A NEW SPECIES OF *MENE* (PERCIFORMES: MENIDAE) FROM THE PALEOCENE OF SOUTH AMERICA, WITH NOTES ON PALEOENVIRONMENT AND A BRIEF REVIEW OF MENID FISHES

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ABSTRACT—A new species of menid fish, †*Mene purdyi*, is described from northwestern Peru. A Paleocene age (late Thanetian) is estimated for the specimen based on biostratigraphic analysis of planktonic foraminifers recovered from the surrounding matrix. Possible explanations for discrepancies between this result and previous interpretations of an Oligocene age are explored. Stable isotopic analysis of foraminifers associated with the fossil allows for general characterization of the thermal profile of the depositional environment. The small temperature gap between distinct depth-ecological foraminifer assemblages inferred from $\delta^{18}O$ values indicates a low vertical temperature gradient, possibly reflecting a depositional environment dominated by upwelling. Although incomplete, the three-dimensional preservation of this specimen allows for detailed description of much of the skull, the first two vertebrae and the posttemporals. Numerous characters distinguish the new taxon from previously described menids, the most conspicuous being its exceptionally large size. Comments on the relationships of this new taxon to other menid fishes are premature until the osteology of fossil and living forms are better documented. Extinct species are briefly reviewed in order to facilitate future studies of Menidae. An examination of the distribution of fossil menids reveals that the group was once widespread, demonstrating a circum-global pattern during much of the Tertiary, consistent with the historical Tethys.

INTRODUCTION

Menidae (moonfishes) are a morphologically distinctive group represented by a single Recent and numerous fossil species. Members of this family are easily recognized by their laterally compressed disc-like bodies, dorsally oriented mouth large, distinctly shaped maxillae and long ascending processes of the premaxillae, anteroposteriorly elongated dorsal and anal fins with relatively short rays, and narrow pelvic fins with a compressed and greatly elongated second ray. This unique morphology is conserved over the known fossil history of this group, and characterizes the only extant member of Menidae, *Mene maculata* Bloch and Schneider, 1801. This Recent form is found throughout the Indo-Pacific, ranging from the eastern coast of Africa, India, the Philippines, northern Australia, and Japan. Springer (1982) regarded Matsubara's (1955) report of *Mene* in Hawaiian waters as dubious. *Mene maculata* typically inhabits deeper costal waters, especially around coral reefs (Carpenter et al., 1997). Some fossil species may have had similar environmental preferences (Bellwood, 1996). *Mene* is known to school (Lee et al., 1988) and is often found near the bottom, where it feeds primarily on copepods, shrimp, and fish larvae (Luo, 1982).

The phylogenetic affinities of *Mene* have been the subject of some historical debate. Gayet (1980) proposed an ancestry lying with †*Aipichthyoides*, an early acanthomorph from the Cretaceous (Cenomanian) of Israel. However, the characters cited in support of this hypothesis are unconvincing. Gross external similarity likely led Montilla (1935) to suggest that these compressed, deep-bodied fishes are allied to the lampridiform *Lampris*. *Mene* does share some characters with the basal acanthomorph clade Lampridiformes, including a frontal vault and elongate ascending processes of the premaxillae, but it lacks the two remaining lampridiform synapomorphies identified by Olney et al. (1993), and, more importantly, shares numerous synapomorphies of higher acanthomorph clades.

Most authors have agreed upon placement of Menidae within the perciform suborder Percoidei. However, Springer, in Springer and Johnson (2004), proposed that the affinities of *Mene* lie with more plesiomorphic acanthomorphs, based on its possession of an esophageal raphe and ventral attachment of the obliquus posterioris (sic) at the level of the fourth ceratobranchial, both of which are lacking in most percomorphs. Johnson did not agree with this and numerous other assertions in that paper (see last paragraph in First Author's Preface; Springer and Johnson, 2004:1). A phylogenetic analysis by Springer and Orrell (2004) placed *Mene* as the sister group of *Macroramphosus* (traditionally considered a syngnathoid gasterosteiform) based on characters of the gill-arch muscles and skeleton described in Springer and Johnson (2004). These disparate genera were included within a highly unlikely clade comprising Beryciformes, Stephanoberyciformes, *Icosteus*, *Polymixia*, *Raniceps*, and Ophidiiformes, the monophyly of which was supported by the two aforementioned characters. However, with one exception (the percomorph interarcual cartilage), this analysis did not include the numerous synapomorphies identified by Johnson and Patterson (1993) that *Mene* shares (numbers in parentheses) with successively less inclusive acanthomorph clades leading from the basal Lampridiformes to the derived Percomorpha: (a) Euacanthomorpha, comprising all acanthomorphs except Lampridiformes (4 of 4); (b) Holacanthopterygii, comprising Paracanthopterygii plus Acanthopterygii (3 of 3); (c) Acanthopterygii (2 of 3, the third inapplicable); (d) an unnamed clade comprising Zeiformes plus Euacanthopterygii (3 of 3); (e) Euacanthopterygii, comprising Beryciformes plus Percomorpha (3 of 5); (f) Percomorpha (7 of 8). Consequently, we reject the placement of *Mene* by Springer and Orrell (2004) with basal acanthomorphs and conclude that its relationships lie within the Percomorpha, probably with some members of the perciform suborder Percoidei.

The specific relationship of *Mene* to other percoids is unclear, and several alternative schemes have been considered. Regan (1909) and Sedgewick (1905) suggested affinities with Coryphaenidae (dolphinfishes) and Bramidae (pomfrets), while a majority of authors have noted similarities to Carangidae (jacks) (e.g.,

Weber and de Beaufort, 1931). Leis (1994) proposed that *Mene* is the sister group of the carangoids based on six shared characters, and that the monotypic family Lactariidae is the sister group to the clade comprising Menidae + Carangoidei (Nematistiidae, Coryphaenidae, Echeneididae, and Carangidae). However, Leis (1994:142) considered his hypothesis tentative, noting that it is "suggested by several demonstrably equivocal characters and two characters of uncertain reliability," and that "evidence from larvae will be crucial to testing it." Some molecular studies corroborate Leis' (1994) surmise, placing *Mene* sister to a clade containing the carangids *Trachinotus* and *Chloroscombrus* and the echeneidid *Echeneis* (Chen et al., 2003:fig. 5). However, we adopt a conservative approach and consider the relationships of *Mene* within the Percoidei as uncertain.

Menid fishes have an extensive fossil record (see Discussion: Fossil Menids). Here we describe a new species of *Mene* from the Paleocene of South America, which has important implications for the historical biogeography of the group. This find also highlights the possibility of a new fossil ichthyofauna in marine deposits of western South America, the significance of which for interpreting the Paleogene radiation of percomorphs is discussed.

MATERIALS EXAMINED

Menidae

Mene maculata Bloch and Schneider (1801): five complete skeletal specimens: two cleared and double stained: USNM 347107; USNM 102665; three dry skeletons: AMNH 98805; AMNH 98806; AMNH 98809.

†*Mene rhombea* Volta (1796): six complete fossil specimens, all from the middle Eocene (Lutetian) of Monte Bolca, Italy: BM(NH) P.29284; CM 4493; CM 4310; CM 4484; CM 4365; CM 5236.

†*Mene oblonga* Agassiz (1833): seven complete fossil specimens, all from the middle Eocene (Lutetian) of Monte Bolca, Italy: BM(NH) P.2087; BM(NH) P.4134; BM(NH) P.23800-1; CM 4020; CM 4492 and 4344 (part and counterpart); CM 4333; CM 4337.

METHODS

Fossil Preparation

As the siliceous matrix surrounding the fossil made mechanical preparation difficult, computer tomography (CT) was explored as an alternative. Exploratory scans proved marginally successful, yielding some details not readily apparent from external observations. However, due to varying degrees of permineralization, the relatively broad scan length of the machine (1 mm), and the low-density gradient between the matrix and the fossil, CT scan images proved inadequate for the examination of potentially diagnostic osteological characters. As a consequence, more conventional preparation techniques were pursued.

Matrix was removed using a flexible shaft grinder equipped with a diamond-tipped burr. A post-mortem displacement gap between the occiput and the anterior articular surface of the first vertebral centrum was wide enough to accommodate a diamond saw, which permitted the removal of these elements for more detailed examination.

Foraminifer Collection and Isotopic Analysis

Portions of matrix were removed with a diamond saw and broken down with a mortar and pestle. The resulting powder was allowed to soak in water for a period of approximately 12 hours to loosen any carbonate cement that may have been present. Afterwards, the slurry was poured into a funnel lined with filter paper in order to collect the sediment fraction, which was then allowed to air-dry. The resulting samples were sorted with a series of standard sieves and each size fraction was examined under a stereomicroscope. Foraminifers were separated by taxon and size fraction. Analyses were made at the University of California, Santa Cruz on a VG Optima mass spectrometer with a precision of 0.05% for δ^{13}C and 0.08% for δ^{18}O. Carerra Marble, which has been calibrated to National Institute of Standards and Technology isotopic reference material NBS-18 and NBS-19 for conversion to the Vienna Peedee belemnite (VPDB) scale, is used as the in-house standard. All values reported here are relative to VPDB.

Sites for comparison of isotopic results with those from this study were chosen based on their temporal and spatial (paleolatitudinal) proximity to the type locality for the new menid. One of the studies used to compare thermal profiles (Lu and Keller, 1996) indicated neither the number of individual foraminifers contributing to species isotopic averages nor standard deviations. Therefore, the isotopic values for thermocline (†*Subbotina*) and mixed-layer (†*Acaranina* + †*Morozovella*) communities were calculated as unweighted averages of the mean δ^{18}O values of each member genus of the assemblage for this and all other localities. We acknowledge that this is methodologically undesirable, but the absence of critical data from the literature precluded a more rigorous approach.

Abbreviations

Institutional—AMNH, American Museum of Natural History, New York, New York; **BMNH**, The Natural History Museum, London; **CAMSM**, Sedgwick Museum, University of Cambridge, Cambridge; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **MGPD**, Museo di Geologia e Paleontolgia dell'Università delgi Studi di Padova, Padua; **PIN**, Paleontological Institute and Museum, Academy of Science, Moscow; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Dagger Symbol—Taxa preceded by the dagger symbol (†) are known exclusively from fossil remains.

Anatomical—Abbreviations followed by (**r**) or (**l**) refer to a right or left bone, respectively. Numbers following vertebral abbreviations refer to the number of the centrum. **aa**, anguloarticular; **ach**, anterior ceratohyal; **c.o.hym**, opercular condyle of the hyomandibula; **a.n**, neural arch; **boc**, basioccipital; **br**, branchiostegal ray; **c.a**, abdominal centrum; **d.la**, depression on the lateral surface of the lacrimal; **ecp**, ectopterygoid; **edp**, endopterygoid; **epo**, epiotic; **ex**, exoccipital; **f.mtp**, foramen in the metapterygoid; **f.o.hym**, opercular facet of hyomanidbula; **fr**, frontal; **gr.a.hy**, groove for the hyoid artery; **hym**, hyomandibula; **io**, infraorbital; **iop**, interopercle; **la**, lacrimal; **mtp**, metapterygoid; **op**, opercle; **pal**, palatine; **par**, parietal; **pch**, posterior ceratohyal; **pop**, preopercle; **pt**, posttemporal; **pto**, pterotic; **qu**, quadrate; **r.d.pt**, dorsal ramus of posttemporal; **r.l.pt**, lateral ramus of posttemporal; **r.v.pt**, ventral ramus of posttemporal; **ri.soc**, strengthened anteriorly-inclined ridge of supraoccipital; **s.n**, neural spine; **so**, sclerotic ossicle; **soc**, supraoccipital; **sop**, subopercle; **sph**, sphenotic; **vo**, vomer.

SYSTEMATIC PALEONTOLOGY

Subdivision TELEOSTEI sensu Patterson and Rosen, 1977
Order PERCIFORMES sensu Johnson and Patterson, 1993
Suborder PERCOIDEI sensu Johnson and Patterson, 1993
Family MENIDAE Gill, 1885
Genus *MENE* Lacépède, 1803
†*MENE PURDYI*, sp. nov.
(Figs. 2, 3, 5, 6; Table 1)

Holotype—USNM 494403, an incomplete skull and first two vertebrae. Cranial material is preserved in three dimensions, with little or no post-mortem compression.

Additional Specimens—The holotype is the only known specimen.

Locality and Age—The precise collection locality of the specimen is unclear. The only geographical data associated with the fossil indicates that it was collected from the Máncora Formation of northwestern Peru, "S. of Negritos (Lagunitos?)" (Fig. 1). At its type locality, this formation consists of a series of sandstones and conglomerates deposited in nearshore marine and brackish environments (Iddings and Olsson, 1928). This lithology differs markedly from that of the matrix that surrounds the fossil, which is composed of hemipelagic sediments and microcrystalline silica. Perhaps more alarmingly, the age of the specimen as suggested by biostratigraphic anaylsis is incongruous with that of the purported source formation. Iddings and Olsson (1928) established an Oligocene age for the Máncora Formation, although more recent studies have questioned this assignment, suggesting that the formation may be even younger (Zuñiga and Cruzado C., 1979). The planktonic foraminifers collected from the matrix (†*Acaranina nitida*, †*A. soldadoensis*, †*Chiloguembelina crinita*, †*Globanomalina chapmani*, †*Morozovella aequa*, †*M. gracilis*, †*M. marginodentata*, †*M. subbotinae*, †*M. velascoensis*, and †*Subbotina velascoensis*) are members of a late Paleocene assemblage and yield a narrow age estimate of 56.5–54.7 Ma (P4c–P5; late Thanetian) (Olsson et al., 1999).

The reworking of the fossil menid from older rocks could be responsible for the disparities in both age and lithology between recent analytical results and field collection data. This hypothesis is consistent with Iddings and Olsson's (1928) observation that the basal Máncora Formation contains reworked fossils and fossiliferous boulders from stratigraphically lower formations. Alternatively, this specimen may have been collected as surface float, displaced from its original stratigraphic context, and merely assigned to the Máncora Formation based on proximity. Regardless of the details of collection, it seems that such well-preserved fish fossils are not entirely uncommon at the locality;
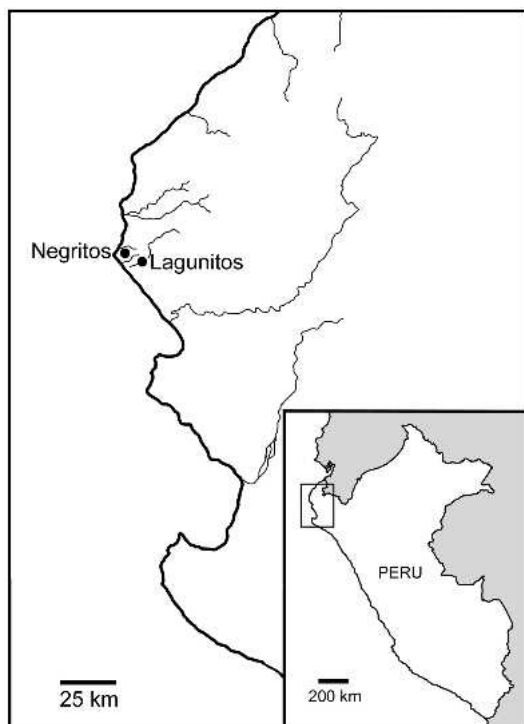
a similarly preserved, undescribed billfish skull housed at USNM was also recovered by Olsson and has collection data identical to that of †*Mene purdyi*, sp. nov.

Diagnosis—†*Mene purdyi*, sp. nov., differs from all other menids by the following combination of characters: (1) considerably larger size than any other extant or extinct menid (Fig. 2); (2), a neurocranium that is three times longer than the outer diameter of the sclerotic ossicle, compared to lower values in other menids; (3) an imperforate supraoccipital crest, unlike the Recent *Mene maculata*; (4) a posteriorly reclined accessory ridge posterior to and continuous with the anteriorly inclined ridge of the supraoccipital crest, which is either absent or poorly developed in *M. maculata*, †*M. oblonga*, and †*M. rhombea* (the condition is insufficiently described or not preserved in other fossil menids); (5) a lacrimal with a strongly concave posterior margin dorsal to the pronounced posterior depression on its lateral face, unlike *M. maculata*, in which the equivalent margin is markedly convex (Fig. 2); (6) absence of the ventral prong of the anguloarticular, a feature present in *M. maculata*, †*M. oblonga*, and †*M. rhombea*; (7) an angle between posterior prong of the anguloarticular and the posterior border of the bone of approximately 90º, in contrast to the more acute angle seen in other menids; (8) a broad preopercle with a relatively elongate anterior arm in comparison to other menids, which generally have a narrower preopercle (Fig. 2); (9) an opercle with a smoothly convex posterior border, unlike in *M. maculata* and †*M. rhombea*, where this same margin has a distinct concavity. Although the supraoccipital crest is not preserved in its entirety, it is inferred that this feature was relatively lower than that found in most other menids (see Description: Neurocranium).

Discussion—†*Mene purdyi* shows several characters found in menids, including: a cavernous vault formed by the frontal bones; a pronounced supraoccipital crest ornamented with a distinctive, anteriorly-inclined ridge; well-formed sclerotic ossicles; a lateral plateau on the hyomandibula ornamented with a set of narrow striae; close association of the first and second neural arches; forked posttemporals with a distinct lateral prong. All of these characters are readily observed in Recent preparations and well-preserved fossil material. Although not directly visible in the compressed specimens from Monte Bolca, the presence of vault in †*M. rhombea* and †*M. oblonga* seems likely based on the apparent crushing of the dorsal projections of the frontals.

The unusual, three-dimensional preservation of the single specimen of †*Mene purdyi* reveals characters found in the Recent *M. maculata* that are not clearly observed in other fossil menids due to either inadequate preparation or poor preservation. These characters include: a vomer with two parallel grooves separated by a median ridge on its anterodorsal face; a laterally-oriented prong of the sphenoid; a series of narrow infraorbital bones and a large lacrimal with a conspicuous depression on its lateral surface posteriorly; a diamond-shaped palatine prong; a well-developed foramen in the metapterygoid near its anteroventral corner; distinctively-shaped anterior ceratohyal and posterior ceratohyal; a posteriorly oriented flange of the first centrum that overlaps the second abdominal centrum.

Etymology—The specific epithet *purdyi* honors Robert Purdy, museum specialist in the Department of Paleobiology, National Museum of Natural History, who directed us to this interesting specimen.

DESCRIPTION

Size and Measurements—Measurements taken directly from the specimen are listed in Table 1. Isometric scaling based on the cranial measurements of the holotype of †*Mene purdyi* and *M. maculata* yields a mean estimated standard length of roughly 340 mm for the new taxon; the total length for such an individual would likely exceed 400 mm. This is far greater than the maxi-

FIGURE 1. Map showing approximate collection locality of †*Mene purdyi*, sp. nov., holotype (USNM 494403), Paleocene (Thanetian), northwestern Peru. The site of collection is given only as "S. of Negritos (Lagunitos?)".
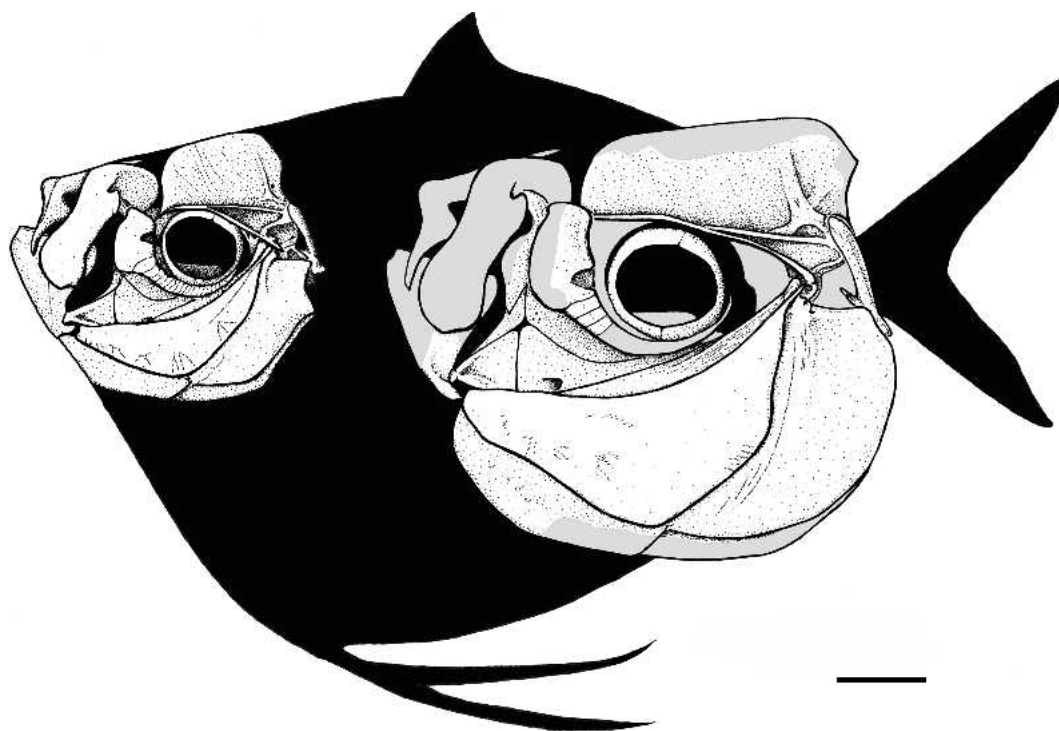
FIGURE 2. Reconstruction demonstrating the large size of †*Mene purdyi*, sp. nov. Body silhouette and skull (left) are those of an exceptionally large specimen of the extant *Mene maculata* (TL = 250 mm; scaled isometrically from AMNH 98805 and 98806), while isolated skull (right) is a reconstruction of †*Mene purdyi* (USNM 494403), holotype, Paleocene (Thanetian), northwestern Peru. Regions infilled with gray are reconstructed based on other Menidae. Scale bar represents 20 mm.

mum size recorded for any other menid (Fig. 2). The extant *M. maculata* commonly reaches a total length of 180 mm, with a maximum of approximately 240 mm (Carpenter et al., 1997). Previously described fossil Menidae that are known from multiple individuals are either smaller than the modern form or attain a comparable maximum total length: †*M. phosphaticus*, approximately 94 mm (both known specimens incomplete anteriorly; estimate based on isometric scaling from *M. maculata*) (Astre, 1927); †*M. triangulum*, 145 mm (Danil'chenko, 1968); †*M. rhombea*, 220 mm (Blot, 1969); †*M oblonga*, 270 mm (Blot, 1969).

Neurocranium—The vomer (Fig. 3B) is the most anteriorly located ossification of the neurocranium and has a smoothly convex ventral margin in anterior view. Two distinct grooves separated by a ridge are found on the anterodorsal surface of this bone; similar features are found on the vomer of *Mene maculata*.

The most conspicuous feature of the braincase is the well-formed dorsal crest that extends nearly the entire length of the skull along its midline. The anterior third of this crest appears to be formed by the frontals, although the division between these bones and the supraoccipital is not clear, and its position must be inferred from the condition in other menids. Viewed head-on, the frontals diverge at the dorsal margin of the crest and flare laterally, forming a vault whose aperture resembles an inverted "V". The intersection of the frontals is located slightly below the dorsal margin of the crest in *Mene maculata*. Since the dorsal intersection of the frontals is visible, it seems likely that the height of the crest in †*M. purdyi* was not considerably greater than the preserved portion, assuming that the gross structure of the complete crest and vault was similar to that of the Recent form. In lateral view, the anterior margin of the frontal (Fig. 3) forms a near right angle with the roof of the skull. The supraoccipital (Fig. 3C, D) lies posterior to the frontals and is continuous with them. A conspicuous, anterodorsally-projecting ridge

(**ri.soc**, Fig. 3C, D) ornaments the posterior portion of the smooth surface of this thin bone. A similar structure is apparent in the other species of *Mene* examined. An additional, fainter thickening projects posterodorsally from this pronounced ridge and rapidly fades with distance from it. This feature does not appear to have a well-defined equivalent in other menids. There is no evidence of a small fenestration posterior to the anteriorly-inclined ridge as in *M. maculata*.

As with its junction with the supraoccipital, the sutures between the frontal and other surrounding bones are indistinct and must be estimated though comparison with the extant species. A strengthened ridge, extending from the posterior margin of the frontal across the parietal (**par(r)**, Fig. 3C, D), is well preserved on the right surface of the specimen and is reminiscent of a nearly identical feature in *Mene maculata*. Immediately posterior to the parietal is the epitotic (Fig. 3 C, D) whose most salient feature is a posterodorsally oriented thickening of bone that terminates in a concave surface for articulation with the posttemporal. The pterotic (Fig. 3C, D) lies ventral to the epiotic, and has a laterally projecting shelf. A small extension of bone is visible posterodorsal to the orbit on both sides of the specimen (Fig. 3). This corresponds to a similar prong that projects laterally from the sphenotic of *M. maculata*. Although comparisons with *M. maculata* suggest that additional portions of the sphenotic may be visible on the fossil, this cannot be confirmed due to ill-defined divisions between bones.

The occipital condyle is of typical tripartite form (Fig. 3D). The exoccipitals border the foramen magnum ventrally and have facets that articulate with those on the first vertebra (Fig. 3D). The basioccipital (Fig. 3D) is exposed ventral to the exoccipitals and has a deeply concave articular surface.

Circumorbital Bones—Like *Mene maculata* (Fig. 3A), †*M. purdyi* has well formed infraorbital (Fig. 3C, D) and sclerotic (Fig. 3) ossifications, all of which are best preserved on the right
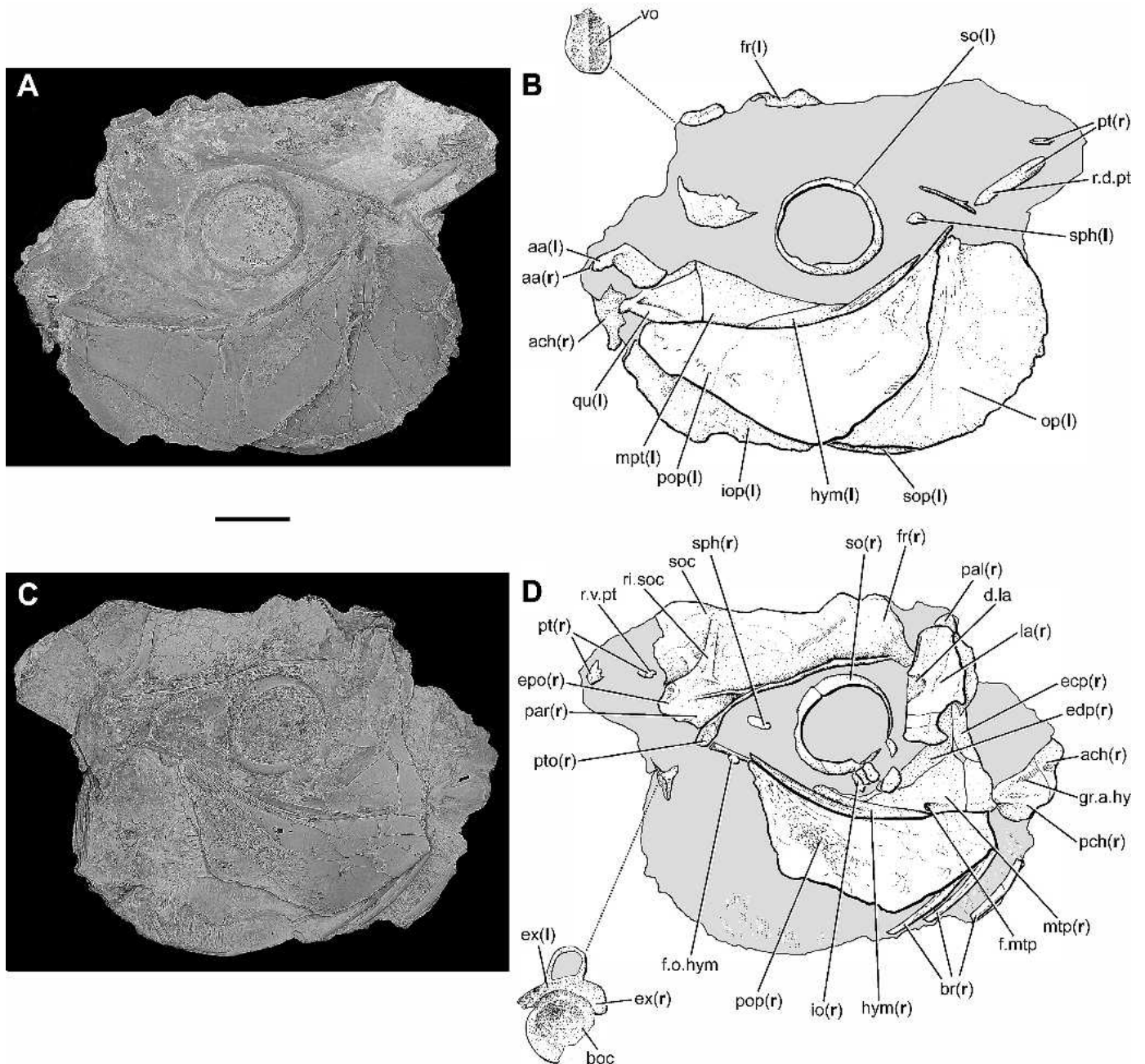
FIGURE 3.   Partial skull of †*Mene purdyi*, sp. nov., holotype (USNM 494403), Paleocene (Thanetian), northwestern Peru. **A**, photograph of left lateral surface; **B**, interpretive drawing of left lateral surface; **C**, photograph of right lateral surface; **D**, interpretive drawing of left lateral surface. Abbreviations are as listed in METHODS. Areas of drawings with solid gray infill indicate matrix. Scale bar equals 20 mm for lateral views of skull. For inset interpretive drawings in B (vomer, anterior view) and D (occiput, posterior view), scale bar equals 10 mm (inset drawings enlarged by a factor of two).

side of the specimen (Fig. 3C, D). The most anterior member of the infraorbital series**,** the lacrimal (Fig. 3C, D), is greatly expanded relative to the succeeding infraorbitals. The lacrimal has a distinctive depression (**d.la**, Fig. 3C, D) on its posterior half, while the remainder of its lateral surface is covered with a series of radiating pores of the infraorbital sensory canal. The posterior border of this bone is markedly concave dorsal to the lateral depression, unlike the convex posterior profile of the equivalent ossification in *M. maculata* (Figs. 2, 4A). It is not immediately clear if the two elongated elements directly ventral to the lacrimal are artifacts of breakage or if they represent separate infra-

orbitals. Comparisons with Recent material support the latter interpretation, which is reflected in the reconstruction (Fig. 2). Not including these equivocal structures, no fewer than six narrow, rectangular infraorbitals (Fig. 3C, D) are preserved, and some of these appear to be in approximate life position relative to one another. These ossifications are too poorly preserved to observe the course of the infraorbital canal through each bone. It is unclear how many infraorbital bones were present in †*M. purdyi*; *M. maculata* has an extensive infraorbital series, consisting of over 20 separate ossifications (Fig. 4B).

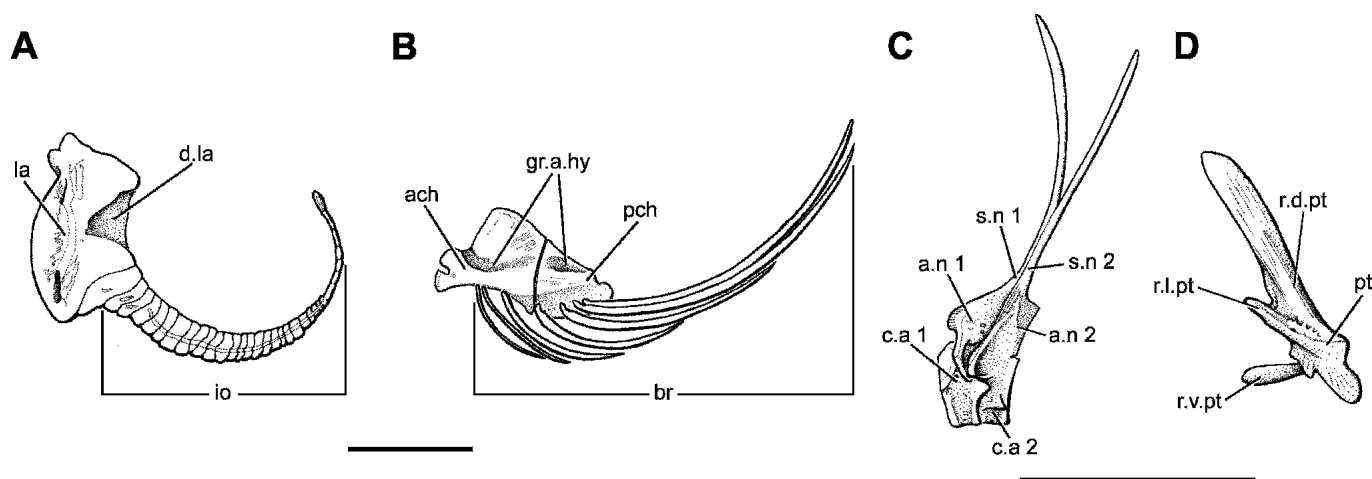   The well-developed sclerotic ossicle (Fig. 3) of †*Mene purdyi* is

FIGURE 4. Camera lucida drawings of left-hand elements of the extant *Mene maculata* (USNM 347107) **A**, infraorbital series, including enlarged first infraorbital (lacrimal); **B**, partial hyoid complex consisting of anterior ceratohyal and posterior ceratohyal with branchiostegal rays (distalmost tip of posteriormost branchiostegal omitted); **C**, first two vertebrae (note the "capture" of the first neural spine by the second vertebra); **D**, posttemporal. Abbreviations are as listed in Methods. First scalebar is applicable to A and B, while the second scalebar is for C and D. Scale bars equal 5 mm.

composed of two curved sheets of bone, each of which roughly defines a semicircle and joins its complement dorsally and ventrally. The dorsal intersection of these two halves is clearest, while the ventral junction is obscured by damage to the bone. These ossifications are essentially identical to those in *M. maculata*.

Jaws and Suspensorium—Portions of the jaws and suspensorium are preserved on both faces of the fossil. Beginning with a posteriorly-reclined intersection with the pterotic and sphenotic of the neurocranium, the sliver-shaped hyomandibula (Fig. 3) curves gently along the anterodorsal margin of the preopercle. The hyomandibula tapers from its articulation with the base of the skull and has a robust, posterolaterally-oriented condyle (**c.o.hym**, Fig. 3C, D) for articulation with the opercle. Anteroventral to this knob, the hyomandibula comprises two distinct planar surfaces—one oriented laterally, the other dorsally. This geometry produces a laterally facing plateau on the hyomandibula, vaguely reminiscent of (but almost certainly not homologous to) the dermohyal of some early actinopterygians (Gardiner, 1984:fig. 104). A series of conspicuous raised striations, running parallel to the length of the bone, ornaments this surface. The angle between the lateral and dorsal planes of the hyomandibula abruptly increases in the anteriormost third of the element, resulting in the obliteration of these individual surfaces as they merge into a smooth plane. The anterior third of the dorsal margin of the hyomandibula abuts the posteroventral border of the plate-like metapterygoid (Fig. 3). This ossification is roughly triangular in outline, with a gently concave dorsal margin and convex ventral border. A conspicuous foramen (**f.mtp**, Fig. 3C, D) is present on the anterior half of its ventral margin, near the anterior termination of the bone; a similar perforation is found in *Mene maculata* (Fig. 2). As in other menids (Fig. 2; Cramer, 1906; Danil'chenko, 1968; Blot, 1969), the laterally exposed portion of the quadrate (Fig. 3) defines an equilateral triangle. Its dorsal margin abuts the metapterygoid, while its ventral portions are overlapped by the subopercle. Both the dorsal and ventral borders of the quadrate are thickened to form robust ridges that intersect just posterior to a well-formed articular condyle at the anterior angle of the bone. The sliver-like ectopterygoid (Fig. 3) traces the dorsal surface of the quadrate. The ectopterygoid broadens and curves anterodorsally where it reaches the level of the posterior margin of the quadrate. The

palatine (Fig. 3C, D) joins the "V"-shaped dorsal border of the ectopterygoid, and terminates dorsally with a distinctive diamond-shaped prong that extends well above the dorsal surface of the vomer, a feature also found in *M. maculata* (Fig. 2). The combined anterior margins of the ectopterygoid and palatine define an obtuse angle. The endopterygoid (Fig. 3C, D) lies posterior to the palatine, bordered on its ventral margin by the metapteryagoid. This broad bone curves medially in its dorsal regions before being obscured by matrix. Several distinct pores are visible near the anteroventral corner of the endopterygoid.

Neither the maxillae nor premaxillae are preserved in the specimen, but portions of the lower jaw are present and are considerably displaced, having been rotated approximately 90° clockwise in lateral view. Both the right and left anguloarticulars (Fig. 3A, B) are preserved on the left side of the fossil. Both bones are incomplete and only the left element has a considerable portion free from the matrix. The anguloarticulars have a well-developed process for articulation with the articular condyle of the quadrate. A narrow prong, similar to that found in other menids, extends past the articular surface of this bone. A thickening on the anteroventral margin of the anguloarticular is confluent with the posterior projection. The intersection of this prong with the posterior margin of the anguloarticular defines a near right angle; in *Mene maculata*, the equivalent angle is conspicuously acute (Fig. 2). Unlike other menids in which the condition is clearly preserved (Blot, 1969:fig. 85), †*M. purdyi* lacks a second, ventrally-oriented prong on its anguloarticular.

Opercular Series, Branchiostegal Rays, and Ceratohyal—The bones of the opercular series are best preserved on the left side of the specimen (Fig. 3A, B). The opercle (Fig. 3A, B) is broad and deep, and has a well-developed process at its anterodorsal corner. This process has a crenulated dorsal margin, and is continuous ventrally with a broad strip of thickened bone that lies just posterior to the overlap area of the preopercle. The dorsal margin of the opercle is slightly concave, while the posterior border defines a continuous, smoothly convex curve. This is different from the condition in *Mene maculata* (Fig. 2) and †*M. rhombea* (Blot, 1969:fig. 85), in which the posterior margin of the opercle bears a conspicuous excavation. On the left side of the fossil, a thin strip of the broken bone located medial to the ventral margin of the opercle is interpreted as the subopercle; this element is too incomplete to comment further. The lunate

preopercle (Fig. 3) overlaps the anterior edge of the opercle and is nearly complete. This relatively broad bone tapers dorsally, terminating in a prong, but ends bluntly anteriorly. The anterodorsal margin of the preopercle is gently concave, while the posterior and ventral margins are somewhat more angular. Although the right opercle has distinctive texturing on its dorsal arm, examination of its antimere and the equivalent element in *M. maculata* indicates that much of this 'ornamentation' is internal structure exposed by delamination of the bone. Two dendritic impressions for the preopercular sensory canal are visible posterior to a series of minute perforations on the anterior limb of the bone. The interopercle (Fig. 3A, B) lies medial to the preopercle. This incomplete bone is broad and relatively deep, and has a subtle texturing similar to that found on the equivalent bone of *M. maculata*.

Thin fragments of gill filaments are strewn throughout the matrix posterior and ventral to the exposed bones of the skull. Three branchiostegal rays, each incomplete proximally and distally, are located just below the preopercle on the left face of the specimen (Fig. 3C, D). The morphology of these elements is unremarkable; each is gently curved and has a longitudinal groove on its lateral face. Comparison of these robust branchiostegals to the complete series of *Mene maculata* (Fig. 4B) suggests that they represent the three most posterior members of the series that have been displaced anteriorly. The right posterior ceratohyal (Fig. 3C, D) and the most posterior portions of the right anterior ceratohyal (Fig. 3C, D) lie anterodorsal to the branchiostegals. The preserved region of the hyoid complex in the new taxon agrees well with the morphology of the equivalent bones in *M. maculata* (Fig. 4B). With the exception of a small notch, the posterior margin of the posterior ceratohyal is rounded. Starting from the upper edge of this notch, a low ridge runs anteriorly and terminates midway along the length of the bone. Two distinct depressions are located on the posterior ceratohyal dorsal to this thickening. The first of these is approximately horizontal and lies a short distance above the ridge. The axis of the second, more anterodorsally located depression is roughly parallel to the dorsal margin of the posterior ceratohyal. This feature has a complement on the anterior ceratohyal, and is separated from it by a thickening at the junction of these two ossifications. This discontinuous groove (**gr.a.hy**, Fig. 3C, D) likely accommodated the hyoid artery. The apparent foramen in the posterior ceratohyal that is nested within this groove is an artifact resulting from damage incurred during preparation.

Vertebral Column—The first two vertebrae of †*Mene purdyi* (Fig. 5) are strikingly similar to those of *M. maculata* (Fig. 4C). A long, well-developed parapophysis emerges from the lateral

surface of the first centrum (**c.a 1**, Fig. 5). A large pit is located on the lateral surface of the vertebra just below this process. Posterior to this pit is a triangular flange that tapers posteriorly and overlaps the centrum of the second vertebra (Fig. 5), as in the extant species (Fig. 4C). The large facets on the first centrum for articulation with the exoccipital condyles are clear even in lateral view. Although the anterior articular surface of the first centrum is convex ventrally and along its outer circumference, it curves gently into a large depression offset dorsally from its center. It is not clear if the first neural arch (Fig. 5) is fused to the centrum or loosely attached like that of *M. maculata* (Fig. 4C). The arch is broken dorsally and the first neural spine is not preserved, making it impossible to determine if this ossification was 'captured' by the second neural spine, as in other fossil menids (Blot, 1969) and *M. maculata* (Fig. 4C; Leis, 1992). The second vertebra (Fig. 5) is nearly complete, with an intact neural spine (Fig. 5) that sweeps posterodorsally. As in the Recent *M. maculata* (Fig. 4C), a series of fine anterodorsally oriented grooves ornaments the lateral faces of the neural arch (Fig. 5) where it is fused to the centrum. The anterior margin of the second neural arch directly abuts the posterior margin of the first neural arch. This condition is present in Menidae, Lactariidae, Nematisiidae, and several other percoid taxa (Leis, 1992), although the overall morphology of these vertebrae is most consistent with that of menids. Large parapophyses originate from the anterodorsal portion of the second centrum as ridges and flare into thin, horizontally oriented projections. Examination of the posterior face of the second vertebra reveals a well-defined neural canal and a deeply concave articular face of the centrum.

Pectoral Girdle—The right and left posttemporals (Figs. 3, 6) are the only pectoral girdle elements preserved in this specimen, and are a near perfect match for those of *Mene maculata* (Fig. 4D). The left bone (Fig. 6) is completely freed from matrix, but is incomplete, missing its ventral ramus. Although concealed by matrix, its right counterpart is intact, thus permitting the description of much of the bone. The posttemporal is fork-shaped, with two major rami that join at the posteroventral corner of the ossification. A small lateral prong (**r.l.pt**, Fig. 6) emerges from this junction and has a distinctive distal end, characterized by a series of crenulations. The dorsal ramus (**r.d.pt**, Fig. 6) broadens distally, and is marked by a concavity on the ventral surface of its distal reaches where it would have articulated with the pterotic. Only the distal portion of the ventral arm of the right posttemporal is exposed on the right surface of the fossil (**r.v.pt**, Fig. 3C, D). This ramus is shorter and less robust than its dorsal counterpart, and appears to be of constant breadth along its visible
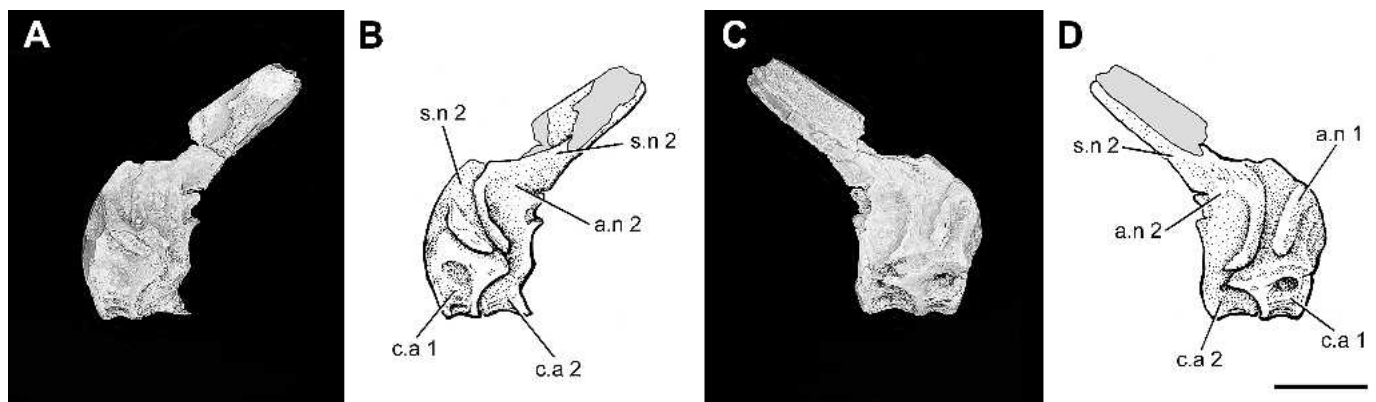

FIGURE 5.   First and second centra of †*Mene purdyi*, sp. nov., holotype (USNM 494403), Paleocene (Thanetian), northwestern Peru. **A**, photograph of left lateral surface; **B**, interpretive drawing of left lateral surface; **C**, photograph of right lateral surface; **D**, interpretive drawing of right lateral surface. Abbreviations are as listed in Methods. Areas of drawings with solid gray infill indicate matrix. Note the close application of the first and second neural arches, a characteristic of Menidae (Lies, 1994). Scale bar equals 10 mm.
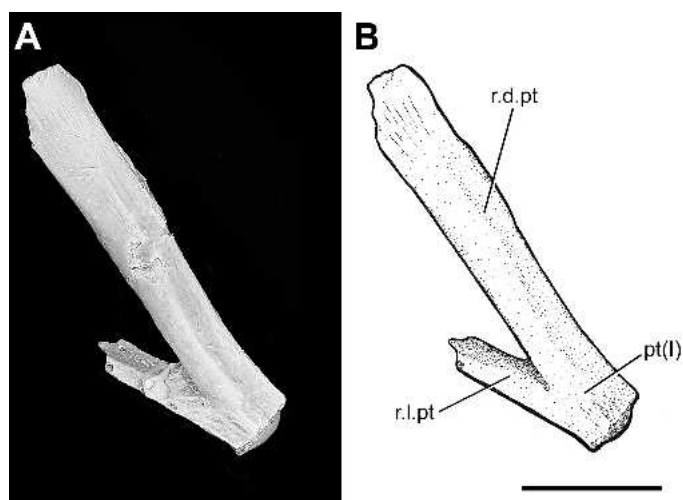
FIGURE 6. Left posttemporal of †*Mene purdyi*, sp. nov., holotype (USNM 494403), Paleocene (Thanetian), northwestern Peru. **A**, photograph of left lateral surface; **B**, interpretive line drawing of left lateral surface. Abbreviations are as listed in Methods. Scale bar equals 10 mm.

length, similar to the equivalent feature in *M. maculata* (**r.v.pt**, Fig. 4D).

DISCUSSION

Paleoenvironmental Interpretation

Although the geological context of this specimen is incompletely known, isotopic analysis of planktonic foraminifers recovered from the matrix allows for preliminary reconstruction of the depositional environment independent of more traditional approaches (Fig. 7A). Stable oxygen isotope ratios in foraminifer tests reflect the $\delta^{18}O$ value of ambient seawater, which, in turn, is a function of temperature (Steens et al., 1992). Based on relative $\delta^{18}O$ values, depth ecologies have been inferred for extinct foraminifers. The genera †*Acaranina* and †*Morozovella* are believed to have occupied the photic zone and mixed layer, whereas the contemporary †*Subbotina* inhabited deeper waters near the thermocline (Shackleton et al., 1985); each of these taxa is represented in the sample collected from the matrix surrounding the fossil menid. Although sample sizes are admittedly very small (†*Acaranina*, n = 7; †*Morozovella*, n = 2; †*Subbotina*, n = 3), we suggest that the isotopic data derived from these samples are nevertheless suitable for highly generalized characterization of the thermal character of the paleoenvironment (see additional qualifications in METHODS).

Utilizing the conversion factor of 0.23 ‰·°C^{-1} (Epstein et al., 1953), estimates of absolute temperature differences between surface-dwelling and thermocline-dwelling foraminferal assemblages (ΔT_{S-T}) can be made from $\delta^{18}O$ values. Larger ΔT_{S-T} values indicate a more stratified water column (relatively colder water at depth), whereas small differences are suggestive of a shallower thermal profile (relatively homogenous temperatures). The late Paleocene ocean appears to have been characterized by low vertical temperature gradients (Bralower et al., 1995), an observation that is broadly consistent with the low ΔT_{S-T} value (2.08 °C) estimated using the foraminifers collected from the matrix of †*Mene purdyi*. However, comparison of this ΔT_{S-T} value to those of coeval oceanic Pacific sites of roughly comparable paleolatitude suggests that the thermal profile at the site of deposition may have been different in a qualitative sense (Fig. 7B). DSDP Site 577 (Sample 577-9-2[80–82]; ΔT_{S-T} = 3.90 °C; tabulated from Lu and Keller, 1996), which was located in the
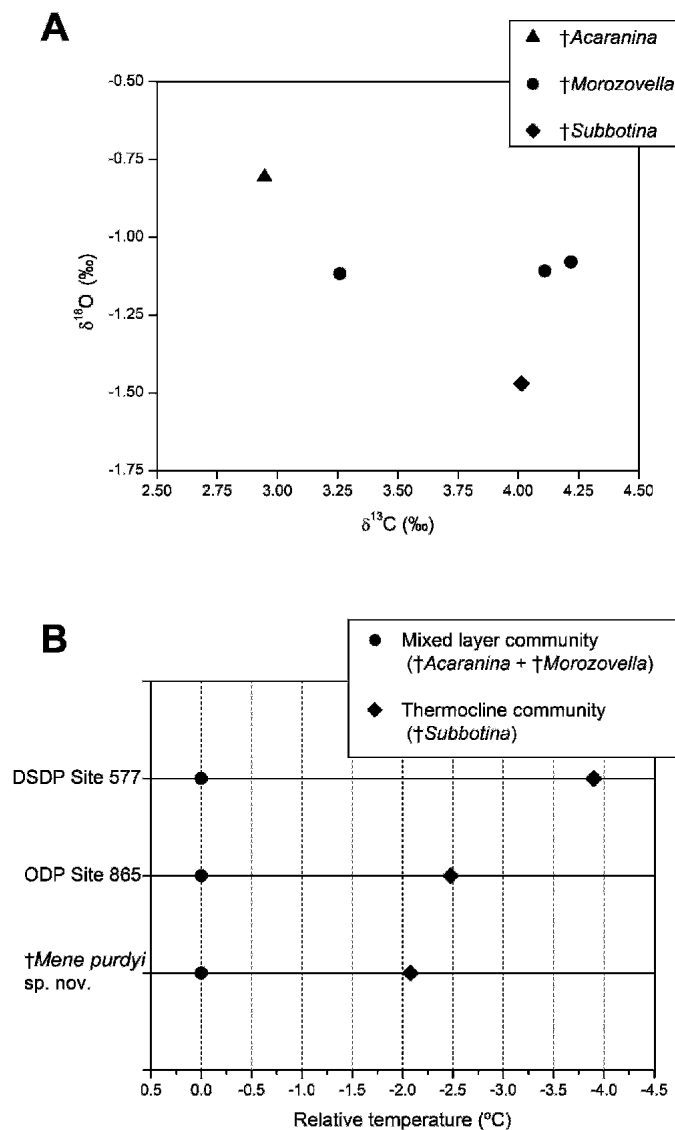

FIGURE 7. Stable isotope data from planktonic foraminifera recovered from the matrix of †*Mene purdyi*, sp. nov., holotype (USNM 494403), Paleocene (Thanetian), northwestern Peru. **A**, raw $\delta^{18}O$ and $\delta^{13}C$ data, values expressed in per mil (‰); **B**, comparison of the thermal profiles of roughly contemporaneous oceanic sites. Near-surface temperatures as inferred from the mixed-layer †*Acaranina* + †*Morozovella* assemblage are set to zero. DSDP Site 577 (Sample 577–9-2(80–82); ΔT_{S-T} = 3.90 °C; data tabulated from Lu and Keller, 1996), was located in the central Pacific during the late Paleocene, as was ODP Site 865 (Zone CP8; ΔT_{S-T} = 2.48 °C; data tabulated from Bralower et al., 1995). Relatively low ΔT_{S-T} values determined for the environment in which †*Mene purdyi* was deposited could possibly reflect Paleocene upwelling dynamics.

central Pacific during the late Paleocene at a paleolatitude of 15–22°N, has a ΔT_{S-T} value nearly twice that determined for the depositional environment of the new menid. ODP Site 865 (Zone CP8; ΔT_{S-T} = 2.48 °C; tabulated from Bralower et al., 1995), which was located on the mid-Pacific Allison Guyot with an estimated late Paleocene paleolatitude of 2°N, has a considerably smaller ΔT_{S-T} value than that of the previous site, although that determined for the Peruvian locality is smaller still.

Upwelling is a possible factor contributing to this comparatively low ΔT_{S-T} value. Foraminifers collected from modern upwelling zones yield isotopic values qualitatively consistent

with those determined for the Peruvian sample. Steens et al. (1992) reported that the difference in oxygen isotopic signals between the surface-dwelling *Globogerina bulloides* and the thermocline-dwelling *Neogloboquadrina dutertrei*, the modern depth-ecological equivalents of †*Acaranina*/†*Morozovella* and †*Subbotina*, respectively, approaches zero in modern upwelling zones, resulting in low ΔT_{S-T} values relative to those from non-upwelling regions. Allison Guyot would almost certainly have been more subject to upwelling than the purely oceanic DPDP Site 577, thus accounting for the gross similarity between ΔT_{S-T} values estimated for this site and the Peruvian locality.

The lithology of the matrix of †*Mene purdyi* is consistent with the environmental profile inferred from isotopic analysis. In particular, the high silica content of the surrounding rock offers the most compelling sedimentological evidence for deposition in a region dominated by upwelling processes. Modern upwelling zones are characterized by high levels of bioproductivity, and are typically underlain by silica-rich sediments and oozes (Stow et al., 1996). Deposition in an upwelling zone is not entirely unexpected, as upwelling dynamics are known to have been in place in northwestern South America as early as the Late Cretaceous (Cenomanian; Macellari and de Vries, 1987).

The find of a fossil menid in an offshore upwelling zone is noteworthy. The Recent *Mene maculata* is often associated with reef environments (Carpenter et al., 1997), and the Eocene ichthyofauna of Monte Bolca, which contains two species of *Mene*, has been interpreted as an inshore coral reef assemblage (Bell-wood, 1996). Among menids, †*M. triangulum* appears to have lived in an environment most similar to that of †*M. purdyi*. This species is the most common member of the Paleocene Danatinsk ichthyofauna of Turkmenistan, which has a strong pelagic character (Bannikov and Tyler, 1995). According to the paleoenvironmental interpretation of the Paleocene Mo-clay of Denmark advocated by Bonde (1997), an unnamed menid from these deposits may also been an inhabitant of an offshore upwelling zone. It seems inadvisable to speculate further on the possible ecological evolution within *Mene* until the relationships between its constituent species are established, but it is nevertheless apparent that this genus occupied a wide range of habitats in the Paleogene.

Fossil Menids

Menids are among the earliest percoid fishes reliably known from the fossil record. Several centropomid- or serranid-like percoids are the contemporaries of what may be the oldest menid, from the early Paleocene (Danian; but see qualifications below). Numerous unequivocally late Paleocene (Thanetian) forms are coeval with several other members of the Percoidei, including serranids, carangids, and the enigmatic genus †*Exillia* (Patterson, 1993a, 1993b; Bannikov and Tyler, 1994). The disparate percoid lineages that appeared rather suddenly by the end of the Paleocene suggest that the diversification of this group may have occurred in the Late Cretaceous (Patterson, 1993a).

Including the new taxon described herein, fossil Menidae have been recovered from Cenozoic sediments on all continents except Antarctica and Australia. Many of these extinct species are represented by multiple, complete, well-preserved specimens (Fig. 8). The relationship of †*Mene purdyi* to these forms is not considered at this time. Apart from being beyond the scope of the current report, a rigorous phylogenetic analysis of fossil menids is not possible until the osteology of the extant *M. maculata* as well as its relationships to other percoid fishes have been more comprehensively examined. The listing included here is intended to facilitate any future studies of Menidae.

Paleocene—(1) †*Mene phosphatica* Astre, 1927, from the Lower Paleocene phosphates of Gafsa, Tunisia (Fig. 8A). A Montian (Danian; Harland et al., 1990) age was specified for this taxon, and was accepted by Patterson (1993b). However, an early Eocene age seems more probable, as the most recent studies indicate that the alternating phosphates and marly limestones of the Gafsa-Metlaoui Basin were deposited in the Ypresian (Zaïer et al., 1998).

Priem (1907) described an incomplete specimen missing its skull and dorsal fin and identified it as "*Mene* aff *rhombeus*." Astre (1927) documented an additional example, also lacking cranial material, and suggested that both Tunisian fossils were members of a new taxon, †*M. phosphaticus*. Five morphological differences are reported between the North African material and †*M. rhombea* from Monte Bolca (Astre, 1927). Priem's (1907) specimen is deposited in l'Ecole des Mines de Paris.

(2) †*Mene purdyi* from the upper Paleocene (Thanetian) of Peru (Figs. 2, 3, 5, 6; Table 1). See above for complete description and discussion.

(3) An undescribed species of *Mene* is a common find in the Fur Formation of the Danish Mo-clay (Bonde, 1997). The age of the Mo-clay has been a point of contention, but the beds that yield *Mene* appear to be upper Paleocene (Thanetian; O'B Knox, 1984). Bonde (1997) asserted that the Danish menid differs from the species described from Turkmenistan and Monte Bolca, but a formal description is still wanting.

(4) †*Mene triangulum* Danil'chenko, 1968, from the Danatinsk Formation of Kopetdag, in southwestern Turkmenistan (Fig. 8B). The age of the fish bed at this locality has been the subject of debate (Patterson, 1993a), although evidence now suggests these deposits are Thanetian in age, synchronous with late Paleocene anoxic events (Bannikov and Parin, 1997). †*Mene triangulum* is the most abundant species at this locality, with at least 20 specimens known that range in size from 40 to 145 mm in total length (Danil'chenko, 1968). A greatly elongated fourth ray of the dorsal fin that often exceeds the total length of the fish is the most distinctive feature of this species. The holotype (PIN 2179/19) is deposited in the Paleontological Institute, Moscow.

Eocene—(5) †*Leiomene kapurdiensis* Gupta and Yazdani, 1976, from the lower Eocene (Ypresian) Fuller's Earth of the Barmer district, Rajasthan, India. Only a single specimen, with an estimated standard length of 36 mm, has been described. Gupta and Yazdani (1976) suggested that †*Leiomene* is intermediate in structure between Menidae and Leiognathidae (ponyfishes). However, none of the characters that putatively link this genus to leiognathids are convincing, and those features that are claimed to distinguish it from menids are either within the range of variation of the described species of *Mene* or appear attributable to damage or imperfect preservation. Furthermore, †*Leiomene* shares with menids a set of derived characters, including the absence of median fin spines and greatly elongated pelvic fins. Like *Mene*, †*Leiomene* has nine abdominal centra (leiognathids have ten abdominal vertebrae; Yabumoto and Uyeno, 1994). The specimen is incomplete posteriorly, but preserves at least eleven caudal centra. The body is notably shallower than that of most other menids, most closely resembling that of †*Mene oblonga* from Monte Bolca.

There are no features of the single described specimen that appear to merit placement in its own genus, separate from *Mene*. We therefore tentatively suggest that †*Leiomene* be considered a junior synonym of *Mene*, but withhold final judgment until the Indian specimen has been more satisfactorily described. The type specimen (PV5-a and its counterpart PV5-b) is housed in the collections of the Zoological Society of India, Calcutta.

(6) †*Mene rhombea* Volta, 1796, from the middle Eocene (Lutetian) of Monte Bolca, Italy (Fig. 8C). Of the 52 specimens for which Blot (1969) indicated dimensions, the smallest individual had total length of 35 mm while the largest measured 220 mm. Of all menids, including the extant *M. maculata*, this species has been the subject of the most thorough osteological review, having been examined by Cramer (1906) and more recently by Blot
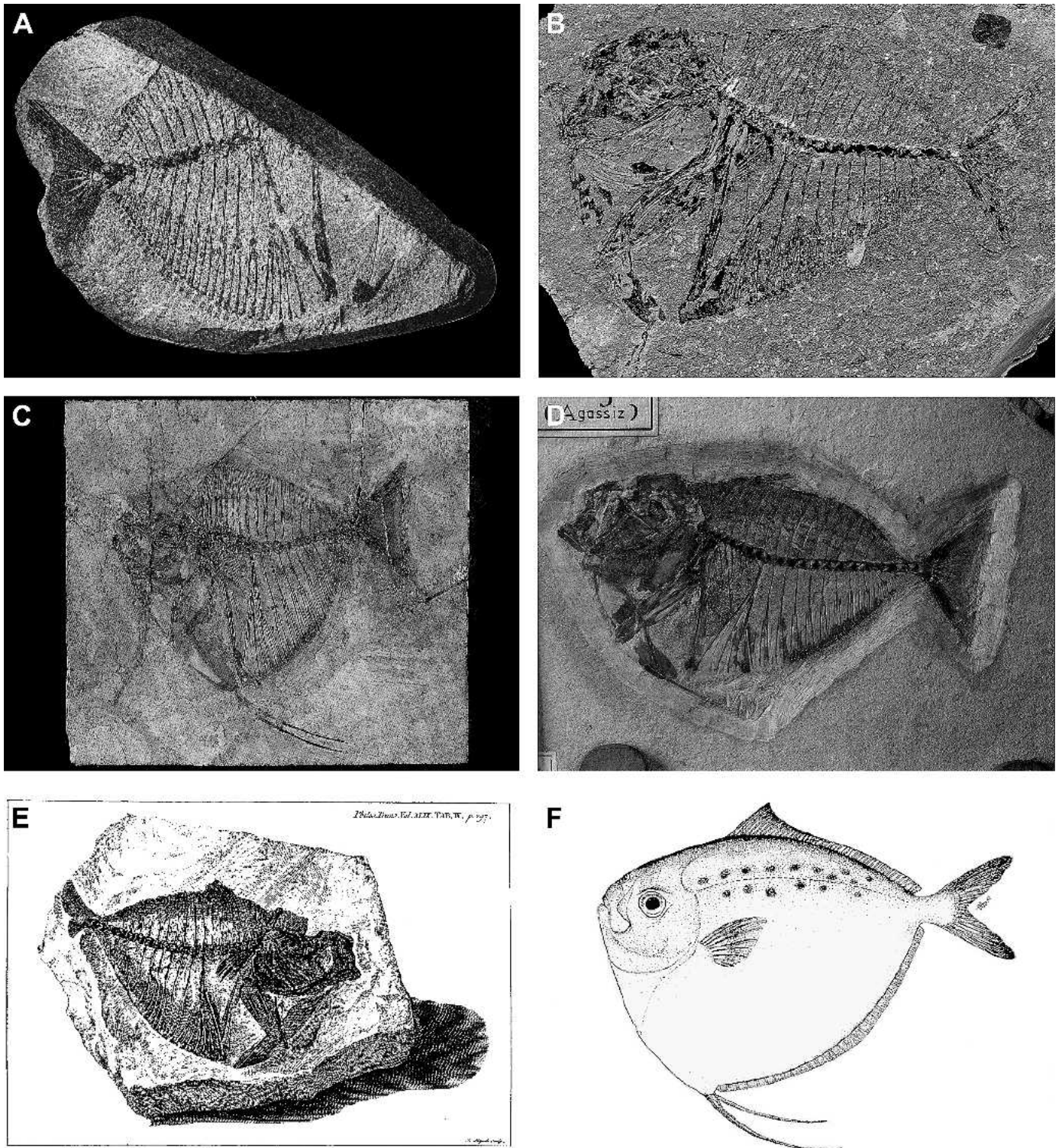
FIGURE 8. Menidae known from well-preserved skeletal (non-otolith) or Recent material. **A**, †*M. phosphatica* Astre (1927) from the Early Paleocene (Danian) of Tunisia (from Priem, 1907); **B**, †*M. triangulum* Danil'chenko (1968) from the Late Paleocene of Turkmenistan (holotype, PIN 2979/19); **C**, †*M. rhombea* Volta (1796) from the middle Eocene of Monte Bolca, Italy (CAMSM C31432); **D**, †*M. oblonga* Agassiz (1833–1834) from the middle Eocene of Monte Bolca, Italy (26237 MGPD); **E**, †*M. novaehispaniae* Eastman (1914) from the Oligocene of Antigua (from Byam, 1755); **G**, *M. maculata* Bloch and Schneider (1801) from the Recent Indo-Pacific (from Carpenter et al., 1997).

(1969). Blot (1969) was unable to locate the holotype (Volta, 1796:pl. 18) and designated a specimen (24) figured by Agassiz (1833–1844:pl. 38) and now deposited in the Paläontologisches Museum, Munich, as the neotype.

(7) †*Mene oblonga* Agassiz, 1833–1844, from the middle Eocene (Lutetian) of Monte Bolca, Italy (Fig. 8D). This species co-occurs with †*M. rhombea*, but is far less common (Blot, 1969; Eastman, 1911). †*Mene oblonga* is immediately distinguishable

TABLE 1. Selected measurements from the skull of †*Mene purdyi* (USNM 494403), holotype, Paleocene (Thanetian), northwestern Peru

Neurocranium (length from vomer to occipital condyles)	90.4
Sclerotic ossicle (inner diameter)	23.2
Sclerotic ossicle (outer diameter)	27.6
Opercle (depth)	61.4
Crest (length)	65.8
Posttemporal (length of dorsal arm)	30.2
Quadrate (height along posterior border)	14.0
Hyomandibula (length)	59.3
Subopercle (length)	52.1
Quadrate (length of ventral margin)	19.7
Palatine (height)	26.6
Metapterygoid foramen (length)	3.8
Preopercle (height)	67.9
Preopercle (length)	62.5
Preopercle (dorsal arm tip to anterior arm tip)	82.0
Posterior ceratohyal (length)	15.3

Measurements in mm.

from most other menids by its comparatively shallow body. Blot (1969) provided numerous additional characters that distinguish †*M. oblonga* from †*M. rhombea*. The designated holotype of this species (MNHN 10890-10891) is deposited in the Museum National d'Histoire Naturelle, Paris.

Multiple Eocene taxa have been defined on the basis of isolated otoliths. It is possible that at least some taxa erected for otolith morphotypes may be redundant, referring to menids described based upon skeletal remains. †*Menidarum occultus* Nolf and Bajpai, 1992, has been found in the (8) Lutetian Harudi Formation of western India and the (9) early Bartonian Nanggulan Formation of Java, consistent with the distribution of modern menids. Several finds, however, fall outside the range of the extant *Mene maculata*. (10) †*Mene sekharani* Nolf and Capetta (1976) is known from the Paris Basin, while (11) Ypresian sediments in southwestern France yield the otoliths of †*Menidarum ornatissimus* Nolf (1985). Undescribed menid otoliths are known from the (12) Bartonian marls of Northern Spain and the (13) Priabonian Yazoo Clay of Louisiana (Nolf and Bajpai, 1992).

Oligocene—(14) †*Mene oblonga* var. *pusilla* Bassani, 1889, from the Oligocene of Chiavon, Italy, is known from a single fossil, which measures only 28 mm in total length. Bassani (1889) reported that the differences between this lone specimen and the Eocene †*M. oblonga* are minimal, and include relative lengths of vertebral centra, anal fin ray counts, and the profile of the caudal fin. This fossil (4018 MGPD) is conserved in the Museo di Geologia e Paleontolgia dell'Università delgi Studi di Padova, Padua.

(15) †*Mene novaehispaniae* Eastman, 1914, from the Oligocene (Maury et al., 1990) of Antigua, British West Indies (Fig. 8E). The only example of this species was first documented in a letter read before the Royal Philosophical Society of London. The specimen was described only as "an exact portraiture of a fish . . . which we call an old wife" (Byam, 1755:295), and marked the first account of a fossil fish from the New World. It was collected in a quarry elevation of 300 yards (274 m) above sea level, located two miles (3.2 km) inland. Both part and counterpart were well preserved in a chalky matrix (Pond, 1756). This specimen was not formally named until Eastman (1914) erected a new species based on the figure that accompanied the 18th century account, suggesting that its morphology was intermediate between that of the two species of *Mene* from Monte Bolca. Eastman (1914) was unable to locate the original specimen, as were the authors of this paper. It is presumed lost.

Miocene—(16) The only menid remains known thus far are otoliths attributed to *Mene* sp. from the early Miocene Canture Formation of northeastern Venezuela (Nolf and Aguilera, 1998).

Taxa Removed from Menidae

†*Bathysoma lutkeni* Davis, 1890, from the lower Paleocene (Danian) Slatholm Limestone of southern Sweden, was assigned by Davis to the Trichiuridae (cutlassfishes), although Patterson (1964) indicated that this may have been the result of a printer's error, given the conspicuous morphological differences between the deep-bodied and apparently edentulous †*Bathysoma* and elongate, predatory trichiurids. Regardless of gross dissimilarity in form, Jordan (1923), Romer (1945), and Bertin and Arambourg (1958) followed suit and placed the genus in the Gempylidae (snake mackerels). Patterson (1964) assigned †*Bathysoma* to Menidae based on several features shared with the Eocene †*Mene rhombea*, including details of the skull and pectoral girdle, as well as general similarity in body shape. Carroll (1996) maintained this placement. Based on details of the caudal skeleton, Patterson later (1968) reassigned †*Bathysoma* to the lampridiform family Veliferidae, noting a possible relationship to the genus †*Palaeocentrotus* Kühne, 1941. Bannikov (1999) also supported the lampridiform hypothesis, but suggested closer affinities to the family †Turkmenidae, particularly the genus †*Analectis*, and placed †*Bathysoma* in the suborder Veliferoidei as incertae sedis.

Historical Biogeography of Menidae

Although modern menids are represented by a single species confined to the Indo-Pacific, it is clear from fossil evidence that the group was both wider ranging and more diverse during the geological past. A plot of fossil localities (Fig. 9) reveals a circumglobal distribution, consistent with the historical Tethys. This distribution is not limited to menids; numerous fish taxa now confined to the Indo-Pacific were widespread in distribution while the Tethyan seaway formed a circumtropical corridor linking the modern Indo-Pacific and Atlantic realms. Chanidae (milkfishes) and Siganidae (rabbitfishes) are known from the Paleocene of Turkmenistan (Bannikov and Parin, 1997), while the Eocene deposits of Monte Bolca produce skeletal remains of both of these families as well as those of Centriscidae (shrimpfishes), Solenostomidae (ghost pipefishes), Toxotidae (archerfishes), Scatophagidae (scats), Veliferidae (velifers), Enoplosidae (oldwife), Triacanthidae (triplespines), and the ostraciid subfamily Aracaninae (boxfishes) (Blot, 1980; Nelson, 1994). †*Eonaso deani*, a surgeonfish closely related to the extant Pacific genus *Naso*, is known from Antigua (Tyler and Sorbini, 1998; Tyler, 2000) and is probably Oligocene in age. It is likely that this specimen came from the same locality as †*Mene novaehispaniae*.

This geographical trend is not limited to body fossils; the otolith record also reveals broader historical ranges for many taxa now confined to the Indo-Pacific. Plotosid catfishes are known from the Miocene of the Dominican Republic (Nolf and Stringer, 1992) and Venezuela (Nolf and Aguilera, 1998), while otoliths indistinguishable from those of the extant laternfish *Diaphus regani* are reported from the Miocene of Italy (Nolf and Aguilera, 1998). Paleogene Lactariidae are known from Germany, Texas, Barbados, and France (Nolf, 1985; Schwarzhans, 1996), while Miocene lactariids have been recovered from France and Portugal (Steurbaut, 1984).

Numerous Indo-west Pacific fish taxa are not found on the Pacific Plate (eastern Pacific) (Springer, 1982). This pattern is consistent with the distribution of menids, whose only Recent occurrence is on the western margin of the Pacific Plate. Springer (1982) proposed two mechanisms for this empirical pattern: (1) in the "reality hypothesis," taxa absent from the Pacific Plate have never been present on the Plate; (2) in the "extinction hypothesis," taxa absent from the Pacific Plate once occurred there, but have become locally extinct. Springer (1982) concludes

FIGURE 9. Historical biogeography of Menidae. Hollow circles represent finds of skeletal material, whereas solid circles indicate localities yielding isolated otoliths. Numbers within circles are keyed to the text. Note the circum-global Tethyan distribution of menids through much of the Cenozoic.

that the first of these explanations accounts for a majority of cases. However, if examined at the familial or generic level, it seems probable that the absence of menid fishes from the Pacific Plate is due to local extinction events in the eastern Pacific, consistent with Springer's (1982) second surmise. The find of †*Mene purdyi* on the western margin of South America marks a clear occurrence in the eastern Pacific; in light of the apparently circumtropical distribution of Menidae in the Paleogene, it seems likely that menids have historically inhabited the waters above the Pacific Plate. Unfortunately, no fossil menids are known from the islands of the Pacific Plate that might permit rejection of the "reality hypothesis" and consequent acceptance of the "extinction hypothesis" for Menidae.

SUMMARY

†*Mene purdyi*, sp. nov., is the first member of the family Menidae known from South America based on skeletal (non-otolith) remains. Although represented by a single skull, two vertebrae, and two posttemporals, the cranial anatomy of this taxon is known in more detail than that of any other fossil menid. Analysis of foraminifers recovered from the matrix of the fossil suggests that the menid is late Paleocene in age and may have been deposited in an upwelling zone. The find of a menid on the western coast of South America, coupled with the locations of other sites that are known to have produced menid fossils, indicates that this Indo-Pacific family was once cosmopolitan and exhibited a circumglobal distribution. Many extinct menids are known from complete or nearly complete remains, thus making them an excellent candidate for future phylogenetic studies based on skeletal anatomy.

The well-preserved specimen of †*Mene purdyi* and an undescribed billfish of similar provenance suggest that the sedimentary rocks of northwestern Peru may contain a yet unrealized Paleocene fish assemblage. The excellent three-dimensional preservation of these specimens is reminiscent of material from the Eocene London Clay (Casier, 1966; Clouter et al., 2000), and permits examination of structures that are typically obliterated by compression in specimens from other localities. These South American fossils fall in the midst of what appears to have been the explosive diversification of acanthomorphs in general, and percomorphs in particular, during early Paleogene. Our current knowledge of this critical period in acanthomorph history is decidedly provincial, dominated by marine localities from the Eastern Hemisphere (the Danish Mo-Clay, the Danatinsk Formation of Turkmenistan, the London Clay of Great Britain, and Monte Bolca in Italy). The two specimens discovered in museum collections raise the tantalizing possibility that a rich Paleocene marine fish assemblage may lie untapped in northwestern Peru; further fieldwork there may open a critical window to faunal compositions in the western Tethys during this important interval of teleost evolution.

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