TARSALS OF SESPEDECTINAE (LIPOTYPHLA) FROM THE MIDDLE EOCENE OF SOUTHERN CALIFORNIA, AND THE AFFINITIES OF EOCENE ‘ERINACEOMORPHS’

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ABSTRACT—Postcranial morphology of Paleogene lipotyphlans (Mammalia: Laurasiatheria) is poorly known relative to dental morphology. When these elements can be referred, they have proven to be a rich source of data for phylogenetic and ecological inferences. In particular, tarsal morphology has challenged hypothesized relationships of several taxa. We refer isolated tarsals from several early and late Uintan (middle Eocene) localities in the San Diego area to three genera of sespedectine erinaceomorph lipotyphlan, Cryptolestes, Protexroides, and Sespedectes, based on patterns of size, morphology, and abundance. Astragali and calcanei are confidently referred to all three genera, whereas naviculars are more tentatively referred to Protexroides and Sespedectes, and cuboids to Sespedectes. Tarsals of the three genera are morphologically quite uniform, supporting their hypothesized close relationship. The most significant difference is a relatively longer calcaneal tuber in Protexroides. The tarsal morphology of Sespedectinae is most consistent with an unspecialized terrestrial locomotor repertoire. Some distinctive features of the sespedectine tarsus, such as ‘S’-shaped ectal facets and a prominent tuber tibialis on the navicular, are potentially indicative of lipotyphlan affinities. However, there is no support for an exclusive relationship to extant erinaceids (or any other lipotyphlan family) or to other Paleogene erinaceomorphs (Macrocranion, Zionodon). Phylogenetic analysis confirms that sespedectines are most likely relatively basal lipotyphlans and that Erinaceomorpha is not a natural group.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Small-bodied insectivorous eutherian mammals ostensibly allied to extant hedgehogs, shrews, and relatives (Lipotyphla sensu Asher and Helgen, 2010) are a diverse and sometimes abundant component of North American Paleogene mammalian faunas. The vast majority of these taxa are known only from teeth and jaw fragments. In some instances, cranial (Gawne, 1968; Bjork, 1975; Maier, 1979; Fox, 1983; Novacek et al., 1983; MacPhee et al., 1988; Wang and Zhai, 1995; Walsh, 1998; Asher et al., 2002, 2005; Manz et al., 2015) or postcranial (Maier, 1979; Koenigswald and Storch, 1983; Storch, 1993, 1996; Godinot et al., 1996; Hooker, 2001, 2014; Dunn and Rasmussen, 2009; Smith and Smith, 2012; Manz et al., 2015) material has been referred, but this represents only a fraction of early lipotyphlan diversity. In particular, the tarsus, which can provide a rich foundation for functional and phylogenetic inferences, is almost unknown in published descriptions of Paleogene North American lipotyphlans. Dunn and Rasmussen (2009) have described the postcranium, including tarsals, of the Uintan (late middle Eocene) Zionodon. Manz et al. (2015) have described postcranial material of North American nyctitheres, a group with controversial but potential lipotyphlan affinities (Hooker, 2001, 2014; Manz et al., 2015). Other early erinaceomorph tarsal material has been mentioned but remains unpublished (Penkrot et al., 2004; Scott and Boyer, 2006).

The abundance of lipotyphlan dental remains in many faunas begs the question of why postcranial remains are so poorly documented. The reason reflects the more generally infrequent association of dental and postcranial elements of small mammals in the fossil record. Whereas skeletal elements of larger mammals are somewhat resistant to transport, the lightweight postcranial elements of smaller mammals are easily dissociated from dental remains. This is unfortunate because isolated postcranial elements, particularly tarsals, are relatively abundant in many assemblages. The ease with which small dental and postcranial remains are dissociated confounds attempts to confidently reassociate isolated tarsals with taxa established on dental remains.

Discovery of associated or articulated remains can clarify the identity of isolated postcranial elements, but such exceptional specimens are rare. Additionally, articulated remains can themselves be problematic because critical morphological features are often obscured by other bones. An alternative is to use patterns of size and abundance, supplemented by morphology, to establish probable dental identities for isolated postcrania (Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Cicelli, 1983; Godinot et al., 1996; Muizon et al., 1998; Hooker, 2001, 2014; Zack et al., 2005; Tabuce et al., 2006, 2007; Penkrot et al., 2008; Coillot et al., 2013).

There is a danger of circularity in using morphology to aid in reassociations. If used uncritically, a priori morphological expectations can lead to incorrect or poorly supported reassocations. However,
when used carefully and in combination with other factors (e.g., relative size and abundance), morphology can help to produce stronger hypotheses of reassociation, particularly by excluding alternative identifications. To take one relevant example, Hooker (2001, 2014) has reassocaited a substantial amount of isolated postcranial material to the extinct ?lipotyphlan family Nyctitheriidae. Initial reassociations of proximal tarsal elements were made based on a combination of all three factors (size, abundance, and morphology; Hooker, 2001). These reassociations have subsequently been confirmed by the description of associated nyctither skeletons (Manz et al., 2015).

Extensive exposures of middle to late Eocene strata in San Diego County, California, have produced a rich fossil mammal fauna (summarized by Walsh, 1996) including a diversity of early lipotyphlans (Novacek, 1976, 1985; Walsh, 1998). This faunal sequence presents an additional opportunity to use size, abundance, and morphology to reassocate postcranial elements with lipotyphlan taxa described from dental remains.

Although small samples of Wasatchian, Bridgerian, and Duchesnean vertebrates are known from San Diego County, most specimens derive from the rich Uintan record, including distinct early and late Uintan faunas (Walsh, 1996, 1998; Walsh et al., 1996). Early Uintan faunas derive from the Friars Formation in southwest San Diego County and Member B of the Santiago Formation in northwest San Diego County. Late Uintan faunas come from the Stadium Conglomerate, Mission Valley Formation, and Miramar Sandstone Member of the Pomerado Conglomerate in southwest San Diego County and Member C of the Santiago Formation in northwest San Diego County. A transitional, late early Uintan fauna derives from the lower member of the Stadium Conglomerate in southwest San Diego County.

Members of the subfamily Sespedectinae are an abundant component of the lipotyphlan assemblage throughout the San Diego County Uintan (Novacek, 1976, 1985; Walsh, 1998). Sespedectines are a group of erinaceomorph lipotyphlans endemic to North America and restricted to Eocene faunas. Erinaceomorpha includes extant hedgehogs (Erinaceidae) as well as extinct forms thought to be most closely related to erinaceids. With the exception of the recently described Colphocherus from the earliest Eocene of Mississippi and Wyoming (Beard and Dawson, 2009; Rose et al., 2012), sespedectines are restricted to middle and late Eocene faunas of California and Texas (Stock, 1935; Novacek, 1976, 1985; Walsh, 1998; Campisano et al., 2014). Relative to other early erinaceomorphs, sespedectines are characterized by a “large, complex P3 [and] bunodont molar cusp pattern” (Novacek, 1985:1). These dental features have led some workers to propose a relationship to small-bodied ‘condylarthrs’ (Russell, 1964; Russell et al., 1975) rather than lipotyphlans. Most assessments, however, indicate a relationship to erinaceomorphs, with sespedectines placed in either Dormaaliidae (Novacek, 1985; Novacek et al., 1985; Walsh, 1998) or an independent Sespedectidae (McKenna and Bell, 1997; Rose, 2006; Gunnell et al., 2008).

Early Uintan assemblages from San Diego County contain abundant remains of a single, relatively small-bodied sespedectine Crypholestes vaughni (Novacek, 1976; Walsh, 1998). Both C. vaughni and a larger, undescribed species of Crypholestes are present in the late early Uintan fauna from the lower member of the Stadium Conglomerate. Late Uintan assemblages typically contain two sespedectines, the relatively small Sespedectes singularis and the larger Protérioixoides davisi (Walsh, 1998). Sespedectes singularis is one of the most abundant small mammals at many localities, whereas P. davisi is less abundant but still well represented.

To date, published sespedectine fossil material has comprised craniodental remains. A skeletal association of the sespedectine Protérioixoides is mentioned but not described by Walsh (1998). This specimen (SDSNH 58944) includes humeri, a pelvis, and a femur in association with a rostrum. In addition, the existence of isolated tarsals potentially referable to Sespedectes and Protérioixoides are mentioned by Novacek (1985) and Walsh (1998), respectively. We report here on newly reassocaited elements of the proximal tarsus for all three Californian sespedectine genera (Crypholestes, Protérioixoides, and Sespedectes). This material permits a reassessment of the paleoecology and phylogenetic position of Sespedectinae as well as more extensive comparisons with other better known Eocene erinaceomorphs.

Institutional Abbreviations—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; SDSNH, Department of Paleontology, San Diego Natural History Museum, San Diego, California, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UFM[MI], Mammalogy collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.; USNM-M, United States National Museum of Natural History, Division of Mammals, Washington, D.C., U.S.A.

MATERIALS AND METHODS

Specimens were imaged via computed tomography on a Nikon XTH 225 ST at the Duke University Shared Materials Instrumentation Facility (SMIF). Scanned specimens were modeled using Slicer 4.3.1 and models were subsequently manipulated in MeshLab. Measurements were taken using Adobe Photoshop. All specimens are illustrated as being from the left side, with right elements reversed.

Material Examined

SDSNH Locality 3832, Friars Formation, Early Uintan—Crypholestes vaughni: SDSNH 51363, a left astragalus.

SDSNH Locality 4020, Mission Valley Formation, Late Uintan—Protérioixoides davisi: SDSNH 60945, a left astragalus; 60948, a left calcaneum; 60949, a right calcaneum; 62504, a right calcaneum; 62505, a left astragalus. Sespedectes singularis: SDSNH 62899, a right astragalus; 69212, a right calcaneum; 69616, a right calcaneum; 62662a–i, four left and five right unassociated calcanei; 62663a–i, three left and six right unassociated astragali; 69615a–c, two left and one right unassociated astragal.

SDSNH Locality 4526, Upper Tongue, Friars Formation, Early Uintan—Crypholestes vaughni: SDSNH 76838, a left calcaneum.

SDSNH Locality 4693, Upper Tongue, Friars Formation, Early Uintan—Crypholestes vaughni: SDSNH 85880, a left calcaneum; 85881, a left calcaneum; 85883, a left astragalus.

SDSNH Locality 4715, Mission Valley Formation, Late Uintan—Protérioixoides davisi: SDSNH 94571, a right calcaneum; 94572, a right calcaneum; 94573, a left calcaneum; 94574, a right astragal.

SDSNH Locality 4888, Mission Valley Formation, Late Uintan—Protérioixoides davisi: SDSNH 96376, a left astragalus; 96377, a left astragalus; 96380, a right astragal.

In addition to the specimens examined in detail for this study, there are numerous additional sespedectine proximal tarsals in the collections of the SDSNH. In particular, there are many additional tarsals of Sespedectes singularis from SDSNH locality 4020.

Comparative Material Examined

Comparisons were made with tarsals of the extinct ‘erinaceomorphs’ Macrocranion junnei and Zionodon spp. as well as with representatives of all living lipotyphlan families.

Macrocranion junnei—UCMP 216445–51, 216453–4, 216457, 216459–60, 216500–11.
Identification and Reassociation

Tarsals were identified from numerous early and late Uintan localities. The single largest sample examined, including almost 2500 cataloged specimens, comes from SDSNH locality 4020 from the late Uintan Cloud 9 Local Fauna, Mission Valley Formation (Walsh, 1996). The sample from SDSNH 4020 is dominated by specimens of *Sespedectes singularis* and the small rodent *Simimys* sp., which constitute 24.4% and 32.1% of all cataloged specimens, respectively. The proximal tarsal sample is likewise dominated by two small morphs of each element, one of which is clearly a rodent, referable to *Simimys*. The other common morph of each element shares features with some living lipotyphlans, consistent with referral to *Sespedectes*. The size of the potential *Sespedectes* tarsals (Table 1) also appears consistent with this tentative identification. The tarsals are very similar in size to those referable to *Simimys* sp. Check teeth of *Sespedectes singularis* are slightly larger than those of *Simimys* sp., but presumed insectivores such as *Sespedectes* typically have somewhat larger teeth for their body mass than presumed herbivores such as *Simimys* (Legendre, 1986). In addition to SDSNH 4020, the same tarsal morph occurs in other late Uintan San Diego faunas (e.g., SDSNH locality 4888), where *Sespedectes* is ubiquitous and abundant.

At many of the localities where *Sespedectes* tarsals occur, larger astragali and calcanei (Table 2) of very similar morphology are also present. These tarsals are probably referable to *Proterixoides davisi*, a larger sespedectine from the late Uintan. The size differences between these tarsals and the suspected *Sespedectes* tarsals are consistent with the size differences between *P. davisi* and *S. singularis* dentitions. Tarsals comparable to *Sespedectes* in size and morphology also occur in early Uintan local faunas (Table 2). These can be tentatively referred to the early Uintan sespedectine *Crypholestes vaughlini*, which is closely similar to *S. singularis* in size and dental morphology.

The morphology of the probable sespedectine tarsals is inconsistent with referral to common Uintan taxa other than potential representatives of Lipotyphla. Other Uintan taxa including representatives small enough to be potentially reassigned with these tarsals include Metatheria, Primates, and Rodentia. North American Paleogene metatherian tarsals are well documented (e.g., Szalay, 1994; Sánchez-Villagra et al., 2007; Horovitz et al., 2008; Rose et al., 2012) and differ dramatically from the material under consideration here. Paleogene primate tarsals (Szalay and Decker, 1974; Szalay and Drahnow, 1980; Gebo et al., 1991, 2012; Dagosto et al., 1999; Dunn et al., 2006; Dunn, 2010) are likewise highly distinctive and differ substantially from the potential sespedectine tarsals. Early rodent tarsals (Wood, 1962; Rose and Chinnery, 2004; Dunn and Rasmussen, 2007) are more similar, but significant differences still exist. Among the more notable differences, rodent astragali have a much more asymmetric and deeply grooved tibial facet, a shallower fibular facet, and a more transverse, dorsiventrally flattened head. Rodent calcanei lack a fibular facet, which is prominent in the potential sespedectine calcanei, have a sustentacular facet without a distal extension, and have a much rounder cuboid facet.

By a process of elimination, a lipotyphlan identification is most likely and appropriate. Although a variety of lipotyphlans have been described from the San Diego Uintan (Stock, 1935; Novacek, 1976, 1985; Lillegren et al., 1981; Walsh, 1998), most of these are far too small and/or rare in their respective local faunas to be plausibly reassociated with the tarsals in question. In particular, *P. davisi* is much larger than other late Uintan lipotyphlans and no other taxon is close to being of the appropriate size to be reassOCIated with the larger late Uintan tarsals.

Metric data further support reassocation of the tarsals to representatives of Sespedectinae. Measurements of sespedectine teeth and potential tarsals (Table 3) were plotted against the data set used by Coillot et al. (2013) to evaluate dental-tarsal reassociations in the earliest Eocene Dormaal fauna (Fig. 1). This comparative data set includes a diversity of Paleocene and Eocene mammals spanning a wide range of body sizes, ecologies, and postulated phylogenetic affinities. All potential sespedectine dental-tarsal pairs fall close to but below the regression lines for astragali and calcanei, indicating that tarsal size is somewhat

![FIGURE 1. A, natural logarithm of mean astragalar lengths plotted against mean m2 area. B, natural logarithm of mean calcaneal lengths plotted against natural logarithm of mean m2 area. Sespedectines have been plotted against a diversity of Paleocene/Eocene mammals using data from Coillot et al. (2013). Mean area of sespedectine m2s calculated from measurements in Novacek (1976) for *Crypholestes*, Novacek (1985) for *Sespedectes*, and Walsh (1998) for *Proterixoides*. Tarsal measurements taken from specimens described here. open circles = taxa from Coillot et al. (2013); solid squares = *Proterixoides*; solid diamonds = *Sespedectes*; solid triangles = *Crypholestes*.](image-url)
smaller than would be expected based on dental size, but within the overall range of variation displayed by this sample.

In addition to astragali and calcanei, isolated cuboids and naviculars can be tentatively reassigned with Sespedectes and an isolated navicular with Proterixoides. The morphology of these elements makes identification as Proterixoides and Sespedectes likely but more tentative than is the case with astragali and calcanei. With respect to navicular morphology, small and large morphs are very similar, consistent with their representing Sespedectes and Proterixoides. The shape of the astragalar facet matches the morphology of the sespedectine astragalar head better than that of rodents, the most likely alternative identification. Specifically, the long axis of the astragalar facet is more parasagittally oriented than would be expected of a rodent. Additionally, sespedectine naviculars have a tuber tibialis, a proximal projection on the medial side of the navicular that is absent in living and fossil rodents but occurs in most living lipotyphlans (Hooker, 2014).

Isolated cuboids from SDSNH locality 4020 are tentatively reassigned with Sespedectes based on the orientation of the calcaneal facet. In the cuboids assigned to Sespedectes, the calcaneal facet is oriented proximolaterally. In the other similarly sized cuboid morph from this locality, the calcaneal facet faces directly proximally, with no lateral tilt. The former morphology matches the orientation of the calcaneal cuboid facet in Sespedectes, whereas the latter agrees with the morphology in Simimys.

DESCRIPTION

Although they differ in size, there is little morphological variation among sespedectine tarsals. For the most part, variation among specimens of a single taxon is comparable to variation between taxa. The most notable differences concern overall robusticity and proportions. Proterixoides tarsals are the most robust, whereas those of Crypholestes are the least. Proterixoides also has a distinctly larger astragalar body and shorter neck than the other two genera, as well as a longer calcaneal tuber. The descriptions in the following section are applicable to all three taxa, except where noted.

Astragalus

The sespedectine astragalar body is relatively large, deep, and square, whereas the head and neck are comparatively small (Fig. 2). The tibial facet is slightly wider than long and moderately grooved (Fig. 2A, F, G, L, M, R). The sharply defined medial and lateral ridges of the tibial facet are strongly convex, with a small radius of curvature. The lateral ridge is longer than the medial ridge but not dramatically so. Distally, the tibial facet is shallowly excavated between the medial and lateral ridges (Fig. 2A, G, M); in two specimens of Sespedectes (SDSNH 62663d, 69615a), there is a flat surface (Fig. 3A), possibly a squatting facet, on the medial half of the body immediately distal to the tibial facet. Proximally, there is no astragalar foramen and the central portion of tibial facet extends to the proximal margin of the bone (Fig. 2E, K, Q).

The medial surface of the body is vertical and is largely occupied by the malleolar portion of the tibial facet (Fig. 2D, J, P), which is much deeper distally than proximally; in Proterixoides, the distal margin of the malleolar facet is bounded by a weak ridge (Fig. 2J). At the proximoventral margin of the medial surface of the body, separated from the tibial facet by a shallow depression, the surface for attachment of the astragalotibial portion of the deltoid ligament is small and faces medially (Fig. 2D, J, P).

Like the malleolar portion of the tibial facet, the fibular facet on the lateral surface of the body is vertical and is much deeper distally than proximally (Fig. 2C, I, O). At its ventrodistal margin, the fibular facet curves to face dorsally, forming a prominent

**FIGURE 2.** Astragali of Sespedectinae. Sespedectes singularis right astragalus (reversed), SDSNH 62899, in A, dorsal, B, ventral, C, lateral, D, medial, E, proximal, and F, distal views. Proterixoides davisi left astragalus, SDSNH 60945, in G, dorsal, H, ventral, I, lateral, J, medial, K, proximal, and L, distal views. Crypholestes vaughni left astragalus, SDSNH 85883, in M, dorsal, N, ventral, O, lateral, P, medial, Q, proximal, and R, distal views. Abbreviations: aef, astragalar cuboid facet; aff, astragalar cuboid facet; an, astragalar neck; asf, sustentacular facet; dl, surface for deltoid ligament; lp, lateral process; mtf, medial tibial facet; nf, navicular facet; ppt, proximomedial plantar tuberosity; tf, tibial facet. Scale bars equal 1 mm.
narrowing of the proximal sustentacular facet (arrow). The right astragalus (reversed), SDSNH 62663d, in oblique and posterolateral views to show the presence of a possible squatting facet. B, Sespedectes singularis right astragalus (reversed), SDSNH 69615c, in oblique and anteromedial views to show the convexity of the posterior portion of the ectal facet (arrow). C, Proterixoides davisi right astragalus (reversed), SDSNH 96380, in ventral view to show the abrupt narrowing of the proximal sustentacular facet (arrow). Abbreviation: sq, possible squatting facet. Scale bars equal 1 mm.

FIGURE 3. Sespedectine astragalar details and variation. A, Sespedectes singularis right astragalus (reversed), SDSNH 62663d, in oblique and posterolateral views to show the presence of a possible squatting facet. B, Sespedectes singularis right astragalus (reversed), SDSNH 69615c, in oblique and anteromedial views to show the convexity of the posterior portion of the ectal facet (arrow). C, Proterixoides davisi right astragalus (reversed), SDSNH 96380, in ventral view to show the abrupt narrowing of the proximal sustentacular facet (arrow). Abbreviation: sq, possible squatting facet. Scale bars equal 1 mm.

lateral process reflecting the orientation of the ectal facet on the ventral surface of the bone (Fig. 2A, F, G, L, M, R). Proximally, the fibular facet is separated from the ectal facet by a well-defined fossa.

On the proximal margin of the body, the groove for flexor digitorum lateralis is continuous with the proximal margin of the tibial facet and is bounded medially by a moderately developed, ventrally oriented proximomedial plantar tuberosity (Fig. 2E, K, Q). On the ventral surface of the body, the ectal facet faces ventrally and slightly laterally (Fig. 2B, C, H, I, N, O). The long axis of the facet is oblique distal and lateral, and the distal third of the facet overhangs the body laterally, producing the prominent lateral process described above.

The facet is relatively broad proximally and tapers modestly towards its distal margin. The facet is somewhat narrower in Sespedectes than in Proterixoides or Crypholestes. Most of the ectal facet is moderately concave, but the proximal margin is convex (Fig. 3B), giving the entire facet an ‘S’-shaped profile. The convex portion is more extensive in Sespedectes and Crypholestes than in Proterixoides.

The ectal and sustentacular facets are separated by a narrow but relatively deep groove. The moderate-sized sustentacular facet is ovoid and gently convex, with its axis of curvature oblique and paralleling the long axis of the neck (Fig. 2B, H, N). Proximally, the facet tapers towards the medial side, particularly in Proterixoides (Fig. 3C), leaving a narrow strip on the underside of the proximomedial tuberosity. Distally, there is a similar but more poorly defined extension towards the lateral margin of the navicular facet. Distomedially, the sustentacular facet is separated from the navicular facet by a shallow but broad sulcus, which is best developed in Proterixoides and Crypholestes.

The neck is short, robust, and medially directed (Fig. 2A, B, G, H, M, N). The head is only modestly wider than the neck. The navicular facet occupies the distal and medial surfaces of the head (Fig. 2D, F, J, L, P, R). The medial portion of the navicular facet extends well proximally along the medial aspect of the neck, nearly reaching the level of the tibial facet. The facet is ovoid, approaching subcircular in distal view, with a long axis directed transversely and slightly dorsoventrally. The facet is uniformly and strongly convex, including its extension onto the medial margin of the head and neck. In dorsal view, the margin of the facet makes a sharp transition between the distal and medial facing portions of the facet. On the ventral surface of the head, just proximal to the medial half of the navicular facet, is a small, ventrally facing surface that may represent a small cuboid facet (Fig. 2B, H, N).

Calcaneum

The calcaneal tuber and body are approximately equivalent in length in Proterixoides, whereas the tuber is distinctly shorter in Sespedectes and particularly Crypholestes (Fig. 4). The body is

neither particularly elongate nor short. The proximal endplate of the tuber is subdivided into a convex dorsal surface oriented proximally and slightly laterally due to projection of its medial edge and a flat, triangular ventral surface that is oriented more ventrally than proximally (Fig. 4A, E, G, K, M, Q). The two surfaces are separated by a shallow groove but are continuous at their medial margin. The dorsal surface likely marks the insertion of m. triceps surae, whereas the ventral surface is probably for contact with the ground, with the foot in a plantigrade position. The calcaneal tuber itself is narrow but deep in Proterixoides and Sespedectes (Fig. 4A–D, G–J). In Crypholestes, the tuber is more robust and is closer to subcircular in cross-section (Fig. 4M, P). Near its proximal end, there is a variably developed excavation on the ventral half of the medial side of the tuber (e.g., Fig. 4H, J), giving the impression of an abrupt widening of the proximal end of the tuber in ventral view.

The ectal facet is oriented medially and somewhat distally (Fig. 4A, D, G, J, M, P). The proximal portion, extending onto the base of the tuber, is concave, matching the convexity of the proximal portion of the astragalus facet. The distal portion is narrower and convex. Proximomedial to the distal half of the ectal facet is a prominent, dorsally oriented fibular facet (Fig. 4A, G, M). The fibular facet is not as proximally extensive as the ectal facet, is strongly convex, and tapers distally. Proximal to the fibular facet is a depression bounded medially by the ectal facet. Laterally, the fibular facet is supported by a deep, flat projection. Between the fibular facet and peroneal tubercle on the lateral aspect of the body is a shallow groove for m. fibularis brevis (Fig. 4C, I, O). In some specimens (e.g., P. davisi, SDSNH 62504: S. singularis, SDSNH 69212), the dorsal margin of the groove is extended onto the tuber by a low ridge (Fig. 3I), whereas in others (e.g., P. davisi, SDSNH 60948: S. singularis, SDSNH 62662c), the ridge is poorly developed.

Distomedial to the ectal facet and separated by a shallow groove, the sustentacular facet is almost dorsally oriented and occupies most of the sustentaculum (Fig. 4A, G, H). There is almost no proximodistal overlap between the ectal and sustentacular facets. The facet itself is subcircular, although there is variable development of a distomedial extension towards the body (e.g., Fig. 4A). On the proximomedial margin of the sustentaculum is a narrow, proximally oriented extension of the sustentacular facet. On the ventral side of the sustentaculum is a broad groove for the tendon of m. flexor digitorum lateralis (Fig. 4B, H, N). The lateral margin of the groove is typically defined by a ridge on the calcaneal body (e.g., Fig. 4H).

The cuboid facet is incompletely preserved in calcanei of Crypholestes (Fig. 4R). In the other two taxa, the facet is diamond-shaped and subequal in depth and width, with the dorsal margin variably angular (e.g., Fig. 4L) or more smoothly curved (Fig. 4F). The ventromedial margin is slightly concave, whereas the remaining margins are straight or convex. The surface of the cuboid facet is almost flat in Proterixoides. In Sespedectes, there is a weak concavity in a primarily mediolateral plane. Ventral to the cuboid facet, the plantar tubercle reaches the distal margin of the bone, but it is separated from the facet by a shallow depression (Fig. 4D, J, P). The tubercle is well developed and projects ventral to the remainder of the bone, giving the calcaneum a concave, slightly bowed ventral profile. In ventral view, the plantar tubercle is positioned medial to the transverse midpoint of the calcaneal tuber (Fig. 4B, H, N).

The peroneal tubercle is relatively short proximodistally, is positioned somewhat proximal to the cuboid facet, and overlaps the distal end of the sustentacular facet (Fig. 4A, B, G, H, N). Lateral projection is substantial, especially in Crypholestes (only the base of the tuber is preserved in available specimens of Proterixoides). The lateral margin of the tubercle is expanded
and deeply bifurcated in specimens of *Sespedectes* (Fig. 4C, F), but is not split in *Crypholestes* (Fig. 4O).

**Navicular**

The navicular is moderately deep relative to its length and width (Fig. 5). In proximal view, the astragalar facet is ovoid, deeper dorsoventrally than wide mediolaterally (Fig. 5A, G, H), and continues onto a strongly proximally projecting tuber tibialis at its ventromedial margin (Fig. 5A, E–G, K, L). The facet is moderately concave, with the apparent concavity exaggerated by the extension onto the tuber tibialis. The lateral margin of the facet is straight where it meets the cuboid facet. The cuboid facet occupies most of the lateral surface of the bone (Fig. 5C, I). It is considerably deeper dorsoventrally than elongate proximodistally. Its proximal and distal margins are concave and convex, respectively. The facet is flat except for its ventral margin, which curves onto the dorsal margin of the plantar process (Fig. 5A, E, G, K). The dorsal margin of the cuboid facet is concave where it meets a shallow, non-articulating, depression. The plantar process at the ventrolateral corner of the bone is distinct but relatively small (Fig. 5A, C, F, G, I, L). It does not project distal to the remainder of the bone.

The distal surface of the navicular is occupied by facets for the ectocuneiform laterally and the mesocuneiform medially (Fig. 5B, H). The two facets are similar in size and shape, being slightly deeper than wide. The ectocuneiform facet is slightly dorsal to the mesocuneiform facet, but they share a lengthy border. The ectocuneiform facet is nearly flat and faces distally and slightly laterally. The mesocuneiform facet is somewhat concave dorsolaterally to ventromedially and faces somewhat medially as well as distally. Both facets are separated from the plantar process by concavities.

At the ventromedial margin of the navicular, distal to the tuber tibialis, is a surface that appears to be a facet for the entocuneiform (Fig. 5D, F, J, L). The facet is saddle-shaped, concave proximodistally and convex dorsoventrally. The facet is continuous distally with the ventromedial corner of the mesocuneiform facet, but they are separated by a sharp ridge. The distal margin of the facet has a stronger medial projection in *Proterixoides* than in *Sespedectes*. 

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**FIGURE 4.** Calcanei of Sespedectinae. *Sespedectes singularis* right calcaneum (reversed), SDSNH 69616, in A, dorsal, B, ventral, C, lateral, D, medial, E, proximal, and F, distal views. *Proterixoides davisi* right calcaneum (reversed), SDSNH 60949, in G, dorsal, H, ventral, I, lateral, J, medial, K, proximal, and L, distal views. *Crypholestes vaughni* left calcanei, SDSNH 76838 and 85880, in M, dorsal (85880), N, ventral (76880), O, lateral (76838), P, medial (85880), Q, proximal (85880), and R, distal (85880) views. **Abbreviations:** ccf, calcaneal cuboid facet; cef, calcaneal ectal facet; cff, calcaneal fibular facet; csf, calcaneal sustentacular facet; ct, calcaneal tuber; fbg, groove for m. fibularis brevis; fbr, ridge for m. fibularis brevis; flr, ridge for m. flexor digitorum lateralis; pet, peroneal tubercle; plt, plantar tubercle; te, calcaneal tuber endplate. Scale bars equal 1 mm.
Cuboid

The cuboid of *Sespedectes* is relatively stocky, with the proximal end somewhat wider than the distal end (Fig. 6). In dorsal view, the medial and lateral margins of the bone are concave, particularly the lateral margin (Fig. 6A). The dorsal margin of the bone is straight, and the calcaneal facet does not overhang the body (Fig. 6C). The primary orientation of the calcaneal facet is proximal, but it does slope somewhat laterally and dorsally (Fig. 6A, C, E). The facet is approximately 1.5 times wider than deep in proximal view, and its surface is slightly convex dorsally, curving ventrolaterally. Where it meets the astragalar facet, the ventromedial margin of the calcaneal facet forms a distinct proximal projection (Fig. 6A, C).

On the medial surface of the cuboid, the astragalar facet is small, proximodistally short, and does not reach the dorsal margin of the bone (Fig. 6D, E). It is weakly concave and oriented nearly equally proximally and medially. Immediately distal to the astragalar facet is a large, flat facet for the navicular and ectocuneiform that occupies most of the medial surface of the bone (Fig. 6D). It is difficult to distinguish the two constituent facets, but in SDSNH 69032d it appears to be divided at approximately mid-length, with the navicular portion oriented medially and the ectocuneiform portion slightly distomedially. The facet is widest proximally, tapering distodorsally, but with a ventral expansion at mid-length. As with the astragalar facet, the navicular facet does not reach the dorsal margin of the bone proximally, leaving a small gap between the navicular and calcaneal facets. There is a small continuation of the navicular facet, set at a right angle to the main facet, at the proximal margin of the ventral surface of the cuboid, on the prong formed by the ventromedial margin of the calcaneal facet (Fig. 6B, D). There is also a small distal ectocuneiform facet at the ventral margin of the distal articular surface of the bone (Fig. 6D).

The plantar process is broad, covering most of the middle two thirds of the ventral surface of the bone, but does not project substantially ventral to the body of the cuboid (Fig. 6B–D). Laterally, the plantar process overhangs the margin of the cuboid in many
specimens. On its ventral margin, the process defines a very narrow groove for the tendon of m. fibularis longus (Fig. 6C).

On the distal surface of the cuboid, there is no differentiation between facets for metatarsals IV and V (Fig. 6F). The combined facet is subtriangular, with the dorsal edge much wider than the ventral and with the ventral and lateral boundaries smoothly continuous. The medial margin is notched at the level of the ventral edge of the distal ectocuneiform facet. The metatarsal facet is gently concave dorsoventrally.

**Tarsal Function**

The calcaneal tuber is moderately elongate in sespedectines, particularly *Proterixoides*. A relatively elongate tuber may be indicative of some digging or climbing behavior, both activities that require some degree of power in plantarflexion (Salton and Szalay, 2004).

At the crurotarsal joint, the deep astragalar body with parallel medial and lateral surfaces in sespedectines contrasts with some arboreally adapted taxa in which these surfaces can be dorsally convergent, the latter morphology potentially facilitating transverse movements at the tibiotarsal joint. The extensive arc described by the tibial facet, nearly continuing onto the ventral surface of the bone, would permit the considerable range of dorsiflexion and plantarflexion typical of terrestrially adapted mammals. On the other hand, the mild excavation of the tibial facet resembles living scansional mammals (e.g., *Echimops*; Salton and Szalay, 2004) and does not suggest extreme specialization for rapid terrestrial locomotion.

The sigmoidal ectal facets on the sespedectine astragalus and calcaneum would lock the subastragalar joint. This contrasts with many arboreal taxa, in which inversion and eversion are shared between the subastragalar and transverse tarsal joints (Szalay and Decker, 1974; Szalay and Drawhorn, 1980) as well as with some terrestrial taxa in which parasagittal movement at the subastragalar joint is enhanced (Schaeffer, 1947). The lack of overlap between the calcaneal ectal and sustentacular facets is a similarity to many scansional and arboreal mammals, although this feature does not discriminate habitat preferences well in extant rodents (Rose and Chinnery, 2004).

The large size of the peroneal tubercle of the calcaneum suggests large mm. fibularis longus and brevis. These muscles act primarily as everters of the pes, and the presence of well-developed everters is consistent with movement over uneven substrates that necessitate a variety of positions of the pes. However, the peroneal tubercle is also relatively distal, a morphology that is more typical of terrestrial mammals than arboreal ones, where the tubercle tends to be at or proximal to the level of the sustentacular facet (Rose and Chinnery, 2004).

The short, medially projecting astragalar neck of sespedectines suggests generalized locomotor habits. Small-bodied cursorial mammals tend to show distal elongation of the tarsus, particularly the astragalar neck, part of a general trend to increase stride length via distal elongation of the limbs in cursoria (Hildebrand, 1985). Medial deflection of the astragalar head is also inconsistent with specialized cursorial locomotion. In cursors, the head is often directly distal to the body. On the other hand, arboreal taxa that make habitual use of inverted foot postures tend to show stronger medial deflection than is seen in sespedectines (Gebo, 1988; Salton and Szalay, 2004).

At the transverse tarsal joint, the relatively round, uniformly convex astragalar head in sespedectines would permit multiaxial movements, consistent with movement across uneven substrates. The distal orientation of the calcaneal cuboid facet aligns it transversely with the navicular facet on the astragalus, permitting rotation of the cuboid and navicular as a unit relative to the astragalus and calcaneum. This would facilitate inversion and eversion at the transverse tarsal joint and is more typical of scansional and arboreal mammals (e.g., Szalay and Decker, 1974). In addition, whereas the cuboid facet is essentially flat in *Proterixoides*, it is slightly concave mediolaterally in Sespedectes, which could enhance its capacity for inversion and eversion.

The overall picture of locomotor habits that emerges from the sespedectine tarsus suggests relatively unspecialized terrestrial or scansional locomotion. There are no indicators of strong adaptation to climbing, digging, or rapid terrestrial locomotion. In fact, a locomotor ecology similar to extant shrews and hedgehogs appears likely. Whether this reflects common ancestry, convergence, or shared retention of plesiomorphic locomotor patterns requires more detailed comparisons with other living and extinct lipotyphlans.

**COMPARISONS WITH EOCENE ERINACEOMORPHA**

Identification of sespedectine tarsals makes it possible to reevaluate the affinities of Sespedectinae with respect to other Eocene ‘erinaceomorphs’ known from postcranial remains (*Macrocranion*, *Zionodon*) and extant Erinaceids. Like other early lipotyphlans, most early ‘erinaceomorph’ taxa are known only from dental remains. Exceptions include complete skeletons of *Pholidocercus* and two species of *Macrocranion* from the middle Eocene Messel Konservat-Lagerstätte (Koenigswald and Storch, 1983; Storch, 1993, 1996). Unfortunately, the articulated and crushed nature of Messel specimens does not always permit easy comparisons with isolated elements and direct comparisons are currently not possible with *Pholidocercus*. In the case of *Macrocranion*, one Messel specimen exposes part of the tarsus (Godinot et al., 1996), permitting identification of isolated tarsals from earliest Eocene deposits at Dormaal, Belgium (Godinot et al., 1996; Coillot et al., 2013), and several quarries in the Willwood Formation, Bighorn Basin, Wyoming (Penkrot et al., 2004, 2013). In addition, dental postcranial skeletal associations are known for two species of the relatively large Uintan ‘erinaceomorph’ *Zionodon* (Dunn and Rasmussen, 2009). These associations have been used to refer additional, isolated elements to *Zionodon*.

Comparisons of sespedectine proximal tarsals with those of *Macrocranion junrei* (Penkrot et al., 2004) and *Zionodon* spp. show substantial differences from both contemporaneous taxa. On the body of the astragalus, the tibial facet is narrower relative to length in both *Macrocranion* and *Zionodon* than in Sespedectinae and is somewhat more deeply excavated (Fig. 7A–C, U–W). In the former taxa, the lateral ridge of the tibial facet is taller than the medial ridge, whereas the ridges are subequal in height in sespedectines (Fig. 7A–C). In contrast to both *Macrocranion* and the sespedectines, *Zionodon* has an astragalar foramen on the dorsal surface of the astragalus body (Fig. 7C). The distal end of the tibial facet shows a deep excavation in *Macrocranion* (Fig. 7B) that is lacking in *Zionodon* and sespedectines, in both of which the distal margin of the facet is linear. Laterally, *Macrocranion* and *Zionodon* share a uniformly deep fibular facet (Fig. 7L, M), contrasting with a facet that is very shallow proximally and deep distally in Sespedectinae (Fig. 7K). At the proximomedial corner of the astragalus body, *Macrocranion* and *Zionodon* both have a well-defined, triangular surface for ligament attachment facing dorsally (Fig. 7B, C); this surface is relatively larger in *Zionodon* than in *Macrocranion*. In Sespedectinae, the equivalent surface is poorly defined and faces medially (Fig. 7P). Ventral to this region, the proximomedial plantar tuberosity is lower and less prominent in *Macrocranion* than in Sespedectinae, whereas the groove for m. flexor digitorum lateralis is narrower in *Macrocranion* than in sespedectines (this region is damaged in known *Zionodon* astragali). At the distomedial corner of the astragal body, *Macrocranion* and *Zionodon* both have distinct cotylar fossae for articulation with
the medial malleolus of the tibia (Fig. 7B, C), an additional feature that is lacking in Sespedectinae.

On the ventral surface of the astragalus, the long axis of the ectal facet has less of a mediolateral orientation in Macrocranion and Zionodon than in sespedectines (Fig. 7G, H, damaged in Fig. 7F); as a result, the lateral process is less well developed in the former taxa. In addition, the curvature of the ectal facet differs substantially, being uniformly concave in Macrocranion and Zionodon (Fig. 7G, H), and lacking the distinctive ‘S’ shape of sespedectines (Fig. 7F). Distally, the ectal facet of Macrocranion tapers, but it remains broader in Zionodon and sespedectines. The sustentacular facet of Macrocranion lacks a clear distomedial boundary with the navicular facet (Fig. 7G), whereas the two facets are separated by a well-defined gutter in Zionodon and Sespedectinae (Fig. 7F, H). This may reflect the fact that the sustentacular facet is much larger in Macrocranion than in either sespedectines or Zionodon.

On the distal end of the astragalus, Macrocranion and Zionodon have relatively larger heads than do sespedectines (Fig. 7U–W). The head does not project as far medially relative to the body in Macrocranion as in Sespedectinae and Zionodon (Fig. 7A–C). The astragalar head itself is ovoid, with sharp boundaries to the navicular facet in Macrocranion and Zionodon (Fig. 7V, W). In these taxa, the head is narrow and the long axis of the navicular facet is almost dorsoventral, particularly in Macrocranion. In Sespedectinae, the long and short axes are more similar in length, particularly in Proterixoides (Fig. 2L), and the long axis is more transverse. The arc of the navicular facet extends onto the dorsal surface of the neck in Macrocranion and Zionodon. In the former taxon, the facet comes to a point close to the level of the tibial facet. In Sespedectinae, the lateral portion of the navicular facet is restricted to the distal surface of the head.

Proximally on the calcaneum, the tuber of Macrocranion is relatively longer and narrower than in sespedectines (Fig. 8B), particularly Sespedectes and Cryptolestes (Fig. 8A). A shorter, more robust tuber is shared by Zionodon satanus (Dunn and Rasmussen, 2009). In sespedectines, the difference in width is particularly noticeable at the proximal end of the tuber, reflecting an expansion of the endplate in sespedectines that is not present in Macrocranion (Fig. 8B).
FIGURE 8. Comparison of the calcaneal morphologies of *Sespedectes singularis* (SDSNH 69212, right calcaneum, reversed) (A, F, K, P, U) with the Eocene ‘erinaceomorphs’ *Macrocranion junnei* (UCMP 216511, right calcaneum, reversed) (B, G, L, Q, V) and *Zionodon walshi* (CM 71142, left calcaneum) (C, H, M, R, W), the erinaceid *Atelerix albiventris* (UF[M] 24247, left calcaneum) (D, I, N, S, X), and the soricid *Suncus murinus* (UF[M] 27599, left calcaneum) (E, J, O, T, Y). A–E, dorsal, F–J, ventral, K–O, lateral, P–T, medial, and U–Y, distal views. Scale bars equal 1 mm.
As would be expected from astragalar morphology, the ectal facet is smoothly convex in Macrocranion and Zionodon (Fig. 8B, C), lacking the ‘S’ shape present in sespedectines. The ectal facet faces distomedially in Macrocranion (Fig. 8B) versus more medially in sespedectines and Zionodon (Fig. 8A, C). In both Macrocranion and Zionodon, the long axis of the facet is substantially shorter than in sespedectines. Lateral to the ectal facet, all three taxa share a well-developed fibular facet, but it differs in shape. In Macrocranion, the facet is elongate and narrow and parallels the entire length of the ectal facet (Fig. 8B). In Zionodon and, particularly, Sespedectinae, the facet is shorter and is restricted to the distal portion of the ectal facet (Fig. 8A, C).

The sustentaculum and sustentacular facet are smaller and less medially extensive in Macrocranion (Fig. 8B) than in sespedectines or Zionodon (Fig. 8A, C). However, in both Zionodon and Macrocranion, the facet itself has extensive proximodistal overlap with the ectal facet, whereas this overlap is minimal in Sespedectinae. On the ventral side of the sustentaculum, Zionodon possesses, but Macrocranion lacks, the distinct groove for m. flexor digitorum lateralis that is present in sespedectines (Fig. 8K–M).

In both sespedectines and Macrocranion, the peroneal tubercle does not reach the distal margin of the bone (Fig. 8A, B) (the distolateral corner of the bone is not preserved in any Zionodon calcaneum), but it is slightly more distal in Macrocranion. Additionally, the peroneal tubercle is less well differentiated from the body of the calcaneum in Macrocranion than in Sespedectinae, and is not as laterally projecting. Instead, the tubercle appears slightly distally directed in dorsal view.

At the distal end of the calcaneum, the plantar tubercle is much more prominent in sespedectines than in Macrocranion (Fig. 8F, G, P, Q), although it is positioned similarly at the distal edge of the bone. In Zionodon, the tubercle is distinct in being well proximal to the distal margin of the calcaneum (Fig. 8H, R); it is also poorly defined, more comparable to Macrocranion. The cuboid facet is wider than deep in Macrocranion and Zionodon (Fig. 8V, W), whereas the proportions are more subequal in Sespedectinae (Fig. 8U). In all taxa, the facet is relatively flat, but there is some dorsoventral concavity in Macrocranion and Zionodon that is lacking in sespedectines. The orientation of the cuboid facet with respect to the long axis of the calcaneum also differs substantially. In Macrocranion and Zionodon, the facet has a distomedial orientation and in Macrocranion, a slight ventral deflection (Fig. 8Q, R), whereas in Sespedectinae, the facet faces more distally with less medial angulation and no dorsal or ventral deflection (Fig. 8P).

For the most part, the differences between Macrocranion and Zionodon on the one hand and members of Sespedectinae on the other are consistent with the former being more specialized for terrestrial locomotion than the latter. To a greater extent than sespedectines, the tarsal morphology of Zionodon and particularly that of Macrocranion would facilitate para-sagittal movements while restricting mobility in other planes. This is consistent with previous reconstructions of Macrocranion as cursorial or saltatorial (Storch, 1993, 1996). Zionodon was reconstructed as showing a mixture of features indicative of different locomotor styles, but was considered to be primarily terrestrial (Dunn and Rasmussen, 2009).

The comparisons also suggest that sespedectines are unlikely to be closely allied to either Macrocranion or Zionodon. There is somewhat greater similarity between Zionodon and members of Sespedectinae than between Macrocranion and Sespedectinae, but this probably reflects the derived morphology of Macrocranion rather than indicating a relationship between the first two taxa. Macrocranion and Zionodon show greater similarities to each other, and a few features such as the orientation of the calcaneal ectal facet and the presence of a cotylar fossa could indicate that they share a distant relationship to each other. Alternatively, because many of the similarities shared by Macrocranion and Zionodon are associated with terrestrial locomotion in a diversity of mammals, they could easily have been acquired convergently.

**COMPARISONS WITH EXTANT LIPOTYPHLA**

In addition to Macrocranion and Zionodon, comparisons were made with tarsals of the taxa listed in Materials and Methods, which broadly samples the taxonomic and morphological diversity of the four extant families. Based on these comparisons, sespedectines share one significant feature with extant hyomyine Erinaceinae that is not shared by Macrocranion or Zionodon: the presence of ‘S’-shaped ectal facets on the astragalus and calcaneum. This feature is also present in soricids (e.g., Fig. 7O) and some talpids (e.g., *Condylura cristata*) but is generally uncommon in mammals. The presence of a tuber tibialis on naviculars tentatively reassigned with sespedectines is also suggestive of a lipotyphlan affinity, because this is present in all extant lipotyphlans exclusive of *Solenodon*. However, whereas both of these features suggest a relationship to non-*Solenodon* lipotyphlans in general, neither provides evidence of an exclusive relationship to Erinaceinae. In fact, tarsals of Soricidae share significant features with erinaceids that are not present in sespedectines.

On the astragalus, the lateral side of the tibial facet is substantially more elongate than the medial side in soricids and erinaceids (Fig. 7D, E, N, O), contrasting with the more nearly subequal medial and lateral margins in sespedectines (Fig. 7A, K). In addition, the lateral half of the tibial facet has a very large radius of curvature in both soricids and erinaceids (Fig. 7N, O), contrasting with a more tightly curved morphology in sespedectines (Fig. 7K).

On the ventral surface of the astragalus, the distal end of the ectal facet does not project laterally in soricids and erinaceids (Fig. 7I, J). As a result, there is no lateral process in dorsal view (Fig. 7D, E). This contrasts with sespedectines, which have a projecting ectal facet and a very prominent lateral process (Fig. 7A, F).

On the calcaneum, the ectal facet of sespedectines (Fig. 8A, P) is oriented more distally than in soricids and erinaceids (Fig. 8D, E, S, T), although less so than in Eocene ‘erinaceomorphs.’ As a result of the differences in orientation, the ectal facet does not extend as far proximally along the tuber in sespedectines, resulting in a relatively more elongate tüber. Additionally, the peroneal process does not project as far laterally from the calcaneal body in soricids and erinaceids (Fig. 8D, E, X, Y). The similarities shared by erinaceids and soricids to the exclusion of sespedectines are inconsistent with the hypothesis that sespedectines and erinaceids share a phylogenetic relationship to the exclusion of other living lipotyphlans.

**PHYLOGENETIC ANALYSIS**

The comparisons suggest two preliminary conclusions regarding sespedectine relationships. First, nothing in the tarsus of sespedectines suggests a close relationship to other Eocene ‘erinaceomorphs.’ Second, whereas sespedectine proximal tarsals are broadly similar to tarsals of extant erinaceids, there is little evidence for an exclusive relationship. Instead, tarsal morphology suggests that soricids, at least, may be closer to erinaceids than are sespedectines. Both of these statements are testable via phylogenetic analysis. Ideally, an appropriate character-taxon matrix should broadly sample living and extinct small-bodied insectivorous placental taxa, including living representatives of Lipotyphla and fossil taxa that may or may not be allied to this group. Of existing character-taxon matrices, those used by Hooker (2014) and Manz et al. (2015) to investigate nyctitherine affinities most closely meet this requirement. Both matrices broadly sample dental and osteological characters and both sample representatives of Lipotyphla and several relevant extinct groups (*Nyctitheriidae, Adapisoriculidae, and Macrocranion*).
Of the two, Hooker’s taxonomic sample is more focused, because Manz and colleagues include a nearly exhaustive sample of Cretaceous placentalts, reflecting the derivation of the latter matrix from Wible et al.’s (2007, 2009) analyses. Hooker (2014) also gives greater weight to the morphology of the proximal tarsus, with 41 of 310 characters describing variation in the astragalus and calcaneum versus 26 of 415 in Manz et al.’s (2015) matrix.

To test the relationships of Sespedectinae, three sespedectine operational taxonomic units (OTUs) were added to Hooker’s (2014) matrix: Cryptolestes vaughni, Proteroxoides davisi, and Sespedectes spp. In addition to sespedectines, Ziododon and three other Paleogene erinaceomorphs, Litotherus spp., Patriolestes novaceki, and Scenopagus spp., were also added. The first named genus was included because of its well-documented postcranial, particularly tarsal, morphology. The remaining three have been argued to be related to sespedectines (Robinson, 1966; Gingerich, 1983; Walsh, 1998) and may help link the morphology of Sespedectinae to that of other erinaceomorphs.

The pliosoricid Batselia, an additional early lipotyphlan for which the tarsus has been recently described (Smith and Smith, 2012), was also added. Finally, to improve sampling of crown-group lipotyphlans, two additional extant lipotyphlan OTUs were added, Solenodon and a composite Talpidae. For the latter, Uropsilus soricipes was used for dental and postcranial scorings, whereas Talpa europaea was used for cranial scorings. Scorings for several other taxa (Macroramion, Purgatorius, and Micromomyidae) were updated based on newly published material (Chester et al., 2015) or observations of unpublished specimens. Finally, two of Hooker’s (2014) characters (3 and 50) were modified to reflect variation seen in newly added or modified taxa. Details of specimens examined, modified characters, and new and revised scorings can be found in Appendices S1–S3 (Supplementary Data 1). The matrix was analyzed in TNT (Goloboff et al., 2003) following the procedures outlined by Hooker (2014).

Results

Analysis of the modified matrix produced 16 most parsimonious trees (tree length = 3028; consistency index = 0.195; retention index = 0.454). The strict consensus tree (Fig. 9A) is poorly resolved. Major groupings recovered by the strict consensus include Ferae, Chirotiera, Anagalida (Glires plus Macroscelidea and their relatives), Primates (including Plesiadiapiformes plus Nyctitheriidae, and a clade of living and extinct lipotyphlans, with the latter two groups recovered as sister taxa. Resolution within Lipotyphla is poor, but all trees recover monophyly of Sespedectinae. All trees also recover a clade comprising living erinaceids, soricids, and talpids. In no tree is any Paleogene erinaceomorph resolved as a stem erinaceid.

The majority-rule topology has more structure (Fig. 9B). Most lepimictomorphs (Leptictidae, Pantolestidae, Pseudorhynchoconyi dae) form a pectinate series basal to Anagalida (sensu McKenna and Bell, 1997). The sister taxon to this clade of generally terrestrial, terrestrial, and adapted taxa is a heterogenous assemblage comprising Chirotiera, Sundatheria, Arctocyonidae, and Pentacodontidae. Within Lipotyphla, resolution is improved, with sespedectines recovered as members of the crown group, forming the sister taxon to the erinaceid/soricid/talpid clade. Aside from Scenopagus, which forms the sister taxon to Batselia/Solenodon clade in all trees, remaining Paleogene erinaceomorphs are identified as stem lipotyphlans by the majority-rule tree, with Ziododon, Macroramion, and Patriolestes forming a clade.

The most significant sources of non-resolution among the most parsimonious trees (MPTs) are three taxa, Protungulatum, Leptictidinae, and Plagionomidae. In 12 of 16 MPTs, the first is recovered with other arctocyonids, the second is paraphyletic with respect to Anagalida, and the third is the sister taxon of Cynocephalus. In the remaining four trees, however, Protungulatum is nested deeply within an otherwise monophyletic Leptictidomorpha, and Plagionomidae recovered between Leptictidomorpha and Anagalida. Trees with the latter topology also have Pentacodontidae paraphyletic and basal to most of the ingroup. Aside from inconsistent relationships within Sespedectinae, Litotherus is responsible for non-resolution within Lipotyphla. All trees recover the basic morphology seen in the majority-rule tree, but Litotherus can occupy one of three positions: basal to all other lipotyphlans (eight trees) positioned between Sespedectinae and the erinaceid/soricid/talpid clade (four trees), or as the sister taxon of Ziododon (four trees).

Discussion

The results of the phylogenetic analysis are poorly resolved and, where resolution is present, generally weakly supported based on Bremer support values. Trees recovered by Hooker’s (2014) original analysis of this matrix also had low Bremer support at most nodes, particularly those subtending more inclusive clades. This should not be surprising given the broader uncertainty concerning the interrelationships of placental mammals and the conflict between morphological and molecular hypotheses of relationships (Asher et al., 2003; Wible et al., 2009; O’Leary et al., 2013). Several aspects of the new topology are unexpected and unlikely, most notably the grouping of Loxolopus and Arctocyon with bats, tree shrews, and flying lemur and the variable placement of either Protungulatum or Anagalida within Leptictidomorpha. However, aspects of the topology recovered by the original analysis appear equally implausible, such as the linkage of carnivorous eutherians with Euarchonta.

Identification of a stable, well-supported morphological phylogeny of eutherian mammals that is compatible with molecular topologies remains a major unresolved goal of the study of mammalian evolution and one that is far beyond the scope of this study. More germane to the present study, reanalysis of Hooker’s (2014) matrix does recover a monophyletic Lipotyphla. The major difference from the consensus molecular topology is the recovery of Soricidae and Talpidae as sister taxa, rather than linking the former with Erinaceidae (Douady et al., 2002; Roca et al., 2004; Bininda-Emonds et al., 2007; O’Leary et al., 2013). However, this is consistent with some other recent studies (Cabría et al., 2006; Meredith et al., 2011). This indicates that results of the analysis are likely to be a useful indicator of the relationships of sespedectines and other purported extinct lipotyphlans to extant members of the order.

The analysis does not support a special relationship between Sespedectinae and Erinaceidae. Although all trees place Sesp edectinae within the lipotyphlan crown group, it is resolved basal to the clade comprising Soricidae, Talpidae, and Erinaceidae. Exclusion of sespedectines from the clade of ‘higher’ lipotyphlans reflects the shared presence of a suite of dental and tarsal features in soricids, talpids, and erinaceids that are not present in sespedectines. In the case of dental morphology, several features (tall m1 enodontid, lingual hypoconulid, buccal cristid obliqua) reflect a distinctive talonid morphology shared by ‘higher’ lipotyphlans. These features also differentiate living hedgehogs from other Paleogene ‘erinaceomorphs.’

Placement of Sespedectinae within crown Lipotyphla, separated from other erinaceomorphs, appears to be driven by two primary factors. First, several tarsal features (larger medial plantar tuberosity, transversely shortened astragalus, navicular facet, sigmoidal or unevenly convex calcaneal ectal facet, and entagul Navicular tuberosity) link sespedectines with erinaceids, soricids, and talpids to the exclusion of Macroranion and Ziododon. Second, a suite of cranial (low dentary coronoid process, angular process elevated, posterior infraorbital foramen above P5, elongate anterior process of frontal, and reduced jugal) and postcranial (four or more sacral vertebrae, weak supinator crest, reduced public
symphysis, short medial malleolus, tall medial trochlear ridge, and weak annular ligament attachments on first phalanges) features unites living lipotyphlans to the exclusion of Macrocranion and, where it can be determined, Zionodon. Almost all of the latter features are presently unknown in sespedectines, but the combination of tarsal features pulling Sespedectinae within crown Lipotyphla and skeletal features excluding Macrocranion and Zionodon from the crown group is enough to render Paleogene erinaceomorphs diphyletic.

Some dental features also support the node uniting sespedectines and ‘higher’ lipotyphlans (small, single-rooted upper canine, single-rooted P2/p2, low p4 paraconid, and M2 postcingulum bypassing postprotocrista to reach metacingularum), but most of these are also found in a variable number of other Paleogene ‘erinaceomorph’ taxa, including, in some instances, Macrocranion. In the present analysis, they merely link sespedectines and ‘higher’ lipotyphlans to the exclusion of Solenodon and its reconstructed relatives.

Overall, there is no support for placement of any of the sampled Paleogene ‘erinaceomorphs’ in Erinaceomorpha, and only sespedectines and Scenopagus are consistently recovered as crown lipotyphlans. Although numerous other Paleocene and Eocene taxa known primarily or exclusively from dental remains have been placed in Erinaceomorpha, the fact that a diversity of better-known forms cannot be linked with erinaceids suggests that these assignments should be viewed cautiously. Some or all of these taxa may eventually prove to be stem erinaceids, but for the moment, they are probably best viewed as Lipotyphla incertae sedis in the absence of support from non-dental features. In particular, the first appearance of ‘erinaceomorphs’ in the fossil record should not be used to constrain the timing of the first appearance of crown Lipotyphla in calibrating molecular clocks.

FIGURE 9. A, strict consensus of 16 trees from analysis of the matrix modified from Hooker (2014). B, majority-rule consensus of the same 16 trees. See text for tree statistics. Paleogene erinaceomorphs are indicated in bold, with sespedectines further emphasized by arrows. Numbers below nodes in A represent Bremer support values for those nodes with values greater than 1.
and the results of past studies that have done so (e.g., Springer et al., 2003) are likely to be inaccurate.

Aside from sespedectines, the only Paleogene ‘lipotyphlans’ that are consistently placed within the crown group are the pleiosoricid Butselia and the ‘erinaceomorph’ Scenopagus. All trees recover Butselia as the sister taxon of Solenodon, a relationship that receives modest branch support. Dental morphology appears to underlie this relationship, and it is true that Butselia and Solenodon share a particularly sectorial dental morphology, with strong emphasis on shear between the trigonid and ectoloph. Additionally, both taxa have a small i1 combined with an enlarged i2, an unusual morphology that is otherwise unique within the ingroup. Postcranial morphology is not particularly supportive of this relationship, but neither taxon is particularly similar to any other sampled taxon in this regard. The possibility of a pleiosoricid-solenodontid link is best viewed tentatively pending additional testing. The placement of Scenopagus basal to this grouping is much more weakly supported and appears to rest solely on the presence of a somewhat more sectorial talonid in Scenopagus than in other ‘erinaceomorphs.’

**TABLE 1.** Measurements (mm) of tarsals of *Proterixoides davisi* and *Crypholestes vaughni*.

| Specimen   | Side | AL | AW | CaL | CaW | NL | NW | CuL | CuW |
|------------|------|----|----|-----|-----|----|----|-----|-----|
| SDSNH 62663a | L    | 2.1 | 1.7 |     |     |    |    |     |     |
| SDSNH 62663c | L    | 2.5 | 2.0 |     |     |    |    |     |     |
| SDSNH 62663d | R    | 1.9 |     |     |     |    |    |     |     |
| SDSNH 62663e | R    | 2.5 | 2.1 |     |     |    |    |     |     |
| SDSNH 62899 | R    | 2.1 | 1.7 |     |     |    |    |     |     |
| SDSNH 69032a | L    | 1.6 | 1.4 |     |     |    |    |     |     |
| SDSNH 69032b | L    | 1.3 | 1.2 |     |     |    |    |     |     |
| SDSNH 69033a | L    | 1.2 | 1.1 |     |     |    |    |     |     |
| SDSNH 69033b | L    | 1.0 |     |     |     |    |    |     |     |

**TABLE 2.** Measurements (mm) of tarsals of *Proterixoides davisi* and *Crypholestes vaughni*.

| Specimen           | Side | AL | AW | CaL | CaW | NL | NW | CuL | CuW |
|--------------------|------|----|----|-----|-----|----|----|-----|-----|
| *Proterixoides davisi* |      |    |    |     |     |    |    |     |     |
| SDSNH 60945       | L    | 4.5 | 4.1 |     |     |    |    |     |     |
| SDSNH 62505       | L    | 4.7 | 4.2 |     |     |    |    |     |     |
| SDSNH 94574       | R    | 5.0 | 4.1 |     |     |    |    |     |     |
| SDSNH 96376       | L    | 4.3 | 3.6 |     |     |    |    |     |     |
| SDSNH 96377       | L    | 4.6 | 3.9 |     |     |    |    |     |     |
| SDSNH 96380       | R    | 4.8 | 4.2 |     |     |    |    |     |     |
| SDSNH 96394       | L    | 7.9 |     |     |     |    |    |     |     |
| SDSNH 96395       | R    | 7.7 | 3.9 |     |     |    |    |     |     |
| SDSNH 62504       | R    | 8.0 | 4.3 |     |     |    |    |     |     |
| SDSNH 94571       | L    | 3.8 |     |     |     |    |    |     |     |
| SDSNH 94572       | R    | 7.3 |     |     |     |    |    |     |     |
| SDSNH 94573       | L    | 8.6 |     |     |     |    |    |     |     |
| SDSNH 96390       | R    | 2.8 | 2.4 |     |     |    |    |     |     |
| *Crypholestes vaughni* |      |    |    |     |     |    |    |     |     |
| SDSNH 51360       | L    | 2.2 | 1.8 |     |     |    |    |     |     |
| SDSNH 85883       | L    | 2.2 | 1.7 |     |     |    |    |     |     |
| SDSNH 76838       | L    | 2.0 |     |     |     |    |    |     |     |
| SDSNH 85880       | L    | 3.5 |     |     |     |    |    |     |     |
| SDSNH 85881       | L    | 3.3 |     |     |     |    |    |     |     |

**Abbreviations:** AL, maximum astragalar length; AW, maximum astragalar width; CaL, maximum calcaneal length; CaW, maximum calcaneal width; CuL, maximum cuboid length; CuW, maximum cuboid width; NL, maximum navicular length; NW, maximum navicular width.

**TABLE 3.** Summary statistics for sespedectine tarsals.

| Dimension                   | N | Mean (mm) | SD | CV  |
|-----------------------------|---|-----------|----|-----|
| *Proterixoides davisi*      |  |  |     |     |
| Astragalar length           | 8 | 2.5       | 0.23| 9.2 |
| Astragalar width             | 8 | 1.9       | 0.16| 8.3 |
| Calcaneum length            | 6 | 3.8       | 0.42| 11.1|
| Calcaneum width              | 3 | 2.2       | 0.45| 20.6|
| Navicular length             | 3 | 1.4       | 0.22| 16.0|
| Navicular width              | 4 | 1.2       | 0.15| 12.4|
| Cuboid length                | 12| 1.5       | 0.15| 9.9 |
| Cuboid width                 | 12| 1.3       | 0.14| 10.5|
| *Proterixoides vaughni*     |  |  |     |     |
| Astragalar length            | 6 | 4.6       | 0.22| 4.6 |
| Astragalar width             | 6 | 4.0       | 0.23| 5.8 |
| Calcaneum length             | 5 | 7.9       | 0.47| 6.0 |
| Calcaneum width              | 3 | 4.0       | 0.27| 6.8 |
| Navicular length             | 1 | 2.8       | ——  | ——  |
| Navicular width              | 1 | 2.4       | ——  | ——  |

**Abbreviations:** CV, coefficient of variation; N, sample size; SD, standard deviation.

**CONCLUSIONS**

Referral of tarsal material to members of Sespedectinae confirms previous hypotheses that *Crypholestes, Proterixoides*, and *Sespedectes* are closely related to one another (Novacek, 1985). All three genera share a very similar astragalar and calcaneal morphology and naviculars of *Proterixoides* and *Sespedectes* are also very similar. What differences exist primarily involve size and proportions. Most notably, *Proterixoides* is much larger and has a relatively longer calcaneal tuber.

Sespedectine tarsal morphology suggests relatively generalized terrestrial or scansorial habits. There is no indication of significant adaptation to arboreal or cursorial locomotion, contrasting with some other potential Paleogene litoptypalans (e.g., *Nyctitheriidae* and *Macrocranion*, respectively). The generalized morphology of sespedectines suggests a lifestyle comparable to living erinaceids and soricids.

The tarsal morphology of *Sespedectinae* is broadly comparable to that of non-*Solenodon* litoptypalans and shares some relatively distinctive features (e.g., S-shaped ectal facets) with living erinaceids, soricids, and talpids. However, tarsals of the latter taxa, particularly erinaceids and soricids, are more similar to each other than they are to sespedectines. Most notably, the lateral side of the astragalar tibial facet in erinaceids and soricids is strikingly elongate and flattened, a distinctive morphology that is poorly developed or absent in sespedectines.
Sespedeentine tarsal morphology is less similar to that of the Paleogene ‘erinaceomorphs’ Macrocranion and Zionodon. Both of the latter show much more specialized terrestrial adaptation in the tarsus. Neither shows any meaningful derived similarity to Erinaceidae or other extant lipotyphlans. Taken together, the evidence from tarsal morphology casts doubt on the validity of Erinaceomorph.

This conclusion is confirmed by analysis of a modified version of Hooker’s (2014) character-taxon matrix, including sespedeetines and other new or modified terminal taxa. Sespedeetines are recovered as lipotyphlans, basal to erinaceids, soricids, and taphids, but more closely related to these taxa than to Solenodon. Macrocranion and Zionodon are excluded from the lipotyphlan crown group, and there is no support for a special relationship between any Eocene ‘erinaceomorph’ and Erinaceidae. This indicates that Erinaceomorph is likely to be a polyphyletic assemblage of dentally similar taxa. The results of this study highlight the value of reassociating isolated postcrania with taxa known from dental remains.

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