

the tongue by the bill removes the nectar from the tongue; it is still not clear, however, how the nectar moves from the anterior portion of the bill into the esophagus. The nectar may adhere to the base of the extruded tongue, being brought to the base of the bill when the tongue is retracted. Suction may help transport nectar into the esophagus: our film shows a bulge in the throat region as the tongue is being extended.

Among hummingbirds, long bills are believed to be beneficial because they facilitate probing of flowers with long corollas (Wolf et al. 1972). Our results provide a mechanism for such a benefit: at flowers with long corollas, long bills may yield greater rates of licking than short bills, because long bills permit maintenance of small distances between nectar and the bill tips, which squeeze loads of nectar off of the tongue. It is therefore not surprising that the bills of hummingbirds tend to be similar in length to the corollas that are visited by the birds (Wolf et al. 1972, 1976). Such matching should result in short transit times by the tongue between the nectar source and the inside of the bill.

Although previously measured negative correlations between extraction rate and corolla length are most pronounced when feeders contain unnaturally large volumes of food, such correlations are still statistically significant when food volumes are similar to those found naturally in flowers (Hainsworth and Wolf 1979). This finding, coupled with our results, suggests that long bills evolved, at least in part, because increased bill length increases rates of licking from flowers with long corollas. Long corollas probably coevolved because of pollination benefits associated with specialization on pollinators (Wolf et al. 1976).

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Tarsometatarsus of *Protostrix* from the mid-Eocene of Wyoming

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Two, probably three (Rich and Bohaska 1976, 1981), families of owls are known from Paleogene sediments of North America and Europe, most taxa being represented by only one or two fragmentary bones. One family, the Protostrigidae, which is endemic to North America, contains two genera, *Eos-trix* and *Protostrix*. Although several specimens (and species) of *Protostrix* are known (Brodkorb 1971), thus far no tarsometatarsus of any species in this genus has been recognized, and it has been difficult to make comparisons with other fossil owls, most

frequently represented by this durable, hind-limb element. It is of some taxonomic interest, then, that a distal fragment of a tarsometatarsus in the Vertebrate Paleontology collections of the American Museum of Natural History appears to represent *Protostrix*.

In 1913 Shufeldt described the distal end of the right tarsometatarsus (AMNH No. 2629, see Fig. 1) among a number of bones that he proposed were from "some medium sized falconine species" (p. 295), which had been collected in 1903 from the lower

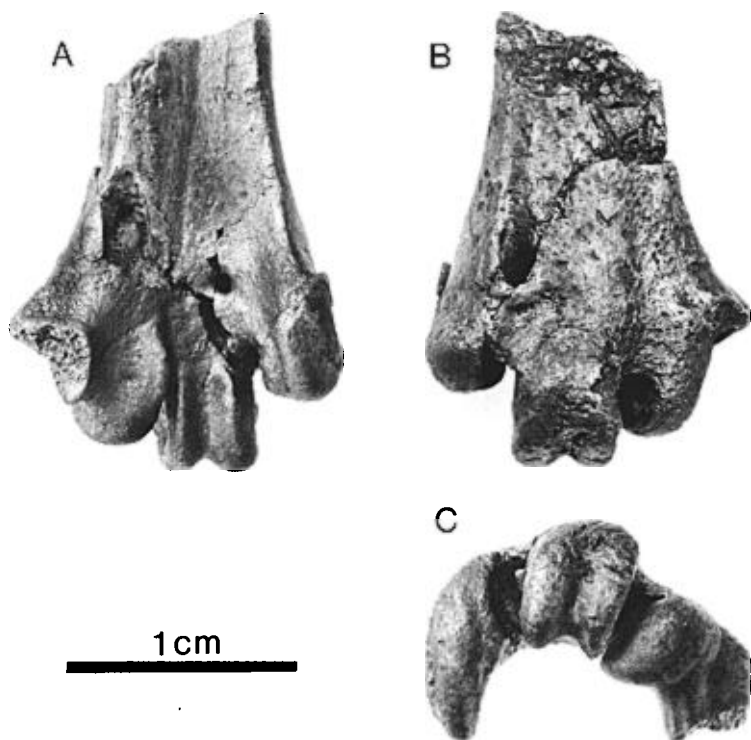


Fig. 1. *Protostrix cf. leposteus* (AMNH 2629) from the mid-Eocene Bridger Formation of Grizzly Buttes, Wyoming. A, posterior; B, anterior; and C, distal views. Photographs by C. Tarka.

part of the mid-Eocene, Bridger Formation of the Grizzly Buttes, Green River Basin, Wyoming. He also mentioned the "upper part of the shaft of the tarsometatarsus" and the "upper extremity of left coracoid" that were "all from the same individual." How he made this association is not explained, and at the time of this study I was unable to locate either of these additional two specimens. Thus, this paper deals only with the distal right tarsometatarsus that he reported. Reexamination of this specimen has shown it to be a strigiform that shares more characters with the Eocene *Eostrix* (Wetmore 1938, Martin and Black 1971) than with any other strigiform; it also exhibits unique characters of its own.

AMNH 2629 is clearly a strigiform as is indicated by the shallow, narrow middle trochlea (III) relative to the inner and outer trochleae; the extremely broad inner trochlea with an elongate wing; the distal extension of the inner trochlea beyond the outer trochlea (IV), being exceeded only slightly by trochlea III; the anteroposterior compression of the shaft with deep posterior channelling; and the elongate inner

and outer trochleae that extend far posteriorly, resulting in the highly arched condition of the trochleae in distal view.

Of owls known from the Paleogene, only seven species and four genera are represented by tarsometatarsi and thus are directly comparable to the Grizzly Buttes specimen: *Ogygoptynx wetmorei* (early Paleocene, North America), *Eostrix mimica* (early Eocene, N.A.), *E. martinellii* (Eocene, N.A.), *Necrobyas harpax*, *N. rossignoli*, *N. edwardsi*, and *Asio* (originally placed in the genus *Otus*) *henrici* (all Eocene-Oligocene, Europe).

AMNH 2629 differs from the North American forms as follows: *Ogygoptynx* (Rich and Bohaska 1976, 1981) has an inner trochlea (II) that extends farther distally than trochlea III, instead of III being longest; a trochlea IV that is located farther proximad on the shaft, terminating at about the point where the proximal end of trochlea III originates instead of being distal to this origin; and in distal view, a trochlea IV that is shifted farther posteriorly relative to other trochleae and an articular surface that is

TABLE 1. Comparison of hind limb measurements of early Tertiary owls of North America and Europe (in mm). Abbreviations include: AMNH, Amer. Mus. Nat. Hist., Dept. Vert. Paleo., New York; KU, Univ. Kansas, Lawrence; MHNL, Mus. Hist. Nat., Lyon; MM, Munich Mus.; NMV, Natl. Mus. Victoria, Melbourne; PM, Mus. Natl. Hist. Nat., Paris; and YPM, Yale Peabody Mus., New Haven.

Measurement	AMNH 2629	<i>Protostrix</i> <i>leptosteus</i> YPM 512	<i>Protostrix</i> <i>lydekkeri</i> AMNH 5165	<i>Eostrix</i> <i>mimica</i>	<i>Eostrix</i> <i>martinellii</i>	<i>Strigogyps</i> <i>dubius</i>
				USNM 15156, 14774	KU 16601	MHNL PQ 1073 (cast)
Tibiotarsus						
1. Transverse breadth across condyles	—	13.5 ^a	~16.5 ^b	11.5	—	21.1
2. Transverse breadth at distal end of shaft	—	~10.9 ^b	11.9 ^b	8.9	—	—
3. Maximum antero-posterior diameter of condyles	—	>9.8 ^c	12.9 ^b	9.9	—	30.3
Tarsometatarsus						
4. Maximum width of distal end	14.3	—	—	13.2	9.8	—
5. Width of trochlea III	>4.3	—	—	≥4.8 ^c	3.5	—
6. Depth of trochlea II	6.3	—	—	>5.2 ^c	6.1	—
7. Depth of trochlea III	5.8	—	—	6.1 ^c	4.3	—
8. Depth of trochlea IV	8.8	—	—	>6.5 ^c	—	—

^a From Wetmore (1937:85).

^b Measured from illustration or given in Wetmore (1933).

^c Measured from cast of specimen.

broader and flattened distally. *Eostrix* (based mainly on *E. martinellii*, KU 16601) (Wetmore 1938, Brodkorb 1971, Martin and Black 1972) has an asymmetric trochlea III with the lateral border decidedly deeper than the internal border, unlike the symmetrical trochlea in AMNH 2629, and a trochlea IV that appears to be narrower and more anteroposteriorly elongated and deeper.

Of the European Paleogene owls, all species of *Necrobyas* (*N. edwardsi*, *N. harpax*, *N. rossignoli*) as well as *Asio henrici* are smaller than AMNH 2629 (Milne-Edwards 1892; Gaillard 1908, 1938). *Strigogyps dubius* (Gaillard 1908) is decidedly larger. AMNH 2629 further differs as follows: *N. harpax*, *N. rossignoli*, and *N. edwardsi* have a relatively broader trochlea III; trochlea IV is more recurved, not straight, along the lateral margin (when viewed distally); trochleae are more highly arched; and the distal end is decidedly deeper, relative to width, producing a deep, more enclosed tendinal canal. In both *N. harpax* and *N. edwardsi* the posterior part of trochlea II, when viewed distally, is decidedly narrower than the anterior, unlike the broad posterior wing in *Protostrix*; in anterior view, the proximal end of trochlea II lacks the prominent internal projection present in *Protostrix*; trochlea II projects about as far distad as trochlea III, whereas III is distinctly longer in AMNH 2629.

Asio henrici has a more robust trochlea II with a narrower wing (viewed distally); a more asymmetric trochlea III, where the external border is much deep-

er than the internal border and the external border is not straight but decidedly convex externally; a trochlea IV that is decidedly deeper and more recurved internally; trochleae that are more highly arched; and a distal end that is deeper and more mediolaterally compressed.

Clearly, AMNH 2629 exhibits more overall similarity to the North American Protostrigidae than to any other group, but it is distinct from *Eostrix*. It was recovered from the same area in the Grizzly Buttes near Fort Bridger, Wyoming, as was the type tibiotarsus (YPM 512) of *Protostrix leptosteus* (Marsh 1871, Wetmore 1937), and is within the size range expected for this large protostrigid (see Table 1), being smaller than expected for *P. lydekkeri* (Shufeldt 1913), if one assumes that proportions of *Eostrix mimica* are reasonable ones to expect for *Protostrix*. Of course, this may be an invalid assumption; until an associated specimen of *Protostrix* is found, this assumption cannot be demonstrated conclusively. It seems reasonable, then, that AMNH 2629 probably represents the remains of *P. leptosteus*, which reinforces the suggestion that *Protostrix* and *Eostrix*, although similar in many characters, are distinct within the Protostrigidae, and that the protostrigids are distinct from both the North American *Ogygoptynx* and the European owls of Paleogene age.

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TABLE 1. Continued.

<i>Necrobyas edwardsii</i> Gaillard 1938	<i>Necrobyas harpax</i> Milne- Edwards 1892	<i>Necrobyas rossignoli</i> Milne- Edwards 1892	<i>Asio henrici</i>				<i>Bubo virginianus</i> NMV B9788	<i>Ninox novaeseelandiae</i> NMV B12401
			PM Qu 3117	PM Qu 3118	PM Qu 3119	Milne- Edwards 1892		
—	—	—	—	—	8.2	—	15.7	8.8
—	—	—	—	—	6.7	—	12.1	7.0
—	—	—	—	—	7.1	—	12.1	7.6
11.0	10.0	9.3	9.1	8.8	—	9.0	16.9	10.5
—	—	—	3.8	3.8	—	—	6.5	4.1
—	—	—	5.1	5.3	—	—	8.6	5.6
—	—	—	4.0	4.1	—	—	8.0	4.1
—	—	—	—	6.4	—	—	10.3	6.4

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