Phylogenetic Revision of the Fish Families Luvaridae and †Kushlukiidae (Acanthuroidei), with a New Genus and Two New Species of Eocene Luvarids

ALEXANDRE F. BANNIKOV

and

JAMES C. TYLER

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ABSTRACT

Bannikov, Alexandre F., and James C. Tyler. Phylogenetic Revision of the Fish Families Luvaridae and †Kushlukiidae (Acanthuroidei), with a New Genus and Two New Species of Eocene Luvarids. *Smithsonian Contributions to Paleobiology*, number 81, 45 pages, 20 figures, 1995.—Ten synapomorphies are described that support the proposed sister group relationship of the Eocene Kushlukiidae and the Eocene to Recent Luvaridae as the superfamilial clade Luvaroidea at the node between the siganid and zanclid+acanthurid clades of acanthuroid fishes. The Kushlukiidae previously have been known only on the basis of *Kushlukia permira* Danilchenko from the Eocene of Turkmenistan, but another species of that age is shown to have been present in India; the latter is not given a new specific name because the two specimens of it are only fragments. In addition to the well known Recent species *Luvarus imperialis*, three fossil species have been referred to the Luvaridae: *Proluvarus necopinatus* Danilchenko from the Eocene of Turkmenistan is here recognied as a valid species of *Luvarus*, with *Proluvarus* becoming a junior synonym of *Luvarus; Eoluvarus bondei* Sahni and Choudhary from the Eocene of India is shown to be not a luvarid but, rather, a member of the fossil perciform family Exelliidae, the affinities of which family are poorly understood; *Luvarus praeimperialis* Arambourg from the Oligocene of Iran is shown to be not a luvarid but, rather, a representative of the new genus *Aluvarus* of such uncertain affinity that we simply place it incertae sedis among the percomorphs.

Among the materials used by Danilchenko in the description of *Proluvarus necopinatus* only the holotype and the five other largest specimens (about 326–495 mm SL) represent that species. All of the other specimens are smaller than about 215 mm SL and represent two new species of a new genus of luvarid, *Avitoluvarus dianae* and *A. mariannae*.

Numerous derived features are used to define both the Kushlukiidae and Luvaridae. Within the Luvaridae, the preponderance of derived features is found in *Luvarus*, whereas *Avitoluvarus* has only two unequivocal synapomorphies.

The Luvaroidea, therefore, are represented by the Eocene Kushlukiidae with one genus and two species (*Kushlukia permira* and *K.* sp.) and the Luvaridae with one Eocene genus with two species (*Avitoluvarus dianae* and *A. mariannae*) and one genus, *Luvarus*, with one Eocene species, *L. necopinatus*, and one Recent species, *L. imperialis*.

Contents

Dedication

This contribution is dedicated to Pavel Georgiyevich Danilchenko, 26 December 1903 to 6 January 1993, our our esteemed colleague and pioneering investigator of the Cenozoic fish fauna of the former USSR; the research reported herein is based mostly on the fossil materials collected by him during his expeditions to Turkmenistan between 1959 and 1964.

Phylogenetic Revision of the Fish Families Luvaridae and †Kushlukiidae (Acanthuroidei), with a New Genus and Two New Species of Eocene Luvarids

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Introduction

The family Luvaridae is best known by its only Recent representative, the rarely collected epipelagic "louvar" of worldwide distribution in tropical to temperate seas, *Luvarus imperialis* Rafinesque (1810). This species has been the subject of a vast literature on its records of capture around the world, its external features, and its remarkable and prolonged juvenile metamorphosis before reaching its adult size of just under two meters in length.

Gregory and Conrad (1943) provided the first comprehensive description and analysis of the morphological features of *L. imperialis*. However, they were still unable to decide whether the "louvar" was a carangoid or a scombroid, into which groups it had usually been placed previously, although some authors had assigned it to its own suborder (e.g., Berg, 1940; Matsubara, 1963; Lindberg, 1971) or order (e.g., Roule, 1924) of uncertain affinities. Regan (1902) proposed that *L. imperialis* was an acanthuroid, but immediately rejected his own hypothesis and related the "louvar" to scombroids (Regan, 1903), like most other workers. Gosline (1968) placed it among the xiphioids, as distinct from scombroids.

The history of the classificatory instability surrounding *L. imperialis* was reviewed by Tyler et al. (1989), whose descriptions of the morphology of *L. imperialis* were based for the first time on cleared and stained materials and on both larval and adult specimens. Using a comparable data base on the larval and adult morphology of acanthuroids, the phylogenetic

analysis in Tyler et al. (1989) supported Regan's first surmise of *L. imperialis* being an acanthuroid. The data in Tyler et al. (1989) strongly supported the hypothesis that the families of acanthuroids have the following phyletic sequence: siganids-luvarids-zanclids-acanthurids. This sequence has been corroborated by myological and additional osteological evidence (Winterbottom, 1993; Guiasu and Winterbottom, 1993; Winterbottom and McLennan, 1993).

Although our knowledge of the extant *L. imperialis* has greatly improved over time, reports of putative fossil luvarids are relatively few and recent, and most of them are shown herein not to be luvarid-like fishes.

The first reported putative luvarid was *Luvarus praeimperialis* Arambourg (1967), based on two incomplete specimens from the Lower Oligocene of Iran. Based on the original description, Tyler et al. (1989) were led to doubt that it is a luvarid or even an acanthuroid. We have examined the type specimens of *L. praeimperialis* and in an addendum to this work we show that this species has essentially no luvarid (e.g., it does not have a reduced number of vertebrae or a pterygial truss, and the caudal fin has nine rather than 16 rays and there is no hypurostegy) or acanthuroid specializations and must be removed from that suborder and placed as a new genus, *Aluvarus*, among the percomorphs incertae sedis because of a highly unusual combination of derived features otherwise unknown among that group.

At about the same time, Danilchenko (1968) described two new genera and species of luvarid-like fishes on the basis of relatively numerous materials from the Lower Eocene (incorrectly given as Upper Paleocene) of Turkmenistan: *Proluvarus necopinatus*, which he placed in the Luvaridae; and *Kushlukia permira*, for which he created the new family Kushlukiidae, placing it with the Luvaridae as the superfamily Luvaroidea of

Alexandre F. Bannikov, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117647 Moscow, Russia. James C. Tyler, National Museum of Natural History, Smithsonian Institution (MRC-106), Washington, D.C. 20560.

the suborder Scombroidei. Based on the original descriptions, Tyler et al. (1989) tentatively considered *Proluvarus* to be generically distinct from *Luvarus,* and the Kushlukiidae to be a distinct family of acanthuroids in need of further study to determine its relationship therein. Without elaboration, Patterson (1993) by implication included *Kushlukia* in the Luvaridae.

We have examined all of Danilchenko's materials of luvarid-like fishes and agree with his assessment of the family-level distinctiveness of *Kushlukia.* We believe that his *Proluvarus necopinatus,* although a valid species, is not generically distinct from *L. imperialis,* and we include *Proluvarus* as a junior synonym of *Luvarus.* The designated holotype of "*necopinatus*" and several other specimens are relatively large (about 326–495 mm SL), whereas the other smaller (about 34–215 mm SL) specimens have differing morphologies from the larger specimens. We presume that Danilchenko noticed at least some of these differences and attributed them to the same kind of stages of ontogenetic transformation that Roule (1924) had so thoroughly described for *L. imperialis.* However, the differences between the larger and smaller specimens are far more morphologically fundamental and unlikely to be manifestations of ontogenetic change in a single species. Our analysis shows that the smaller specimens represent two different species of a new genus of luvarid that we describe herein as *Avitoluvarus dianae* and *A. mariannae.*

More recently, Sahni and Choudhary (1977) described a putative luvarid, *Eoluvarus bondei,* based on a single specimen from the Lower Eocene of India. From the original description and illustration, Tyler et al. (1989) believed this species to be so similar to *Luvarus* that it should be placed in that genus. We have examined the type specimen of *E. bondei* and find that it lacks the acanthuroid features attributed to it (e.g., it does not have a reduced number of vertebrae or a pterygial truss, none of the vertebrae of the caudal peduncle are modified as a "pivot" and "anchor," there are 17 rather than 16 principal caudal-fin rays, although these are just as hyperostegic as in *Luvarus*). In a separate publication, we show that *Eoluvarus* is a valid taxon of the Eocene family Exelliidae (e.g., it has the specialized forward placement of consolidated basal pterygiophores at the anterior end of the dorsal fin, which originates over the eye; see Bannikov and Tyler, 1994, for a revision of the Exelliidae).

Thus, two of the putative species of fossil luvarids are removed from among the acanthuroids and placed elsewhere (*Aluvarus praeimperialis* to the Percomorpha incertae sedis and *Eoluvarus bondei* to the Exelliidae), two others are retained in the Luvaridae *(Luvarus necopinatus)* and Kushlukiidae *(Kushlukia permira),* and two new species are described in a new genus of Luvaridae *(Avitoluvarus dianae* and *A. mariannae).* Additionally, several fragmentary specimens from the Lower Eocene of India, which are a species distinct from *Kushlukia permira,* are described as *Kushlukia* sp., the first report of this family since its original description from the Lower Eocene of Turkmenistan.

Upon learning of our work on the fossil luvarid-like fishes, Colin Patterson (pers. comm.) informed us that, based on newly collected material, *Beerichthys ingens* Casier (1966) is a luvarid. This fossil originally was described from three incomplete skulls from the Eocene of the London Clay and was placed in its own family in the Iniomi. The new materials of *Beerichthys ingens* also are incomplete skulls, although showing more features than the original materials, and it may not be possible to determine whether these fossils are generically or specifically distinct from other luvarids.

METHODS

Standard length (SL) in mm is from the tip of the upper jaw to the end of the hypural plate. Measurements under 100 mm are given to the nearest 0.1 mm when possible; many measurements are given only as approximations (with "estimated" being less precise than "approximately" = "about") to the nearest mm. Principal caudal rays are the branched rays plus the uppermost and the lowermost unbranched ray. Bone terminology, except as noted below, follows that in the detailed osteological description by Tyler et al. (1989) of the only Recent species of the luvarid+kushlukiid clade, *Luvarus imperialis.* None of that description is repeated herein, but with our descriptions of a new genus and two new species of fossil luvarids we contrast the similarities and differences, especially in derived features, between all of the species and genera of luvarids and kushlukiids.

For purposes of outgroup comparison with acanthuroids, we use the term "higher squamipinnes" to include scatophagids and ephippidids, as discussed in Tyler et al. (1989). The term "pterygial truss" refers to the complex suture-like interlocking of the expanded distal portions of the proximal or basal pterygiophores of the dorsal and anal fins with one another to form a firm infrastructure around the dorsal and ventral margins of the body just beneath the skin (see Tyler et al., 1989:65 and fig. 14).

Tyler et al. (1989) followed the numbering convention for interneural spaces commonly used for perciforms (e.g., Johnson, 1984), with the space anterior to the neural spine of the first vertebra called the first interneural space, that between the first and second being the second interneural space, etc. Birdsong et al. (1988) noted that publications on gobies referred to the space between the first and second neural spines as the first interneural space and continued that usage. Before the usage now associated with perciforms becomes further entrenched in the literature, we concur with Baldwin and Johnson (1993) that it should be changed: preneural is a more appropriate name for the space in front of the first neural spine, and the term interneural should be reserved for the spaces actually between adjacent spines, with the first interneural space thus being between the first and second spines, the second space between the second and third spines, etc. We adopt a similar terminology for the space in front of the haemal

spine of the first caudal vertebra (prehaemal) and between haemal spines (first interhaemal space between first and second haemal spines, etc.).

What Tyler et al. (1989) called epipleurals in acanthuroids are herein referred to as epineurals, following the terminology developed by Patterson and Johnson (in press) in their extensive treatise on the homologies and phylogenetic implications of intermuscular bones in fishes.

In those cases in which there are two equally parsimonious scenarios for the distribution of a specialized feature and we use one of these as an equivocal synapomorphy, our preferred hypothesis is that the ancestor had the primitive condition of the outgroups.

Text references in the analytical section to Tyler et al. without date are for the 1989 article on *Luvarus imperialis* and acanthuroid phylogeny.

Abbreviations for the repositories of specimens are as follows: AMNH, American Museum of Natural History; LUVP, Department of Geology, Vertebrate Paleontology Collections, Lucknow University, Lucknow; MNHN, Muséum National d'Histoire Naturelle, Paris; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; USNM, former collections of the United States National Museum now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Materials Examined

Luvaridae

Avitoluvarus dianae, new species. Holotype: PIN 2179/62, about 98 mm SL, a relatively complete skeleton except for missing anteroventral part of head, single plate. Paratypes (11 specimens, 38.5–estimated 120 mm SL): PIN 2179/60, about 115 mm SL, a skeleton that is incomplete anteroventrally and missing most of head, single plate (figured by Danilchenko, 1968, pl. XXXV: fig. 2 as paratype of *Proluvarus necopinatus*); PIN 1762/93, 38.5 mm SL, poorly preserved complete skeleton, single plate; PIN 1762/94, about 46 mm SL, poorly preserved complete skeleton, single plate; PIN 1762/95, estimated 99 mm SL, fragment of skeleton including all but most posterior anal-fin basal pterygiophores, single plate; PIN 1762/96, estimated 98 mm SL, poorly preserved skeleton without head and hypural plate, single plate; PIN 1762/97, estimated 120 mm SL, middle part of body, including 3rd to 13th vertebrae, single plate; PIN 2179/104, estimated 120 mm SL, fragment of body including abdominal region and dorsal part of head, single plate; PIN 2179/105, estimated 105 mm SL, ventral part of skeleton including anterior and middle regions of anal-fin basal pterygiophores, single plate; PIN 2179/106, estimated 49 mm SL, fragment of skeleton including posterior part of head and abdominal vertebrae, in part and counterpart. The following fragments are not designated as paratypes, but they are of a species of *Avitoluvarus,* and, on the basis of the few differential features preserved, we think them more likely

to be *A. dianae* than *A. mariannae:* PIN 2179/107, estimated 142 mm SL, middle part of body including last five abdominal vertebrae and ribs, in part and counterpart; PIN 2179/108, estimated 116 mm SL, anterior part of body including rear half of head and first seven vertebrae, single plate; PIN 2179/109, estimated 125 mm SL, poorly preserved anterodorsal part of skeleton, single plate; PIN 2179/110, estimated 116 mm SL, middle region of body and pectoral fin, single plate; PIN 2179/111, estimated 115 mm SL, first six vertebrae and head with jaws missing, single plate.

One other specimen, PIN 2179/61, was figured by Danilchenko (1968, pl. XXXV: fig. 3; 1980, pl. V: fig. 3) and designated a paratype of *Proluvarus necopinatus,* which on the basis of the illustrations is probably *A. dianae;* this specimen cannot be located in the PIN collections. On the basis of the magnification figure given in the illustrations, this specimen was about 54 mm SL. This missing specimen seems to have formed much of the basis for the composite drawing of *P. necopinatus* in Danilchenko (1968:146, text fig. 17), which, on the basis of the illustrated morphology, is *A. dianae.*

All of the above are from the Lower Eocene part of the Danata (Danatinsk) Formation of the Uylya-Kushlyuk locality, southwest Turkmenistan.

Avitoluvarus mariannae, new species. Holotype: PIN 2179/112, about 150 mm SL, poorly preserved skeleton somewhat incomplete anterodorsally, single plate and a counterpart of posterior part of body. Paratypes (4 specimens, estimated 34–190 mm SL): PIN 1762/98, estimated 48 mm SL, poorly preserved skeleton without caudal peduncle, single plate; PIN 1762/99, estimated 34 mm SL, skeleton incomplete posteriorly, single plate; PIN 2179/113, estimated 190 mm SL, fragment of body including abdominal region and several anterior anal-fin basal pterygiophores, single plate; PIN 2179/114, estimated 96 mm SL, fragment of skeleton including 5th to 15th vertebrae, single plate. The following fragments are not designated as paratypes, but they are of a species of *Avitoluvarus,* and, on the basis of the few differential features preserved, we think them more likely to be *A. mariannae* than *A. dianae:* PIN 2179/115, estimated 207 mm SL, poorly preserved imprint of head, single plate; PIN 2179/116, estimated 170 mm SL, poorly preserved head and pectoral and pelvic girdles, single plate; PIN 2179/117, estimated 154 mm SL, upper middle part of body just behind head, single plate; PIN 2179/118, estimated 187 mm SL, middle part of body including 9th to 17th vertebrae, single plate; PIN 2179/119, estimated 173 mm SL, posterior region of body including 13th to 18th vertebrae, single plate; PIN 2179/120, estimated 192 mm SL, middle of body, in part and counterpart; PIN 1762/100, estimated 150 mm SL, anterior part of body, single plate.

All of the above are from the Lower Eocene part of the Danata Formation of the Uylya-Kushlyuk locality, southwest Turkmenistan.

Avitoluvarus sp. There are 18 specifically indeterminate fragments of the body or head (four in part and counterpart) of

Avitoluvarus in the PIN collections. Except for the fragment of the head (PIN 1762/107, estimated 215 mm SL) illustrated herein, these are all uncatalogued. We estimate these fragments to represent specimens of about 32–215 mm SL, and they are thus within the approximate size range of the specimens of one or the other of the two species of *Avitoluvarus* (34–207 mm SL). All of these fragments are from the same Uylya-Kushlyuk locality as the other specimens of both species of *Avitoluvarus*.

Luvarus necopinatus (Danilchenko), new combination. Holotype: PIN 2179/59, about 340 mm SL, almost complete skeleton, in part and counterpart (figured by Danilchenko, 1968, pl. XXXV: fig. 1). Additional specimens (5 specimens, estimated 326-495 mm SL, none of which were specifically designated as paratypes by Danilchenko but which he had available at PIN): PIN 2179/63, about 337 mm SL, almost complete skeleton except partially incomplete posteriorly and counterpart missing head and middle part of body; PIN 1762/91, estimated 495 mm SL, middle part of body including 4th to 14th vertebrae, single plate; PIN 2179/102, estimated 383 mm SL, fragment of middle of body including first six vertebrae, single plate; PIN 2179/103, estimated 326 mm SL, middle of body from rear of opercular series to end of abdominal vertebrae, in part and counterpart; PIN 1762/92, estimated 340 mm SL, fragment of body including most of head and first five vertebrae, in part and counterpart. All of the above are from the Lower Eocene part of the Danata Formation of the Uylya-Kushlyuk locality, southwest Turkmenistan.

Danilchenko (1968:145) stated that his description of *Proluvarus necopinatus* was based on 10 specimens, 44–330 mm SL, and he designated and illustrated a holotype (PIN 2179/59) and two paratypes (PIN 2179/60, 2179/61), in keeping with the custom of only designating illustrated specimens as paratypes. The length of these specimens was not stated, but these can be approximated from the magnifications given in the legends for the photographs of the three specimens in pl. XXXV (figs. 1–3) (Danilchenko, 1968:172). The holotype (fig. 1) is indicated as very close to our measurement of it of 337 mm SL. One of the two paratypes (PIN 2179/60, fig. 2) is indicated as very close to our measurement of it of 115 mm SL. The other paratype (PIN 2179/61, fig. 3) cannot be located at PIN, but it is indicated as being about 54 mm SL. Both of these paratypes of *P. necopinatus* are herein referred to *Avitoluvarus dianae*. Because there are only six specimens in the PIN collections that are referable to *P. necopinatus*, and these range from about 326–495 mm SL, several of the smaller specimens that Danilchenko included in *P. necopinatus* must be specimens of one or the other of the two species of *Avitoluvarus*, as is the case with the two paratypes being *A. dianae*. We presume that some of these smaller specimens utilized by Danilchenko also represent *A. mariannae*, but we have no way of individually identifying them as such. As discussed under the material of *A. dianae*, the text illustration of *P. necopinatus* (Danilchenko, 1968:146) is based mostly on the former species.

Luvarus imperialis Rafinesque. See Tyler et al. (1989) for the listing of materials on which their descriptions of this species are based. These materials also form the basis of our comparisons of it with the fossil species. We have examined the disarticulated dry skeleton (AMNH 27984, length questionable but an adult of about 91 kg weight) that was used for the description by Gregory and Conrad (1943), and we illustrate its rudimentary fused pelvic fin (the "operculum ani") herein for purposes of comparison with the remarkably similar structure in the Eocene *L. necopinatus*.

Kushlukiidae

Kushlukia permira Danilchenko. Holotype: PIN 2179/64, estimated 183 mm SL, well-preserved complete skeleton except missing caudal peduncle and caudal fin, single plate (figured by Danilchenko, 1968: pl. XXXVI: fig. 1). No paratypes were designated by Danilchenko (1968). Additional specimens (8 specimens, estimated 141–198 mm SL): PIN 2179/65, estimated 187 mm SL, fragment including head and abdominal region, single plate; PIN 2179/66, estimated 141 mm SL, anterior part of body from anterior end of snout to sixth caudal vertebrae, single plate; PIN 1762/101, estimated 150 mm SL, head incomplete posteriorly, single plate; PIN 1762/102, estimated 156 mm SL, fragment of much of upper middle part of body including occiput, abdominal vertebrae, and first three caudal vertebrae, single plate; PIN 1762/103, estimated 190 mm SL, mid-dorsal region of body above vertebral centra, in part and counterpart; PIN 1762/104, estimated 160 mm SL, mid-ventral region of body including lower part of more anterior anal-fin basal pterygiophores, in part and counterpart; PIN 1762/105, estimated 188 mm SL, posterior part of body including nine vertebrae preceding caudal peduncle, in part (incomplete above vertebral centra) and counterpart (region above vertebral centra only); PIN 1762/106, estimated 198 mm SL, posterior part of body including seven mid-caudal vertebrae, in part and counterpart.

All of the above are from the Lower Eocene part of the Danata Formation of the Uylya-Kushlyuk locality, southwest Turkmenistan.

Kushlukia sp. LUVP 12010, estimated 93 mm SL, fragment of middle part of body including first nine caudal vertebrae, about 23.5 mm from front of first to end of ninth centrum, single plate; LUVP 12011–12011A, estimated 98 mm SL, fragment of middle part of body including ten mid-caudal vertebrae, about 30.3 mm from front of first to end of tenth centrum, including the gap between the second and third centra, single plate. These two specimens are from the Fuller's Earth, Lower Eocene, Bothia locality, Barmer District, Rajasthan, India.

Percomorpha Incertae Sedis (Familiae)

Aluvarus praeimperialis (Arambourg), new combination.

Holotype: MNHN 1939-6-250 d and g, estimated 110 mm SL, axial skeleton incomplete ventrally and lacking head and pelvic region, in part and counterpart. Paratype: MNHN 1939-6-252 d and g, estimated 75 mm SL, axial skeleton incomplete anteriorly and lacking head, pectoral, pelvic, and caudal fins, in part and counterpart. These two specimens are from the Lower Eocene (Rupelian) fish-bearing layers of the Elam locality, Iran.

Exelliidae

Eoluvarus bondei Sahni and Choudhary. Holotype: LUVP 12013-12013A, estimated 280 mm SL, almost complete skeleton but missing tip of snout and region of pelvic girdle, in part and counterpart. Fuller's Earth, Lower Eocene, Bothia locality, Barmer District, Rajasthan, India. In the process of placing this species in the Exelliidae we have examined the type specimens and other materials of both of the species previously referred to this family: *E. velifer* (Volta) from the Middle Eocene of Monte Bolca, Italy, and *E. proxima* Danilchenko from the Lower Eocene of Turkmenistan (see Bannikov and Tyler, 1994, for a listing of these materials).

Systematic Descriptions

Order PERCIFORMES, sensu Johnson and Patterson, 1993

Suborder ACANTHUROIDEI, sensu Tyler et al., 1989

Superfamily LUVAROIDEA, sensu novo

DIAGNOSIS.—The Luvaridae+Kushlukiidae clade differs from all other acanthuroid fishes (whose contrasting character states are given in parenthesis) by the following: presence of median pterygial truss around most of body (versus no truss); two or fewer dorsal-fin spines (versus 4–14); no anal spines (versus 3–8); soft-dorsal and anal-fin rays unsegmented (versus segmented); distal end of first anal-fin basal pterygiophore greatly prolonged anteriorly (versus not greatly prolonged, except independently in *Naso*); anus displaced anteriorly (versus not displaced, except independently somewhat so in *Naso*); hypurals 1–4 fused (versus unfused, except independently in *Naso*); caudal-fin rays broadly overlapping hypural plate (versus no overlap or only slightly so); pelvic fin becoming rudimentary with increasing specimen size (versus not becoming rudimentary); teeth greatly reduced in size or lost in adults (versus not reduced or lost) (the first nine of these are proposed as unequivocal synapomorphies of the Luvaroidea, whereas the last one is uncertain or equivocal, see Characters 1–10 in "Analysis of Characters" for details).

COMPOSITION.—Luvaridae Gill and Kushlukiidae Danilchenko.

Family LUVARIDAE Gill, 1885

TYPE GENUS.—*Luvarus* Rafinesque, 1810, by monotypy.

DIAGNOSIS.—Differs from the Kushlukiidae (see the diagnosis of that family for its contrasting character states) as follows: vertebrae 9 + 13 = 22; ventral shaft of first basal pterygiophore of dorsal fin very long and placed in preneural space; middle regions of first two haemal spines curved toward one another; abdominal vertebrae without parapophyses; opercular region rounded; articular relatively large; exceptionally slender neural and haemal spines; proximal shafts of dorsal- and anal-fin basal pterygiophores relatively slender; epineural intermuscular bones usually absent; postcleithrum shaft-like; no long posterior extension of pelvis making contact with anterior extension of first anal-fin basal pterygiophore, and anus under pectoral-fin base; pectoral fin placed in middle of body or lower; coracoid not elongate and postcoracoid process present; premaxilla not beak-like; ascending process of premaxilla short

or absent; scapula of moderate size; neural spines of first two vertebrae long; urohyal of moderate size; a single anal-fin basal pterygiophore in front of first haemal spine; pelvic fin retained as a specialized operculum ani even at large sizes in *Luvarus*, but pelvic fin probably lost at small adult sizes in *Avitoluvarus* (all of the above features are polarizable and discussed in the "Analysis of Characters," whereas the following cannot be polarized and are not included in the analytical section); no ventral flange on parasphenoid under orbit; anterior extension of first anal-fin basal pterygiophore without a constriction; eye not placed especially high in head, remote from profile; dorsal fin with a total of no more than about 18-26 fin-ray elements.

The extensive definition of the Luvaridae given by Tyler et al. (1989) and based largely on *L. imperialis* needs slight emendation on the basis of the fossil species of luvarids: dorsal fin initially with 22 to 26 total elements, including spines, and the anal fin initially with 18 to 26 soft rays, the anterior elements in these fins becoming reduced and lost with increasing specimen size only in *Luvarus*; epineural intermuscular bones absent in all species except *Avitoluvarus dianae*.

COMPOSITION.—Two genera, *Avitoluvarus*, new genus, with two species *(A. dianae* and *A. mariannae)*, both from the Lower Eocene of Turkmenistan, and *Luvarus* Rafinesque (1810), with one species *(L. necopinatus)* from the Lower Eocene of Turkmenistan and another *(L. imperialis)* in the Recent fauna (world-wide in temperate and tropical marine waters). A third genus, *Beerichthys* Casier (1966), with the single species *B. ingens* Casier (1966), from the Lower Eocene of the London Clay, is probably a member of this family and may be a synonym of *Luvarus* (pers. comm., C. Patterson, based on his work in progress).

†*Avitoluvarus*, new genus

Proluvarus Danilchenko, 1968:144 [in part].

TYPE SPECIES.—*Avitoluvarus dianae*, new species, by designation here.

ETYMOLOGY.—The generic epithet is from *avitus* (Latin), for old or ancient, and *Luvarus*, for its sister-group relationship with that genus; masculine.

DIAGNOSIS.—Differs from *Luvarus* (see the diagnosis of that genus for its contrasting character states) by the following: neural and haemal spines of ninth caudal vertebra relatively slender and oriented posteroventrally; centrum of tenth caudal vertebra not much shorter than the others in the caudal peduncle and with slender neural and haemal spines oriented obliquely posteriorly, this and the ninth vertebra not forming an "anchor" and "pivot"; postcleithrum long; shaft of first anal-fin basal pterygiophore relatively stout or long; eye placed relatively higher in head, in about middle of upper half of head; pleural ribs slender; pelvic fin lost at small adult sizes; pterygial truss much shallower and the interdigitations over a less broad area, the depth of the interdigitated surface not exceeding about one-fourth the length of the centra; first two haemal spines

slightly to much thicker and not curved in same direction, the first being concave anteriorly and the second either slightly to distinctly convex anteriorly; teeth present in at least small adults; epineural intermuscular bones present in one species *(A. dianae)* and absent in the other *(A. mariannae)*; most of shafts of anal-fin basal pterygiophores relatively thick in one species *(A. dianae)* and slender in the other *(A. mariannae)*; usually seven to eleven shafts of anal-fin basal pterygiophores placed in first two interhaemal spaces; ascending process of pelvis oriented vertically or posterodorsally, and posterior process relatively long, prominent, and posteriorly oriented; vertebral column articulated high on cranium (see "Analysis of Characters" for details of all of these features).

The specimens of the two species of *Avitoluvarus* range from about 34 to 207 mm SL (to about 215 mm SL for fragments of *A.* sp.). The materials of *Luvarus necopinatus* range from about 326 to 495 mm SL, whereas *L. imperialis* obtains more than 1.8 m SL. We presume that the species of *Avitoluvarus* have smaller adult sizes than those of *Luvarus*.

†*Avitoluvarus dianae*, new species

FIGURES 1–3

Proluvarus necopinatus Danilchenko, 1968: 145, pl. XXXV: figs. 2, 3 [in part]; 1980:165, pl. V: fig. 3.

HOLOTYPE.—PIN 2179/62, see "Material Examined" for details of the holotype and paratypes, totaling 10 specimens of 38.5–120 mm SL, plus five fragments of what are probably this species that are estimated to be about 115–142 mm SL.

TYPE LOCALITY AND HORIZON.—Two km northeast of Uylya-Kushlyuk village, southwest Turkmenistan; lowermost layers of the middle part of the Danata Formation, Lower Eocene (Ypressian). Danilchenko (1968) was in error in thinking that the fish bearing layers of the Danata Formation were Upper Paleocene in age (see Tyler and Bannikov, 1992:2, for details).

DIAGNOSIS.—Differs from *A. mariannae* (see the diagnosis of that species for its contrasting character states) by the following: shaft of first anal-fin basal pterygiophore thick and stout; usually seven shafts of anal-fin basal pterygiophores placed in first two interhaemal spaces; pleural ribs relatively longer and slightly thicker; ventral half of pterygial truss relatively thicker; first two haemal spines relatively thicker; shafts of most anal-fin basal pterygiophores less slender; epineural intermuscular bones present (the above features are polarizable and discussed in the "Analysis of Characters," whereas the following cannot be polarized and are not included in the analytical section); curved regions of first two haemal spines of caudal vertebrae in close proximity; posterior process of pelvis very short; 23 soft anal-fin rays.

ETYMOLOGY.—The specific epithet *dianae* is in honor of Diane M. Tyler, the wife of one of us (JCT) and the editor of the presubmission versions of this and several other joint works by the authors.
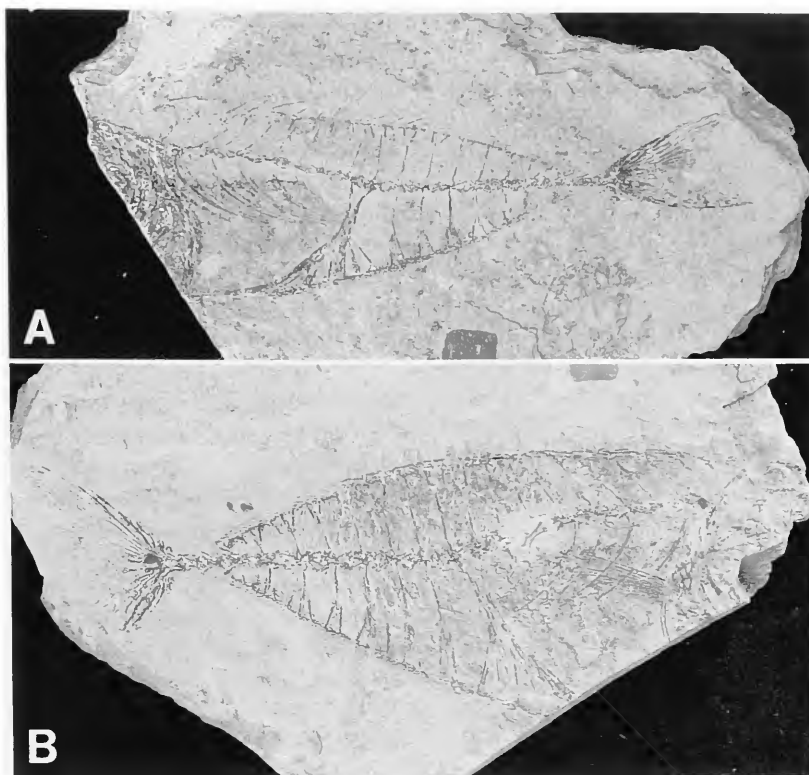
FIGURE 1.—*Avitoluvarus dianae*, new species: A, PIN 2179/62, holotype, about 98 mm SL, skeleton without most of anteroventral region of head, × 1.0; B, PIN 2179/60, paratype, about 115 mm SL, skeleton incomplete anteroventrally, × 1.0; Lower Eocene of Turkmenistan.

DESCRIPTION.—The only two complete skeletons (PIN 1762/93 and 1762/94) are poorly preserved and the two best-preserved specimens (PIN 2179/62, the holotype, and 2179/60, Figure 1) are missing most of the skull.

The body is fusiform in shape, with a slender caudal peduncle. The greatest body depth varies from 26%–38% SL (average 31%). The head is moderately long, 32%–34% SL, the upper profile gently curved, and the mouth small. The round orbit is placed in about the middle of the upper half of the head, and its horizontal diameter varies from 22%–28% of head length.

Skull: The limits of the individual bones of the occipital and otic regions are not clear, but the frontals are apparently relatively wide and the supraoccipital lacks a prominent crest. The ethmoid region was probably largely cartilaginous, although the lateral ethmoids are weakly ossified. The parasphenoid is slender and convex ventrally where exposed below the orbit and ethmoid region. The shaft of the hyomandibular is oriented obliquely anteroventrally, and the dorsal head is somewhat expanded anteriorly. The ventral end of the hyomandibular shaft is well removed from the posterior end of the quadrate. The quadrate is triangular and has a small articular facet for the lower jaw. The limits of the pterygoid bones and palatine are not clear.

The lower jaw articulation is situated under the middle of the ethmoid region, well in front of the level of the anterior edge of the orbit. The lower jaw is approximately triangular. Although the limits of the dentary and articular are not clear, it appears that these bones were of approximately equal size. The dentary bears a single row of small conical teeth. The alveolar process

FIGURE 2.—*Avitoluvarus dianae*, new species, PIN 2179/106, paratype estimated 49 mm SL, fragment of skeleton showing pectoral fin, ribs, and origin of dorsal fin; Lower Eocene of Turkmenistan.
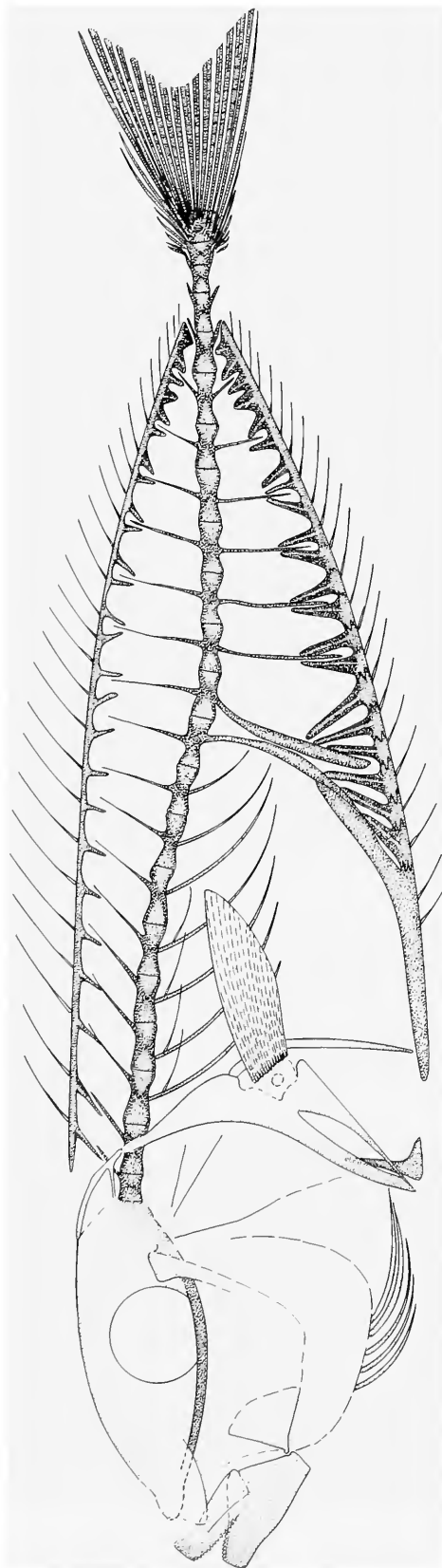
FIGURE 3.—*Avitoluvarus dianae*, new species, reconstruction of skeleton based mainly on the holotype (PIN 2179/62, about 98 mm SL) but with much of head based on paratypes; Lower Eocene of Turkmenistan.

of the premaxilla is slender, elongate, and bears a single row of small conical teeth like those of the dentary, whereas the ascending process of the premaxilla is short but prominent. The maxilla is thin and of increasing width posteroventrally. The thin lachrymal partially covers the maxilla and appears to be prolonged into a slender posterior process similar to that found in *L. imperialis* (Tyler et al., 1989, figs. 4, 16). The region of the orbit is not well-enough preserved to determine whether other infraorbital bones were present behind the lachrymal and under the orbit (a single rudimentary infraorbital is present under the middle of the eye in *L. imperialis*).

The thin, flat bones of the opercular region are poorly preserved, and the limits of most of them are unclear. However, the opercle is approximately triangular and thickened along its anterior edge.

The hyoid and branchial arches are not clear, but five branchiostegal rays are well preserved and exposed.

Pectoral Fin and Girdle: The elongate and flattened posttemporal is situated just above the level of the vertebral column, extending anterodorsally from the region we presume represents the supracleithrum (although this bone is not clearly preserved) to the region of the epiotic. A prominent rod-like intercalar process extends anteriorly from the ventral region of the posttemporal. The cleithrum is large, its upper end inclined anterodorsally and its lower end inclined anteroventrally. The upper limits of the postcleithrum are obscured by the pectoral fin, but the long shaft of the bone below the pectoral-fin base is sturdy and reaches ventrally to contact or almost contact the dorsal edge of the anterior end of the long anterior extension of the first anal-fin basal pterygiophore, apparently helping to anchor the truss in the anterior abdominal region. The long shaft of the postcleithrum has no evidence of division into two pieces, and we presume that the postcleithrum is a single bone. The scapula and actinosts are not well preserved. The coracoid is wide dorsally, including a prominent postcoracoid process, and tapers to a narrow shaft anteroventrally. There is a large unossified region in the girdle between the upper and lower points of contact between the coracoid and cleithrum.

The base of the pectoral fin is situated just below the middle of the body, or slightly above the middle of the distance between the vertebral column and the ventral profile of the body. The pectoral fin has 16 or 17 rays. The length of the pectoral fin is about 18% SL in larger specimens and about 21% SL in smaller specimens.

Pelvic Girdle: The pelvic fins are absent or invisible (or the pelvic region is missing) in all of the present materials, but the two smallest specimens (PIN 1762/93, 38.5 mm SL, and PIN 2179/106, about 46 mm SL) are so poorly preserved that we are not sure whether fins were present at this size, as they are in specimens of *A. mariannae* of about 34 and 48 mm SL. The pelvis is L-shaped, with the long main body (ascending pubic process) oriented vertically or slightly posterodorsally toward the cleithrum, whereas the posterior (ishial) process is short but prominent; there is essentially no anterior (iliac) process.

Vertebral Column: There are 9 + 13 = 22 vertebrae. The vertebral column is elevated anteriorly and articulates high on the rear of the cranium. The length of the abdominal part of the vertebral column is about 77%–82% of the length of the caudal part. All of the centra are amphicoelous. All but the first and a few of the last centra are relatively (in comparison to *Luvarus* and *Kushlukia*) elongate anteroposteriorly and compressed in the middle. The centrum of the first vertebra is shortened and usually mostly obscured by the cranial bones, but is relatively distinct in a few specimens. All of the neural spines are relatively straight and slender, with the neural spine of the first vertebra somewhat shorter than those of the second and subsequent vertebrae. The neural spines of the more anterior abdominal vertebrae are inclined posterodorsally at a more acute angle than those of the last few abdominal and more anterior caudal vertebrae, whereas the neural spines of the more posterior caudal vertebrae are inclined progressively obliquely. The neural spines of all but the more posterior caudal vertebrae are shorter than the corresponding haemal spines. The abdominal vertebrae lack haemal arches and parapophyses. Moderately long and slender pleural ribs that become shorter posteriorly in the series are present on the third to ninth abdominal vertebrae. The pleural ribs are inclined posteroventrally and reach to a level of no more than one-half of the distance between the vertebral column and the ventral profile of the body. Very slender, short epineurals are attached to the proximal regions of the first to at least the fourth pleural ribs.

The proximal region of the haemal spine of the first caudal vertebra is oriented almost vertically and then curves anteroventrally. This haemal spine is widest in its middle region and tapers to a point distally. The second haemal spine is narrow proximally and wide throughout the rest of its length, including at its blunt distal end. The second haemal spine swings anteriorly from its base at the centrum to closely approach the posterior edge of the middle of the first haemal spine, distal to which these two haemal spines diverge. The haemal spines of the third and subsequent caudal vertebrae are slender, almost straight, of decreasing length posteriorly in the series, and slightly longer than the corresponding neural spines. The haemal spines of the third to fifth or sixth caudal vertebrae are oriented relatively vertically, whereas those of the subsequent vertebrae are inclined posteroventrally. The neural and haemal spines of the ninth caudal vertebra are not modified as specialized anchors for the pterygial truss, such as is the case in *Luvarus.*

Caudal Fin and Skeleton: The tenth to thirteenth caudal vertebrae form the caudal peduncle. The ninth and subsequent vertebral centra are of slightly decreasing length in the series (except for the last, which is obscured by fin rays but probably longer in conjunction with the hypural plate than the preceding centrum). The lengths of the obliquely oriented neural and haemal spines of the caudal vertebrae decrease posteriorly in the series until the tenth, whereas those of the eleventh and twelfth are slightly increased in length relative to those of the

tenth. The centrum of the tenth caudal vertebra is not modified as a specialized pivot for the rest of the caudal peduncle, such as is the case in *Luvarus.*

The caudal fin is moderately long and forked. It has 16 principal rays (i,7+7, i) and about seven unbranched and unsegmented procurrent rays above and about six below. Except for the middle two to four rays, the principal rays deeply overlap the hypural plate, epural, and parhypural, especially in the middle regions of the upper and lower lobes, in typical hypurostegy.

Dorsal and Anal Fins: There are a total of about 26 dorsal-fin elements. Because of their state of preservation it is difficult to determine which of these elements anteriorly are spines versus soft rays. However, in the two smallest specimens (38.5 and about 49 mm SL) the first element in the dorsal fin appears to be a spine. It is borne in supernumerary association on the first dorsal-fin basal pterygiophore. All of the soft rays are unsegmented, unbranched, and bilaterally paired. The rays are relatively short; the longest ones, from about the middle of the fin, are about 7%–8% SL. There are about 26 dorsal-fin basal pterygiophores. Except for the last few, the dorsal-fin basal pterygiophores are approximately T-shaped in lateral view, with a ventrally oriented shaft and anteroposteriorly prolonged distal end. These distal expansions of the basal pterygiophores are apparently extensively interdigitated with one another. Although these articulations are not well preserved in most of the material, it is evident that the broad contact between the distal ends of the pterygiophores forms a continuous truss. What portions of the distal expansion that forms the truss are composed by the basal, medial, and distal pterygiophores is unclear. The ventral shafts of at least the first few and last few dorsal-fin basal pterygiophores have longitudinal lateral ridges and medial lamellar flanges. The ventral shaft of the first dorsal-fin basal pterygiophore is the longest in the series and is placed in the preneural space along the anterior edge of the upper half of the neural spine of the first vertebra, with its ventral end remote from the first centrum and neural arch. The shafts of the second to eleventh basal pterygiophores are placed individually in the first to tenth interneural spaces, whereas more posteriorly there are two or sometimes three shafts per interneural space, with no vacant interneural spaces.

The anal fin has 23 soft rays and no spines. The first two rays are borne in supernumerary association toward the rear of the thick anterior elongation of the first anal-fin basal pterygiophore. The anal rays are unbranched, unsegmented, and bilaterally paired, similar to those of the dorsal fin except shorter. There are about 22 anal-fin basal pterygiophores, mostly T-shaped like those of the dorsal fin but with much thicker anteroposterior distal expansions and longer, stouter shafts. The first anal-fin basal pterygiophore has a long and thick anterior extension beneath most of the length of the abdominal cavity and an equally thick posterodorsal process whose upper end articulates along the anterior edge of the lower end of the haemal spine of the first caudal vertebra. The second

and more posterior anal-fin basal pterygiophores have strong longitudinal lateral ridges and prominent medial lamellar flanges. The deep distal expansions of the anal-fin basal pterygiophores are broadly and complexly sutured to one another by elaborate emarginations and interdigitations that are clearly preserved, even though the relative contribution of the medial and distal pterygiophores to this complex cannot be discerned. The shafts of the second to fourth basal pterygiophores are placed between the distal ends of the haemal spines of the first and second vertebrae (first interhaemal space), and those of the fifth to eighth (in the majority of specimens) or fifth to seventh (PIN 1762/95, 2179/60) basal pterygiophores in the second interhaemal space. The succeeding interhaemal spaces accommodate two or three basal pterygiophore shafts. The shafts of the anal-fin basal pterygiophores converge toward the haemal spines more prominently than in the dorsal fin.

Scales: There are faint remains and impressions of numerous minute rounded scale plates on the body (best seen on PIN 2179/104). The largest scales are placed along the bases of the dorsal and anal fins (scales not shown in illustrations) and in front of the fin origins. The scales seem to bear upright

spinules that are directed into the preservation matrix. The lateral line is not evident.

†*Avitoluvarus mariannae,* new species

FIGURES 4–8

Proluvarus necopinatus Danilchenko, 1968:145 [in part]; 1980:165.

HOLOTYPE.—PIN 2179/112, see "Material Examined" for details of the holotype and paratypes, totaling five specimens of about 34–190 mm SL, plus seven fragments of what are probably this species that are estimated to be of about 150–207 mm SL.

TYPE LOCALITY AND HORIZON.—Two km northeast of Uylya-Kushlyuk village, southwest Turkmenistan; lowermost layers of the middle part of the Danata Formation, Lower Eocene (Ypressian).

DIAGNOSIS.—Differs from *A. dianae* (see the diagnosis of that species for its contrasting character states) by the following: shaft of first anal-fin basal pterygiophore relatively more slender; 10 to 11 shafts of anal-fin basal pterygiophores

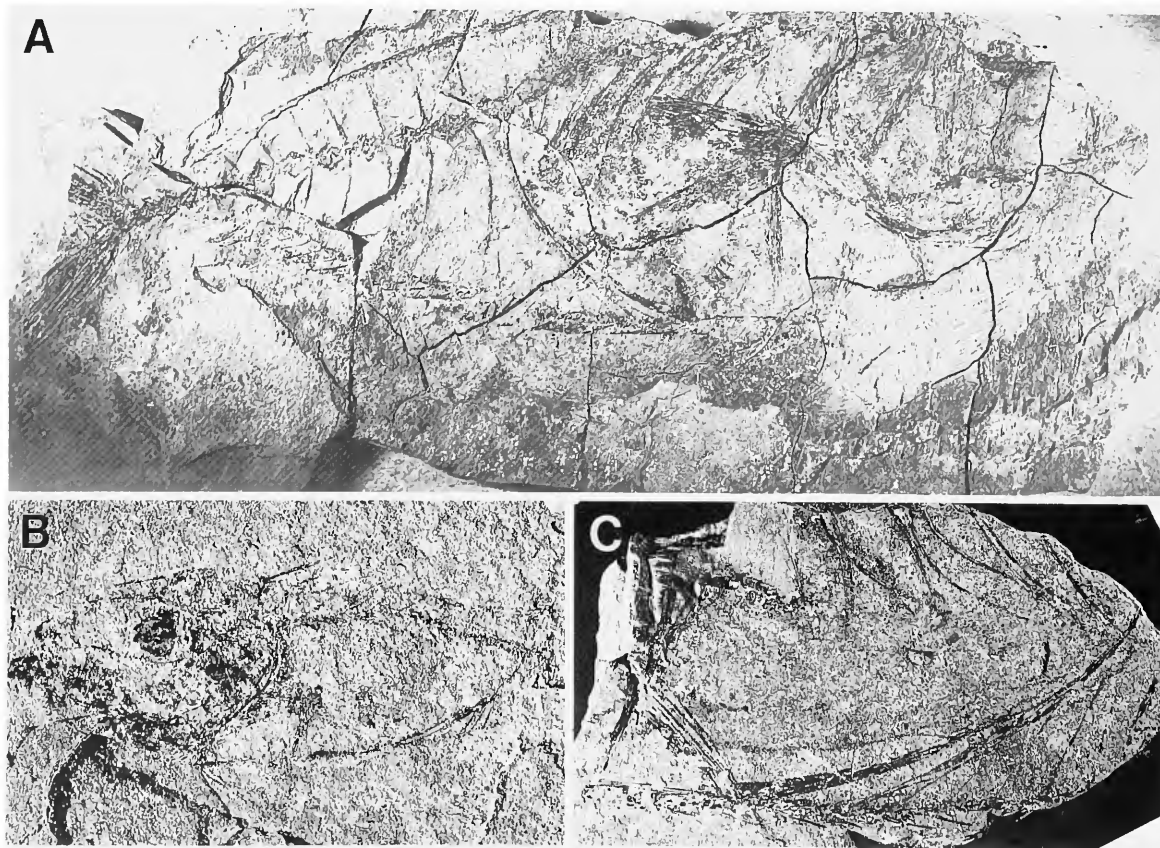FIGURE 4.—*Avitoluvarus mariannae,* new species: A, PIN 2179/112, holotype, about 150 mm SL, imprint of skeleton, × 1.0; B, PIN 1762/99, paratype, estimated 34 mm SL, skeleton of juvenile specimen incomplete posteriorly, × 3.4; C, PIN 2179/113, paratype, estimated 190 mm SL, fragment of skeleton including region of abdominal cavity and anterior pterygiophores of anal fin, × 1.3; Lower Eocene of Turkmenistan.

placed in the first two interhaemal spaces; pleural ribs relatively short and thin; ventral half of pterygial truss very shallow; first two haemal spines only slightly thickened; shafts of most anal-fin basal pterygiophores exceptionally slender; epineural intermuscular bones absent (the above features are polarizable and discussed in the "Analysis of Characters," whereas the following cannot be polarized and are not included in the analytical section); curved regions of first two haemal spines of caudal vertebrae not in close proximity; posterior process of pelvis slightly elongate; 26 soft anal-fin rays.

ETYMOLOGY.—The specific epithet *mariannae* is in honor of the daughter of one of us (AFB), Marianna Alexandrovna Bannikova.

DESCRIPTION.—None of the materials are especially well preserved and only two specimens (PIN 2179/112 and 1762/98) represent relatively complete skeletons, and a few morphological features of this species in relation to the other two fossil luvarids remain unclear. Our impression is that *A. mariannae* is less well ossified than *A. dianae*.

The body is fusiform is shape, with a slender caudal peduncle. The greatest body depth varies from 25%–34% SL (average 30%). It is apparent that the larger specimens are relatively more deep-bodied than the smaller specimens, but there are not sufficient entire specimens of both large and small size available to be able to quantify this difference. The head is of moderate length, 28%–32% SL, the upper profile probably relatively straight, and the mouth small. The round orbit is placed in about the middle of the upper half of the head, and its horizontal diameter varies from 26%–28% of head length.

Skull: The limits of the individual bones of the weakly ossified occipital and otic regions are not clear, but the frontals are apparently relatively wide and the supraoccipital lacks a prominent crest.

The bones of the cranial roof of the smallest specimen (PIN 1762/99, about 34 mm SL) bear remnants of larval ridges that we presume were probably serrate as in other acanthuroids, even though we cannot absolutely determine the presence of serrations in the poorly preserved materials; one ridge is along the dorsal midline of the supraoccipital, and another is along the lateral border of the frontal and pterotic. Comparable ridges, with serrations, are known for larval *Luvarus imperialis* (see Leis and Richards, 1984, fig. 297; Johnson and Washington, 1987, fig. 6; Tyler et al. 1989, fig. 48) and other acanthuroids and were an important part of the suite of specialized characters indicating the relationship of *Luvarus* with acanthuroids.

The ethmoid region is almost unossified. The parasphenoid is slender and slightly convex where exposed at the lower edge of the orbit in some specimens, but it is apparently displaced somewhat dorsally to almost the middle of the orbit in PIN 1762/98. The shaft of the hyomandibular is almost vertical or oriented only slightly anteroventrally. The metapterygoid is of moderate size; the other pterygoid bones and the palatine are unclear. The quadrate is large, broad, subtriangular, and has a small articular facet for the lower jaw.

FIGURE 5.—*Avitoluvarus mariannae*, new species, PIN 1762/98, paratype, estimated 48 mm SL, skeleton of juvenile specimen without caudal peduncle, × 2.0; Lower Eocene of Turkmenistan.

The lower jaw articulation is situated under the middle of the ethmoid region, well in front of the level of the anterior edge of the orbit. The lower jaw is short but deep, with the dentary and articular seeming to be of about equal size. The symphysis of the dentary is deep and the dentary bears a single row of small conical teeth (see Figure 9 for a photograph of the teeth in the jaws of a specimen of *A.* sp.). The alveolar process of the premaxilla is slender, elongate, and bears a single row of small conical teeth, whereas the ascending process is short but prominent. The maxilla and lachrymal (and infraorbital regions) are not well-enough preserved in any of the materials to describe.

The thin, flat bones of the opercular region are poorly preserved, with the limits of the preopercle, subopercle, and interopercle unclear. However, the opercle is subtriangular and has at least three bony ridges radiating from the occipital condyle: one of these is along the anterior border of the bone and the other two in the middle of the opercle.

The hyoid and branchial arches are not clear, but there are five branchiostegal rays (and possibly a sixth ray in one specimen but we think this is more likely a ray displaced from the opposite side).

Pectoral Fin and Girdle: The slender and elongate posttemporal is visible in only one specimen (PIN 1762/99, as shown in the reconstruction); it extends from the top rear of the head posteriorly and slightly ventrally over the region above the level of the first two centra but is so poorly preserved at its lower end that we can discern neither an intercalar process nor the articulation with the pectoral girdle. The large cleithrum is gently curved into a C-shape, the upper end inclined anterodorsally and the lower end inclined anteroventrally. The upper limits of the postcleithrum are poorly preserved or obscured by the pectoral fin, but the long shaft of the bone below the pectoral-fin base is sturdy and reaches ventrally almost to the dorsal edge of the anterior extension of the first anal-fin basal pterygiophore, except in PIN 1762/98 in which the distal end of the postcleithrum is either slightly shorter than
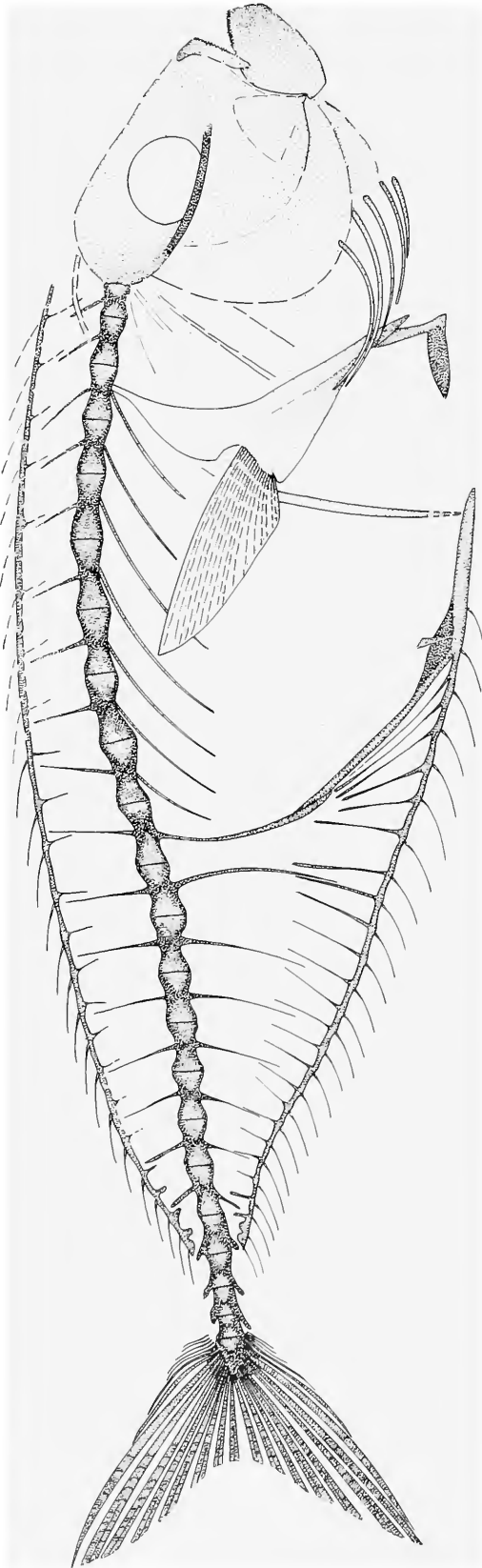
FIGURE 6.—*Avitolavarus mariannae*, new species, reconstruction of skeleton based mostly on the holotype (PIN 2179/112, about 150 mm SL) but with some details from paratypes; Lower Eocene of Turkmenistan.

in other specimens or it is not fully exposed ventrally in the matrix. There is no evidence of a division of the long postcleithral shaft into two pieces, and we presume that the postcleithrum is a single bone. The coracoid is elongate, of decreasing width anteroventrally, with a moderately developed postcoracoid process.

The base of the pectoral fin is situated in the middle of the body, slightly above the middle of the distance between the vertebral column and the ventral profile of the body. The pectoral fin has about 17 rays and its length in the one specimen in which it can be measured (PIN 2179/112) is 17%SL.

Pelvic Fin and Girdle: The pelvis is L-shaped. The long main body is oriented vertically or slightly posterodorsally toward the cleithrum. The posterior process is broad and well developed (i.e., longer than in *A. dianae*). The posterior process is slightly shorter than the ascending process in large specimens (Figure 6) but much longer and more tapered in the two smallest specimens available (about 34 and 48 mm SL, respectively PIN 1762/99 and 98), its length much greater than that of the ascending process (Figure 7), reaching almost to the level of the anterior end of the anterior extension of the first anal-fin basal pterygiophore. There is essentially no anterior pelvic process.

The pelvic fin is not evident in any of the large specimens, and we presume that it is absent at these sizes. Pelvic spines, but not rays, are preserved in the two smallest specimens (about 34 and 48 mm SL, see above). The pelvic spines are long (somewhat longer than the posterior process), slender, and bear serrations along the anterior edge (Figure 7), being similar to the first dorsal spines in these two specimens.

Vertebral Column: There are 9 + 13 = 22 vertebrae. The vertebral column is elevated anteriorly and articulates high on the rear of the cranium. The length of the abdominal part of the vertebral column is about 87% of the length of the caudal part. All of the centra are amphicoelous. All but the first and a few of the last centra are relatively elongate anteroposteriorly and compressed in the middle. The centrum of the first vertebra is shortened. All of the neural spines, except for the few in the caudal peduncle, are straight and exceptionally slender, with the neural spine of the first vertebra somewhat shorter than those of the second and subsequent abdominal vertebrae. The neural spines of the first eight abdominal vertebrae are inclined posterodorsally, whereas those of the last abdominal and first caudal vertebrae are inclined slightly anterodorsally and all of the more posterior abdominal vertebrae are inclined postero-dorsally. The neural spines of all but the more posterior caudal vertebrae are shorter than the corresponding haemal spines. The abdominal vertebrae lack haemal arches and parapophyses. Relatively short and exceptionally slender pleural ribs that become slightly shorter posteriorly in the series are present on the third to ninth abdominal vertebrae. The pleural ribs are inclined posteroventrally and reach to a level less than one-half of the distance between the vertebral column and the ventral profile of the body. We find no evidence of epineurals and are
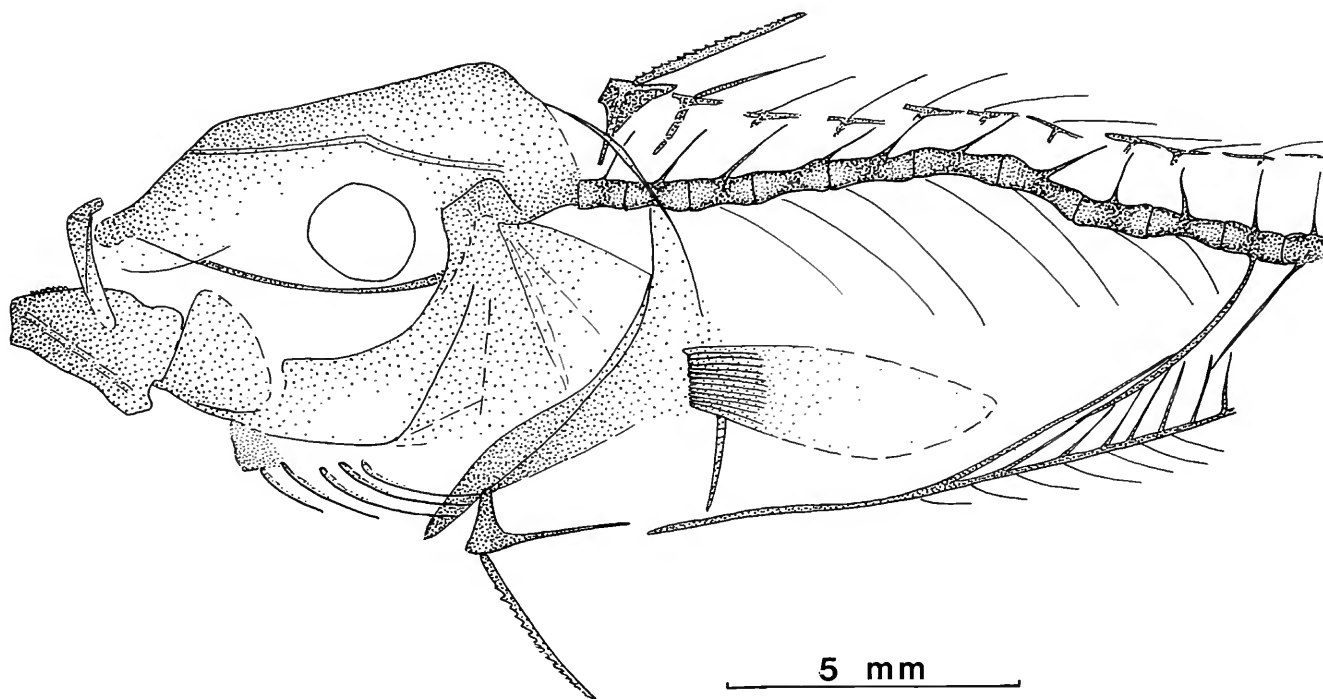
FIGURE 7.—*Avitoluvarus mariannae*, new species, PIN 1762/99, paratype, estimated 34 mm SL, anterior part of skeleton of juvenile specimen; Lower Eocene of Turkmenistan.

confident that none were present because the regions around the upper ends of the pleural ribs where epineurals would be expected to occur are relatively well preserved.

The haemal spine of the first caudal vertebra is only slightly thicker than that of the second caudal vertebra and is only slightly thicker distally than proximally; it is only moderately curved anteroventrally in the lower half of its length. The haemal spine of the second caudal vertebra is very slender and has a gently convex anterior edge, with the middle region only slightly curved forward toward the first haemal spine and a space equal to about one-half of the centrum separating the middle regions of the first and second haemals. The haemal spines of the third and subsequent caudal vertebrae are exceptionally slender, inclined posteroventrally, straight or only very slightly curved, of slightly decreasing length posteriorly in the series, and all but the last few are distinctly longer than the corresponding neural spines. The neural and haemal spines of the ninth caudal vertebra are not modified as specialized anchors for the pterygial truss, such as is the case in *Luvarus*.

CAUDAL FIN AND SKELETON.—The caudal fin and the tenth to thirteenth caudal vertebrae that form the caudal peduncle are preserved only in PIN 2179/112. The ninth and subsequent caudal vertebral centra are of slightly decreasing length posteriorly in the series, except for the last which, in conjunction with the hypural plate, is longer than the preceding centrum. The haemal spines of the tenth and eleventh caudal vertebrae are of progressively increased length. The neural spine of the eleventh caudal vertebra is crest-like and shorter than that of the preceding vertebra. The parhypural is autogenous but other details of the caudal skeleton are obscured by the overlapping caudal-fin rays. The centrum of the tenth vertebra is not modified as a specialized pivot for the rest of the caudal peduncle, such as is the case in *Luvarus*.

The caudal fin is incompletely preserved distally, but, based on the thickness and branching of the basal regions, it was probably forked. It has 16 principal rays (i,7+7, i) and about seven unbranched and unsegmented procurrent rays above and at least five below (total number uncertain). Except for the middle two rays, the principal rays deeply overlap the hypural plate, epural, and parhypural, especially in the middle regions of the upper and lower lobes, in typical hypurostegy.

Dorsal and Anal Fins: There are a total of about 24 dorsal-fin elements. In the two smallest specimens (about 34 and 48 mm SL) the first dorsal-fin element is definitely a spine; it is longer and stouter than the succeeding elements, borne in supernumerary association on the first dorsal-fin basal pterygiophore, and bears serrations along its anterior edge, these being especially clear in PIN 1762/99 (Figure 7). The second element in PIN 1762/99 also appears to be a spine. All of the other elements are clearly soft rays that are unsegmented, unbranched, and bilaterally paired. The rays are relatively short, the longest ones, from about the middle of the fin, about 5% SL. There are about 24 dorsal-fin basal pterygiophores.
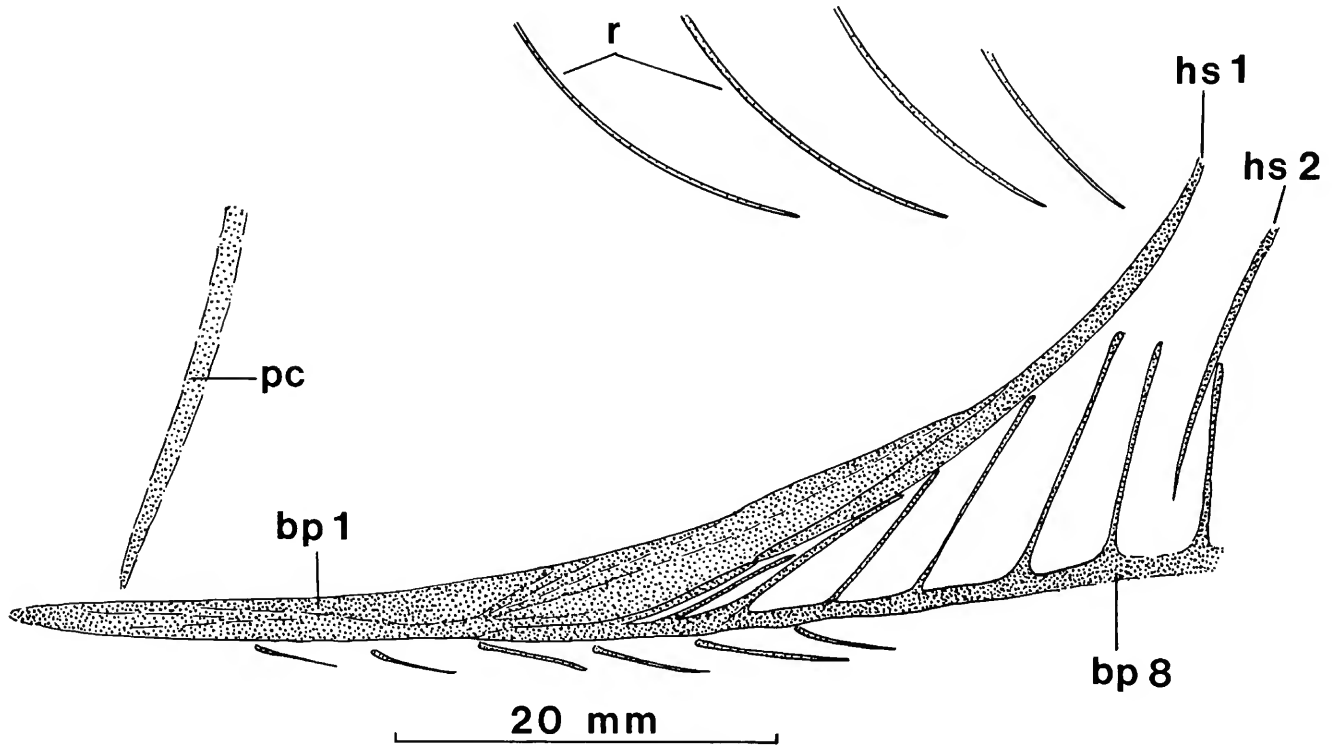
FIGURE 8.—*Avitoluvarus mariannae*, new species, PIN 2179/113, paratype, estimated 190 mm SL, fragment of skeleton showing structure of anterior pterygiophores of anal fin; Lower Eocene of Turkmenistan. (Abbreviations: bp = basal pterygiophores of anal fin (first and eighth); hs = haemal spines (first and second); pc = postcleithrum; r = pleural rib.)

Except for the last few, the dorsal-fin basal pterygiophores are approximately T-shaped in lateral view, with a ventrally oriented shaft and anteroposteriorly prolonged distal end. These distal expansions apparently sutured to one another to form a continuous truss, but, because of the poor state of preservation of the materials, we can determine neither the degree of interdigitation nor the relative contribution to the truss of the basal, medial, and distal pterygiophores. However, this distal suturing of the dorsal-fin basal pterygiophores was probably relatively weak in juveniles because several pterygiophores in the anterior part of the dorsal fin are separated from one another in the 34 mm SL specimen (Figure 7). The ventral shafts of the majority of the dorsal-fin basal pterygiophores are short and slender, with those of the most posterior few pterygiophores very short and slightly expanded into medial plates. The ventral shaft of the first dorsal-fin basal pterygiophore in the 34 mm SL specimen is expanded medially into prominent lamellar plates both anteriorly and posteriorly; this shaft is relatively longer in this juvenile than in the larger specimens, but its ventral end is still well separated from the first centrum and the base of the skull. In all specimens the ventral shaft of the first dorsal-fin basal pterygiophore is placed in the preneural space in front of the distal end of the neural spine of the first vertebra, with its ventral end remote from the

first centrum and neural arch. The shafts of the second to tenth basal pterygiophores are placed individually in the first to ninth interneural spaces, whereas more posteriorly there are either one or two shafts per interneural space, with no vacant interneural spaces.

The anal fin has 26 soft rays and no spines. The first two rays are borne in supernumerary association toward the rear of the thick anterior extension of the first anal-fin basal pterygiophore. The anal rays are unbranched, unsegmented, and bilaterally paired, similar to those of the dorsal fin and perhaps of about the same length. There are about 26 anal-fin basal pterygiophores, mostly T-shaped like those of the dorsal fin but with longer, although equally slender, shafts. The first anal-fin basal pterygiophore has a long and thick anterior extension beneath most of the length of the abdominal cavity and a long but somewhat less stout posterodorsal process whose upper end articulates along the anterior edge of the lower end of the haemal spine of the first caudal vertebra. The second and more posterior anal-fin basal pterygiophores have the distal ends expanded into shallow anterior and posterior processes that form a continuous truss that we presume must have been extensively interdigitated even though we cannot determine the details of this in the poorly preserved materials. The dorsally directed shafts of all but the first few and last few of these
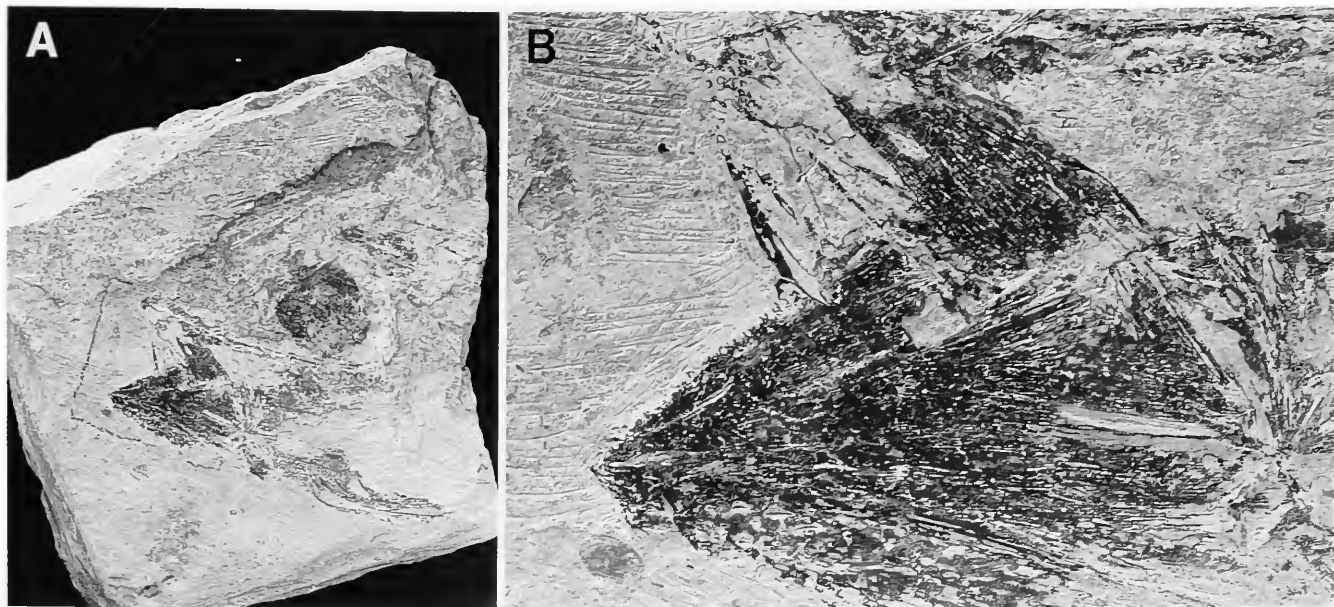
FIGURE 9.—*Avitoluvarus* sp., PIN 1762/107, estimated 215 mm SL: A, head, × 1.0; B, region of upper and lower jaws bearing teeth, × 5.0; Lower Eocene of Turkmenistan.

anal-fin basal pterygiophores are exceptionally slender, far more so than in *A. dianae.* The shafts of the second to eighth (second to seventh in PIN 1762/99 and 2179/113, Figure 8) basal pterygiophores are placed between the haemal spines of the first and second vertebrae (first interhaemal space), and those of the ninth to twelfth basal pterygiophores in the second interhaemal space (this region present and fully preserved only in PIN 1762/98). The succeeding interhaemal spaces usually accommodate two, sometimes three, basal pterygiophore shafts. The shafts of the anal-fin basal pterygiophores are not especially convergent toward the haemal spines.

Scales: There are faint remains and impressions of numerous minute rounded scale plates on the body. The largest scales are present ventrally (and, less certainly, dorsally) along the base of the anal fin and in front of its origin. The lateral line is not evident.

Luvarus Rafinesque, 1810

Luvarus Rafinesque, 1810:22 [type species *L. imperialis* Rafinesque, 1810, by monotypy].

Diana Risso, 1826:267 [type species *D. semilunata* Risso, 1826, by monotypy].

Ausonia Risso, 1826:341 [type species *A. cuvieri* Risso, 1826, by monotypy].

Proctostegus Nardo, 1827a:27, 35 [type *P. proctostegus* Nardo, 1827a, by tautology and monotypy].

Astrodermus Cuvier, 1829:216 (ex Bonelli) [type species *A. guttatus* Cuvier, 1829 (ex Bonelli), by monotypy]. [Subsequently variously spelled: *Astrodermes* by Swainson, 1839:79; *Astrodermis* by Swainson, 1839:440; *Astroderma* by Lowe, 1843:83; *Asterodermus* by Agassiz, 1846:37.]

Scrofaria Gistel, 1848:viii [type species *Ausonia cuvieri* Risso, 1826, as replacement name. Occasionally misspelled *Scafaria.]*

Proluvarus Danilchenko, 1968:144 [in part; type species *P. necopinatus* Danilchenko, 1968, by monotypy and original designation].

We agree with Whitley (1940:326), Fowler (manuscript), and Eschmeyer (1990) that the terms *Hystricinella, Astrodermella,* and *Luvarella* as applied to juvenile developmental stages of *L. imperialis* by Roule (1924:123) are not to be considered as generic names.

TYPE SPECIES.—*Luvarus imperialis* Rafinesque, 1810, by monotypy.

DIAGNOSIS.—Differs from *Avitoluvarus* (see the diagnosis of that genus for its contrasting character states) as follows: neural and haemal spines of ninth caudal vertebra short, upright, and sutured to posterior ends of truss, forming the "anchor" for succeeding or "pivot" vertebra; centrum of tenth caudal vertebra short, with low neural and haemal spines, forming a "pivot" for caudal peduncle; postcleithrum short; shaft of first anal-fin basal pterygiophore short and slender; eye placed low on head, in about middle of head; pleural ribs expanded; pelvic fin retained as a specialized rudiment (operculum ani) in adults; pterygial truss relatively deep and pterygiophores articulated to one another over a relatively broad surface distally, the depth of the interdigitated surface equal to about one-half the length of the centra; first two haemal spines exceptionally slender and curved in approximately the same direction, with both concave anteriorly; loss of teeth in large adults; epineural intermuscular bones absent; most of shafts of anal-fin basal pterygiophores exceptionally slender; usually four shafts of anal-fin basal pterygiophores placed in first two interhaemal spaces; ascending process of pelvis oriented anterodorsally, and posterior process very short and posterodorsally oriented or essentially absent; vertebral column articulated low on cranium (see "Analysis of Characters" for discussion of all of these features).

†*Luvarus necopinatus* (Danilchenko, 1968), new combination

FIGURES 10–12

Proluvarus necopinatus Danilchenko, 1968:145, pl. XXXV: fig. 1 [in part]; 1980:165.

HOLOTYPE.—PIN 2179/59, see "Material Examined" for details of the holotype and other materials, totaling six specimens of about 326–495 mm SL. The two specimens designated as paratypes of this species by Danilchenko are herein referred to *A. dianae*.

TYPE LOCALITY AND HORIZON.—Two km northeast of Uylya-Kushlyuk village, southwest Turkmenistan; lowermost layers of the middle part of the Danata Formation, Lower Eocene (Ypressian).

DIAGNOSIS.—Differs from *L. imperialis* (see the diagnosis of that species for its contrasting character states) by the following: neural spine of first vertebra slender and less long, extending dorsally no more than two-thirds distance between centrum and dorsal pterygial truss; first two haemal spines less curvaceous and less anteriorly swung; more anterior pleural ribs expanded throughout their lengths, increasingly so distally (the above features are polarizable and discussed in the "Analysis of Characters," whereas the following cannot be polarized and are not included in the analytical section); shafts of two anal-fin basal pterygiophores placed in first interhaemal space and two in second interhaemal space; pelvic fins at approximately 300 mm SL more reduced in size, consisting of two at least partially consolidated or fused spines, as well as individually indistinguishable rays.

DESCRIPTION.—Based on the body sizes of the various life history stages of the other representative of this genus, *L. imperialis,* we presume that all of the specimens available of *L. necopinatus* are adults.

The body is fusiform in shape, with a short and very slender caudal peduncle. The greatest body depth varies from 33%–
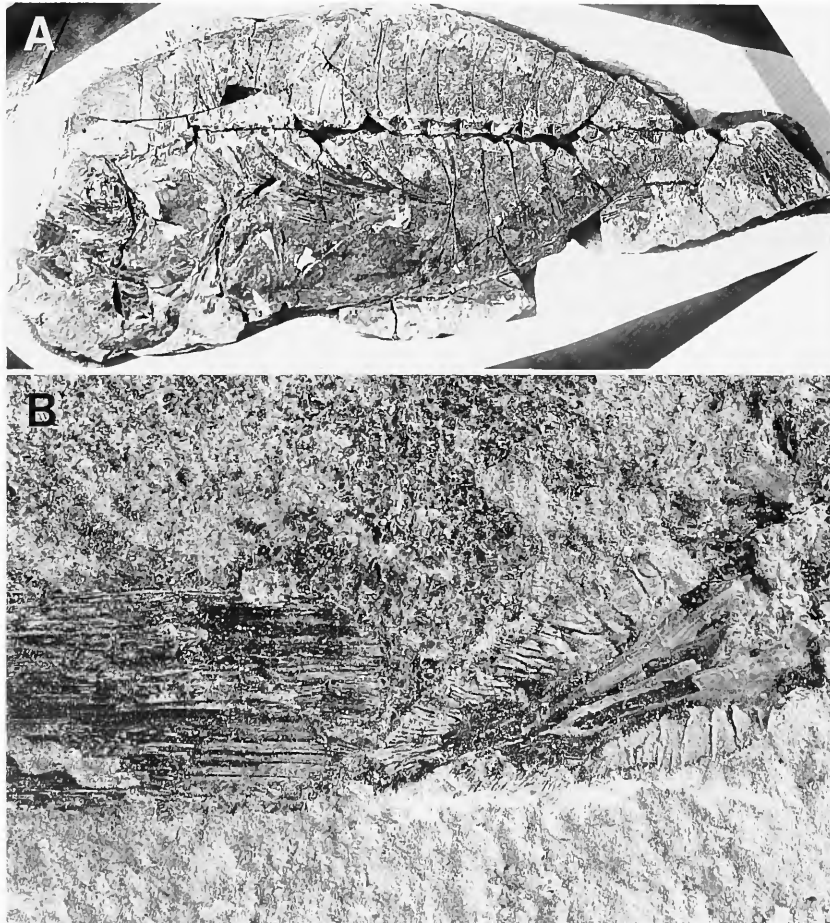

FIGURE 10.—*Luvarus necopinatus*: A, PIN 2179/59, holotype about 340 mm SL, almost complete skeleton, ×0.3; B, PIN 2179/103, estimated 326 mm SL, coalesced pelvic fins (operculum ani), × 5.0; Lower Eocene of Turkmenistan.
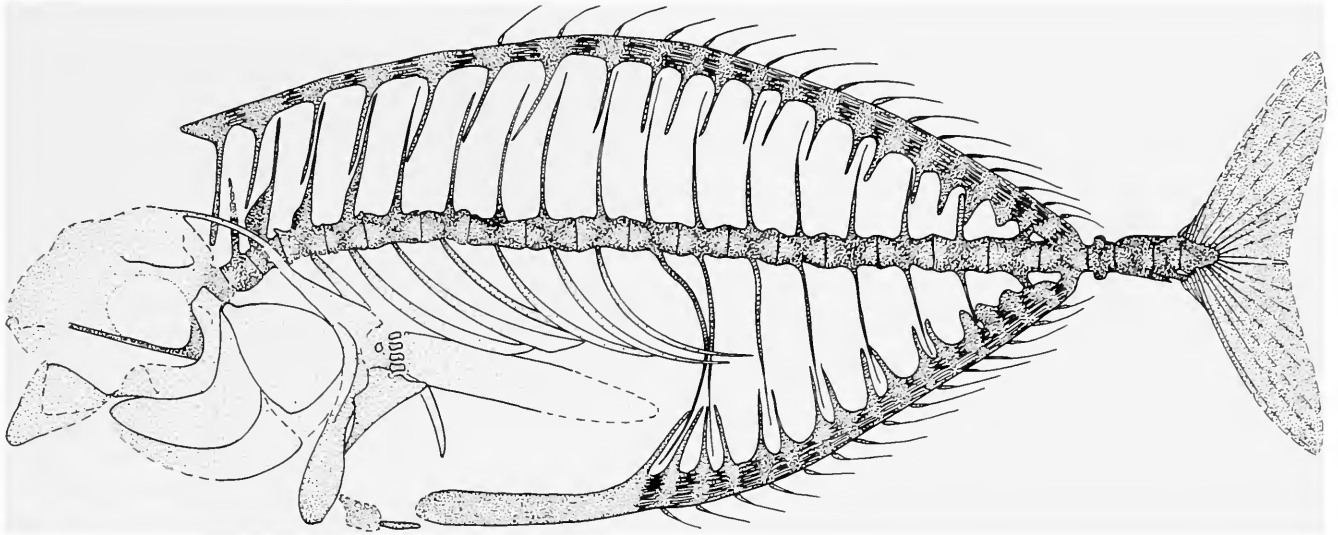
FIGURE 11.—*Luvarus necopinatus*, reconstruction of skeleton based mostly on the holotype (PIN 2179/59, about 340 mm SL) but with some details from other specimens (especially PIN 2179/63 and 2179/103); Lower Eocene of Turkmenistan. (See Figure 12B for details and scale.)

38% SL (average 36%). The head is relatively short, 26%–28% SL, and deep, similar in shape to that in larger specimens of *L. imperialis* (see Gregory and Conrad, 1943, figs. 5, 12). The mouth is small. The round orbit is placed in about the middle of the head and its diameter varies from 22%–25% of head length.

Skull: The limits of the individual bones of the neurocranium are not clear, but the relatively low position of the orbit, below the level of the vertebral articular facet of the basioccipital, indicates that the frontals and supraoccipital were probably relatively large and wide; the supraoccipital probably lacked a prominent crest. The ethmoid region is moderately elongate. The slender and almost straight parasphenoid is evident below the orbit and the rear half of the ethmoid region, whereas posteriorly it is strongly curved upward toward the basioccipital. The shaft of the hyomandibular is almost vertical, and its dorsal head is slightly expanded and bent anteriorly; the middle of the head of the articular facet is upraised and apparently articulated obliquely with the sphenotic anteriorly and the pterotic posteriorly. The quadrate is of moderate size and approximately subtriangular in shape, with a somewhat rounded upper margin, thickened lower edge, and a small articular facet for the lower jaw. A slender symplectic is apparent in some specimens and a large metapterygoid apparently occupied the space between the quadrate and lower end of the hyomandibular shaft. The limits of the pterygoid bones and palatine are unclear.

The lower jaw articulation is situated at the rear of the ethmoid region, only slightly in front of the level of the anterior edge of the orbit. The lower jaw is approximately triangular, its length about 32% of the head length. The dentary is edentulous and its symphysis shallow, its depth increasing greatly toward

the rear. The articular and dentary are approximately equal in size. The bones of the upper jaw are preserved in a single specimen (PIN 2179/63) and only poorly so, with the premaxilla so poorly preserved that we cannot determine whether it was similar to that of *L. imperialis* in lacking an ascending process. The maxilla is constricted just below its dorsal head and becomes much wider ventrally. The vague remains of a lachrymal are indicated on this same specimen.

The opercular region is broad. The preopercle is crescentic, broadest in the middle and with dorsal and ventral limbs of about equal length; the angle between the two limbs is about 85°. The upper half of the anterior edge of the preopercle articulates with the hyomandibular. The opercle is broad, rounded posteriorly and ventrally, with an anterodorsal knob-like articular condyle toward the posterodorsal end of the hyomandibular. Posteroventrally the opercle broadly overlies the thin subopercle. The interopercle is a large, thin, oblong plate, broadest posteriorly where it abuts the anterior end of the subopercle. The upper surface of the interopercle is broadly overlain by the ventral limb of the preopercle.

The hyoid and branchial arches are not visible, and the branchiostegal rays are only partially exposed and impossible to accurately count. Long gill filaments are exposed in PIN 2179/63, in which the opercle is anteriorly displaced.

Pectoral Fin and Girdle: The posttemporal is long and slender, apparently flattened, and extends from just below the level of the vertebral column to the posterodorsal region of the epiotic. An anterior or intercalar process from the lower end of the posttemporal is not exposed in any of the materials but if such is present it would be as long as the intercalar process in *L. imperialis* because of the great distance between the skull

and the lower end of the posttemporal. The supracleithrum is not clearly visible. The cleithrum is large and strongly curved anteriorly at both the upper and lower ends. The lower end of the cleithrum is rounded rather than tapered to a point. The dorsal region of what appears to be a single postcleithrum is obscured by the pectoral fin, but the region below the fin is short and relatively slender, its ventral end well removed from the dorsal edge of the anterior extension of the first anal-fin basal pterygiophore. The scapula is a large, flat plate, thickened along its posterior edge where it bears an articular facet for the uppermost pectoral-fin ray and, below that facet, where it supports the upper actinosts. A small foramen is present in the scapula. The limits between the scapula and coracoid are unclear in most of the materials but in PIN 1762/91 it is clear that the scapula supports the upper two and part of the third actinost whereas the coracoid supports the rest of the third and the fourth actinost. The actinosts are of increasing size from first to fourth and are compressed in the middle (hour-glass shape). The coracoid is broad dorsally and tapered anteroventrally, with a long and broad lamellar-like postcoracoid process.

The base of the pectoral fin is situated below the middle of the body, under the fourth or fifth vertebral centra, at a level a little above the middle of the distance between the vertebral column and the ventral profile of the body. The pectoral fin is relatively long, 19%–21% SL, and although its number of rays is difficult to determine precisely, there were a minimum of 15 rays and more likely about 18.

Pelvic Fin and Girdle: The pelvis is short, with a narrow ascending process, a poorly developed anterior or ishial process, and essentially no posterior process. The axis of the ascending process and main body of the bone lie at about a 45° angle to the vertebral axis.

The region of the pelvic fin is preserved only in the approximately 326 mm SL specimen (PIN 2179/103, Figures 10B, 12A) and the pelvic fin is exposed in dorsoventral view (shown in hypothesized lateral view in the reconstruction, Figure 11). In this specimen the pelvic spines from each side of the body are represented by short (8 mm long) but stout rudiments that lie immediately adjacent to one another in the midline of the belly immediately in front of the anterior end of the anterior extension of the first anal-fin basal pterygiophore. The two rudimentary spines are at least partially fused to one another and to the obliquely striated teardrop-shaped flat plate that surrounds them. Because of the striations on this plate and its position around the pelvic spines, we believe that the plate is composed of coalesced rudimentary pelvic-fin soft rays. This structure in *L. necopinatus* is remarkably similar to what Cuvier and Valenciennes (1833:413) and Rafinesque (1810:22) described and Gregory and Conrad (1943, fig. 9E,F) illustrated and labelled as the operculum ani for large specimens of *L. imperialis* (Figure 12 compares the operculum ani in both species of *Luvarus*). An alternate interpretation, which we think less likely, is that the striated plate represents the posterior process of the pelvis.

Vertebral Column: There are $9 + 13 = 22$ vertebrae. The vertebral column is relatively straight, except that it is curved downward at the anterior end where it articulates low on the rear of the cranium. The length of the abdominal part of the vertebral column is 69% of the length of the caudal part in the only specimen in which this measurement can be obtained (PIN 2179/59). All of the centra are amphicoelous. The centra of the first and second vertebrae are shorter than the others, except for the modified ones of the caudal peduncle. The neural spine of the first vertebra is more slender and shorter than those of the other abdominal and more anterior caudal vertebrae, extending dorsally somewhat less than two-thirds of the distance between the centrum and the ventral edge of the pterygial truss. The neural spines of the other more anterior abdominal vertebrae are somewhat expanded anteriorly in their basal regions (especially that of the second vertebra) but more distally are very slender. From about the sixth abdominal to the sixth caudal vertebrae the neural spines are slender throughout their lengths, which decrease posteriorly in the series, whereas those of the seventh to ninth caudal vertebrae become especially shorter and stouter. The distal ends of the neural spines closely approach the ventral edge of the pterygial truss. The neural spines of all but the more posterior caudal vertebrae are shorter than the corresponding haemal spines. The abdominal vertebrae lack haemal arches and parapophyses. Relatively long and stout pleural ribs that become slightly shorter posteriorly in the series are present on the third to ninth abdominal vertebrae. These pleural ribs are strongly inclined backwards and the first three or four ribs are broadly expanded (best seen in PIN 2179/59), increasingly so to the distal ends, whereas the degree of expansion progressively decreases in the more posterior ribs, with the last being a relatively slender curved shaft. There are no epineurals.

The haemal spines of the first two caudal vertebrae are moderately (first) to slightly (second) curvaceous. The first haemal spine curves posteriorly from its origin on the centrum and its middle region extends to the level of the middle of the second caudal vertebral centrum, below which it curves back anteriorly to the level of its origin. The second haemal spine is only slightly curved posteriorly in the middle region and its distal region is relatively vertically oriented. These two haemal spines are in contact or at least very close proximity with each other in their middle regions. The first six haemal spines are very slender and those of the third to seventh vertebrae are relatively straight and progressively shorter. The neural and haemal spines of the eighth and ninth caudal vertebrae are much shorter and stouter than those anterior to them, in specialized support of the pterygial truss. The neural and haemal spines of the ninth caudal vertebra are especially broad and sturdy, oriented anteriorly, and extensively sutured to the last basal pterygiophores of the dorsal and anal fins, forming the specialized "anchor" (the term of Gregory and Conrad, 1943) for the rear end of the truss in the same manner as in *L. imperialis*.
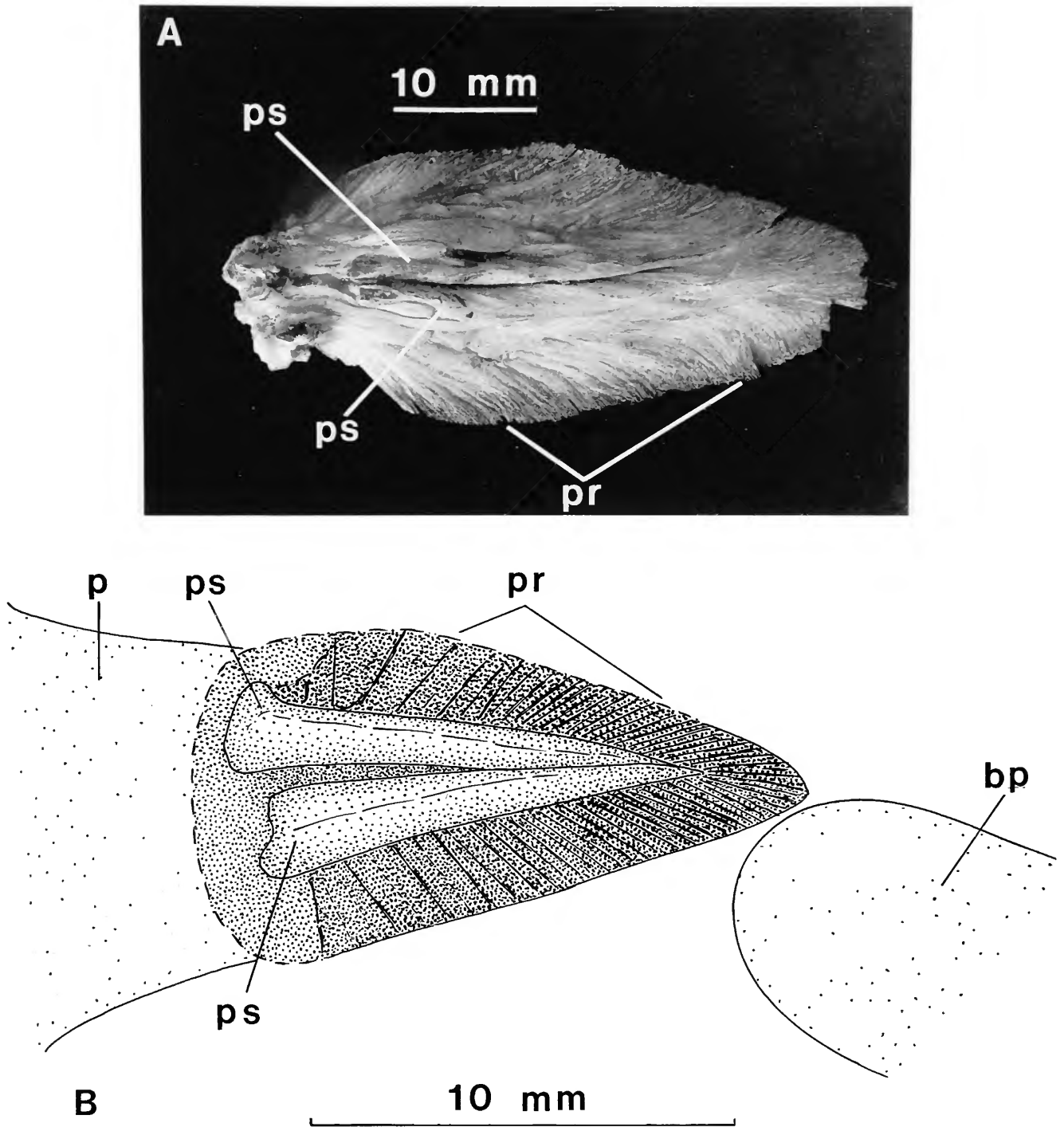
FIGURE 12.—Coalesced pelvic fins (operculum ani) in adult specimens of *Luvarus:* A, *L. imperialis*, AMNH 27984, large adult of unknown length but about 91 kg weight, Recent, western Atlantic off Florida; B, *L. necopinatus*, PIN 2179/103, estimated 326 mm SL, Lower Eocene of Turkmenistan. (Abbreviations: bp = basal pterygiophore of anal fin (first); p = pelvis; pr = pelvic-fin rays; ps = pelvic-fin spine (left and right); Gregory and Conrad (1943:240) interpreted the view of the operculum ani in A to be internal or dorsal, while it cannot be determined whether the view in B is dorsal or ventral.)

Caudal Fin and Skeleton: The tenth to thirteenth caudal vertebrae that form the caudal peduncle are preserved in several specimens but the caudal fin is not complete in any of them. The basal part of the lower caudal-fin lobe is preserved in PIN 2179/59 and the uppermost rays of the upper lobe are preserved in PIN 2179/63. These partial remains lead us to believe that the fin was similar in size, shape, and number of rays to other luvarids; 16 principal rays plus procurrent rays above and below in a forked fin and the bases of the rays broadly overlapping the hypural plate in hypurostegy.

The centrum of the tenth caudal vertebra is much shorter than the ones immediately anterior and posterior to it, and its neural and haemal spines are exceptionally low and vertical, forming the "pivot" (the term of Gregory and Conrad, 1943) for the flexure of the caudal peduncle in the same manner as in *L. imperialis.*

The neural and haemal spines of the eleventh caudal vertebra (PU_3) are directed posteriorly and almost horizontally over the anterior half of the succeeding vertebra. The twelfth and thirteenth vertebrae are best seen in PIN 2179/59 but are only fragmentarily preserved; however, hypurostegy is evident and the entire complex seems to have the same structure as that of the 301 mm SL specimen of *L. imperialis* illustrated by Tyler et al. (1989, fig. 21).

Dorsal and Anal Fins: In the only specimen in which the entire dorsal fin is preserved (PIN 2179/63, about 337 mm SL), there are 17 soft fin rays and no spines. The first dorsal-fin ray in this specimen is borne on the sixth dorsal-fin basal pterygiophore, and we presume that the more anterior rays and spines have been lost with increasing specimen size in the same ontogenetic manner as occurs in *L. imperialis*. All of the rays are unbranched, unsegmented, bilaterally paired, and have small posterior projections from their bases for muscle attachment. The rays are relatively short, the longest (11th) being about 9% SL. There are 22 dorsal-fin basal pterygiophores in the two specimens in which a total count can be obtained (PIN 2179/59 and 63), one more than is the norm for *L. imperialis* (Tyler et al., 1989:21). Except for the last three, each dorsal-fin basal pterygiophore is approximately T-shaped in lateral view, with a ventrally oriented shaft and anteroposteriorly prolonged distal end. The distal ends of these pterygiophores are extensively interdigitated to one another throughout their entire surface of contact, with the depth of the interlocking increasing toward the outer edge of the truss. The first dorsal-fin basal pterygiophore has a well-developed anterior flange from its distal end whereas its ventral shaft is long and robust, placed in the preneural space and reaching to or almost to the rear of the occipital region of the cranium. The ventral shafts of the other dorsal-fin basal pterygiophores, except for the last three or four, are slender and of decreasing length posteriorly in the series. The material is not well-enough preserved for the medial and distal pterygiophores to be seen. Except for one vacant interneural space of variable position, each of the first to tenth interneural spaces accommodates a single basal pterygiophore shaft, whereas more posteriorly there are one to three shafts (or ventral protrusions in the case of the last few pterygiophores) per space. In the three specimens in which we are certain of the position of the vacant interneural space, it varies from the third (PIN 1762/91) to the fourth (PIN 2179/59, as illustrated in the reconstruction based mostly on the holotype) to the fifth (PIN 2179/103) space.

The anal fin has 17 soft rays and no spines. Each ray is borne on the pterygiophore just posterior to the one with which it was probably serially associated, although there are no rays apparent on the first basal pterygiophore. The anal-fin rays are unbranched, unsegmented, and bilaterally paired, like the dorsal-fin rays but very slightly longer. There are 18 anal-fin basal pterygiophores with the same T-shaped structure and size as the corresponding ones in the dorsal fin, except for the first anal pterygiophore. The material is not well-enough preserved to be able to distinguish medial and distal pterygiophores. The first anal-fin basal pterygiophore has a slender posterodorsal shaft of moderate length along the front of the distal end of the first haemal spine, whereas its anterior extension is long and deep, reaching to a level just in front of the ventral end of the postcleithrum and at the posterior edge of the rudimentary pelvic fin. The posterodorsal shafts of the second and third anal-fin basal pterygiophores are placed between the first and second haemal spines (first interhaemal space) and those of the third and fourth in the second interhaemal space. The succeeding interhaemal spaces also usually accommodate two basal pterygiophore shafts. The dorsal ends of the shafts of the more anterior anal-fin basal pterygiophores converge toward the ventral ends of the haemal spines of about the first five caudal vertebrae. The last four basal pterygiophores essentially lack elongate shafts.

Scales: The body is covered with minute rounded scale plates, with somewhat larger scales irregularly scattered around the body. The largest scales (approximately 2.8 mm greatest dimension in a 337 mm SL specimen) are relatively more oval and placed along the bases of the dorsal and anal fins. The scales are not well-enough preserved to determine if sculpturing or spinules were present on the scale plates, and the lateral line is not evident.

Luvarus imperialis Rafinesque, 1810

FIGURE 13

Luvarus imperialis Rafinesque, 1810:22.
Diana semilunata Risso, 1826:267.
Ausonia Cuvieri Risso, 1826:342.
Proctostegus protostegus Nardo, 1827a:27, 35.
Proctostegus prototypus Nardo, 1827b:7.
Astrodermus guttatus Cuvier, 1829:216 (ex Bonelli).
Coryphaena elegans Cuvier in Cuvier and Valenciennes, 1833:353 (ex Risso).
Astrodermus coryphaenoides Cuvier in Cuvier and Valenciennes, 1833:353 (ex Bonelli).
Diana Valenciennesii Cocco and Scuderi, 1835:264.
Astrodermus Elegans Bonaparte, 1839:[unpaginated, 355 subsequently assigned to the referenced page].
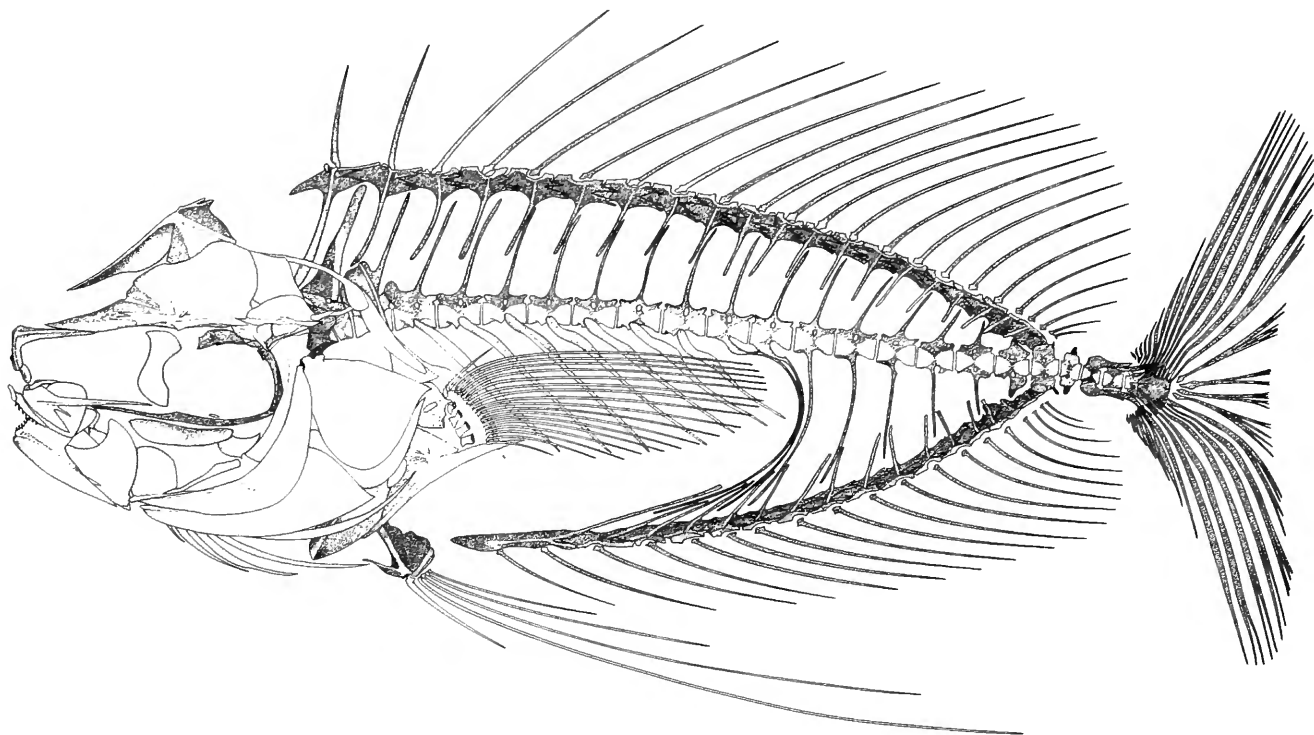
FIGURE 13.—*Luvarus imperialis*, USNM 228612, 79.2 mm SL, lateral view of entire cleared and stained skeleton, from Tyler et al. (1989, fig. 3); Recent, western Atlantic off Brasil.

Astroderma plumbeum Lowe, 1843:83.
Ausonia Cocksii Bullmore, 1866:163.

HOLOTYPE.—None designated by Rafinesque (1810). No neotype has been designated subsequently, and we see no reason to do so here for this relatively easily recognized and relatively well known, even if seldom collected, species that is the only Recent representative of its family.

TYPE LOCALITY AND HORIZON.—Solanto, Italy; Recent.

DIAGNOSIS.—Differs from *L. necopinatus* (see the diagnosis of that species for its contrasting character states) by the following: neural spine of first vertebra long and stout, extending dorsally to lower edge of dorsal pterygial truss; first two haemal spines exceptionally curvaceous and anteriorly swung; pleural ribs expanded only in their basal half or less, with the distal ends tapered to points (the above features are polarizable and discussed in the "Analysis of Characters," whereas the following cannot be polarized and are not included in the analytical section); shafts of three anal-fin basal pterygiophores placed in first interhaemal space and only one shaft in second interhaemal space; pelvic fins at approximately 300 mm SL less reduced in size, small but separated from one another and consisting of a spine and four rays.

DESCRIPTION.—This species has recently been described in detail by Tyler et al. (1989) based on larval and adult cleared and stained materials, as well as alcohol preserved specimens

and large dry skeletons, whereas Gregory and Conrad (1943) gave a detailed description of the dry skeleton of a large (about 91 kg) specimen. We do not repeat any of those descriptive details herein but simply call attention in the diagnosis above to the differences between the Recent *L. imperialis* and the Eocene *L. necopinatus*.

Family †KUSHLUKIIDAE Danilchenko, 1968

TYPE GENUS.—*Kushlukia* Danilchenko, 1968, by monotypy.

DIAGNOSIS.—Differs from the Luvaridae (see the diagnosis of that family for its contrasting character states) as follows: vertebrae 10 + about 19–20 = about 29–30; ventral shaft of first basal pterygiophore of dorsal fin very short and placed in third or fourth interneural space; first two haemal spines parallel or divergent from one another; several of more posterior abdominal vertebrae with parapophyses; opercular region elongate; articular relatively small; neural and haemal spines of caudal vertebrae relatively broad; proximal shafts of dorsal- and anal-fin basal pterygiophores relatively broad; epineural intermuscular bones present; postcleithrum a greatly expanded plate; pelvis with long posterior extension sutured or closely applied to anterior extension of first anal-fin basal pterygiophore, and anus therefore probably on throat; pectoral fin placed high on body; coracoid elongate and lacking
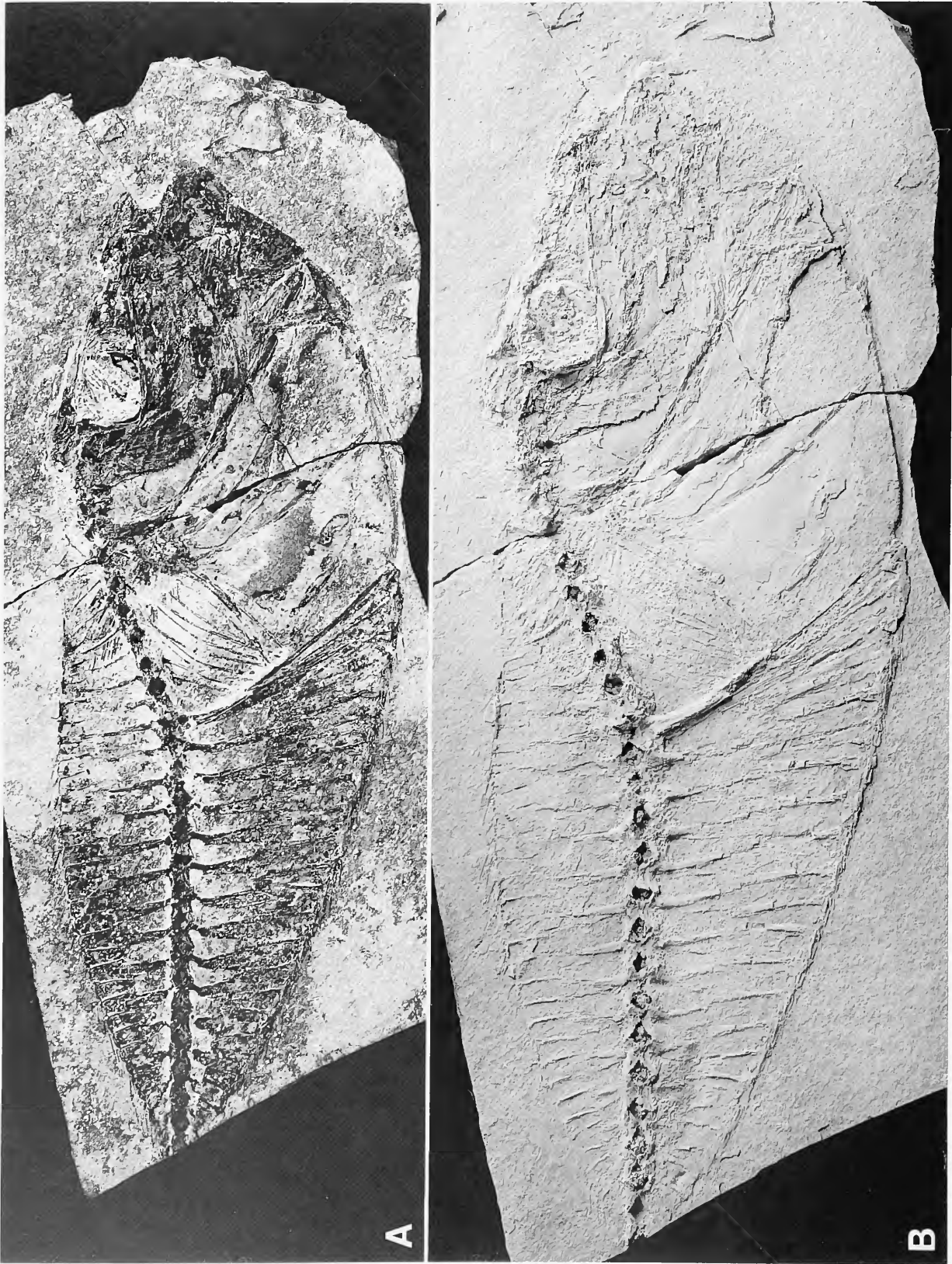
FIGURE 14.—*Kushlukia permira*, PIN 2179/64, holotype, estimated 183 mm SL, skeleton without caudal peduncle: A, natural contrast, × 1.0; B, coated with sublimate of ammonium chloride to improve contrast, × 1.2; Lower Eocene of Turkmenistan.

postcoracoid process; premaxilla beak-like; ascending process of premaxilla of moderate length; scapula small; neural spines of first two vertebrae short; urohyal exceptionally large; two anal-fin basal pterygiophores in front of first haemal spine; complete loss of pelvic fins even at relatively small sizes (all of the above features are polarizable and discussed in the "Analysis of Characters," whereas the following cannot be polarized and are not included in the analytical section); ventral flange present on parasphenoid under orbit; anterior extension of first anal-fin basal pterygiophore with a constriction just in front of distal end of shaft-like portion; eye placed very high in head, close to profile; dorsal fin with a total of at least 30 fin-ray elements.

COMPOSITION.—One genus, *Kushlukia* Danilchenko (1968), with two species, one (*K. permira* Danilchenko, 1968) from the Lower Eocene of Turkmenistan and the other (not specifically named here) from the Lower Eocene of India.

†*Kushlukia* Danilchenko, 1968

Kushlukia Danilchenko, 1968:148.

TYPE SPECIES.—*Kushlukia permira* Danilchenko, 1968, by monotypy and original designation.

DIAGNOSIS.—As for the family, of which it is the only genus.

†*Kushlukia permira* Danilchenko, 1968

FIGURES 14, 15

Kushlukia permira Danilchenko, 1968:148, pl. XXXVI: fig. 1, text fig. 18; 1980:166, pl. VI: fig. 4.

HOLOTYPE.—PIN 2179/64, see "Material Examined" for details of the holotype and other materials, totaling nine specimens of about 141–198 mm SL, which, on the basis of the sizes of the various life history stages in *L. imperialis,* we presume are adults. The caudal fin and caudal peduncle vertebrae are missing in all of the specimens and we presume that the text figure of this species in Danilchenko (1968:149, fig. 18), with a peduncle and caudal fin, is entirely hypothetical for this region.

TYPE LOCALITY AND HORIZON.—Two km northeast of Uylya-Kushlyuk village, southwest Turkmenistan; lowermost layers of the middle part of the Danata Formation, Lower Eocene (Ypressian).

DIAGNOSIS.—Differs from *K.* sp. by the following: the approximately 10 most anterior haemal spines inclined anteroventrally; basal pterygiophores interdigitated to one another only distally (for details of both features see "Analysis of Characters").

DESCRIPTION.—The body is fusiform in shape and, based on the tapering of the body in the posterior region of the dorsal and anal fins, we presume that the caudal peduncle was as short and slender as in luvarids. The greatest body depth is about 35%

SL. The head is of moderate length, 31%–32% SL, with the viscerocranium anteroventrally elongate. The mouth is small, edentulous, and distinctly supraterminal. The round orbit is placed high in the head, very close to the dorsal profile, with a diameter of about 24%–27% of head length.

Skull: The neurocranium is especially low and although the limits of the individual bones in the posterodorsal region of the skull are not distinct, it is clear that the supraoccipital had essentially no crest and that the frontals were narrow interorbitally. The braincase is very short, about 1.5 times shorter than the diameter of the orbit. The ethmoid and lateral ethmoid together form a long and sturdy buttress that tapers anteriorly to the region of the vomer below the upper end of the upper jaw. The parasphenoid is relatively long and straight as exposed under the orbit and ethmoid region and has a prominent ventral flange in the region under the orbit and lateral ethmoid. The shaft of the hyomandibular is strongly inclined anteroventrally, at an angle of about 60° to the vertebral axis. The articular facet of the hyomandibular with the pterotic is oblique to the axis of the hyomandibular shaft. The limits of the pterygoid bones and symplectic are unclear. The quadrate is large, triangular, and elongate anteroventrally; the angle midway between its upper and lower edges converging on the articular facet is about 45°.

The lower jaw articulation is positioned far forward, at a level anterior to the anterior end of the ethmoid-vomerine complex, under the middle of the upper jaw. The lower jaw is short and very deep, with a deep symphysis. Most of the lower jaw is formed by the edentulous dentary, which apparently is intimately bound to the much smaller articular. The region of the lower jaw immediately below its articulation with the quadrate is relatively deep and we presume that this is largely formed from the angular, although we cannot discern a line of articulation here. The maxilla is badly damaged in all of the materials, but it was obviously narrow and placed closely along the rear edge of the premaxilla. The premaxilla is massive, edentulous, tapered at all three angles and therefore beak-like as seen laterally, with a prominent ascending process above the anterior end of the ethmoid-vomerine region. The lower jaw is distinctly protruded relative to the upper jaw.

The opercular region is badly damaged in all of the materials, but it is narrow and anteroventrally elongate. The preopercle is apparently long, narrow, and only gently curved. The opercle is triangular, with a broadly rounded posteroventral border. The hyoid and branchial arches and the branchiostegal rays are obscured or otherwise unrecognizable. Most of the urohyal is exposed in the anteroventral region of the head; it is enormous, filling most of the space between the rear of the lower jaw and the ventral end of the cleithrum, with a thickened region vertically in the middle of its broad surface.

Pectoral Fin and Girdle: The posttemporal is not preserved in place in any of the materials, but a slender and somewhat arched rod of bone in the region above the fourth
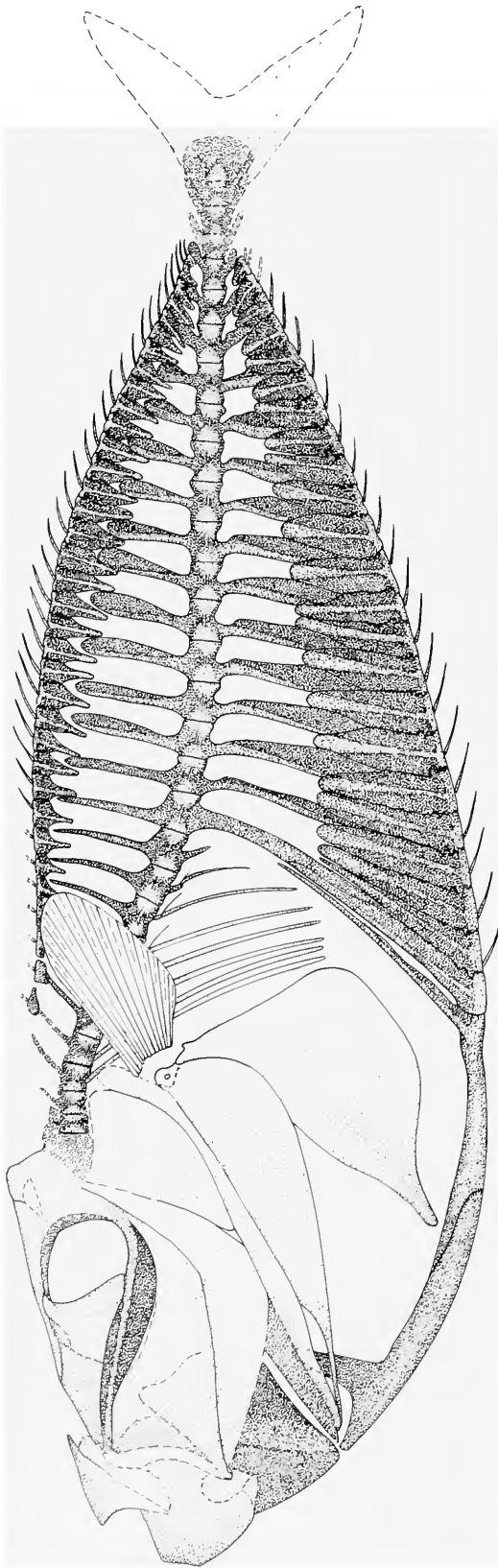
FIGURE 15.—*Kushlukia permira*, reconstruction of skeleton based mostly on the holotype (PIN 2179/64, estimated 183 mm SL) but with some details from paratypes; Lower Eocene of Turkmenistan. (Dashed lines indicate hypothesized morphology.)

vertebra in PIN 2179/64 is probably the anterodorsal wing of the displaced posttemporal (in PIN 2179/65 an elongate rod of bone displaced behind the occipital region also may be a posttemporal). The supracleithrum is not recognizable. The cleithrum is exceptionally narrow and curved upward at its dorsal end just below the third centrum, with the lower four-fifths of its length straight and placed at about a 32° angle to the vertebral axis. The scapula is very small, with the foramen entire. The coracoid is very long, thin, and tapered to a narrow shaft at its anteroventral end, with a longitudinal crest throughout its length and no postcoracoid process. The postcleithrum is an enormous, broad, flat bone that occupies much of the middle of the region of the abdominal cavity between the rear of the upper part of the coracoid and the first anal-fin basal pterygiophore; it is broadly rounded posteriorly, tapers to a sturdy shaft anteroventrally, and has a thickened ridge along its length. We find no evidence of this huge plate being divided into two pieces, nor of a separate element dorsally in the region of the pectoral-fin base that could be interpreted as a separate dorsal postcleithrum, and we therefore assume that the postcleithrum is a single bone as in luvarids and all other acanthuroids except siganids. In the original description of this species, Danilchenko (1968) erroneously described the postcleithrum as an opercle.

The base of the pectoral fin is placed very high on the body, about midway between the levels of the upper one-third to one-fourth of the body, just below the centrum of the fourth vertebra. The pectoral fin is relatively short, but the rays are not preserved well enough in any of the materials for an accurate count to be made; based on the condition in the best preserved specimen, the holotype, we estimate that there were about 14 rays and that the length of the fin was about 14% SL.

Pelvic Girdle: There is no evidence of a pelvic fin anywhere along the great length of the well-preserved pelvis in any of the materials, and we presume that if a pelvic fin is present at smaller sizes than available that it is lost ontogenetically in adults. The main body of the pelvis lies along the ventral border of the anterior half of the abdominal cavity as a deep strut representing enormous posterior (ishial) and broad anterior (iliac) processes, with an ascending (pubic) process that is shorter than the ishial, longer than the iliac, and directed posterodorsally to the lower region of the cleithrum and coracoid. The posterodorsal end of the posterior pelvic process is broadly overlain and apparently fully sutured to the anterior end of the anterior extension of the first anal-fin basal pterygiophore. The anterior end of the anterior pelvic process is situated just behind the posteroventral edge of the urohyal and below the anterior end of the cleithrum. We find no evidence of any anal opening or gap in the long strut of bone formed by the anterior extension of the first anal-fin basal pterygiophore and the posterior and anterior processes of the pelvis, including along the broad area of articulation between these two bones. We conclude that the anus must be placed far forward on the throat at the narrow gap between the anterior end of the anterior

process of the pelvis and the posteroventral end of the urohyal.

Vertebral Column: There are 10 abdominal vertebrae and 15 caudal vertebrae in the trunk anterior to the missing caudal peduncle. Because all luvarids have a tapering posterior region of the trunk similar to that of *K. permira* (although in luvarids only nine rather than 15 pre-peduncular vertebrae) and luvarids all have four caudal peduncle vertebra, we believe it reasonable to assume that *K. permira* had at least four peduncular vertebra, and perhaps five if this region of the body was as comparably more elongate as the pre-peduncular region is in relation to luvarids. Therefore, we assume that *K. permira* had at least 10 + about 19 = 29 vertebrae and perhaps 10 + about 20 = 30. The vertebral column is elevated anteriorly and articulates low on the rear of the cranium. All of the centra are amphicoelous. The centra are slightly compressed in the middle and are subrectangular except for the first four, which are progressively shortened anteroposteriorly. The neural spines of the more anterior abdominal vertebrae are slender (especially the first few) and straight or only slightly curved posterodorsally. The first two neural spines are short, no longer than the depth of their centra, whereas more posteriorly the neural spines are of increasing length and stoutness. The last two abdominal vertebrae have short but prominent parapophyses. Slender pleural ribs are present on the third to ninth or tenth abdominal vertebrae; they are inclined posteriorly and occupy the upper half of the abdominal cavity between the posterodorsal end of the postcleithrum and the upper half of the shaft formed by the first anal-fin basal pterygiophore and the first haemal spine. There are short, slender epineurals attached to either the upper ends of the pleural ribs or to the centra of at least most of the abdominal vertebra.

The haemal spine of the first caudal vertebra is slightly thicker than that of the second and these two haemal spines are parallel or only slightly divergent from one another distally. The haemal spines of all but the last few pre-peduncular caudal vertebrae are essentially straight except where slightly curved basally and are of decreasing length posteriorly in the series. Most of these haemal spines are broadened by medial flanges along the posterior edge behind the thickened anterior edge. The distal ends of the first 10 haemal spines are inclined anteroventrally, decreasingly so posteriorly. The neural spines of the caudal vertebrae are relatively straight, inclined posterodorsally, and similar to the corresponding haemal spines except shorter. The neural and haemal spines of the twelfth to fifteenth caudal vertebrae become progressively shorter and more posteriorly inclined; none of them, including those of the fifteenth (which is the last to support dorsal- and anal-fin basal pterygiophores), are modified as an "anchor" for the pterygial truss, such as is the case in *Luvarus*. Because the fifteenth vertebra is not modified into an "anchor," we believe it likely that future specimens of *K. permira* with the caudal peduncle intact will show that none of the peduncular vertebrae are modified as a "pivot."

Caudal Fin and Skeleton: None of the materials are complete posterior to the fifteenth caudal vertebra.

Dorsal and Anal Fins: There are a total of 29 dorsal-fin soft rays borne on the eighth to thirty-fifth basal pterygiophores (complete only on the holotype), one per pterygiophore except two on the last, with the rays short, unbranched, undivided, and bilaterally paired (the rays probably serially associated with the preceding pterygiophore). On the holotype the first dorsal-fin basal pterygiophore bears a short and slender fin-ray element that is too poorly preserved to determine whether it is a spine or a soft ray. Even though the second to seventh basal pterygiophores of the dorsal fin are poorly preserved, we presume that they also bore fin-ray elements, forming a continuous series between the first and eighth and more posterior basal pterygiophores on which fin rays are preserved. If that be the case, then there are a total of about 36 dorsal fin-ray elements, an unknown small number of which anteriorly may have been small spines. The length of the longest dorsal-fin rays is about 5% SL. The first two dorsal-fin basal pterygiophores are small and have only short ventral processes rather than distinct ventral shafts; the first basal pterygiophore is associated with the top of either the third (PIN 1762/102, as in the reconstruction) or fourth (PIN 2179/64, the holotype) interneural space. The basal pterygiophores are of increasing size from the front to about the middle of the fin and then are of progressively decreasing size. The size of the individual interdigitations between adjacent basal pterygiophores and the depth of the articular contact increases from anteriorly to about the rear of the middle region of the fin and then slightly decreases more posteriorly. Each basal pterygiophore in the middle and rear of the dorsal fin has a sturdy shaft and relatively broad medial flanges both in front of and behind the centrally strengthened rod of the shaft, forming with the distal expansions of the neural spines a broad sheet of bone around the dorsum. Each of the basal pterygiophores of the dorsal fin anterior to the neural spine of the first caudal vertebra is placed individually in an interneural space (third to tenth), whereas most of the interneural spaces of the caudal vertebrae accommodate the shafts of two basal pterygiophores, occasionally one or three, and there are no vacant interneural spaces posterior to the origin of the dorsal fin.

There are 23 soft anal-fin rays and no spines, with the rays unbranched, unsegmented, and bilaterally paired, similar to the dorsal-fin rays but even shorter. The bases of the rays are positioned toward the front of the distal ends of the third to last basal pterygiophores and were probably serially associated with the preceding pterygiophores but the state of preservation is such that we cannot distinguish medial and distal pterygiophores. There are 24 basal pterygiophores, with one ray per pterygiophore, except that the last bears two rays, the elongate first pterygiophore has no ray, and the second pterygiophore has only a serial association with the first ray, positioned anteriorly on the distal end of the third pterygiophore. The first anal-fin basal pterygiophore has a long anterior extension that broadly articulates over the posterodorsal end of the posterior

process of the pelvis; this extension is constricted just in front of the distal end of the shaft-like portion of the pterygiophore. The posterodorsal shaft of the first anal-fin basal pterygiophore is exceptionally long, straight, strengthened by a thickening along its anterior edge, and inclined at about a 55° angle to the vertebral axis. The second and more posterior anal-fin basal pterygiophores are broad and strengthened by a thickened central rod to either side of which is a medial flange; their length decreases posteriorly in the series, and their orientation similarly changes from posteriorly to anteriorly oblique. The anal-fin basal pterygiophores are substantially longer than the corresponding dorsal-fin basal pterygiophores and are articulated broadly to one another by especially deep emarginations and interdigitations. The combination of the broadly expanded anal-fin basal pterygiophores and the expanded distal ends of the haemal spines forms a broad sheet of bone around the ventrum that is continued anteriorly by the strut formed by the anterior extension of the first anal-fin basal pterygiophore and the anterior and posterior processes of the pelvis. The posterodorsal shafts of both the first and second anal-fin basal pterygiophores are placed along the anterior edge of the distal region of the first haemal spine, whereas the shafts of the third to fifth pterygiophores are placed between the haemal spines of the first and second vertebrae (first interhaemal space), and those of the sixth and seventh in the second interhaemal space. The succeeding interhaemal spaces accommodate one or two basal pterygiophore shafts. Near its ventral edge each anal-fin basal pterygiophore bears a lateral foramen (not shown in illustrations) that is open on the more anterior and middle pterygiophores but closed on the posterior ones.

Scales: No scales are evident in any of the materials and it is possible that *K. permira* was scaleless.

†*Kushlukia* sp.

FIGURES 16, 17

LOCALITY AND HORIZON.—Bothia, Barmer District, Rajasthan, India; Fuller's Earth, Lower Eocene (Ypressian).

DEFINITION.—Differs from *K. permira* by the following: second and subsequent haemal spines inclined posteroventrally; basal pterygiophores interdigitated to one another throughout most of their length (for details of both features, see "Analysis of Characters").

DESCRIPTION.—Both specimens of this species are highly incomplete, being represented only by the anterior part of the caudal region of the vertebral column and adjacent basal pterygiophores, and hence our reluctance to formally name it even though it represents a species distinct from *K. permira.* Judging from the proportions of *K. permira,* we estimate that the specimens represented by the two fragments of the Indian species of *Kushlukia* were approximately 93 and 98 mm SL, smaller than the specimens of the Turkmenian species.

LUVP 12010 includes the first to ninth caudal vertebrae and

faint traces of the tenth and eleventh, whereas LUVP 12011–12011A includes 10 caudal vertebrae (and space for one missing vertebra, the third in the series), the first of which is not the first caudal vertebra but perhaps the second or third. All of the centra are subrectangular and in a straight line. The neural and haemal spines are relatively straight, broad, and become progressively shorter posteriorly. The neural spines are inclined posterodorsally and appear to be shorter than the corresponding haemal spines. The haemal spines of the second and subsequent caudal vertebrae are inclined slightly but distinctly posteroventrally. The haemal spine of the first caudal vertebra is oriented anteroventrally and is strongly divergent from the second haemal spine.

Dorsal and Anal Fins: Neither of the specimens has dorsal- or anal-fin rays preserved. The dorsal-fin basal pterygiophores are only very partially preserved, and only on LUVP 12011–12011A, but some of the delicate interdigitations along a few broad areas of articulation between adjacent pterygiophores are well indicated as impressions.

The basal pterygiophores of the anal fin are preserved in both specimens along with the full extent of the closely associated haemal spines of the caudal vertebrae, although the distal ends of these anal-fin basal pterygiophores in LUVP 12011 were apparently removed during specimen preparation. The anal-fin basal pterygiophores are broad and medially expanded into a continuous sheet of bone with fine interdigitating sutures not only distally but throughout most of the length of contact between adjacent pterygiophores up to the level of the distal ends of the haemal spines (as seen in LUVP 12011–12011A; the dorsal ends of the pterygiophores are not well preserved in LUVP 12010). There are usually two, occasionally one or three, basal pterygiophores of the anal fin placed in each of the interhaemal spaces. The anteriormost anal-fin basal pterygiophores are evident only in LUVP 12010 but they are so poorly preserved that we cannot determine how many shafts of basal pterygiophores were placed anterior to the first haemal spine (two as in *K. permira* or only one as in luvarids?) but there were probably three between the first and second haemal spines (first interhaemal space).

The two characteristics (more extensive interdigitation of basal pterygiophores, and posteroventral inclination of second and more posterior haemal spines) by which the Indian specimens of *Kushlukia* differ from the Turkmenian *K. permira* do not seem to be related in the smaller size of the Indian specimens because the inclination of the haemals does not change much ontogenetically in those species of luvarids known from specimens of wide size range, and in those species the degree of interdigitation increases with increasing specimen size (e.g., in *Avitoluvarus mariannae* as described herein and in *Luvarus imperialis* as described by Tyler et al., 1989). Thus, there is every reason to believe that the Indian specimens represent a different species than the Turkmenian *K. permira.*
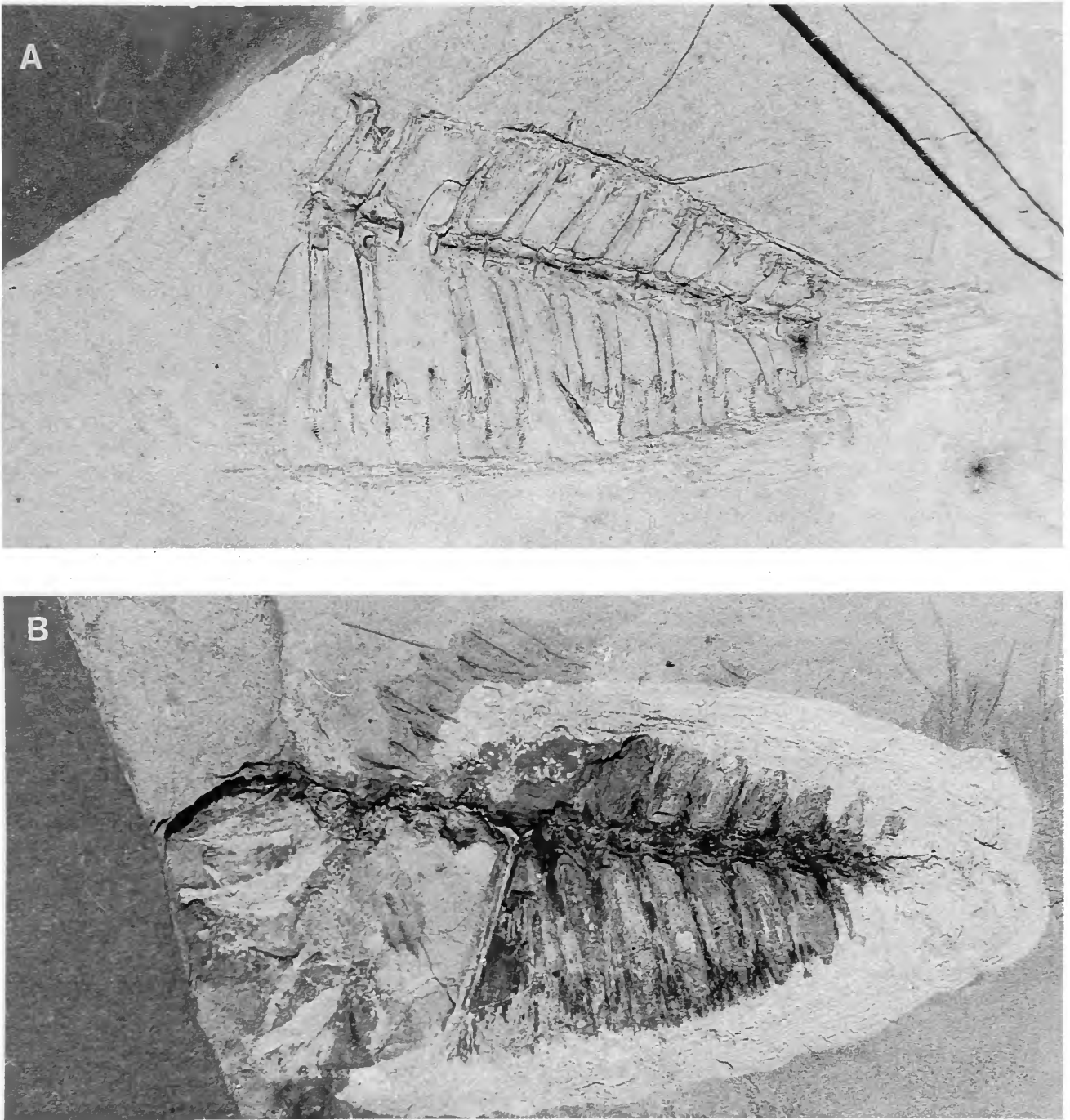
FIGURE 16.—*Kushlukia* sp.: A, LUVP 12011, estimated 98 mm SL, fragment of skeleton, × 3.1; B, LUVP 12010, estimated 93 mm SL, fragment of skeleton, × 2.9; Lower Eocene of Rajasthan, India.

Analysis of Characters

A cladistic analysis by Tyler et al. (1989) of the interrelationships of the families of the Acanthuroidei, based on 90 characters encompassing both larval and adult morphology, provides a highly corroborated hypothesis indicating the following phyletic sequence: Siganidae-Luvaridae-Zanclidae-Acanthuridae (the latter including Nasinae and Acanthurinae),
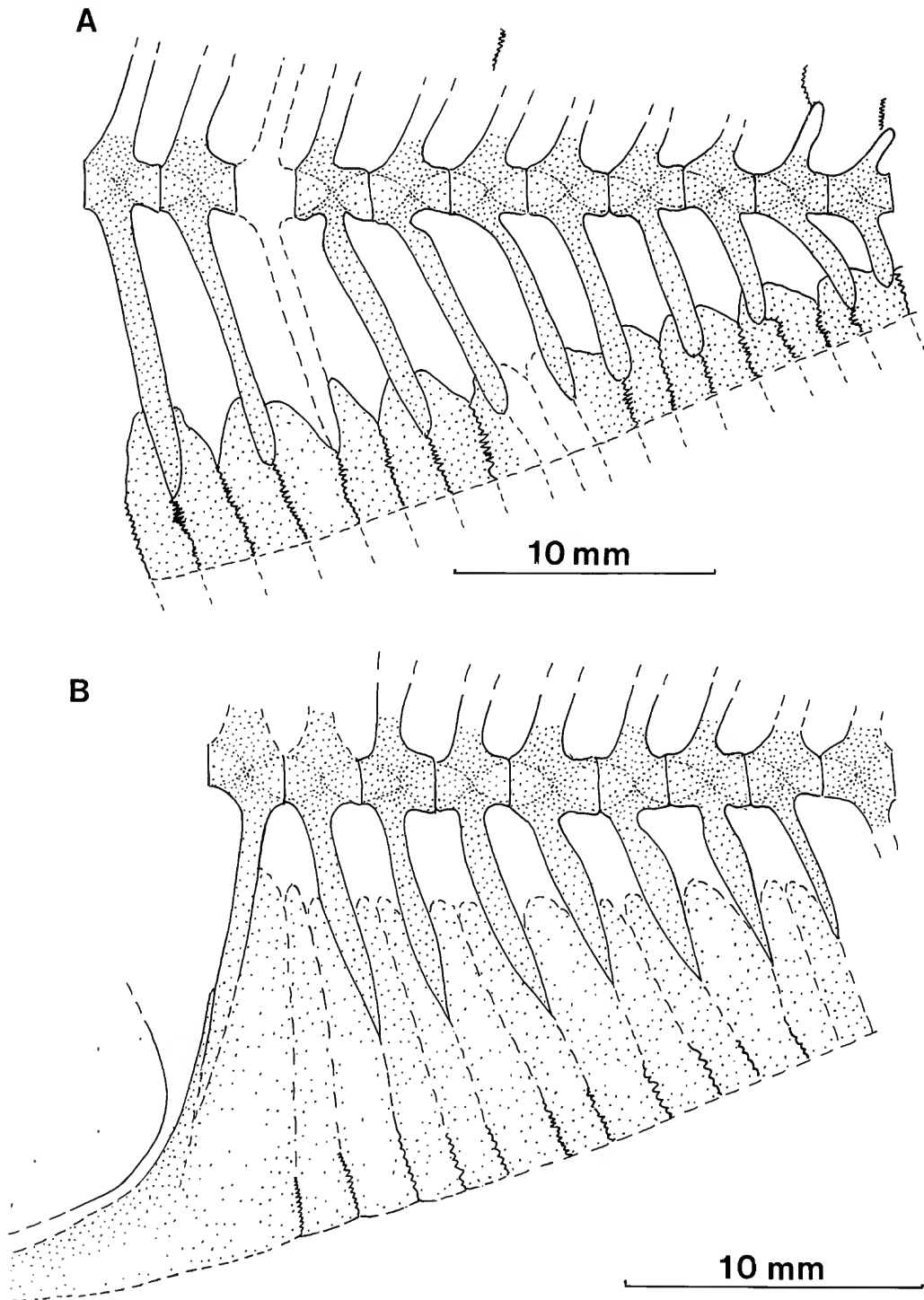
FIGURE 17.—*Kushlukia* sp.: A, most of the more anterior caudal vertebrae (but not the first; third vertebra in series missing) and basal regions of anal-fin basal pterygiophores (much of more distal regions absent), with impressions of a few of the interdigitations between the absent dorsal-fin basal pterygiophores, based on LUVP 12011, estimated 98 mm SL; B, first to ninth caudal vertebrae and more anterior anal-fin basal pterygiophores (extreme distal regions of which may be absent), based on LUVP 12010, estimated 93 mm SL; Lower Eocene of Rajasthan, India.

with Scatophagidae and Ephippididae as the first and second outgroups among the higher squamipinnes. A comparable myological analysis by Winterbottom (1993) based on 46 characters also supports that same sequence of familial relationships, as well as resolving many of the generic-level relationships within the Acanthuridae. As summarized in Winterbottom (1993), a total of 130 myological and larval and adult osteological synapomorphies support that familial phylogeny, and another 56 synapomorphies support the generic phylogeny proposed by Winterbottom with the sequence of *Naso, Prionurus, Paracanthurus-Zebrasoma, Acanthurus-Ctenochaetus* (see Guiasu and Winterbottom, 1993, for the details of the osteologically based portion of the generic phylogeny of the Acanthuridae). Therefore, the familial-level phylogeny of acanthuroids adopted herein for purposes of analysis of luvaroid relationships is robustly supported by both osteology and myology.

However, for the Luvaridae the data in Tyler et al. (1989) and Winterbottom (1993) are based exclusively on the osteology of the Recent *Luvarus imperialis*. For example, Tyler et al. (1989) reviewed the reported fossil record of the luvarids but did not feel confident enough in the descriptions in the literature or of the allocations of some of the species to try to include them in the analysis of characters, especially because many of the critically important character states are not preserved in fossil materials. The present review of all fossil luvarid-like fishes shows that the Luvaridae and Kushlukiidae clade is united by nine unequivocal synapomorphies (and one that is uncertain or equivocal) and that the family Luvaridae is composed of two genera and four species and that the family Kushlukiidae, with one genus and two species, is its sister group. With this expansion of the concept of the luvaroid fishes, the relationships of these two families with other acanthuroid fishes is reassessed below, followed by an analysis of their interrelationships. Because Winterbottom's myological data is not available for fossil materials, we can only compare our new data with the previously established osteological synapomorphies in Tyler et al. (1989), which gives the plesiomorphic conditions in the scatophagids, ephippidids, and other squamipinnes.

For analyses of proposed synapomorphies within the luvarid+kushlukiid clade, we use those two families as sister groups for which the first outgroup is the zanclid+acanthurid clade, the second outgroup the siganids, and the third outgroup the higher squamipinnes (scatophagids and ephippidids).

We use the term "acanthuroid" in the traditional sense to include siganids, luvarids (and now kushlukiids), zanclids, and acanthurids. Bannikov (1991) has suggested that caproids and the Eocene acanthonemids be recognized as acanthuroids and Winterbottom (1993) has advocated the inclusion of scatophagids and ephippidids in that suborder. Such expansions of the inclusiveness of the acanthuroids may prove to be reasonable but we do not follow them herein because our focus in this paper is only on the luvarid-like acanthuroids. Additionally, we have work in progress on other new fossil

materials that may represent taxa even more closely related to the traditional acanthuroids than are some of these other families and that may therefore further change the concept of the acanthuroids. However, our preliminary analysis of these new fossils indicates that they will not change any of our assessments of character polarity within the luvarid+kushlukiid clade.

Relevant Acanthuroid Synapomorphies

Of the 11 previously established osteological synapomorphies of adult acanthuroids, the character states of four of these (characters 3, 5, 8, 11 in Tyler et al.: anterior articulation of second infraorbital; condition of supracleithral sensory canal; supraoccipital articulation with exoccipital; and orientation of fourth pharyngeal tooth plate) are unknown in the fossil materials of the luvarid+kushlukiid clade.

Five of the other acanthuroid synapomorphies apply to the entire luvarid+kushlukiid clade (with the caveat that some of the fossil taxa have parts missing and therefore unknown conditions), as follows. The first neural spine is fused to its centrum (character 1 in Tyler et al.): this is clearly the case in both *L. imperialis* and the fossil *L. necopinatus*, in which the first neural spine is robust; in both species of the fossil luvarid *Avitoluvarus* and in the fossil *Kushlukia* the first neural spine is short and slender and we have no reason to presume that it is other than fused to the centrum. The maxilla and premaxilla are closely bound together as one functional unit (character 6 in Tyler et al.): although not well preserved individually, the maxilla in *Kushlukia* is slender and closely apposed to the rear edge of the beak-like premaxilla and gives every indication of being immovably articulated with it; in the fossil luvarids the maxilla also appears to have been slender and closely apposed to the rear edge of the premaxilla and we have no reason to believe that together they formed other than a single functional unit. The anguloarticular (articular) is much smaller than the dentary, except by reversal in *Luvarus* (character 7 in Tyler et al.): the anguloarticular is clearly relatively small in *Kushlukia*, even though in preservation it is only partially distinct from the retroarticular (angular), but even in combination they are much smaller than the dentary; in the fossil luvarids (*L. necopinatus* and *Avitoluvarus*) the articulations between the component lower jaw bones are not distinct enough for us to determine the relative size of the anguloarticular but if it is as large as in *L. imperialis* then by the same argumentation as in Tyler et al. this is a reversal that applies to all luvarids based on the overall most parsimonious interpretation. The crest of the supraoccipital is very low (character 9 in Tyler et al.): this is clearly the case in *Kushlukia* and all of the fossil luvarids, just as in *L. imperialis*. Predorsal bones are absent (character 10 in Tyler et al.): this is clearly the case in *Kushlukia* and all of the fossil luvarids, just as in *L. imperialis*.

One of the acanthuroid synapomorphies, the reduction in the number of branchiostegals to five or four (character 2 in Tyler

et al.) applies to both species of *Avitoluvarus* but the branchiostegals cannot be counted accurately in the materials available of the other fossil luvaroids, *Luvarus necopinatus* and *Kushlukia permira* (and the head is not preserved in *Kushlukia* sp.).

Only one of the 11 adult osteological synapomorphies (character 4, the long ventral shaft of first basal pterygiophore of dorsal fin placed over or anterior to the neural spine of the first vertebra) of all acanthuroids in Tyler et al. does not apply to the entire luvarid+kushlukiid clade: in both the fossil and Recent luvarids the long shaft of the first pterygiophore is clearly placed in the preneural space, whereas in *Kushlukia* the shaft is very short and placed at the top of either the third or fourth interneural space (between the distal tips of the neural spines of the third and fourth or the fourth and fifth vertebrae). Because of the nine unequivocal synapomorphies that unite the luvarid+kushlukiid clade and the numerous synapomorphies that support the siganid-luvaroid-zanclid-acanthurid sequence, the placement of the first dorsal basal pterygiophore in *Kushlukia* is most parsimoniously interpreted as an independent specialization associated with the reduction of the anterior part of the dorsal fin in that genus of luvaroids. The ancestral condition for acanthuroids, as found in higher squamipinnes, is for the first dorsal pterygiophore to be placed in the first or second interneural space, and both the more forward position in luvarids and most other acanthuroids and the more posterior position in kushlukiids are specializations.

Only one of the character states of the eight osteological synapomorphies of larval acanthuroids in Tyler et al. can be determined from the few small and perhaps late larval fossil specimens of luvaroids available. An approximately 34 mm SL specimen (PIN 1762/99) of the luvarid *Avitoluvarus mariannae* has the specialized acanthuroid serrations on the supernumerary large first dorsal spine (corresponding to the large second spine that follows a rudimentary spine in *L. imperialis*) and the pelvic spine.

Synapomorphies of Luvarid+Kushlukiid and Zanclid+Acanthurid Clade

Of the eight previously established osteological synapomorphies of adult zanclids, acanthurids, and *L. imperialis*, the character states of three of these (characters 29,30,31 in Tyler et al.: no spina occipitalis; soft rays with small lateral spinules; small scale plates with small upright spinules) cannot be determined in the fossil materials of the luvarid+kushlukiid clade (although some type of spinule is present on the scales in *Avitoluvarus dianae*).

Three of the other adult osteological synapomorphies of zanclids, acanthurids, and *L. imperialis* apply to the entire luvarid+kushlukiid clade just as well as previously to *L. imperialis* alone, as follows. The lachrymal is positioned anteriorly, removed from the anterior border of the orbit and not in contact with the lateral ethmoid (character 27 in Tyler et al.): with the exception of the lachrymal, the infraorbitals are

not preserved, if present at all (they are represented by a single rudimentary element in *L. imperialis*), in any of the fossil materials, but the lachrymal is placed far anterior to the orbit in those specimens in which it can be seen and it is obviously not in contact with the lateral ethmoid. The palatine is placed well forward of, and out of contact with, the lateral ethmoid (character 28 in Tyler et al.): the palatine is not well enough preserved with distinctive limits as a separate element in any of the fossil materials, but its position can be estimated from its presumed attachment to the ectopterygoid-quadrate complex, and because this complex is well forward of the lateral ethmoid it is a reasonable assumption that the palatine in the fossil luvarids+kushlukiids is like that of *L. imperialis* in being out of contact with the lateral ethmoid. There is a single postcleithrum (character 32 in Tyler et al.): we find no evidence of a division of the postcleithrum into two pieces in any of the fossil materials, including in the large and well-preserved postcleithrum of *Kushlukia*.

Two of the eight adult osteological synapomorphies (character 25, vertebrae $9 + 13 = 22$; character 26, ventral shaft of first basal pterygiophore of dorsal fin in preneural space) of zanclids, acanthurids, and *L. imperialis* in Tyler et al. apply to the three species of fossil luvarids but not to *Kushlukia*. In *Kushlukia* the vertebrae are about $10 + 19-20 = 29-30$, clearly a specialization of increased number from the ancestral higher squamipinne number of $10 + 14 = 24$, in the opposite direction of the reduced number of 22 found in luvarids, zanclids, and acanthurids (siganids have 23). In *Kushlukia* the first dorsal pterygiophore is in the third or fourth interneural space, but this is only a slight variant of character 4 of Tyler et al. discussed above, with the ventral shaft of the first dorsal-fin basal pterygiophore being distinctly in the preneural space in front of the first neural spine in zanclids, acanthurids, and *L. imperialis* rather than, as in siganids, over the open low neural arch of the first vertebra or in the first interneural space (see Character 12 of this work, below), or in the first or second interneural space in the higher squamipinne outgroups. The far posterior placement of the first dorsal pterygiophore in kushlukiids is shown above to be most parsimoniously interpreted as an independent and opposite specialization of the forward placement in luvarids relative to higher squamipinnes. Given the synapomorphies that unite luvarids and kushlukiids and that clade with other acanthuroids, the increase in number of vertebrae in kushlukiids also is interpreted as an independent and opposite specialization to the decrease in number in luvarids and most other acanthuroids relative to higher squamipinnes.

Synapomorphies of Superfamily Luvaroidea

Nine unequivocal synapomorphies, and another uncertain or equivocal one, establish the monophyly of the Luvaridae and Kushlukiidae in what we recognize as the Superfamily Luvaroidea. Here and following, all character number headings are those of this work and correspond to those in the cladogram (Figure 18).

Character 1. The dorsal- and anal-fin pterygiophores are uniquely modified and broadly sutured into a bony truss around the dorsal and ventral margins of the body just below the skin. The various ossifications of the pterygiophore that interdigitate to form this truss in *L. imperialis* are described in detail in Tyler et al. (their character 33). Although we cannot observe the same detail in the fossil materials, it is obvious that the truss in the fossils is basically the same as in the Recent species of luvarid, except less thickly developed in *Avitoluvarus* than in *Luvarus* and *Kushlukia*. The extensive interdigitation of the distal regions of the pterygiophores as a truss in luvarids and kushlukiids does not occur elsewhere in acanthuroids or higher squamipinnes.

Character 2. There are two or fewer large dorsal-fin spines, and often none in adults. In *L. imperialis* the two prominent dorsal-fin spines are preceded by a buried rudimentary spine that persists to sizes of at least 301 mm SL (Tyler et al., 1989:25; with the number of dorsal-fin spines treated as their character 39). Such a rudiment is unlikely to be seen in our fossil materials. There are no dorsal spines in *L. necopinatus*. If any had been present at small body sizes, they and some of the more anterior fin rays were probably lost ontogenetically. In the one specimen (about 337 mm SL) in which the dorsal fin is fully preserved, the first fin ray occurs on the sixth basal pterygiophore. In both species of *Avitoluvarus* there is at least one dorsal-fin spine and the second element in the fin of *A. mariannae* also is probably a spine (as best seen in a perhaps late larval specimen of about 34 mm SL, Figure 7). There is no evidence of more than two spines in any of the materials. In *Kushlukia* there is no evidence of dorsal-fin spines and all of the dorsal-fin elements appear to be soft rays, although it is possible that any spines, if present, had already been resorbed at the specimen sizes of the materials available (about 141–198 mm SL). Thus, all species of the luvarid+kushlukiid clade as far as is known have no more than two well-developed dorsal-fin spines at all specimen sizes. Among all other acanthuroids there are four to 14 dorsal-fin spines at all specimen sizes, and among the higher squamipinnes there are also at least four dorsal spines.

Character 3. There are no anal-fin spines. In *L. imperialis* there are no anal-fin spines at any specimen sizes and we find no evidence of anal-fin spines in any of our materials of fossil luvarids and kushlukiids. Among all other acanthuroids there are three to eight anal-fin spines, and among the higher squamipinnes there are three or four anal spines. For the sake of convenience in listing the autapomorphies of *L. imperialis,* Tyler et al. (1989:66) combined the number of dorsal and anal spines as a single feature, but now that the reduction in number of dorsal-fin spines and the loss of all anal-fin spines is known to apply to all members of the luvarid+kushlukiid

clade, we consider these as separate synapomorphies.

Character 4. The soft-dorsal and anal-fin rays are unsegmented. In neither our cleared and stained specimens of *L. imperialis* nor any of our fossil materials of species of the luvarid+kushlukiid clade can we detect any segmented articulations or cross-striations in any of the dorsal- and anal-fin rays. These rays are segmented in all other acanthuroids and higher squamipinnes.

Character 5. The distal end of the first anal-fin basal pterygiophore is greatly prolonged anteriorly. In both the fossil and Recent species of luvarids *(Luvarus* and *Avitoluvarus)* the distal end of the first anal-fin basal pterygiophore is prolonged anteriorly to the level of the pectoral-fin base, to a position under the third to fifth abdominal vertebrae (Figures 3, 6, 11, 13). In *A. mariannae* the prolongation is greater in small specimens than in adults, extending in front of the pectoral-fin base and under the first or second vertebrae (Figure 7). In *Kushlukia* the anterior prolongation is even greater, to a level far in front of the pectoral-fin base, under the rear of the orbit (Figure 15). In all other acanthuroids and in higher squamipinnes the anterodistal end of the first anal-fin basal pterygiophore is only slightly to moderately swung forward, to a level well behind the pectoral-fin base and under the last or next to last abdominal vertebrae, with the exception of the acanthurid genus *Naso.* In *Naso* the first anal-fin basal pterygiophore is swung distinctly forward, although not so extremely as in luvarids and kushlukiids and always to a level distinctly behind the pectoral-fin base (Tyler et al., 1989, figs. 23, 25). Given the large number (23; see Character 8, below) of derived features uniting *Naso* with the acanthurids, the less pronounced anterior prolongation of the first anal-fin basal pterygiophore in *Naso* is most parsimoniously interpreted as independent to the relatively greater prolongation in luvaroids.

Character 6. The anus is positioned anteriorly, under or anterior to the level of the vertical through the pectoral-fin base. In both the fossil and Recent species of luvarids *(Luvarus* and *Avitoluvarus)* the anus is displaced forward to a level under the pectoral-fin base in conjunction with the anterior elongation of the distal end of the first basal pterygiophore of the anal fin, with the anus located in the narrow gap between the anterior end of this pterygiophore and the posterior end of the pelvis. In *Kushlukia* the anterior end of the prolonged distal end of the first basal pterygiophore of the anal fin broadly articulates with a long posterior process of the pelvis and we presume that the anus is located even further anteriorly than in luvarids, at the only gap in the bony truss around most of the ventral edge of the body, this being on the throat at the anterior end of the pelvis and the posterior end of the enormous urohyal. In all other acanthuroids and higher squamipinnes the anus is placed well behind the pectoral-fin base, toward the posterior
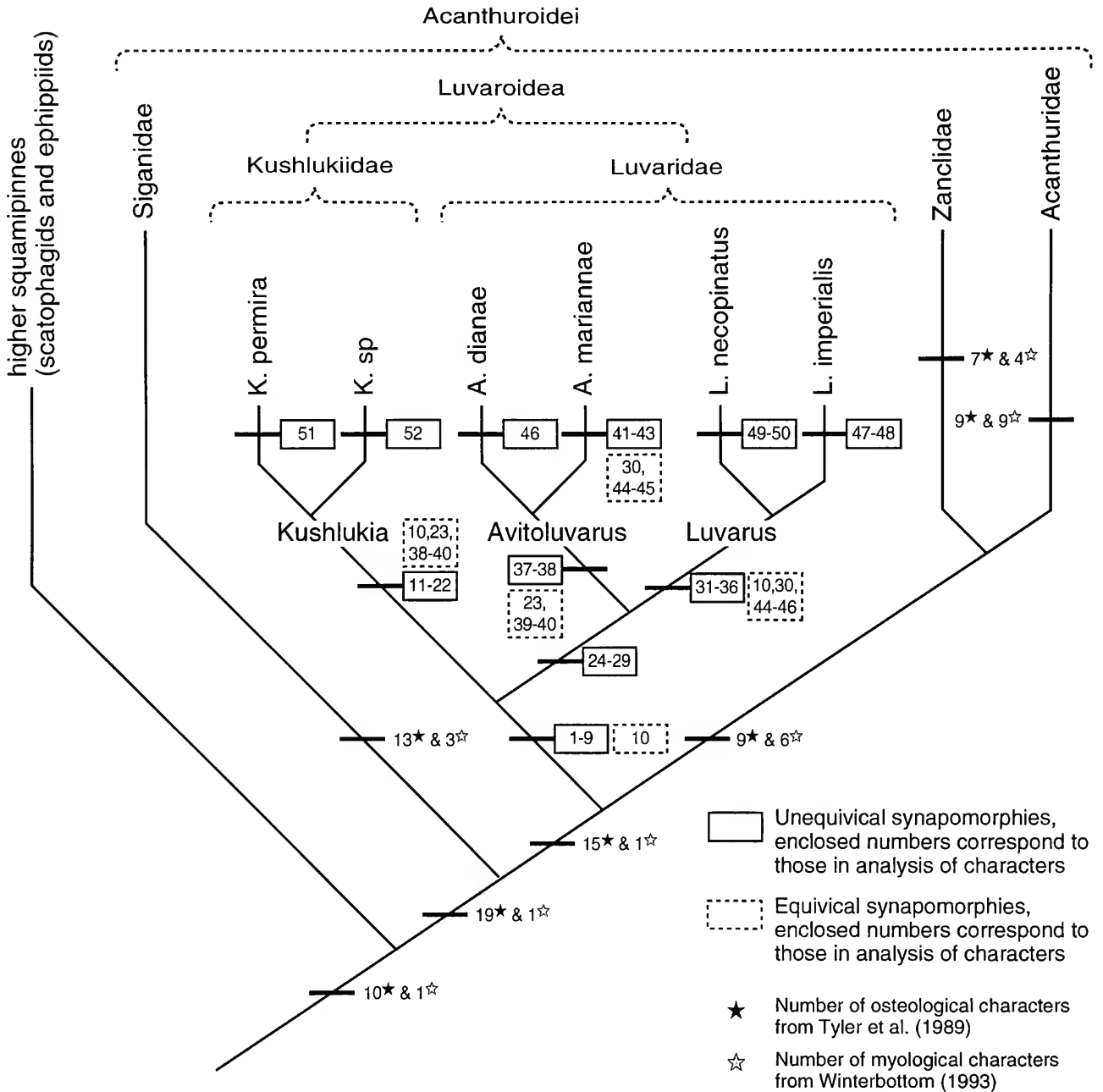
FIGURE 18.—Cladogram of relationships of the Luvaridae and Kushlukiidae; unequivocal synapomorphies in solid line rectangles and equivocal synapomorphies in dashed line rectangles; numbers within rectangles correspond to those of Characters in the "Analysis of Characters"; see Tyler et al. (1989) and Winterbottom (1993) for the characters supporting the phyletic sequence of siganids-luvarids(+kushlukiids)-zanclids-acanthurids and of them with the higher squamipinnes (especially scatophagids and ephippiids).

end of the abdominal cavity, with the exception that most species of the acanthurid genus *Naso*, in which the first anal-fin basal pterygiophore is moderately swung forward and the anus is only moderately but distinctly posterior to the level of the pectoral-fin base. Given the large number (23; see Character 8, below) of derived features uniting *Naso* and the other acanthurids, the moderate anterior displacement of the anus in *Naso*, like

the anterior prolongation of the first anal-fin pterygiophore, is most parsimoniously interpreted as independent of the great anterior displacement in luvarids-kushlukiids.

Character 7. Hypurals 1–4 fuse to form a single hypural plate, with only the uppermost or fifth hypural and the parhypural remaining autogenous. The hypural plate in all of our fossil materials of luvarids (caudal skeleton missing in all specimens of kushlukiids) is as fully fused as in *L. imperialis* (this being character 36 in Tyler et al.). In all acanthuroids and higher squamipinnes hypurals 1–4 remain separate, with the exception of *Naso,* in which these are fused. Given the large number (23; see Character 8, below) of derived features uniting *Naso* with the other acanthurids, hypural fusion in *Naso* is most parsimoniously interpreted as independent of that in luvarids-kushlukiids.

Character 8. The caudal-fin rays deeply overlap the hypural plate. The deep overlapping of the hypural plate by the bases of most of the principal caudal-fin rays (hypurostegy) is apparent in all of our fossil materials of luvarids in which this region is preserved, to the same extent as in comparably sized specimens of *L. imperialis* (this being character 38 in Tyler et al.). The caudal fin and last few vertebrae are not preserved in any of the specimens of *Kushlukia* but the configuration of the vertebral column is otherwise relatively similar to that of luvarids (except for the increased number of vertebrae); therefore, we presume that *Kushlukia* also exhibited hypurostegy. Hypurostegy is not present in other acanthuroids or higher squamipinnes, with the exception of a few species of *Naso* (exemplified by *N. thynnoides,* see Tyler et al., 1989:33, fig. 23) in which the caudal rays slightly overlap the hypural plate, but scarcely enough to qualify as hypurostegy. As with hypural fusion in *Naso,* the slightly overlapping caudal-fin rays in some species of *Naso* is considered independent of the hypurostegy in luvarids-kushlukiids and associated with the semipelagic or slightly offshore habitat of many species of *Naso,* which are united with the other acanthurids by a total of 23 larval and adult osteological and myological synapomorphies (Tyler et al., 1989:57; Winterbottom, 1993:35; Guiasu and Winterbottom, 1993:309).

Character 9. The pelvic fin becomes rudimentary with increasing specimen size or is absent. In *L. imperialis* the pelvic fins from each side become united into a single median plate (operculum ani) apparently representing the fusion product of the right and left pelvic spines and rays at sizes of about 980 mm SL and larger. In *L. necopinatus* the only specimen in which the pelvic fin is preserved is about 326 mm SL and the pelvic fins are consolidated into a short, flat, plate-like structure placed on the midline close to the surface of the body just in front of the anus, very similar to the operculum ani in

large specimens of *L. imperialis.* In *A. dianae* the pelvic fin is either absent or cannot be discerned whereas in *A. mariannae* it is absent in all but the two smallest specimens. In these two late larvae or early juveniles (about 34 and 48 mm SL) of *A. mariannae* the pelvic spines are long and slender, and it seems clear that the pelvic spines are completely lost with increasing specimen size in both species of *Avitoluvarus.* In none of the specimens of *Kushlukia* is a pelvic fin present. In all other acanthuroids and higher squamipinnes the pelvic fin is well developed at all specimen sizes.

Character 10 (tentative). The teeth are greatly reduced in size or lost in adults. In *L. imperialis* the teeth are lost from the lower jaw with increasing specimen size (teeth absent by about 300 mm SL) and become rudimentary in the upper jaw at larger sizes (by about 1 m SL). In *L. necopinatus* the dentary is toothless in those specimens in which it is well preserved, but the premaxilla is not well enough preserved in any of the materials to determine whether or not small teeth were present. In both species of *Avitoluvarus* the premaxilla and dentary bear a single series of small conical teeth (in specimens of about 34–190 mm SL) like those of comparably small specimens of *L. imperialis* (see Figure 9 of jaws of *A.* sp.). We presume that the larger specimens of both species of *Avitoluvarus* are adults, or at least young adults of what we believe are probably smaller species than those of *Luvarus.* If the two species of *Avitoluvarus* obtain somewhat larger sizes than the present materials, it may be discovered that they reduce and loose the teeth in the same manner as *L. imperialis.* In *Kushlukia* none of the specimens (about 141–198 mm SL) have teeth in either jaw. All other acanthuroids and higher squamipinnes have well-developed teeth present at all specimen sizes. Loss of teeth in adults is clearly a derived feature but it is as equally parsimonious to propose that the specialized adult tooth reduction and loss is ancestral for the luvarid+kushlukiid clade as it is that the ancestor had the primitive condition of teeth at all sizes and that adult teeth were lost independently by *Luvarus* and *Kushlukia* but retained by *Avitoluvarus.* Because the rudimentation and loss of teeth in large adults is known for both *Luvarus* and *Kushlukia* but will remain uncertain for *Avitoluvarus* until larger specimens of it are available, we propose this feature as an tentative synapomorphy for the entire luvarid+kushlukiid clade.

Synapomorphies of Family Kushlukiidae

Character 11. The number of vertebrae are greatly increased, to about 29–30 (10+19–20). In *K. permira* there are 10 abdominal vertebrae and 15 in the caudal series until the end of the dorsal and anal fins, posterior to which the caudal peduncular vertebrae are missing.

However, in both *Luvarus* and *Avitoluvarus* there are four vertebrae in the caudal peduncle, posterior to the end of the dorsal and anal fins, and this is also the case in siganids and acanthurids. Zanclids have only three vertebrae in the caudal peduncle. We make the presumption that *Kushlukia* had no less than the same number of caudal peduncle vertebrae (4) as found in the two genera of its sister group (and most other acanthuroids), and that it perhaps had one more than them given the increased number of trunk vertebrae in *Kushlukia* relative to luvarids. Therefore, we presume that *Kushlukia* had a vertebral formula of 10 + 19–20 = 29–30. Luvarids and zanclids+acanthurids (the sister group of luvarids+kushlukiids) all have 9 + 13 = 22 vertebrae, whereas siganids (sister group of the previous four families) and scatophagids have 10 + 13 = 23 and other higher squamipinnes 10 + 14 = 24. It is clear that the increase in number of vertebrae in kushlukiids is a derived feature among acanthuroids, in which the trend has otherwise been to reduce the ancestral number from 24 to 23 (10 abdominal) in siganids, with 22 (9 abdominal) being the ancestral number for the luvarid+kushlukiid and zanclid+acanthurid clade.

Character 12. The short shaft of the first basal pterygiophore of the dorsal fin is placed in the third or fourth interneural space, between the neural spines of the third and fourth or fourth and fifth vertebrae. In luvarids and in zanclids+acanthurids the long shaft of the first dorsal pterygiophore is placed in the preneural space and its proximal end is held to a concavity on the rear of the skull. In siganids the shaft is of moderate length and placed over the open low neural arch of the first vertebra in the Recent *Siganus* but the shaft is longer and placed in the first interneural space in most of the fossil genera (Tyler and Bannikov, manuscript). In the higher squamipinne outgroups the shaft of the first dorsal pterygiophore is placed in the first or second interneural space. The primitive ancestral acanthuroid condition of the first pterygial shaft in the first interneural space is exhibited by fossil siganids, with placement in the preneural space the ancestral condition for all other acanthuroids and the posterior shifting of the placement in kushlukiids considered a derived feature associated with reduction in the anterior part of the dorsal fin either through loss of elements or of their posterior migration.

Character 13. The postcleithrum is greatly expanded. The postcleithrum is a narrow shaft in luvarids, all other acanthuroids, and higher squamipinnes.

Character 14. The pelvis has a long posterior ′ process that is broadly sutured or fused to the anterior extension of the distal end of the first basal pterygiophore of the anal fin, with the anus probably being on the throat at the anterior end of the anterior (iliac) process of the pelvis just behind the urohyal. In luvarids the pelvis does

not have an exceptionally long posterior process and the pelvis does not contact the anterior end of the long anterior extension of the distal end of the first basal pterygiophore of the anal fin. The anus is placed below the pectoral-fin base between the anterior process of the first anal-fin basal pterygiophore and the posterior process of the pelvis. The posterior process of the pelvis is relatively short and the anus is in the posterior part of the abdominal cavity in all other acanthuroids (except independently somewhat advanced in *Naso*, as discussed under Character 6) and higher squamipinnes. The luvarid conditions of the posterior pelvic process and anus placement are more like that of all other acanthuroids and the long posterior process of the pelvis and the placement of the anus on the throat are considered derived features of kushlukiids.

Character 15. The base of the pectoral fin is placed in the upper third of the body depth. In luvarids the pectoral fin is placed in about the middle of the body or distinctly below the middle of the body, whereas in all other acanthuroids and higher squamipinnes it is placed slightly to well below the middle of the body.

Character 16. The coracoid is extremely elongate, reaching to the level of the anterior region of the snout and lacks a posterior (postcoracoid) process below the pectoral-fin base. In luvarids, other acanthuroids, and higher squamipinnes the coracoid is much shorter and there is a posterior process below the pectoral-fin base.

Character 17. The premaxilla is pointed anterodorsally and beak-like. The premaxilla in luvarids, other acanthuroids, and higher squamipinnes has a much different shape, being neither pointed anterodorsally nor beak-like.

Character 18. The scapula is exceptionally small. The scapula in luvarids, other acanthuroids, and higher squamipinnes is of relatively normal perciform size.

Character 19. The neural spines of the first two abdominal vertebrae are very short and slender, their length being no greater than the depth of their centra. In luvarids, all other acanthuroids except siganids, and higher squamipinnes these first two neural spines are broad and much longer than the depth of their centra. In fossil siganids the first neural spine is broad and between slightly longer and twice as long as the depth of the centrum, whereas in the Recent *Siganus* there is a specialized open neural arch and no neural spine. The siganid condition, differing from that of kushlukiids by the broadness of the neural spine (or its absence in *Siganus*), is most parsimoniously interpreted as an independent specialization, with the ancestral condition for the luvarid+kushlukiid and zanclid+acanthurid clade being a long and broad first neural spine that was subsequently reduced in both length and width in kushlukiids.

Character 20. The urohyal is exceptionally large. The urohyal in luvarids, other acanthuroids, and higher squamipinnes is of more normal perciform size.

Character 21. The first two basal pterygiophores of the anal fin have long posterodorsally directed shafts placed in the prehaemal space along the anterior edge of the first haemal spine. In luvarids, other acanthuroids, and higher squamipinnes only the first basal pterygiophore of the anal fin is placed along the anterior edge of the first haemal spine.

Character 22. The ascending process of the premaxilla is of moderate length and projects back along the upper surface of the ethmoid, although it is difficult to characterize the length of the ascending region in a bone that is triangular in outline as preserved in lateral view. In luvarids the ascending process of the premaxilla is either absent or very short, as follows: in *L. imperialis* the dorsal head of the premaxilla is deeply concave for articulation with the head of the palatine and there is no ascending process, the upper jaw bones being closely held to one another in a single functional unit as is typical of all acanthuroids; the premaxilla in *L. necopinatus* is too poorly preserved for the condition of the upper end of the premaxilla to be observed; in both species of *Avitoluvarus* the premaxilla has a very short ascending process. In siganids and acanthurids the ascending process is very short in adults (slightly longer in small juveniles and in the acronurus stage of acanthurids). In zanclids the ascending process is short and slender, but slightly longer than in other adult acanthuroids, about as long as in young siganids and acanthurids. Among the higher squamipinnes (scatophagids, ephippidids) and in pomacanthids the ascending process (especially in conjunction with the rostral cartilage) is longer than in acanthuroids; we would characterize the ascending process in these squamipinnes as moderately long, and the upper jaw bones as more movably articulated to one another than in acanthuroids. In other squamipinnes, such as drepanids, chaetodontids, and monodactylids, the ascending process is very long and the upper jaw bones are very movable and protrusible. Therefore, a long ascending process is considered primitive for the squamipinnes and the reduced moderate length in the higher squamipinnes a derived feature, with the even greater reduction in the length of the ascending process (and in upper jaw bone flexibility) an ancestral feature of acanthuroids (as discussed for character 6 in Tyler et al., 1989:58). Because all acanthuroids have a short or moderately short ascending process, we consider the longer but difficult to define length of the process in *Kushlukia* to be a specialized reversal to the ancestral higher squamipinne condition.

The complete loss of the ascending process in *L. imperialis* is a specialization opposite to that in *Kush-*

lukia, but because the condition of the ascending process is unknown in *L. necopinatus* we cannot determine whether the absence of the process is a synapomorphy of *Luvarus* in relation to the short process in *Avitoluvarus.*

Character 23 (equivocal). There is no evidence of pelvic fins in specimens of the size range available (about 141–198 mm SL). Separate pelvic fins composed of a spine and four rays are present at sizes up to about 300 mm SL in *L. imperialis,* but at larger sizes these fins become consolidated into a fused structure (operculum ani) that persists even in the largest individuals. In *L. necopinatus* the pelvic fin is preserved only in the approximately 326 mm SL specimen, and it is consolidated into an operculum ani. In both species of *Avitoluvarus* pelvic fins are either absent or too small and poorly preserved to be observed in the specimens of about 100–200 mm SL, but in the two smallest specimens (about 34–48 mm SL) available of *A. mariannae* the pelvic spine is well developed, with serrations typical of late larval acanthuroids. We presume that in both species of *Avitoluvarus* the size of the fin becomes reduced with increasing specimen size, although at smaller adult sizes than in *Luvarus.* In all other acanthuroids and higher squamipinnes the pelvic fin is present at all sizes and does not become reduced with increasing specimen size. The presumed complete loss of pelvic fins in *Kushlukia* and *Avitoluvarus* at sizes as small as 100–200 mm SL is therefore a derived feature relative to the retention in *Luvarus* of the fully formed pelvic fins until sizes around 300 mm SL and the consolidation of the fin into an operculum ani that persists at all adults sizes. However, it is equally parsimonious to propose that the ancestor of the luvarid+kushlukiid clade had: gradual reduction of the pelvic fin and consolidation into a persistent operculum ani, with *Kushlukia* and *Avitoluvarus* independently developing the complete loss of the pelvic fin at sizes of about 100 mm SL; or that the fin was completely lost in adults of the ancestor and *Luvarus* has by reversal retained the ancestral condition further into adult development. Our preferred hypothesis here (and in similar situations below) is that, without evidence to the contrary, the primitive condition for the outgroups is also that of the ancestor in question. Therefore, we propose that the ancestor of the luvarid+kushlukiid clade had separate pelvic fins present at least into moderate adult sizes, as in *Luvarus,* and that the relatively earlier reduction and loss of the pelvic fin is independently derived in *Kushlukia* and *Avitoluvarus.*

Synapomorphies of Family Luvaridae

Character 24. The middle regions of the elongate haemal spines of the first two caudal vertebrae distinctly

converge toward one another. In kushlukiids, other acanthuroids, and higher squamipinnes these haemal spines are approximately parallel to one another or slightly divergent.

Character 25. There are no parapophyses on any of the abdominal vertebrae and the pleural ribs are borne on the sides of the centra. In kushlukiids, other acanthuroids, and higher squamipinnes two or more of the more posterior abdominal vertebrae have parapophyses and the pleural ribs are borne on these rather than on the sides of the centra.

Character 26. The area occupied by the four bones of the opercular series is relatively rounded, with the greatest width (horizontally in dorsal region) about two to two and a half times in its length (obliquely). In kushlukiids the opercular region is exceptionally elongate and narrow, its width dorsally about three and a half to four times in its length. In all other acanthuroids and higher squamipinnes the opercular region is also more elongate (although usually slightly less so than in kushlukiids) than rounded, the width about three and a half to five times in the length.

Character 27. The articular (anguloarticular) is relatively large, its length about equal to that of the dentary. In kushlukiids and in all other acanthuroids the articular is reduced in size relative to the higher squamipinne outgroups and the primitive ancestral condition for acanthuroids is a small articular, with the most parsimonious interpretation being that the outgroup condition in luvarids is a reversal. The same argumentation for this character reversal of articular size in luvarids is given by Tyler et al. (1989:58, their character 7 for all acanthuroids) and is supported by the report here of the derived condition in the kushlukiid sister group of luvarids.

Character 28. Most of the shafts of the neural and haemal spines of the caudal vertebrae between the dorsal and anal fins are exceptionally slender and bear no medial flanges. In kushlukiids and all other acanthuroids the shafts are less slender and have variously developed medial flanges along their posterior edges. In the outgroup higher squamipinnes the shafts are also less slender than in luvarids, but medial flanges are essentially absent. The presence of flanges can be considered a synapomorphy of all acanthuroids, with loss of the flanges in luvarids being a reversal.

Character 29. The proximal shafts of the basal pterygiophores of the soft dorsal and anal fins are relatively slender, being moderately reduced in stoutness in *A. dianae* and exceptionally slender in *A. mariannae* and *Luvarus,* and are well separated from one another, with medial flanges either reduced *(A. dianae)* or absent (the other three species). In kushlukiids and other acanthuroids these pterygiophore shafts are less slender and have medial flanges anteriorly and/or especially

posteriorly, or the shafts are in broad contact with one another proximal to the distal articular region. In the outgroup higher squamipinnes the shafts of the pterygiophores usually have less well-developed flanges and are in less extensive contact with one another than in acanthuroids, with the better flange development and greater pterygial contact being a synapomorphy of all acanthuroids, with loss of these features in luvarids being a reversal.

Character 30 (equivocal). Epineural intermuscular bones are usually absent. In both species of *Luvarus* and in *A. mariannae* epineurals are absent but these are present in *A. dianae.* In kushlukiids, all other acanthuroids, and higher squamipinnes epineurals are present. It is clear that the loss of epineurals is a derived feature but it is equally parsimonious to propose that the ancestral luvarid condition was the presence of epineurals that were lost independently by *Luvarus* and *A. mariannae* or that the ancestor of luvarids lost the epineurals and that these were regained by *A. dianae.* Our preferred hypothesis is that the luvarid ancestor had the primitive condition of the outgroups and we therefore propose as an equivocal synapomorphy the independent loss of epineurals by *Luvarus* and *A. mariannae,* with the retention of the primitive ancestral condition by *A. dianae.*

Synapomorphies of *Luvarus*

Character 31. The neural and haemal spines of the ninth caudal vertebra are short, stout, upright, and broadly sutured to the last basal pterygiophores of the dorsal and anal fins to support the especially massive truss. In *Avitoluvarus* these spines of the ninth caudal vertebra are more slender, normally tapered, and directed obliquely just under the rear of the less massive truss and the spines do not suture to the pterygiophores. These neural and haemal spines under the end of the dorsal and anal fins in kushlukiids, other acanthuroids, and higher squamipinnes are similar to those of *Avitoluvarus,* and the condition in *Luvarus* is considered derived.

Character 32. The centrum of the tenth caudal vertebra is substantially shorter than that of the preceding and succeeding vertebrae, and bears low neural and haemal arches without obliquely directed spines, this being the relatively block-like pivot vertebra. In *Avitoluvarus* the centrum of the tenth caudal vertebra is only slightly shorter than that of the preceding centrum and slightly longer than that of the succeeding centrum, being of normal size in the sequence of centra of progressively lesser length posteriorly in the series and bearing short but obliquely oriented neural and haemal spines; it is not modified as a pivot vertebra. In kushlukiids the caudal peduncle vertebrae are missing in all specimens. In all other acanthuroids and higher squamipinnes the first

vertebra of the caudal peduncle (corresponding to the tenth in *Luvarus*) is relatively normal and not modified into a pivot.

Character 33. The postcleithrum is relatively short, and well removed from the anterior extension of the first basal pterygiophore of the anal fin. In *Avitoluvarus* the postcleithrum is significantly longer, reaching ventrally to close to the anterior extension of the first anal-fin basal pterygiophore. In *A. mariannae* most specimens in which it is preserved have a long postcleithrum, as seen in Figures 7, 8, but in the holotype it does not so closely approach the pterygiophore (Figure 6), perhaps because the ventral end is not fully exposed. In kushlukiids the postcleithrum is as long as in *Avitoluvarus*, reaching to the anterior extension of the first anal-fin basal pterygiophore. The length of the postcleithrum is highly variable in other acanthuroids: exceptionally long and reaching the moderate anterior extension of the first anal-fin basal pterygiophore in some siganids, but somewhat shorter in others; long and reaching down more than three-fourths the depth of the abdominal cavity in zanclids; and of moderate to relatively great length in acanthurids, sometimes reaching close to either the posterior process of the pelvis or the anterior extension of the first anal-fin basal pterygiophore. In any case, the most parsimonious interpretation is that a relatively long postcleithrum is ancestral for luvarids+kushlukiids and that the shorter postcleithrum is a derived feature of *Luvarus*.

Character 34. The proximal shaft of the first basal pterygiophore of the anal fin is relatively short and slender. In *Avitoluvarus* the proximal shaft of this pterygiophore is broader (as in *A. dianae*) or somewhat broader and significantly longer (as in *A. mariannae*). In kushlukiids this shaft is moderately broad and very long. In all other acanthuroids and higher squamipinnes this shaft is very long and broad.

Character 35. The eye is placed relatively low in the head, with the middle of the eye in about the middle of the head. In *Avitoluvarus* the eye is placed higher, with the middle of the eye in about the middle of the upper half of the head. In kushlukiids the eye is very high in the head, with the middle of the eye in the middle of the upper third of the head. In other acanthuroids and higher squamipinnes the eye is placed relatively high in the head, with its middle in about the upper half of the head.

Character 36. Most of the pleural ribs are broadly expanded along half *(L. imperialis)* or all *(L. necopinatus)* of their lengths. In *Avitoluvarus*, kushlukiids, all other acanthuroids, and higher squamipinnes the pleural ribs are more slender and rod-like.

Synapomorphies of *Avitoluvarus*

Character 37. The truss formed by the interdigitation of the distal regions of the pterygiophores of the dorsal and anal fins is relatively shallow and less extensively interdigitated, with the depth of the interdigitated region equal to about one-fourth of the length of the vertebral centra in the middle of the body. In *Luvarus* the pterygial truss is relatively deeper and the distal regions of the pterygiophores are extensively interdigitated with one another over a broad surface, with the depth of the interdigitated region equal to about one-half of the length of the vertebral centra in the middle of the body. In kushlukiids the truss is as deep as in *Luvarus* and the region of interdigitation is just as extensive as in *Luvarus* but the individual interdigitations are broader or less fine than in *Luvarus*. There is no comparable structure in any of the other acanthuroids or higher squamipinnes to aid in the polarization of this character. It is most parsimonious to propose that when the truss first arose in the ancestor of the luvarid+kushlukiid clade that it was thick and extensively interdigitated as in *Kushlukia* and *Luvarus* and that the thickness and degree of interdigitation was then reduced in *Avitoluvarus* (one step after acquisition of the original truss), versus the truss originally being thin and relatively weakly interdigitated and then becoming thicker and more extensively interdigitated independently in *Kushlukia* and *Luvarus* (two steps after truss acquisition).

Character 38. The proximal shafts of a total of seven to 11 (rarely six) basal pterygiophores of the anal fin are placed in the first two interhaemal spaces (between first and third haemal spines). In *Luvarus* there are four pterygial shafts placed in the first two interhaemal spaces, and in kushlukiids five. In zanclids there are five pterygiophores in these spaces and in all acanthurids except *Naso* there are four; in *Naso* there are 10 to 11 pterygiophores in these spaces associated with the far forward displacement of the first basal pterygiophore of the anal fin. In siganids there are two or three pterygiophores in these spaces. In the higher squamipinnes the number of pterygiophores in the first two interhaemal spaces varies from two to four. It is clear that a low number of no more than five pterygiophores in the first two interhaemal spaces is primitive for acanthuroids, and that the increase to seven to 11 in *Avitoluvarus* is derived. Given the numerous synapomorphies linking *Naso* with the acanthurids, the increase in number of pterygiophores in the first two interhaemal spaces in this genus is independent of that in *Avitoluvarus*.

Character 39 (equivocal). The ascending portion of the pelvis (basiptergium) is oriented vertically *(A. dianae)* or posterodorsally *(A. mariannae)* toward the pectoral girdle. In *Luvarus* the ascending portion is oriented anterodorsally. In kushlukiids the ascending portion is oriented posterodorsally, as in *A. mariannae*. In all other acanthuroids and higher squamipinnes the ascending portion is longer than in luvarids and kushlukiids and is oriented obliquely anterodorsally. It is

clear that the vertical or posterodorsal orientation of the ascending portion of the pelvis is derived but it is equally parsimonious to propose that the ancestral condition in the luvarid+kushlukiid clade was: anterodorsal orientation as in *Luvarus*, with *Kushlukia* and *Avitoluvarus* independently acquiring the derived condition; or that it became vertically or posterodorsally oriented in the ancestor and the primitive orientation in *Luvarus* is a reversal to the condition in all other acanthuroids and higher squamipinnes. Our preferred hypothesis is that the ancestor had the primitive condition of the outgroups and therefore we consider the vertical to posterodorsal orientation in *Avitoluvarus* an equivocal synapomorphy distinguishing it from *Luvarus*, with the posterodorsal orientation independently acquired in *Kushlukia*.

Character 40 (equivocal). The vertebral column articulates high on the cranium. In *Luvarus* the column articulates low on the cranium, whereas in kushlukiids it articulates as high on the cranium as in *Avitoluvarus*. In all other acanthuroids and higher squamipinnes the column articulates low on the cranium. While it is clear that the high articulation of the column on the cranium is a derived feature, it is equally parsimonious to propose that the ancestral condition for the luvarid+kushlukiid clade was: low on the cranium as in *Luvarus*, with *Kushlukia* and *Avitoluvarus* independently acquiring the derived condition; or that the articulation became high in the ancestor and the primitive condition in *Luvarus* is a reversal to the condition in all other acanthuroids and higher squamipinnes. Our preferred hypothesis is that the ancestor had the primitive condition of the outgroups and therefore we consider the high articulation in *Avitoluvarus* an equivocal synapomorphy distinguishing it from *Luvarus*, with the high articulation independently acquired in *Kushlukia*.

Autapomorphies of *Avitoluvarus mariannae*

Character 41. The shafts of a total of 10 to 11 basal pterygiophores of the anal fin are placed in the first two interhaemal spaces (six or seven in the first and four in the second). In *A. dianae* there are a total of seven (occasionally six) pterygiophore shafts in these first two interhaemal spaces (three in the first and four, sometimes only three, in the second). Accepting the argumentation given for Character 38 above, with two to five pterygiophore shafts in the first two interhaemal spaces as the primitive condition for acanthuroids, the greater increase in number of pterygiophores in these two spaces in *A. mariannae* is a more derived condition than the lesser increase in *A. dianae* (assuming an ordered transformation series).

Character 42. The pleural ribs are relatively short and thin, ending at the level of about the upper third of the abdominal cavity. In *A. dianae* these ribs are relatively longer and slightly thicker, extending to about the level of the middle of the abdominal cavity. In *Luvarus* the ribs are wide and extend to about the middle of the abdominal cavity. In *Kushlukia* the ribs are slightly thickened and extend to about the middle of the abdominal cavity, about as in *A. dianae*. In other acanthuroids the ribs are of moderate thickness and usually reach to about the middle of the abdominal cavity or below, but this is highly variable. In an especially deep-bodied genus like *Zanclus* the ribs are relatively long but only reach to the level of the upper third of the abdominal cavity. Nevertheless, it is clear that ribs of moderate width and of a length that reaches to at least the middle of the abdominal cavity are primitive and that the shorter and more slender ribs in *A. mariannae* are derived.

Character 43. The ventral half of the pterygial truss, formed from the distal ends of the anal-fin basal pterygiophores, is very shallow. In *A. dianae* the anal-fin pterygial truss is thicker than the dorsal-fin truss and thicker than either the dorsal or ventral portions in *A. mariannae*. Accepting the argumentation given for Character 37 above, the deep pterygial truss as found in *Luvarus* and *Kushlukia* is the primitive condition for the luvarid+kushlukiid clade, and the thinner truss of *Avitoluvarus* is a secondary reduction, with the greater degree of specialized reduction found in *A. mariannae* more derived than the lesser degree of reduction in *A. dianae* (assuming an ordered transformation series).

Character 44 (equivocal). The first two haemal spines are only slightly thickened. In *A. dianae* these two haemal spines are much thicker than any of the others. In *Luvarus* these two haemals are very slender, even more so than in *A. mariannae*. In kushlukiids the first two spines are relatively thick and sturdy, as they are in all other acanthuroids and higher squamipinnes. It is clear that the slenderness of these two spines is a derived feature but it is equally parsimonious to propose that the ancestral condition for luvarids was: for these two haemals to be as thick as in other acanthuroids and slenderness to have been obtained independently by *Luvarus* and *A. mariannae*; or that these two haemals became slender in the ancestor and the thickened condition in *A. dianae* is a reversal to the condition of all other acanthuroids and higher squamipinnes. Our preferred hypothesis is that the luvarid ancestor had the primitive condition of the outgroups and therefore we consider the slender first two haemals of *A. mariannae* an equivocal autapomorphy distinguishing it from *A. dianae*, with the even more slender first two haemals in *Luvarus* independently acquired.

Character 45 (equivocal). The shafts of the second and more posterior anal-fin basal pterygiophores, except

for the last few, are exceptionally slender. In *A. dianae* these shafts have narrow but distinct medial flanges that somewhat increase in width toward the distal end, as seen laterally. In *Luvarus* the shafts of the anal-fin basal pterygiophores are as slender *(L. imperialis)* or almost as slender *(L. necopinatus)* as in *A. mariannae*. In kushlu-kiids, all other acanthuroids, and higher squamipinnes the shafts of these pterygiophores are of at least moderate stoutness and width, and usually have some development of medial flanges. It is clear that narrowing of the shafts is a derived feature but it is equally parsimonious to propose that the ancestral condition for luvarids was: for these anal-fin pterygial shafts to be of moderate stoutness and bearing medial flanges as in other acanthuroids, with narrowing and loss of flanges to have been developed independently by *Luvarus* and *A. mariannae*; or that these pterygial shafts became slender and flangeless in the ancestor and the thickened condition in *A. dianae* is a reversal to the condition of all other acanthuroids and higher squamipinnes. Our preferred hypothesis is that the luvarid ancestor had the primitive condition of the outgroups and therefore we consider the slender pterygial shafts of *A. mariannae* an equivocal autapomorphy distinguishing it from *A. dianae*, with the slender shafts in *Luvarus* independently acquired.

Autapomorphy of *Avitoluvarus dianae*

Character 46. The posterodorsally oriented proxi-mal shaft of the first anal-fin basal pterygiophore is especially thick and stout. In *A. mariannae* this shaft is much more slender. This shaft is exceptionally slender in both species of *Luvarus*. In kushlukiids this shaft is moderately slender, as in *A. mariannae*. In all other acanthuroids and higher squamipinnes this shaft is stout. The slenderization of this shaft is a derived feature, but it is most parsimonious to propose that the stout shaft of *A. dianae* is a reversal from a luvarid+kushlukiid ancestor that had a relatively slender shaft retained by all members of the clade except *A. dianae* (two steps), rather than the ancestor having a stout shaft that was retained by *A. dianae* whereas the slender shaft was developed inde-pendently in kushlukiids, *Luvarus*, and *A. mariannae* (three steps).

Autapomorphies of *Luvarus imperialis*

Character 47. The neural spine of the first abdomi-nal vertebra is stout and exceptionally long, extending dorsally to the lower edge of the dorsal-fin pterygial truss. In *L. necopinatus* the first neural spine is slender and relatively shorter, extending dorsally a little less than two-thirds the distance between the centrum and the truss. In both species of *Avitoluvarus* the first neural spine is also slender (as judged from its poorly preserved

remains) and extends about two-thirds the distance between the centrum and the truss. In kushlukiids the first few neural spines are not clearly preserved but judging from those behind them and the space available for them, they obviously were short and slender. In all other acanthuroids and higher squamipinnes the first neural spine is relative short, and often more slender than those just posterior to it, and usually reaches dorsally to no more than one-half the distance between the centrum and the distal regions of the anterior dorsal-fin basal pterygiophores. The exceptionally long and stout first neural spine in *L. imperialis* is obviously a uniquely derived feature.

Character 48. The haemal spines of the first and second caudal vertebrae are both exceptionally curva-ceous, the first haemal spine curved posteriorly in its middle region, reaching the level of the anterior half of the centrum of the third caudal vertebra, whereas its distal end is curved far anteriorly, reaching the level of the middle of the centrum of the preceding vertebra (last abdominal). In *L. necopinatus* the first two haemal spines are only slightly (the second spine) to moderately (the first spine) curvaceous, the first curved posteriorly in its middle region to the level of about the middle of the centrum of the second caudal vertebra and its distal end curved anteriorly to the level of the middle of its centrum. In both species of *Avitoluvarus* the first two haemals are only moderately curved, as in *L. necopinatus*, whereas these spines in kushlukiids and other acanthuroids are not strongly curved toward each other in the middle regions, usually being more or less parallel (and sometimes in contact for much of their lengths) or even slightly divergent. It is clear that the curvature of the first two haemals toward one another in the middle region is a synapomorphy of luvarids (Character 24) and that the more extreme version of that curvature in *L. imperialis* is derived relative to the lesser degree of curvature in *L. necopinatus* (assuming an ordered transformation series).

Autapomorphies of *Luvarus necopinatus*

Character 49. The more anterior pleural ribs are expanded throughout their length, increasingly so dis-tally. In *L. imperialis* the pleural ribs are only expanded in the upper half of their lengths and taper to points distally. The ribs are not expanded in *Avitoluvarus*, kushlukiids, and other acanthuroids. It is clear that rib expansion is a synapomorphy of luvarids (Character 36) and that the more extreme version of that expansion in *L. necopinatus* is derived relative to the lesser expansion in *L. imperialis* (assuming an ordered transformation series).

Character 50. There is a vacant interneural space posterior to the origin of the dorsal fin, variably the third

to fifth interneural space. In *L. imperialis* there are no vacant interneural spaces posterior to the origin of the dorsal fin, whose first basal pterygiophore is inserted in the preneural space. Both species of *Avitoluvarus* are like *L. imperialis* in having no vacant interneural spaces and the shaft of the first dorsal-fin basal pterygiophore inserted in the preneural space. In *Kushlukia* the anterior end of the dorsal fin is more posterior in position than in luvarids, with the small first dorsal-fin basal pterygiophore placed at the top of the third or fourth interneural space but with no vacant interneural spaces posterior to the origin of the dorsal fin. In acanthurids and zanclids the third interneural space is vacant and in siganids the fifth or sixth interneural space is vacant. Among higher squamipinnes the sixth or seventh (rarely fifth or eighth) interneural space is vacant in scatophagids, whereas the sixth space is vacant in ephipiids (except none in *Platax*); and the fifth is vacant in drepanids. Therefore, we consider the presence of a vacant interneural space behind the origin of the dorsal fin as ancestral for acanthuroids, with the most parsimonious interpretation being that the ancestor of the luvarid+kushlukiid clade lost the vacant interneural space and that the vacant space behind the dorsal-fin origin in *L. necopinatus* is a reversal (two steps) rather than a vacant space being ancestral for luvarids+kushlukiids and the loss of the vacancy independent in *Kushlukia*, *Avitoluvarus*, and *L. imperialis* (three steps).

Autapomorphy of *Kushlukia permira*

Character 51. The haemal spines of all but the more posterior caudal vertebrae are inclined anteroventrally. In *K.* sp. the haemal spines of all but the first caudal vertebra are inclined posteroventrally. In luvarids the haemal spines are either relatively vertical or inclined posteroventrally, except for the first two with the derived condition of being curved toward one another (with the third and fourth haemals in *L. imperialis* also inclined anteroventrally). In all other acanthuroids and higher squamipinnes these haemal spines are also either relatively vertical or inclined posteroventrally. The anteroventral inclination of the haemal spines of most of the caudal vertebrae is obviously a derived feature of *K. permira*.

Autapomorphy of *Kushlukia* sp.

Character 52. The basal pterygiophores of the dorsal- and anal-fin trusses are interdigitated to one another throughout most of their length, the interdigitation extending proximally to the distal tips of the neural and haemal spines. In *K. permira* only the distal regions of these pterygiophores are interdigitated to one another,

and this is also the case in all four species of luvarids. Other acanthuroids lack the truss that characterizes the luvarid+kushlukiid clade, but when the basal pterygiophores are articulated on one another it is only at their distal ends, except in some species of *Naso*. In the latter there is increased interdigitation of the anal fin basal pterygiophores, which is most parsimoniously interpreted as an independent acquisition. It is clear that the extensive interdigitation of the pterygiophores throughout most of their lengths should be interpreted as a derived feature of *K.* sp.

Conclusion

The luvaroid fishes are represented today only by the large (over 1.8 m SL and 140 kg weight) and rarely collected oceanic pelagic *Luvarus imperialis* found worldwide in tropical and temperate marine waters. However, luvaroids were rather diversified about 55 million years ago in the Lower Eocene, especially as represented in the species known from the mostly pelagic marine (Tethyan) ichthyofauna of Turkmenistan (Danilchenko, 1968; Bannikov, 1993). Even in that limited sample of its diversity as preserved in Turkmenistan, there were two families of luvaroids, the Kushlukiidae and Luvaridae, both with relatively smaller species of up to about 150 to 500 mm SL, the first with a single species, *Kushlukia permira*, and the second with two genera and three species, *Luvarus necopinatus*, which is not much different morphologically than the Recent *L. imperialis*, and *Avitoluvarus dianae* and *A. mariannae*.

Outside of Turkmenistan, the fossil luvaroids presently are represented only by a few fragments of two species. One is a species of *Kushlukia* from the Lower Eocene of India that is distinct from *K. permira* but not named herein because only parts of its vertebral column have yet been found. The other is known from several incomplete skulls from the Lower Eocene of the London Clay and is probably a species of luvarid, perhaps of a *Luvarus* (originally described as an iniomoid, *Beerichthys ingens* Casier, 1966).

One suspects that yet much more will come to light about the diversification of the fossil luvaroids from future excavations in other locations with Tethys Sea pelagic ichthyofaunas. That luvaroids are not yet known from the rich and beautifully preserved late Tethyan marine ichthyofauna of Monte Bolca, Italy, is probably because most of those fishes are inshore and shallow benthic rather than offshore and pelagic. But one can hope that by chance some luvaroid fishes did wander into the Monte Bolca locality to be well preserved and found among the materials continuing to be retrieved there.

Addendum

†*Aluvarus*, new genus

Luvarus.—Arambourg, 1967:172 [in part; with *Luvarus praeimperialis* Arambourg improperly included in that genus].

TYPE SPECIES.—*Luvarus praeimperialis* Arambourg, 1967 [by monotypy and designation here].

ETYMOLOGY.—The generic epithet is from *A* (Greek), for "not" or "different than," plus *Luvarus,* for the original generic allocation of its type species; masculine.

DIAGNOSIS.—Body moderately elongate, with short and shallow caudal peduncle. About 28 vertebrae (26 preserved and space for an estimated two more between anterior end of preserved column and rear of skull), with the neural and haemal spines of all but the three vertebrae preceding the caudal skeleton exceptionally short, forming low ridges along the centra; none of the more posterior vertebrae reduced in size or specialized other than the caudal skeleton. Caudal skeleton highly consolidated, the hypurals and parhypural fully fused to the centrum and only a single autogenous element, an epural. Caudal fin with a total of nine rays, four above and five below, the uppermost ray and the lowermost ray unbranched, the middle seven rays branched, no procurrent rays (i,3 + 4,i = 9 principal); bases of rays articulated along posterior edge of hypural plate, not significantly overlapping the plate. Dorsal and anal fins long-based and continuous, the fin-ray elements short, slender, unsegmented, unbranched, and at least mostly composed of soft rays (although the most anterior ends of the dorsal and anal fins where a few spines might have occurred are variously either poorly preserved or absent). Dorsal- and anal-fin basal pterygiophores somewhat expanded anteroposteriorly at distal end and probably relatively continuous with one another, with exceptionally slender proximal shafts, the more posterior of which closely approach the low neural and haemal spines; an approximately one to one ratio between basal pterygiophores and vertebrae. A long and continuous band of enlarged scales present along the bases of the dorsal and anal fins, some with posterolaterally directed spiny processes.

COMPOSITION.—A single species, *Aluvarus praeimperialis* (Arambourg, 1967), Lower Oligocene of Iran.

REMARKS.—Arambourg (1967) placed this Oligocene species in *Luvarus* based on what we believe were several misinterpretations of the features in the two incomplete skeletons available, and inadequate appreciation of how many of its other characteristics were exceptionally different from luvarids (and other acanthuroids).

The misinterpretations concern the supposed pterygial truss and the caudal skeleton and fin.

What Arambourg described as a luvarid-like pterygial truss of basal pterygiophores that were anteroposteriorly expanded and sutured together distally appears to us to be composed mostly of anteroposteriorly elongate and abutting or perhaps slightly overlapping enlarged scale plates along the bases of the dorsal and anal fins. Some of these scales have laterally or posterolaterally projecting spiny processes. The distal ends of the basal pterygiophores seem to us to be expanded only as thin medial flanges that are more or less rounded in ventral outline to either side of the distal ends of the very thin proximal shafts. These relatively thin moderate expansions of the distal ends of the pterygiophores probably were in contact with one another but this region is hidden from view by the overlying enlarged scale plates. However, there is no evidence that these distal ends of the basal pterygiophores were broadly thickened and extensively interdigitated into a luvarid-like truss. The enlarged scale plates do seem to closely abut against one another or to slightly overlap at the apposed ends and it is this structure that we believe Arambourg thought was a pterygial truss. Some of the lateral processes of the scales have both anteriorly and posteriorly directed prongs.

Arambourg may have believed that the long slender proximal ends of the basal pterygiophores were similar to those of luvarids, and in a sense they are, although even more slender. However, the relationship of the proximal ends of the basal pterygiophores to the vertebral column in *Aluvarus* and in luvarids is strikingly different, with the distal ends of the less slender shafts of the pterygiophores in luvarids closely associated with long neural and haemal spines but those of *Aluvarus* not so associated, the neural and haemal spines of the latter being exceptionally low; luvarids also tend to have a few more basal pterygiophores than vertebrae, especially in the anal fin.

Arambourg believed that the caudal-fin rays were of reduced and variable number (10 in the holotype and 13 in the paratype) relative to the 16 in luvarids but that they deeply overlapped the hypural plate in hypurostegy as in luvarids. We believe that there is an exceptionally specialized condition of only nine caudal-fin rays, four above and five below, and that these do not significantly overlap the hypural plate. The hypurals are all fully consolidated with the terminal centrum (PU_1) but the surface of the hypural plate has prominent ridges and grooves radiating out from the rear of the centrum to the posterior edge of the plate. We believe that these ridges were mistaken for the bases of deeply overlapping caudal-fin rays in the original description and that these were not seen to end at the posterior end of the hypural plate, with only nine rays abutting against the end of the plate in the holotype. The caudal fin is absent in the paratype, but the ridges and grooves on its hypural plate are more prominent than on the holotype and Arambourg apparently counted these ridges in arriving at his interpretation of a larger number of caudal rays in it than in the holotype. In short, the caudal skeleton and fin are not at all similar to those of any luvarid+kushlukiid (which have 16 principal rays and hypurostegy) or acanthuroid.

The relatively large number of vertebrae (about 28) in *A. praeimperialis* is similar to that in *Kushlukia* (about 29–30) but because *Aluvarus* has none of the synapomorphies of either kushlukiids or luvarids, or of other families of the acanthuroid clade, the number of vertebrae in *Aluvarus* is herein interpreted as a specialization independent of that in *Kushlukia* alone among acanthuroids (22-23 vertebrae).

Although the above indicates that *Aluvarus* is neither a luvaroid nor closely related to other acanthuroid families, we cannot exclude the possibility that it is the sister group of some

more expansive group of acanthuroid-like fishes because the condition of none of the 11 adult osteological synapomorphies that Tyler et al. (1989) found to characterize the acanthuroids can be determined in the partial skeleton of *Aluvarus*. We have not been able to associate its unique combination of specialized features (about 28 vertebrae, most of which have very low neural and haemal spines; consolidated caudal skeleton with ridged hypural plate; nine caudal-fin rays, with only four in upper half and five below and no procurrent rays; exceptionally slender proximal shafts of basal pterygiophores; enlarged scales with spiny processes forming continuous band along dorsal and anal fins) with any particular order of acanthopterygians, including any of the zeiform+euacanthopterygii groups (sensu Johnson and Patterson, 1993) or suborders of perciforms. In fact, we place *Aluvarus* among the percomorphs mainly because of the great reduction in the number of caudal-fin rays and the consolidation of the caudal skeleton (hypural fusion; no separate second ural centrum), although a zeiform relationship is not thereby excluded (especially because the scales along the bases of the dorsal and anal fins are reminiscent of those of many zeids).

Our efforts to place *Aluvarus* among the percomorphs is of course greatly hampered by the lack of a well-preserved entire head, the missing pelvic fin region, uncertainty about the kind of fin-ray elements at the anterior ends of the dorsal and anal fins, and by not knowing the conditions of any of the characters that are useful in assessing higher acanthopterygian relationships (e.g., characters 1 through 26 in Johnson and Patterson, 1993, cannot be determined). Only more complete specimens of *Aluvarus* will help resolve its relationships.

†*Aluvarus praeimperialis* (Arambourg, 1967), new combination

FIGURES 19, 20

Luvarus praeimperialis Arambourg, 1967:172, pl. XVII: figs. 2, 4.

HOLOTYPE.—MNHN 1936-6-250 d and g, see "Material Examined" for details of this and the single paratype, of about 110 and 75 mm SL, respectively, the head incomplete or missing and the pelvic region missing in both specimens.

TYPE LOCALITY AND HORIZON.—Fish bearing layers of the Elam locality, Iran; Lower Oligocene (Rupelian).

DIAGNOSIS.—As for the genus, of which *A. praeimperialis* is the only presently known representative. Additionally, the following characters may prove useful in distinguishing it from other closely related species: dorsal and anal fins separated from the caudal fin by the lengths of the last two vertebrae (PU$_{1-2}$); pharyngeal teeth slender, conical, curved; and, according to Arambourg (1967:173-174), dorsal fin-ray elements about 23, anal-fin ray elements about 16 or 17 (but most anterior elements of both fins perhaps not preserved, and pectoral fin (which is placed very low on the body) with about 16 rays.

DESCRIPTION.—We do not further describe this species beyond the diagnosis above and our remarks, which correct what we consider to be the misinterpretations in the original description that led to it inaccurately being included in the Luvaridae.
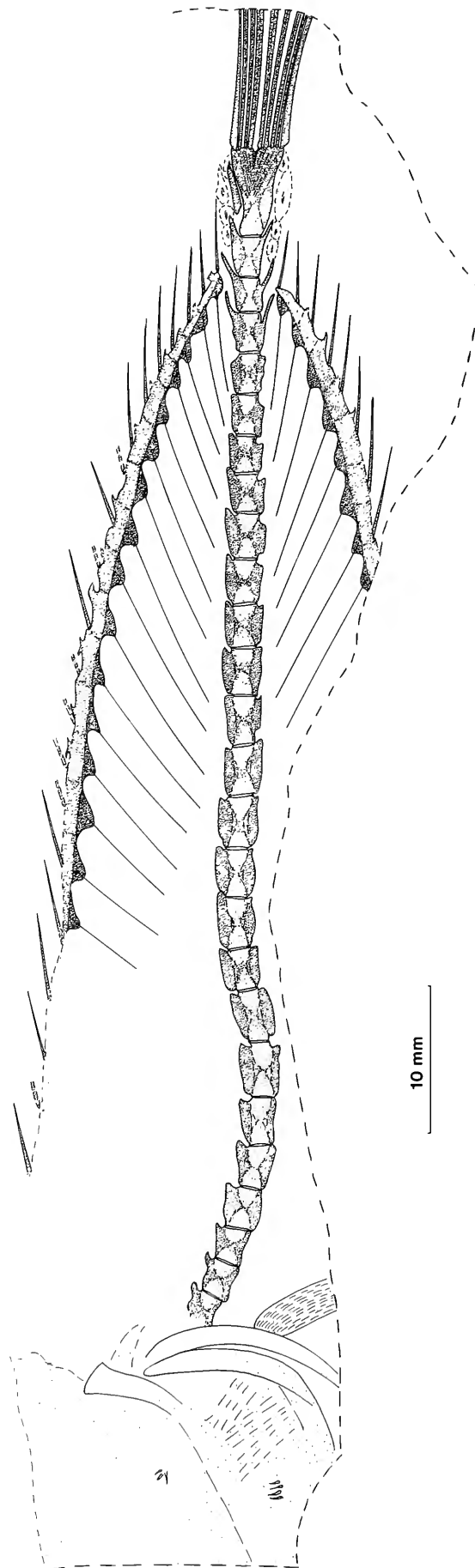

FIGURE 19.—*Aluvarus praeimperialis*, reconstruction of skeleton, based on the holotype (MNHN 1939-6-250 d and g, estimated 110 mm SL); Lower Oligocene of Iran.
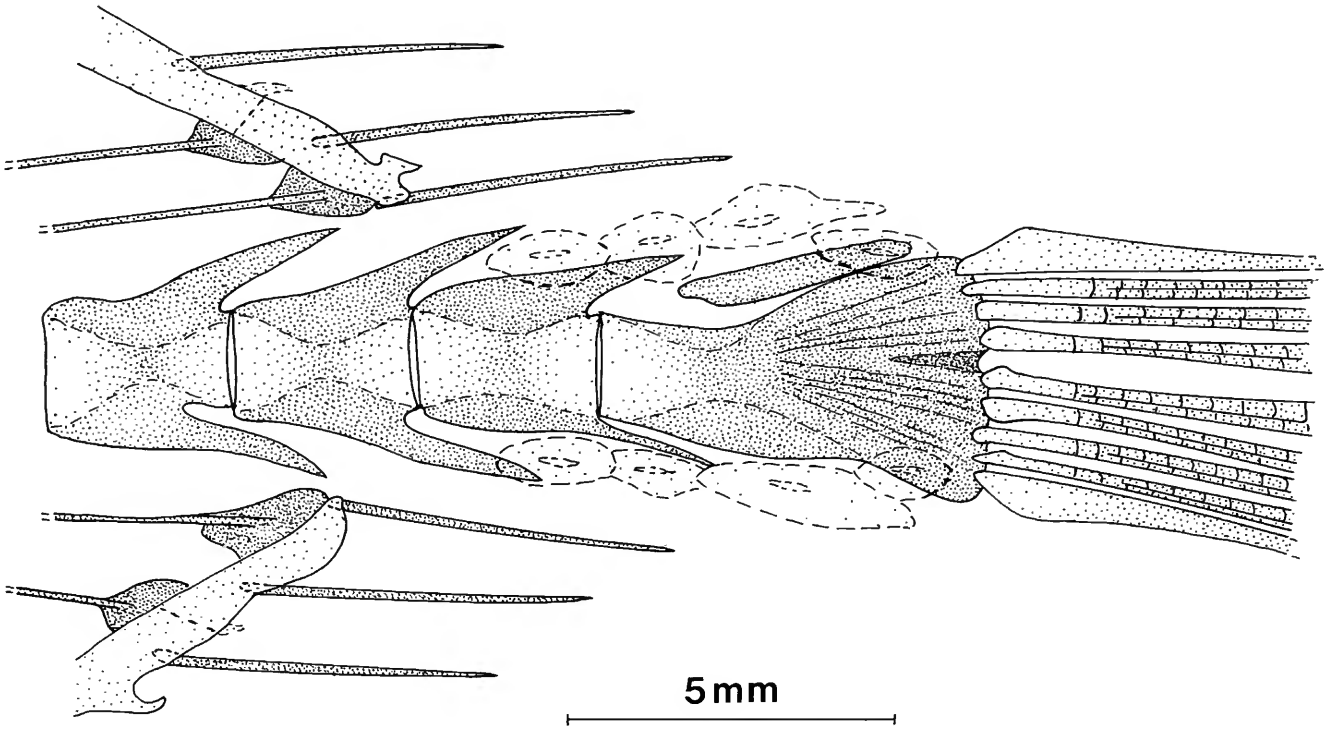
10 mm

FIGURE 20.—*Alwarus praeimperialis*, reconstruction of caudal skeleton, based on the holotype (MNHN 1939-6-250 d and g, estimated 110 mm SL); Lower Oligocene of Iran.

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