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The Scutulum and the Pre-Auricular Aponeurosis in Bats

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ABSTRACT

The external ear in eutherian mammals is composed of the annular, auricular (pinna), and scutellar cartilages. The latter extends between the pinnae, across the top of the head, and lies at the intersection of numerous auricular muscles and is thought to be a sesamoid element. In bats, this scutulum consists of two distinct regions, (1) a thin squama that is in contact with the underlying temporalis fascia and (2) a lateral bossed portion that is lightly tethered to the medial surface of the pinna. The planar size, shape, and proportions of the squama vary by taxa, as does the relative size and thickness of the boss. The origins, insertions, and relative functions of the auricular muscles are complicated. Here, 30 muscles were tallied as to their primary attachment to the pinnae, scutula, or a pre-auricular musculo-aponeurotic plate that is derived from the epicranius. In contrast to Yangochiroptera, the origins and insertions of many auricular muscles have shifted from the scutulum to this aponeurotic plate, in both the Rhinolophidae and Hipposideridae. We propose that this functional shift is a derived character related primarily to the rapid translations and rotations of the pinna in high-duty-cycle rhinolophid and hipposiderid bats.

1 | Introduction

The external ear of eutherian mammals is well developed and functions to collect and channel sound waves toward the external auditory meatus (or ear canal) for acoustic processing. It is generally composed of three elastic cartilages, the annular, auricular (pinna), and the scutulum. The annular cartilage is ring-shaped and fixed to the external acoustic meatus by fibrous tissue that permits some degree of movement with the pinna. The pinna is a distinctive external feature of the outer ear in mammals, usually spoon or cone-shaped, and lies distal to the annular cartilage. Its size varies considerably across taxa due to its functional relationship with sound collection and localization and even thermoregulation in some species. The scutulum has several synonyms: scutellum, scutellar or scutiform cartilages, clypeus, rotula, and the Schildknorpel (shield cartilage) and Schildchen (little shield) in German. Histologically, it is an elastic cartilage but it has also been described in rabbits as fibrocartilage with a thick perichondrium (Huber 1924–25; Lamb and Sawin 1963).

The scutulum consists of two distinct regions, (1) a thin squama that is in contact with the underlying temporalis muscle and (2) a lateral bossed portion that is lightly tethered to the medial surface of the pinna. The planar size, shape, and proportion of the squama vary by taxa (Table 1a). However, many of those studies did not look at the scutulum in isolation and their descriptions of “shape” were based on that portion of cartilage that was exposed beneath the attached muscles, and those reflecting the completeness of the dissection. Squama are typically thicker at their lateral border and the thickness and shape of this bossed edge is unremarkable in most mammals.

The scutulum is located between the pinnae and within the intersection of several auricular muscles. There, it acts as a

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TABLE 1a | Shape of the scutulum in 16 terrestrial mammals.

Taxon	Shape	Authors
Artiodactyla (alphabetical)		
Babyrousa celebensis	Quadrangular	Kneepkens and Macdonald (2010)
Bos tarus	Quadrangular	Al-Sadi and Hasso (2012)
Bubalus bubalis	Quadrangular	Al-Sadi and Hasso (2012)
Camelus dromedarius	Quadrangular	Sisson (1975)
Equus asinus	Quadrangular	Sisson (1975); Sharsher et al. (2020)
Equus caballus	Ovoid	Budras et al. (2011)
Equus caballus	Quadrangular	Sisson (1914)
Equus caballus	Triangular	Bradley (1923)
Ovis aries	Quadrangular	May (1970); Sisson (1975)
Sus domesticus	V-Shaped	Gandhi (1975)
Carnivora (alphabetical)		
Canis familiaris	Bilobed	Evans (1993)
Canis familiaris	V-Shaped	Ellenport (1975); Huber (1922, 1923)
Felis catus	Quadrangular	Crouch (1969)
Felis catus	Rod-like	Diogo et al. (2012)
Felis catus	Triangular	Huber (1930a)
Leptailurus serval	Triangular	Diogo et al. (2012)
Nasua narica	Triangular	Compton (1973)
Pantera tigris	Triangular	Diogo et al. (2012)
Other		
Didelphis virginiana	Triangular	Huber (1930b)
Oryctolagus cuniculus	Triangular	Farag (2008)
Oryctolagus cuniculus	Quadrangular	Lamb and Sawin (1963)
Lemuridae	Absent	Huber (1930a)
Hominidae	Absent	Huber (1930b)

sesamoid element that glides over the subjacent temporal fascia and may provide mechanical advantage for the muscles associated with differential movements of the pinnae and scutulum.

There are four sets of these auricular muscles that are situated rostral, caudal, dorsal, and ventral to the scutulum, all of which are innervated by the seventh cranial nerve. These muscles move both the scutulum and the pinna in predictable ways. Typically, the rostral group rotates the pinna medially and draws the face of the pinna forward; the caudal group rotates the pinna laterally and moves the face of the auricle rearwards; the dorsal group elevates the ear and adducts the pinnae and scutulum; the ventral group depresses the ear which abducts both the scutulum and pinna.

When the word "*scutulo*" (Latin: platter) appears in the literature, it is usually in reference to these auricular muscles, for example, scutulo-auricularis. Any description of the specific form, function, and movement of the scutulum itself is limited, if not neglected, throughout 120+ years of veterinary atlases and general textbooks (Budras et al. 2011; Crouch 1969; Ellenport 1975; Evans 1993; Gandhi 1975; Getty 1975; Kainer 1993; May 1970; Reighard and Jennings 1902); detailed comparative studies of the musculature of the external ear (Al-Sadi and Hasso 2012; Compton 1973; Diogo et al. 2012; Farag 2008; Huber 1922, 1923, 1924, 1930a, 1930b, 1931; Kneepkens and Macdonald 2010; Lamb and Sawin 1963; Minkoff et al. 1979; Zherebtsova 2012); its location merely as a landmark for veterinary surgery (Chow, Bennett, and Whittington 2011; Kushnir et al. 2018; Sharsher et al. 2020); and a convenient point for the insertion for data transponders into livestock (Conill et al. 2000; Klindtworth et al. 1999; Shojaeipour et al. 2021).

Anterior to the scutulum, a musculo-aponeurotic layer has been observed in a variety of taxa. This is formed by the fusion of the frontalis, occipitalis, and several auricular muscles. This structure is referred to variably as a pre-auricular aponeurosis, terminal line, einheitliche Sehnenplatte (Huber 1924–25, 1930a; Wiedersheim 1895), or more simply as a tendon plate (Tp). The Tp is attached to the anterior edge of the scutula in several taxa (Schneider and Möhres 1960).

In bats, the scutulum, auricular musculature, and the Tp have received some attention (Huber 1924–25; Schneider 1961; Schneider and Möhres 1960). This is in stark contrast to the number of studies that concern the size, shape, and acoustical properties of the pinna in bats (e.g., Boas 1912; Griffin et al. 1962; Pye, Flinn, and Pye 1962; Pye and Roberts 1970; Mogdans, Ostwald, and Schnitzler 1988; Raghunath Rao and Ben-Arie 1996; Walker, Peremans, and Hallam 1998; and more recently by Gao et al. 2011; Ma and Müller 2011; Qiu and Müller 2020; Wohlgemuth, Kothari, and Moss 2016; Yin et al. 2017; Yin and Müller 2019; Zhang et al. 2019). Heretofore, the most cohesive work on the scutula in bats is limited to three taxa—*Asellia tridens*, *Rhinolophus ferrumequinum*, and *Myotis myotis* (Schneider 1961; Schneider and Möhres 1960). Their careful dissections and detailed drawings were the impetus for the present work.

Here, we present a comparative anatomical study on 18 species of bat with some comments on functionality. The primary goal of this work was to extend the taxonomic breadth of our knowledge of the scutulum and Tp in bats.

We expected that (1) the scutulum is not a simple sesamoid element, (2) the Tp and scutulum work in a reciprocal manner to provide points of attachment for the auricular musculature, (3) the relative size and shape of these elements vary by taxa, and (4) these elements scale primarily with dimensions of the pinna, rather than the size of the bat.

TABLE 1b | Shape and size of the scutulum in 18 species of bat.

Taxon (by family)	Shape	Authors	Family	Size	EP′	SDL
Cynopterus sphinx	Quadrangular	Present study	Pteropodidae	Small	44	S
Rousettus sp.	Quadrangular	Medvedeva (1989)	Pteropodidae	Small	51	L
Taphozous hildegardeae	Quadrangular	Present study	Emballonuridae	Large	11	SD
Diclidurus isabellus	Quadrangular	Present study	Emballonuridae	Small	30	S
Nycteris thebaica	Ovoid	Present study	Nycteridae	Large	76	SD
Asellia tridens	Quadrangular	Schneider (1961)	Hipposideridae	Large	64	L
Hipposideros caffer	Quadrangular	Present study	Hipposideridae	Large	60	S
Rhinolophus eloquens	Quadrangular	Present study	Rhinolophidae	Large	88	SD
Rhinolophus ferrumequinum	Quadrangular	Schneider and Möhres (1960)	Rhinolophidae	Large	64	SD
Noctilio leporinus	Quadrangular	Present study	Noctilionoidea	Large	34	SD
Pteronotus parnelli	Hourglass	Present study	Mormoopidae	Small	15	SD
Mormoops megalophylla	Hourglass	Present study	Mormoopidae	Small	—	S
Myotis myotis	V-Shaped	Schneider (1961)	Vespertilionidae	Small	15	L
Nyctalus noctula	Quadrangular	Medvedeva (1989)	Vespertilionidae	Large	—	L
Molossus molossus	Quadrangular	Present study	Molossidae	Large	36	S
Tadarida brasiliensis	Triangular	Present study	Molossidae	Small	24	S
Otomops martiensseni	Quadrangular	Present study	Molossidae	Large	36	SD
Myopterus daubentonii	Quadrangular	Present study	Molossidae	Large	—	S

Abbreviations: EP′ = cephalometric angle between the palate and horizontal semicircular canals (see Pedersen 1993 and Pedersen and Müller 2013), gray shading = nasal emitting taxa, SDL where S = scanned, D = dissected, L = drawn from the literature.

2 | Materials and Methods

Microcomputed topography (μCT) was used to visualize the scutulum in 18 species of bat (Table 1a). Most specimens were provided by the Royal Ontario Museum (ROM) and scanned at East Tennessee State University using a Bruker Skyscan 1273 μCT scanner both before and after contrast enhancement with Lugol's iodine (Gignac et al. 2016). Each head was submerged in iodine for 7 days before being rescanned. The *Tadarida brasiliensis* and *Molossus molossus* specimens were provided by the Field Museum of Natural History and scanned using a Phoenix *V*|tome|x S μCT scanner housed at The University of Chicago. The *Cynopterus sphinx* specimen came from the laboratory of Tim Smith and was scanned twice (traditional and contrast-enhanced) with a General Electric phoenix V|tome|x M 240 μCT scanner at the University of Florida Nanoscale Research Facility.

Image registration of the traditional and contrast-enhanced scans for each specimen was done in Dragonfly (Object Research Systems, Quebec, Canada). Following which, the scutulum was segmented from the contrast-enhanced data set and the skull from the traditional data set. This ensured that our rendered 3D models of the scutulum's position relative to the skull were accurate. All scans are available on MorphoSource (https://www.morphosource.org) with a unique identifier (Table 2).

The pinna and scutulum are both cartilaginous and they absorbed similar amounts of iodine and, therefore, had a similar appearance (Figure 1). The skin lining the pinna and the subscutularis muscle served as ready landmarks when identify the scutulum in the contrast-enhanced scans. However, the periphery of a very thin scutulum could be difficult to determine in our μCT data sets. Conversely, there were instances where the scan showed an outline of a structure that could not be confirmed by dissection, but we believe these to be the result of adjacent structures confounding the segmentation process due to similarity in iodine uptake. Where possible, precise visualization of the scutular shape was achieved through dissection. Upon comparing the traditional and contrast-enhanced μCT data sets of *Otomops martiensseni* it became obvious to us that the scutulum of this species is heavily mineralized and can be visualized with traditional μCT alone. Therefore, we included three other molossid species (*Myopterus daubentonii, M. molossus*, and *T. brasiliensis*) for which we had traditional μCT data sets (Table 2).

Nearly 70 auricular muscle names were extracted from the literature cited herein. This nomenclature is historically complicated (ICVGAN [International Committee on Veterinary Gross Anatomical Nomenclature] 2017) yet many terms were easily synonymized, reducing this number to 30. These were subsequently tallied as to their attachments to the following in this order: Tp, scutulum, epicranius, and pinna (Table 3). Muscle attachments were documented for seven species via gross dissection under a Wild M5A dissection microscope (Table 1b). Data for additional taxa were critically evaluated and drawn from the literature.

Scutular size (large/small) was tallied as a simple ratio of the "maximum dimension of the squama" to the diameter of the auditory bulla when viewed laterally (Table 1a). The cephalometric angle between the palate and horizontal semicircular

TABLE 2 | Taxa used in this study and μCT scanning data.

Species (by facility)	Catalog #	Facility		Settings[a]	Identifier
Diclidurus isabellus	ROM109126	ETSU	Bone	12, 80, 187	ark:/87602/m4/495265
	Guyana		diceCT	12, 80, 187	ark:/87602/m4/548267
Hipposideros caffer	ROM39119	ETSU	Bone	12, 80, 187	ark:/87602/m4/495381
	Cameroon		diceCT	11, 80, 187	ark:/87602/m4/548280
Mormoops megalophylla	ROM54156	ETSU	Bone	11, 80, 187	ark:/87602/m4/495272
	Columbia		diceCT	12, 80, 187	ark:/87602/m4/548273
Noctilio leporinus	ROM58797	ETSU	Bone	13, 80, 187	ark:/87602/m4/495392
	Guyana		diceCT	11, 80, 187	ark:/87602/m4/548312
Nycteris thebaica	ROM73409	ETSU	Bone	11, 80, 187	ark:/87602/m4/495467
	Kenya		diceCT	12, 80, 187	ark:/87602/m4/548610
Otomops martiensseni	ROM66037	ETSU	Bone	11, 80, 187	ark:/87602/m4/495565
	Kenya		diceCT	12, 80, 187	ark:/87602/m4/548270
Pteronotus parnelli	ROM89770	ETSU	Bone	13, 80, 187	ark:/87602/m4/495406
	Jamaica		diceCT	11, 80, 187	ark:/87602/m4/548331
Rhinolophus eloquens	ROM56287	ETSU	Bone	13, 80, 187	ark:/87602/m4/495461
	Kenya		diceCT	13, 80, 187	ark:/87602/m4/548261
Rhinolophus ferrumequinum	SDSU2092	ETSU	Bone	12, 70, 214	ark:/87602/m4/549753
	China		diceCT	12, 70, 214	ark:/87602/m4/549770
Taphozous hildegardeae	ROM73478	ETSU	Bone	11, 80, 187	ark:/87602/m4/495568
	Kenya		diceCT	12, 80, 187	ark:/87602/m4/548264
Cynopterus sphinx	I-TS Cyno1	UF-NRF	Bone	20, 100, 100	ark:/87602/m4/365511
			diceCT	20, 100, 140	ark:/87602/m4/365359
Myopterus daubentonii	AMNH49228	UF-NRF	Bone	30, 100, 200	ark:/87602/m4/519270
	D. R. Congo				
Molossus molossus	FMNH204426	UC	Bone	—	—
	Puerto Rico				
Tadarida brasiliensis	FMNH55697	UC	Bone	—	—
	USA				

Abbreviations: ETSU = East Tennessee State University, ROM = Royal Ontario Museum, SDSU = South Dakota State University, UC = University of Chicago, UF-NRF = University of Florida Nanoscale Research Facility.

[a] Settings: pixel spacing (μm), voltage (kV), and amperage (μA).

canals distinguished rhinolophid and hipposiderid bats from other extant chiropterans (Pedersen 1993). This angle, EP′, is included in Table 1b for reference.

Taxonomically, the Rhinolophidae (106 species) and the Hipposideridae (91 species) are successful taxonomic radiations within the traditional Yangochiroptera. Both families are characterized by their use of the nasal passages as a waveguide during echolocation. We subsequently refer to these taxa as the Old-World nasal-emitting bats [OWNE] (after Pedersen 1993).

3 | Results

The scutulum typically consisted of a thin squama with a bossed lateral edge (Figures 2 and 3). The thickness of the squama decreased evenly toward the midline of the skull, finally merging into the superficial fascia. The extent to which a scutulum was lifted away from the neurocranium reflects the thickness of the underlying temporalis muscle and the subscutular musculature (Figure 3a–d). Many squama were thin enough to be nearly translucent and those of the molossids appeared to be calcified. Scutula varied considerably in size, where those of *Cynopterus*, *Mormoops*, and *Pteronotus* were diminutive while others were considerably larger (*Noctilio, Otomops*) (Figure 2). Squama are typically quadrangular. The scutula in OWNE are often depicted as triangular (Schneider 1961; Schneider and Möhres 1960), but careful dissection shows them to be quadrangular with the anteromedial 1/3 of the element being very thin and transparent (Table 1a). Taken together, the lamina and boss exhibit three general forms:

1. Simple lamina with a pronounced boss: The boss is tethered loosely to the adjacent pinna by connective tissue at the opposing ends of the boss. The arrangement of this connective tissue gave the impression of a two-point hinge

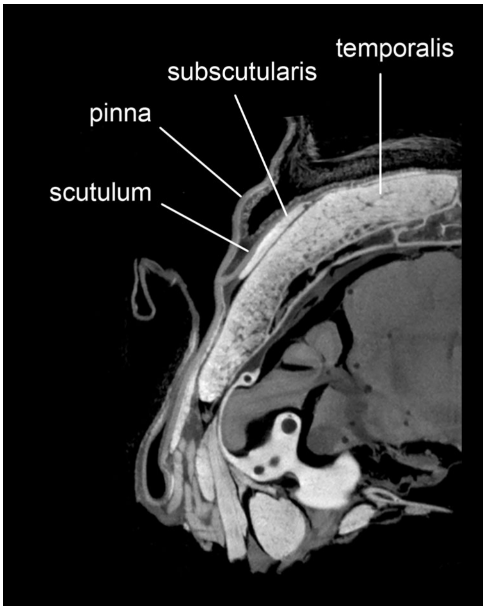

FIGURE 1 | DiceCT 2d slice of the head of *Hipposideros caffer*. Since the pinna and scutulum are both cartilaginous, they absorb a similar amount of iodine and have a similar appearance. The subscapularis muscle sits directly underneath the scutulum and was used as a landmark for identification.

that reinforces the tipping of the pinna medially or laterally about the large boss (*Noctilio*, *Taphozous*). This type of scutulum is characteristic of many Yangochiroptera.

2. Complicated lamina with a concave boss that faces ventrolaterally: The bossing neatly attends the convex outer surface of the auricle. The degree of contact varies in proportion to the curvature of the boss, the relative sizes of the scutulum and pinna, and the degree to which the squama and boss flare dorsolaterally away from the underlying temporalis fascia. The latter creates a unique subscutular fossa that is lined by a thin cushion of fat (corpus adiposum auriculae) which was removed in the photograph in Figure 1. As seen above, the boss was loosely tethered to the adjacent auricle at two points by connective tissue (Figure 1). A line drawn between these two points is roughly orthogonal to the long axis of the pinna. In combination, the tethers, the concave surface of the boss, and the depth of the subscutular fossa gave the impression of a socket joint equipped with a c-shaped meniscus for articulation with the pinna. The tethers of connective tissue should not interfere with the tipping of the pinna laterally in the socket, but it is unclear if the tethers would limit the rotation of the pinna within the socket. This type of scutulum is characteristic of *Rhinolophus*.
3. Large squama with an insignificant boss: These squama extend anteriorly as elongated plates that converge toward the midline, extending within the pinnae almost to the tip of the ear.

The yangochiropterans in this study have a Tp but these vary in both size and the number of muscles that are attached to them. Many of these Tps are quite narrow and are better referred to as terminal lines (Table 3). The Tp is best developed in OWNE bats (Figure 4). Two arrangements of connective tissue associated with the Tp warrant histological study in the future. First, the Tp in *Noctilio* extends laterally as a stiff strap-like element that blends imperceptibly into the oval tendon of the fronto-auricularis muscle. Second, the scutula of *Nycteris* do not have a bossed lateral edge, rather the squama is fused to the adjacent pinna apparently without interruption. The anterolateral edges of each scutulum extend as an elastic rod that bends toward the midline and becomes a narrow ligamentous element as it passes across the midline of the head.

The ratio between the number of muscles that insert on the scutulum to those that are relocated to the Tp (Table 3) is depicted graphically in Figures 4 and 5. The extreme form of which is *Asellia* with 14 slips of muscle attached to its Tp, whereas *Myotis* has but two.

Taxa are readily parsed into three broad categories (left to right, Figure 5): (1) those with relatively simple pinnae plus bats that do not laryngeally echolocate, (2) carnivores plus yangochiropterans that echolocate laryngeally, and (3) OWNE that echolocate laryngeally and have reapportioned their auricular muscles from the scutulum to the Tp. It is noteworthy that the pteropodid, *Rousettus*, is clustered with quadrupeds, rather than with OWNE.

The cephalometric angle, EP′, is large in OWNE (> 60°), which distinguishes them from the other bats in this study which have angles < 60° (Table 1b).

4 | Discussion

4.1 | Taxonomic Distribution and Derivation of the Scutulum

The scutulum is primarily a sesamoid element in mammals, whether it helps coordinate the action of auricular muscles or provides them with some mechanical advantage. Scutula are found in representative rodents, lagomorphs, ungulates, and carnivores (Table 1a). The data for additional taxa is sparse. The scutula of opossums are not well-defined (Minkoff et al. 1979) and Boas and Paulli (1908) could not identify scutula in *Centetes* (*Tenrec*) *ecaudatus*, yet the arrangement of the auricular muscles suggested they did have them at one time. The scutula in lemuroids and primates are also missing, arguably due to their well-developed mimetic facial musculature (Wiedersheim 1895).

The development of the scutulum has been neglected. Baum and Dobers (1905) suggested that the scutulum detaches from the spina helix of the pinna during development, this separation being the result of the pull of the attached auricular muscles. However, Boas (1912) found no indication of this in his detailed dissections of the external ear in 13 species of bat as well as dissections of other mammals. Subsequently, Huber (1924–25) posited that the scutulum evolved as a simple sesamoid element embedded within the tensile fields of the auricular musculature, a view that holds today.

The development of this element may not be complicated, that is, Lamb and Sawin (1963) demonstrated how the *dachs* gene

TABLE 3 | Differential muscle attachments for seven terrestrial mammals and 11 species of bat.

	Oryctolagus	*Equus*	*Babyrousa*	*Didelphis*	*Rousettus*	*Canis*	*Felis*	*Nasua*	*Taphozous*	*Nyctalus*	*Noctilio*	*Pteronotus*	*Myotis*	*Otomops*	*Nycteris*	*R. eloquens*	*R. ferrume-quinum*	*Asellia*
Frontalis epicranius				E	E				E		E		Tp	Tp				
Frontalis scutularis	S	S	S	S	S		Tp		E	Tp		TP				Tp	Tp	
Frontalis auricularis					P		Tp	S	P			TP		E	Tp			
Frontalis temporalis		S	S										S			Tp	Tp	
Fronto-scutularis frontalis superioris						P		Tp							Tp			Tp
Fronto-scutularis frontalis inferioris						Tp		Tp							Tp			Tp
Fronto-scutularis temporalis superioris										P	S							Tp
Fronto-scutularis temporalis inferioris										P	S							Tp
Auricularis anterior superioris				S	P	S	S		Tp	P	Tp	S	P		Tp	Tp	Tp	Tp
Auricularis anterior medialis							S		Tp		Tp	S	S		Tp	Tp	Tp	Tp
Auricularis anterior inferioris	P			S	P	Tp	Tp						P		P	P	P	Tp
Sphincter colli				S		S	S	Tp		E			E					
Mandibulo-scutularis				S														
Zygomatico-scutularis					S		S					S						
Zygomatico-auricularis	P	P				S		P	P	P			P	P	Tp	Tp	Tp	Tp
Interscutularis	S	S	P	S	S	S	S	S	S		S	P	S	S	Tp	Tp	Tp	Tp
Scutulo-auricularis	S	S			S				S	S	S	P						
Scutulo-auricularis anterioris	S																	
Scutulo-auricularis superioris						S												
Scutulo-auricularis superioris dorsalis		S	S					S						S				
Scutulo-auricularis superioris medialis		S	S											S				

(Continues)

TABLE 3 | (Continued)

	Oryctolagus	*Equus*	*Babyrousa*	*Didelphis*	*Rousettus*	*Canis*	*Felis*	*Nasua*	*Taphozous*	*Nyctalus*	*Noctilio*	*Pteronotus*	*Myotis*	*Otomops*	*Nycteris*	*R. eloquens*	*R. ferrumequinum*	*Asellia*
Scutulo-auricularis superioris ventralis		S	S											S				
Cervico-scutularis epicranius	S		E	E	E	E	E	E	E	E	Tp	P	Tp	Tp	Tp	Tp	Tp	Tp
Cervico-scutularis scutularis	S	S	S	S	S	S	S	S	S	S	S	P	E	S	S	S	S	S
Cervico-scutularis auricularis			P		P	P	P		S	P	P	P	P	P				
Parieto-auricularis		P	P					P										
Cervico-auricularis superioris major	P							P							P	P	P	P
Cervico-auricularis superioris minor	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Cervico-auricularis profundus minor	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Cervico-auricularis profundus major	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Tendon plate present	No	No	No	No	No	Yes	Yes	Yes	Yes	Line	Yes	Line	Line	Yes	Yes	Yes	Yes	Yes
# of muscles	12	13	13	12	14	14	14	14	14	13	13	13	14	13	14	13	13	15
Pinna	6	5	6	3	7	5	4	6	5	8	4	8	7	5	5	5	5	4
Epicranius	0	0	1	2	2	1	1	1	3	2	1	0	2	1	0	0	0	0
Scutulum	6	8	6	7	5	6	6	4	4	2	5	3	3	5	1	1	1	1
Tendon plate (Tp)	0	0	0	0	0	2	3	3	2	1	3	2	2	2	8	7	7	10
Tp/Scutulum x 10	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**3.3**	**5.0**	**7.5**	**5.0**	**5.0**	**6.0**	**6.7**	**6.7**	**4.0**	**80.0**	**70.0**	**70.0**	**100.0**

Note: Attachments are prioritized in the following order: Tp = tendon plate, S = scutulum, E = epicranius, and P = pinna. The last row (bold face) is a ratio of the number of muscles attached to the Tp divided by the number attached to the scutulum, all multiplied by 10. These data were used to generate Figure 5.
Abbreviations: E = epicranius, P = pinna, S = scutulum,Tp = tendon plate, and line = terminal line.

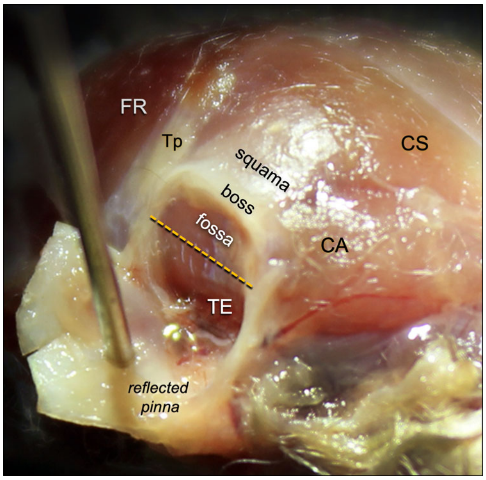

FIGURE 2 | Dissection of left scutulum in *Rhinolophus ferrumequinum*. Note the arched boss and the distinct subscutular fossa. The boss is tethered loosely to the adjacent pinna by connective tissue at the opposing ends of the boss, here indicated by the dotted orange line. This arrangement suggests a two-point hinge that may stabilize the tipping of the pinna medially or laterally about the boss. CA = cervicoauricularis, CS = cervicoscutularis, FR = frontalis, TE = temporalis, Tp = tendon plate.

(*dach1*) reduces the scutulum to a loose frame of connective tissue in affected rabbits. The auricular musculature is thereby displaced leading to a significant loss of function.

4.2 | Scutular Diversity

Manipulation of pinna, before and after dissection indicates that the three different types of scutular squama are primarily responsible for the general sesamoid functions of the scutulum. However, it is impossible to understand other scutular functions without considering the variety of linkages between the scutulum and the adjacent pinna. We have identified four of these.

1. Hinge-joint: The lateral edge of this type of scutulum bears a thick linear boss (e.g., *Noctilio*, *Taphozous*, and despite its size, *Pteronotus*) that is tethered to the pinna by short strands of connective tissue that extend from the ends of the boss. This arrangement suggests a simple hinge whereby the pinna rolls across the boss (fulcrum). Manipulation of dissected specimens indicated that these tethers restrict, but do not prevent, simple longitudinal rotations of the pinna against the scutulum. This infers that the tethers are there to stabilize the contact between the boss and the pinna during ear movements. In turn, axial rotations of the pinna are transferred in part to the interface between the scutular squama and the head.
2. Socket joint: This unique articulation is characterized by a concave boss lined with a c-shaped meniscus, which projects laterally over a subscutular fossa. A thin cushion of fat (corpus adiposum auriculae) lines this fossa, which accommodates the eminenta concha of the auricle. This is clearly represented by *Rhinolophus* (Figure 2), and, to a lesser extent, in *Hipposideros* and *Noctilio* (Figure 3). Given the presence of the same tethers (above) and the presence of relative size of the boss, this design may retain some function as a fulcrum. We suspect a continuum of form and function exists between the fulcrum and socket types of joint, with this socket form being the most derived. However, this socket design most likely stabilizes the bulk of the pinna during complex ear movements, particularly those lateral rotations when the pinna is held upright. It is entirely unclear how these tethers function, given the complexity of the movements associated with this unique articulation.

   The rate at which an individual pinna can move through a complete cycle varies amongst taxa: 80–83 Hz in several hipposiderids (Pye and Roberts 1970; Schneider 1961; Yin and Müller 2019), 40–50 Hz in several *Rhinolophus* (Gao et al. 2011; Griffin et al. 1962; Pye, Flinn, and Pye 1962; Pye and Roberts 1970), and < 25 Hz in *M. myotis* and *Eptesicus fuscus*, respectively (Schneider 1961; Wohlgemuth et al. 2016). These frequencies correlate well with the speed of the pinna tip: 1.25 m/s in *Hipposideros* and 0.8 m/s in *Rhinolophus* (Qiu and Müller 2020; Yin and Müller 2019). At such speeds, OWNE pinnae actively create Doppler shifts to encode additional sensory information (Gao et al. 2011; Yin and Müller 2019). Putting emitted echolocation frequencies aside, it is only in OWNE that we find a construct that includes this socket-like scutulum, exceptionally high pinna speeds, and an extensive Tp.
3. Fusion: In direct contrast to mobile hinge and socket joints, the pinna is effectively fused to the scutulum in *Nycteris*. There is no significant bossing of the relatively linear, lateral edge of the scutulum, the posterior-most third of which was fused to the pinna without interruption. In addition, the squama consists of a flattened toroid whose void is spanned by a very thin translucent membrane (presumably the perichondrium), through which the subscutularis is clearly visible. The anterolateral edges of each scutulum extend as an elastic rod that bends toward the midline (Figure 3b) and becomes a narrow ligamentous element as it passes across the midline of the head. Such drastic changes in the histological composition and thickness of these ligaments and cartilages are perhaps the greatest challenge when building accurate 3D models. Given this unique anatomy and taxonomic placement, further study of *Nycteris* is clearly warranted.
4. Support: In this limited sample, there are two molossids that exhibit both large pinnae and scutula—*Otomops* and *Myopterus* (Figure 3d). Ostensibly, large ears need a large, stable platform for their attachment to the head, this certainly being the case in flight. Large ears generate considerable drag during flight, but this is somewhat offset by the lift generated by the pinnae themselves at speed (Gardiner, Codd, and Nudds 2011; Johansson et al. 2016). To increase the lift-to-drag ratio, the ears can be brought to the front of the head and/or the aspect ratio of the pinnae can be reduced as done in most molossids. In some, the pinnae converge and fuse to form a "canard wing" (Bullen and McKenzie 2001, 2008; Vaughan 1966). Under the presumed loads imposed by such a wing, the size of those associated scutula should scale with the size of the relatively immobile pinnae. This is illustrated in a

comparison of molossids with large ears (*Myopterus, Otomops*) and those with smaller ears that is, *Tadarida* and *Molossus* (Figure 3d). Certainly, stability at the base of the pinna will help reduce deformation of the scapha in flight, which would interfere with the reception of echoes (Keeley and Keeley 2021; Keeley, Keeley, and Houlahan 2018) and will reduce control over lift, roll, pitch, and yaw movements of the bat (Bullen and McKenzie 2001, 2008; Gardiner, Codd, and Nudds 2011; Håkansson et al. 2017; Johansson et al. 2016; Vanderelst

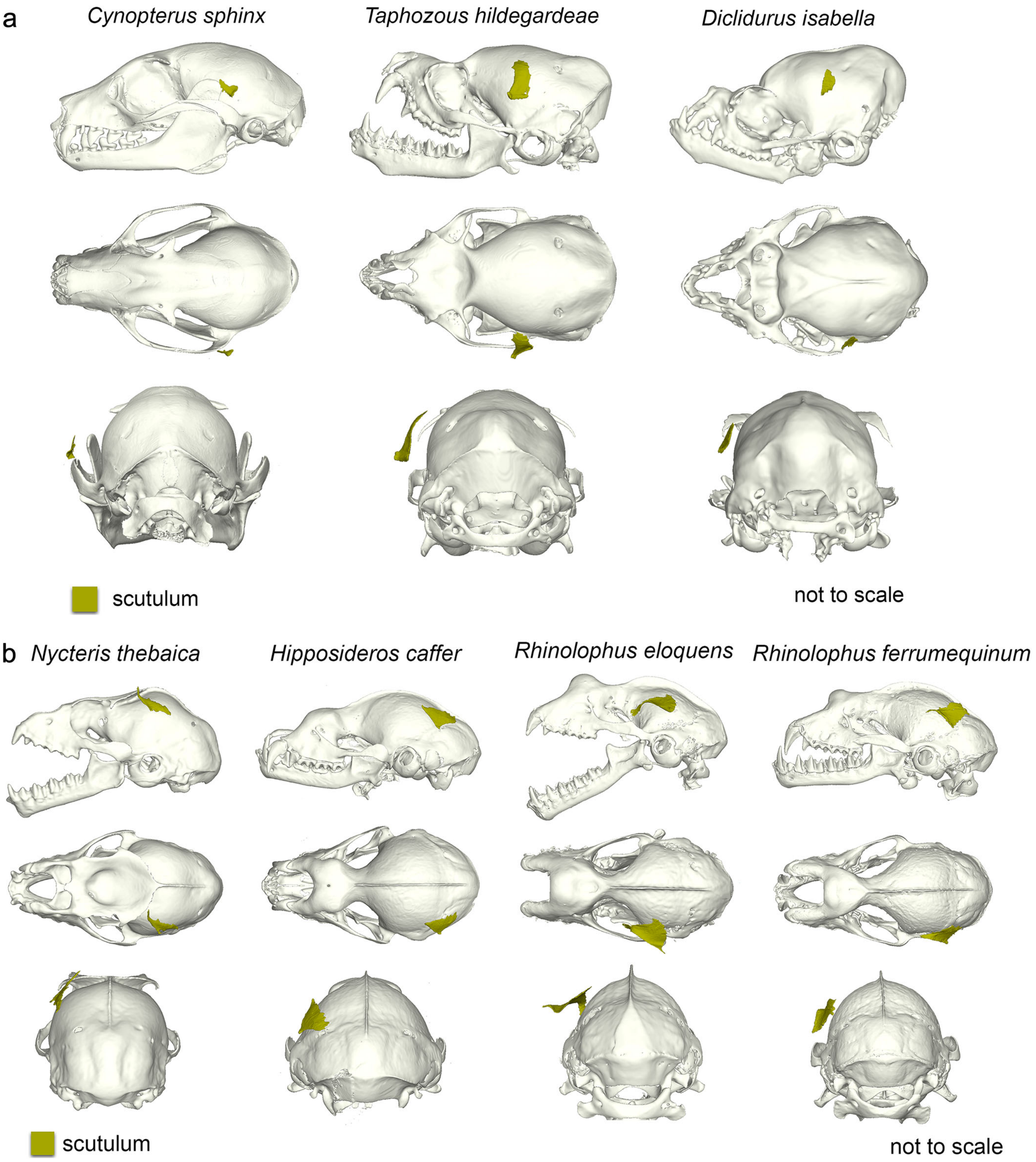

FIGURE 3 | (A) DiceCT 3D models of the skull and scutula of *Cynopterus sphinx, Taphozous hildegardeae*, and *Diclidurus Isabella*. (B) diceCT 3D models of the skull and scutula of *Nycteris thebaica. Hipposideros caffer, Rhinolophus eloquens*, and *Rhinolophus ferrumequinum*. (C) diceCT 3D models of the skull and scutula of *Noctilio leporinus, Pteronotus parnellii*, and *Mormoops megalophylla*. (D) diceCT 3D models of the skull and scutula of *Molossus molossus, Tadarida brasiliensis, Otomops martiensseni*, and *Myopterus daubentonii*.

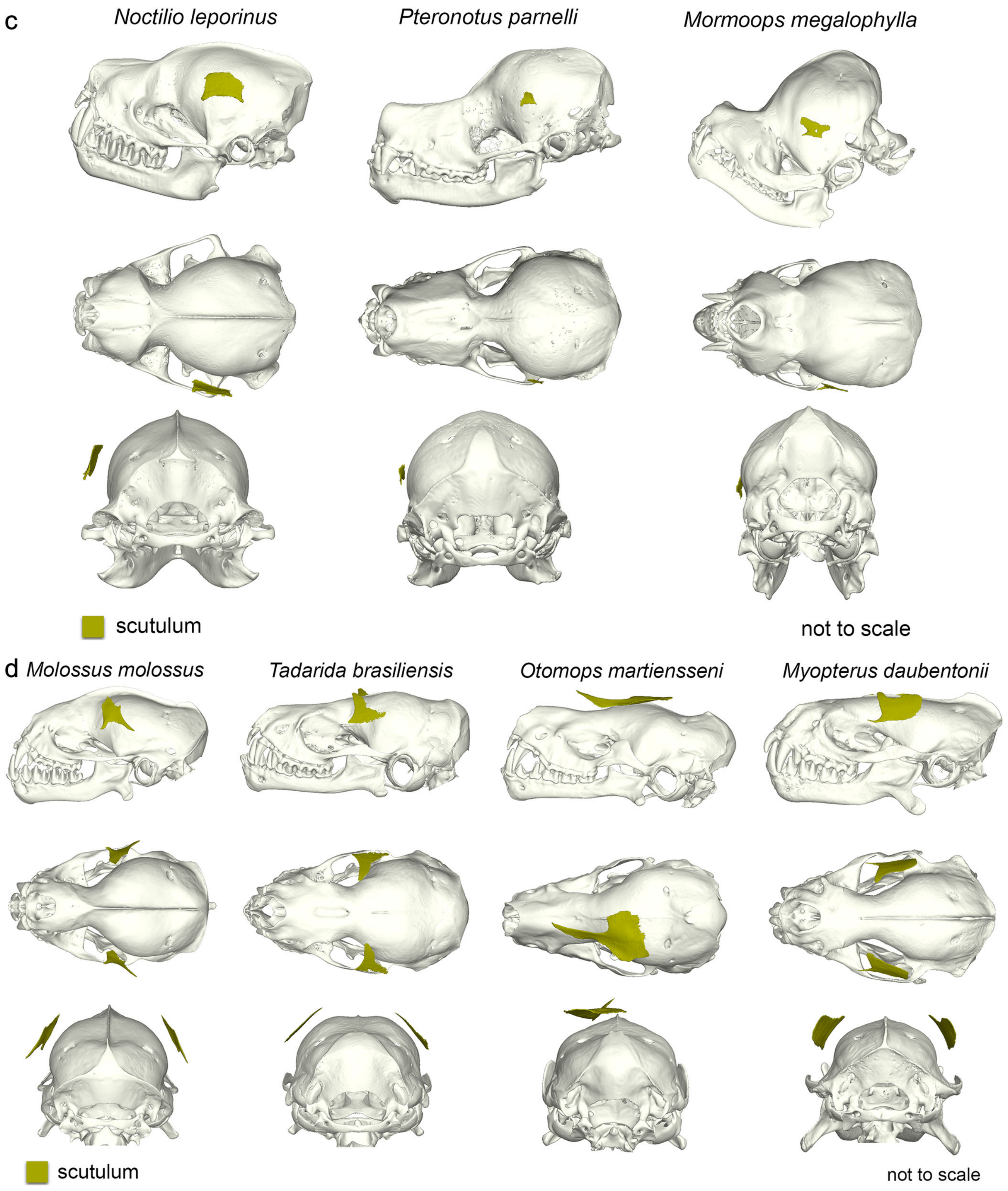

FIGURE 3 | (Continued)

et al. 2015). The intrinsic stability of the pinna is thought to be augmented by (1) pleated rows of muscles (transversus auriculae) and their connective tissues, and (2) a rod-like cartilage spine that runs most the length of the pinna which has its own muscle—the arrector auriculae (Schneider 1961, Schneider and Möhres 1960). In *Otomops*, the large scutula taper as they project forward until they become integrated into the pinna (Figure 3d). Manipulation of our specimens indicated that these unique scutula double the bending resistance of the pinna in the sagittal plane. We are currently building models to evaluate these stresses.

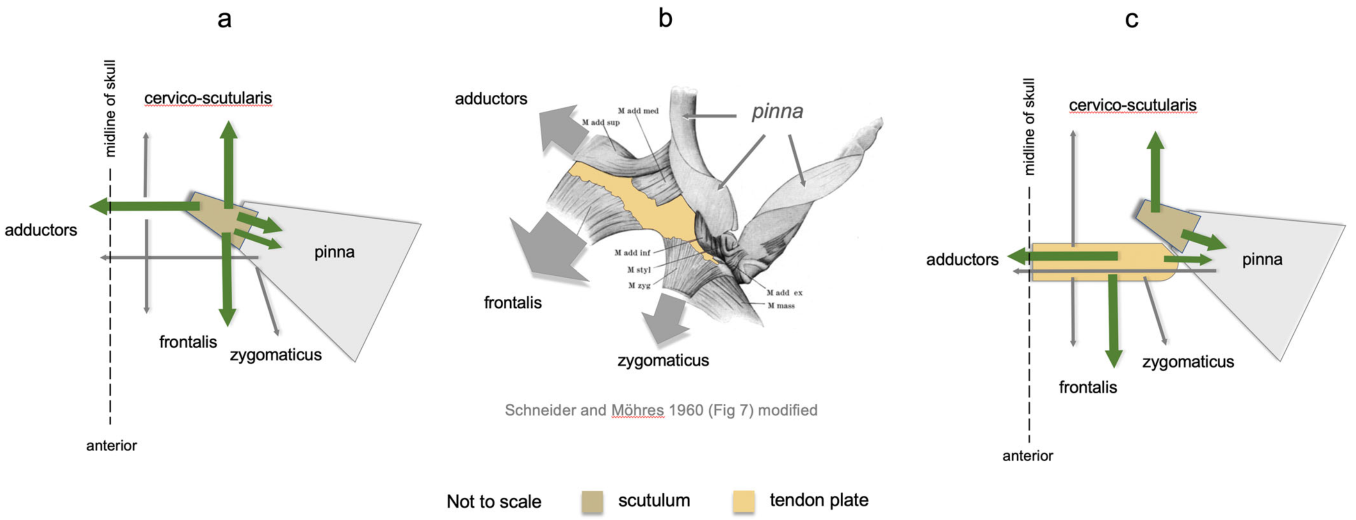

FIGURE 4 | Cartoons depicting the relationships among the scutulum, Tp, and pinna. (A) Generalized schematic for those animals in this study that do not have a well-developed Tp. (B) This diagram of the Tp in *Rhinolophus ferrumequinum* shows the depth and breadth of this aponeurosis and several muscles that relocated from the scutulum, pinna, and epicranius to the Tp. This is Figure 7 (modified) from Schneider and Möhres 1960. (C) Generalized schematic for OWNE wherein several muscles have moved from the scutula to the Tp. OWNE = old-world nasal-emitting bats, Tp = tendon plate.

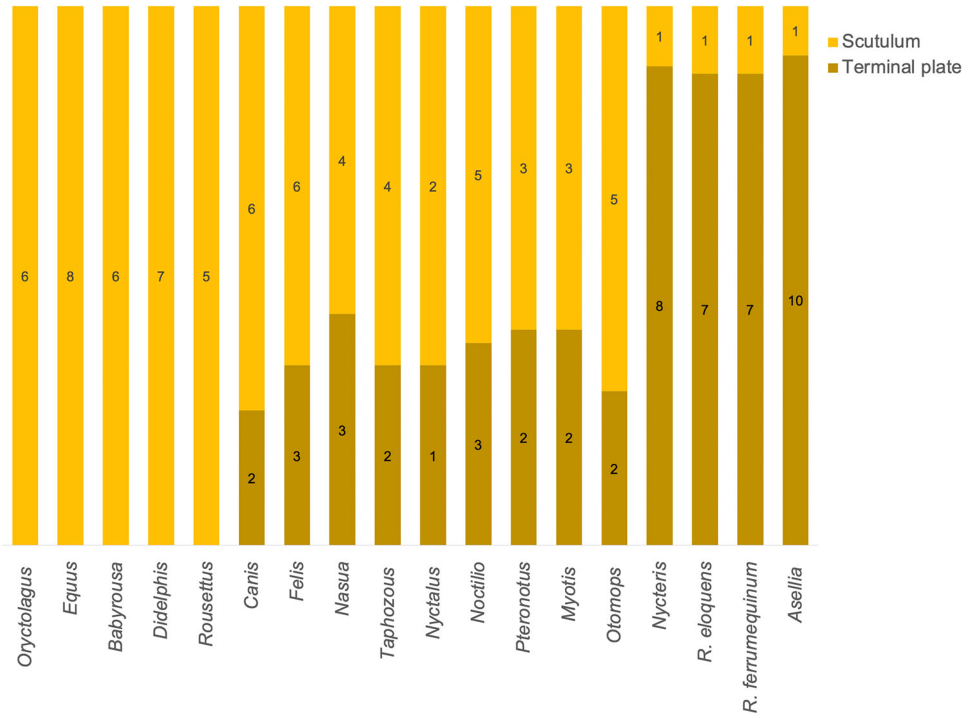

FIGURE 5 | Summary graphic the ratio of the number of muscles that attach to the scutulum to those muscles that have relocated to the Tp (Table 3). Taxa are distributed in three broad categories, left to right: (1) those with simple pinnae and do not laryngeally echolocate, (2) carnivores and yangochiropterans that exhibit a small Tp, and (3) OWNE that have a socket-joint type of scutulum and well-developed Tp. Tp = tendon plate.

4.3 | Sound Production and Movements of the Pinna

Pteropodids use a variety of behaviors to produce sound for echolocation: *Cynopterus brachyotis*, *Eonycteris spelaea*, and *Macroglossus sobrinus* clap the wing tips together (Boonman, Bumrungsri, and Yovel 2014; Holland, Waters, and Rayner 2004) *Rousettus aegyptiacus and R. amplexicaudatus* use tongue-clicking (Holland, Waters, and Rayner 2004), and Schoeman and Goodman (2012) have suggested that the vocalizations made by *Eidolon dupreanum* may be evidence of incipient laryngeal echolocation. The pinnae of pteropodids, marsupials, and most placental mammals are essentially spoon-shaped, with well-differentiated pre- and post-auricular muscle groups (Huber 1930b). The speed and mobility of these simple pinnae vary amongst taxa, but few exhibit modifications that would “tune” the pinna to a specific range of frequencies. Accordingly, the pinnae of pteropodids neither exhibit directional specialization (Obrist et al. 1993) nor do their auricular cartilages approach the complexity found in the ears of most bats (Boas 1912). In *Rousettus*, and perhaps pteropodids in general, the pinnae move in phase with each other during sound detection (Holland, 2009), but this generalization needs to be confirmed. In summary, the external ears of pteropodids represent a primitive arrangement, more closely allied with non-bats than with microchiropterans.

The diversity of pinna morphology among microchiropterans is most remarkable (Ma and Müller 2011; Mogdans, Ostwald, and Schnitzler 1988; Müller 2010; Walker, Peremans, and Hallam 1998). The intricate modifications of their pinna carry out important signal-processing operations before the echo is received by the ear drum. These modifications include horizontal pleats (Keeley and Keeley 2021; Keeley, Keeley, and Houlahan 2018), vertical sound-diffracting flaps (Müller, Lu, and Buck 2008; Wang and Müller 2009), and a variety of notches and folds. The tragus and antitragus are dynamic mobile elements near the base of the pinna that also contribute to signal processing (Chiu and Moss 2007; Müller 2004; Müller, Lu, and Buck 2008; Zhuang et al. 2023). These structures are found only within the external ears of laryngeally echolocating bats. Their pinnae move alternately fore-and-aft, 180′ out-of-phase, wherein hipposiderid bats exhibit exceptional cycle rates (80–83 Hz) and ear tip velocities (~1.25 m/s). The pinnae in OWNE are remarkably dynamic, wherein their movements include both rigid and nonrigid deformations (Gao et al. 2011), each of which has its own acoustic functions (Yin et al. 2017). There is a general correlation between the size of the pinna and the frequency of the emitted call in microchiropterans (Obrist et al. 1993). This is minimally correlated in those bats that emit frequency-modulated, low-duty-cycle calls. However, there is a strong, significant correlation between the dimensions of the ear and call frequency in hipposiderid bats (OWNE), which emit constant-frequency, high-duty cycle echolocative calls.

4.4 | Post-Auricular Muscles

Primitive laurasiatherians are thought to have two post-auricular muscles, each of which has three heads: the cervico-scutularis (C-S epicranialis, scutularis, and auriculares) and the cervico-auricularis (C-A superficialis, medialis, and profundus) (Chi, Meguro, et al. 2023; Chi, Tu, et al. 2023). The C-S and its fasciae lay superficial to the cervico-auriculares, placing these six muscular heads in an overtly simplistic 3-over-3 layout (Table 3). This arrangement is found in the Pteropodidae, the Yangochiroptera (Chi, Meguro, et al. 2023; Schneider 1961), most entries in Table 3, but not in OWNE. The three heads of the C-A muscle mostly originate on the sagittal crest in pteropodids, whereas the origins of these muscles in microchiropterans have relocated sequentially to the nuchal crest, in part or in whole (Chi, Meguro, et al. 2023; Chi, Tu, et al. 2023; Medvedeva 1989; Schneider 1961; Schneider and Möhres 1960; and this study). This latter arrangement distinguishes the Microchiroptera from both pteropodids and non-bat laurasiatherians, inferring this as the derived state for Chiroptera (Chi, Meguro, et al. 2023).

OWNE have six muscular slips that form two distinct groups as well, albeit in a 2-over-4 arrangement wherein the C-S has two heads (epicranialis and scutularis) and the cervico-auriculares has four (superioris major and minor, and the profundus major and minor), which is a derived condition for bats (Table 3). This nomenclature follows that of Schneider (1961), but it does not easily synonymize with that suggested for general case in bats (Chi, Meguro, et al. 2023), nor with idiosyncratic terminology (e.g., Medvedeva 1989). As such, we suggest the following homologies (Chi, Meguro, et al. 2023; Schneider 1961): C-S auricularis = C-A sup. major, C-A superficialis = C-A sup. minor, C-A medialis = C-A prof. minor, C-A profundus = C-A prof. major. It is most likely that the C-S auricularis in most bats has been transformed into the C-A superficialis major in OWNE. This is supported by the fact that both are the most superficial muscles near the vertex of the skull in both the 3-over-3 and 2-over-4 post-auricular muscle arrangements.

4.5 | Redistribution of Muscles From the Scutulum to the Tp

The Tp and terminal lines appear in several mammalian taxa. Most are small, isolated aponeuroses that connect the frontalis muscle to preauricular muscles or directly to the pinna (Huber 1930a; Reighard and Jennings 1902; Wiedersheim 1895), or to the anterior edge of the scutulum (Huber 1923; Schneider and Möhres 1960). The Tp is not found in *Didelphis*, *Oryctolagus*, *Babyrousa, Equus*, Lemuridae, Hominidae, and *Rousettus*, but the carnivores (*Canis*, *Felis*, and *Nasua)* have well-developed Tp (Table 3). All yangochiropterans in this study have either terminal lines or a small Tp which vary in the number of muscles that are attached to them. The Tp in OWNE bats is a broad tendon common to many pre-auricular muscles (Figure 4) and scutula that bear very few (Schneider and Möhres 1960). The ratio of the number of “muscles that attach to the scutulum” to those “muscles that have relocated to the Tp” is depicted in Figure 5.

Taxa in this study are distributed in three broad categories, left to right: (1) those taxa with simple pinnae and do not laryngeally echolocate, (2) carnivores and yangochiropterans that exhibit a terminal line or a small Tp, and (3) OWNE that have a socket-joint type of scutulum and a well-developed Tp.

In OWNE, parts or the entirety of the following muscles have relocated to the Tp: zygomatico-auricularis, inter-scutularis, and the C-S epicranius. Some obvious “shifts,” for example, auricularis anterior, reflect synonym issues (auricularis anterior vs. scutulo-auricularis), rather than some aspect of the functional matrix around the Tp.

We presume that by unloading the scutulum, it is free to adopt new functions. The most obvious of which is the shift from being a hinge joint to becoming the more complicated socket joint seen only in OWNE. It is most likely that the evolution of this joint has been driven by both pinna speed and the range of pinna movements. If so, there would seem to be a division of labor. By relocating many of the pre-auricular muscles to the Tp, the scutulum is bypassed, perhaps leaving it to function as a socket joint in relative isolation. In this scenario, the large Tp in OWNE may serve as an elastic storage element which would be more responsive to high-speed movements of the pinnae than would the scutula and their associated muscles and connective tissues.

The various components of the frontalis muscle typically originate on the frontal bone. Our dissections of *R. ferrumequinum* show that this muscle runs from the Tp to the lateral edges of the noseleaf via a thin aponeurosis, that is, it does not attach to bone. Usui, Khannoon, and Tokita (2022) noted the lack of a boney origin for this muscle as well in embryos of this species. Further work is necessary, but it is intriguing to think that the Tp is tacitly involved in the control of both the pinnae and the noseleaf as well.

4.6 | The Tp and Head Posture

Cephalometric data have shown that the skulls of microchiropteran bats follow one of two mutually exclusive sets of construction rules based on the ultimate use of either the oral cavity or the nasal passages as a waveguide when projecting sound (Pedersen 1993, 1995; Pedersen and Müller 2013). In general, the rostrum of oral-emitting bats is stereotypically located well above the inertial axis of the head in flight (dorsiflexed), whereas nasal-emitting bats fly with their rostrum at or well below the inertial axis of the head (ventro-flexed)—this typifies both OWNE and Phyllostomidae, with very few exceptions (Table 1b). Apart from the sternodermatines, many phylostomids exhibit flexibility in their use of either nasal- or oral-emisson, despite the construction of their skulls (Gessinger et al. 2021). In most OWNE, the distribution of bone associated with their exaggerated head postures, suggests that these skulls are poorly designed to resist torsional/bending forces. The Tp is a broad, conformational sheet of connective tissue that is well-developed only in OWNE. This points to two testable hypotheses: (1) are their exaggerated head postures driving the size and location of the Tp, and (2) did the Tp (also) evolve as an elastic element to compensate for a perceived loss of boney integrity in the midface?

It is also interesting to speculate that transition from the 3-over-3 to the 2-over-4 arrangement of post-auricular muscles in OWNE was driven by the downward rotation of the rostrum and the subsequent translation of the Tp forward, such that the ancestral C-S muscle is distracted, with the C-A scutularis and C-A epicranius retaining their connection to the Tp, and the C-S auricularis retaining its connection with the vertex of the skull.

4.7 | Yinpterochiroptera

There has been considerable debate over whether early chiropterans could echolocate, laryngeally or otherwise (Fenton 2010; Simmons et al. 2008, 2010; Snipes and Carter 2021; Thiagavel et al. 2018; Veselka et al. 2010) and the fossil record is understandably mute regarding the evolution of cartilaginous structures like the scutulum and pinna, let alone the Tp (Simmons et al. 2008, 2010). Genome-based phylogenetics has suggested that the non-echolocating pteropodids and the highly sophisticated OWNE are closely related to each other within the Yinpterochiroptera (Eick, Jacobs, and Matthee 2005; Hutcheon and Kirsch 2006; Springer et al. 2001; Teeling et al. 2002). Even if released from the morphological strictures of ultrasonic echolocation (Giannini and Simmons 2012), there is little or nothing about pteropodid anatomy (hyoid suspension, dentition, brains, cranial development, cranial vasculature, neuro-acoustic systems, thoracic compliance, reproductive biology, and now scutular morphology) that would support such a relationship (Jones et al. 2002; Nojiri et al. 2021; Usui et al. 2024; see discussion in Pedersen and Timm 2012). These data and that from the current study do not uphold Yinpterochiroptera, rather they support the traditional phylogeny of bats as composed of the Yangochiroptera, Yinochiroptera, and the Pteropodidae (Jones et al. 2002; Simmons and Geisler 1998).

5 | Conclusion

We expanded the taxonomic breadth of our knowledge of the scutulum and Tp to include 18 species of bat. Our description of the range of scutular morphology, the redistribution of auricular muscles, and the novelty of the Tp have greatly improved our understanding of the mechanical linkage between the head and pinnae. The scutulum is not a simple sesamoid element, and the relative size and shape of these elements vary by taxa and scale primarily with dimensions of the pinna and presumably the complexity of pinna movements. The relationship between the size of the scutulum and Tp across taxa does not exist as a continuum related to function as expected, rather, it is a dichotomy driven by the order of magnitude difference in the relative muscularity of the Tp among taxa.

In this study, bats fell into one of three groups: (1) pteropodid, (2) oral-emitting, and (3) nasal-emitting bats. However, to put this into perspective, the advent of nasal-emitting bats required a dramatic redesign of the rostrum and skull base during development. This subsequently effected changes in head posture and the probability of a nascent noseleaf. Nasal emission is, therefore, a key innovation responsible for two of the most dramatic morphological radiations in the Chiroptera—phyllostomids in the New World (~200 species) and hipposiderid and rhinolophid bats in the Old World (~200 species combined) (reviews by Pedersen and Timm 2012; Pedersen and Müller 2013). The nasal emitters subsequently developed their own neuroacoustic and auditory systems in parallel, if not in isolation.

We are left with two intriguing questions: (1) Did the socket-type of scutulum and the Tp coevolve to become the key innovation that led to the most technologically advanced and arguably the most derived taxon in the Order? and (2) Phyllostomids were not included in this study, but do the linkages between their heads and pinnae follow the OWNE example, or what structures have they coopted and modified to best support movements of the pinna?

Experimental work in the future is clearly warranted but will be limited by the high cycle speeds (80 Hz) of the pinna, the small sizes of the scutulum, and the diversity of the auricular muscles across taxa. Our sample size is being increased and the taxonomic diversity expanded to include the Megadermatidae and Rhinopomatidae. The highly diverse phyllostomids will receive a separate study where we can better address allometry and feeding guild associations. We are currently building 3D models with our enhanced μCT data set for *Otomops*, to examine how their large scutulae have been dramatically modified to increase the structural integrity of the pinnae in flight.

Author Contributions

Scott C. Pedersen: investigation (lead), analysis of the data, generation of tables and figures, primary writing. **Chelsie C. G. Snipes:** collected, scanned, and interpreted the diceCT data, digital segmentations and visualizations of scutula. **Richard T. Carter:** collected, scanned, and interpreted the diceCT data, digital segmentations of scutula. **Rolf Müller:** provision of specimens for dissection, critical guidance throughout.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All scans are available on MorphoSource (https://www.morphosource.org) with a unique identifier (Table 2).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/jmor.70006.

References

Al-Sadi, S., and A. A. Hasso. 2012. “Comparative Study of the Auricle and External Acoustic Meatus of the Cattle and Buffalo.” *Iraqi Journal of Veterinary Sciences* 26: 65–72.

Baum, H., and R. Dobers. 1905. “Die Entwickelung des Äusseren Ohres bei Schwein und Schaf.” *Beiträge und Referate zur Anatomie und Entwickelungsgeschichte* 28: 587–690. https://doi.org/10.1007/BF02274654.

Boas, J. E. V. 1912. *Ohrknorpel und äusseres ohr der Säugetiere; eine vergleichend-anatomische Untersuchung*. Kopenhagen: Nielsen & Lydiche.

Boas, J. E. V., and S. Paulli. 1908. *The Elephant's Head—Studies in the Comparative Anatomy of the Organs of the Head of the Indian Elephant and Other Mammals*. Jena: Gustav Fischer.

Boonman, A., S. Bumrungsri, and Y. Yovel. 2014. “Nonecholocating Fruit Bats Produce Biosonar Clicks With Their Wings.” *Current Biology* 24: 2962–2967.

Bradley, C. O. 1923. *The Topographical Anatomy of the Head and Neck of the Horse*, 228. Edinburgh: Green & Son.

Budras, K. D., O. M. Sack, S. Röck, A. Horowitz, and R. Berg. 2011. *Anatomy of the Horse*. 6th ed. Hannover, Germany: Schlütersche Verlagsgesellschaft mbH & Co. KG.

Bullen, R., and N. L. McKenzie. 2001. “Bat Airframe Design—Flight Performance, Stability and Control in Relation to Foraging Ecology.” *Australian Journal of Zoology* 49: 235–261. https://doi.org/10.1071/ZO00037.

Bullen, R. D., and N. L. McKenzie. 2008. “Aerodynamic Cleanliness in Bats.” *Australian Journal of Zoology* 56: 281–296.

Chi, T. C., F. Meguro, M. Takechi, et al. 2023. “Anatomy and Homology of the Caudal Auricular Muscles in Greater Short-Nosed Fruit Bat (*Cynopterus sphinx*).” *Journal of Veterinary Medical Science* 85: 571–577. https://doi.org/10.1292/jvms.23-0088.

Chi, T. C., V. T. Tu, J. Sohn, J. Kimura, and D. Koyabu. 2023. “Caudal Auricular Muscle Variations and the Evolution of Echolocation Behavior in Pteropodid Bats.” *Journal of Veterinary Medical Science* 85: 625–630. https://doi.org/10.1292/jvms.23-0128.

Chiu, C., and C. F. Moss. 2007. “The Role of the External Ear in Vertical Sound Localization in the Free Flying Bat, *Eptesicus fuscus*.” *Journal of the Acoustical Society of America* 121: 2227–2235. https://doi.org/10.1121/1.2434760.

Chow, E. P., R. A. Bennett, and J. K. Whittington. 2011. “Total Ear Canal Ablation and Lateral Bulla Osteotomy for Treatment of Otitis Externa and Media in a Rabbit.” *Journal of the American Veterinary Medical Association* 239: 228–232.

Compton, R. W. 1973. “Morphological, Physiological, and Behavioural Studies of the Facial Musculature of the Coati (*Nasua*).” *Brain, Behavior and Evolution* 7: 85–103.

Conill, C., G. Caja, R. Nehring, and O. Ribó. 2000. “Effects of Injection Position and Transponder Size on the Performances of Passive Injectable Transponders Used for the Electronic Identification of Cattle.” *Journal of Animal Science* 78: 3001–3009.

Crouch, J. E. 1969. *Text-Atlas of Cat Anatomy*. Philadelphia: Lea & Febiger.

Diogo, R., F. Pastor, F. de Paz, et al. 2012. “The Head and Neck Muscles of the Serval and Tiger: Homologies, Evolution, and Proposal of a Mammalian and a Veterinary Muscle Ontology.” *Anatomical Record* 295: 2157–2178.

Eick, G. N., D. S. Jacobs, and C. A. Matthee. 2005. “A Nuclear DNA Phylogenetic Perspective on the Evolution of Echolocation and Historical Biogeography of Extant Bats (Chiroptera).” *Molecular Biology and Evolution* 22: 1869–1886.

Ellenport, C. R. 1975. “The Ear of Carnivores.” In *The Anatomy of the Domestic Animals*, edited by R. Getty, 5th ed. Philadelphia: W. B. Sounders Co.

Evans, H. E. 1993. *Miller's Anatomy of the Dog*. Philadelphia: W. B. Saunders.

Farag, F. M. M. 2008. “Some Gross Anatomical Studies on the External Acoustic Meatus and Cartilages of the External Ear in the Rabbit.” *Kafrelsheikh Veterinary Medical Journal* 6: 174–195.

Fenton, M. B. 2010. “Convergences in the Diversification of Bats.” *Current Zoology* 56: 454–468.

Gandhi, S. S. 1975. “The Middle Ear.” In *The Anatomy of the Domestic Animals*, edited by R. Getty, 5th ed. Philadelphia: W. B. Sounders Co.

Gao, L., S. Balakrishnan, W. He, Z. Yan, and R. Müller. 2011. “Ear Deformations Give Bats a Physical Mechanism for Fast Adaptation of Ultrasonic Beampatterns.” *Physical Review Letters* 107: 214301.

Gardiner, J. D., J. R. Codd, and R. L. Nudds. 2011. “An Association Between Ear and Tail Morphologies of Bats and Their Foraging Style.” *Canadian Journal of Zoology* 89: 90–99.

Gessinger, G., R. Page, L. Wilfert, A. Surlykke, S. Brinkløv, and M. Tschapka. 2021. “Phylogenetic Patterns in Mouth Posture and Echolocation Emission Behavior of Phyllostomid Bats.” *Frontiers in Ecology and Evolution* 9: 630481. https://doi.org/10.3389/fevo.2021.630481.

Getty, R. 1975. "Equine Digestive System." In *The Anatomy of the Domestic Animals*, edited by R. Getty, 5th ed. Philadelphia: W. B. Sounders Co.

Giannini, N. P., and N. B. Simmons. 2012. "Toward an Integrative Theory of on the Origin of Bat Flight." In *Evolutionary History of Bats: Fossils Molecules and Morphology*, edited by G. F. Gunnell and N. B. Simmons, 353–384. Cambridge: Cambridge University.

Gignac, P. M., N. J. Kley, J. A. Clarke, et al. 2016. "Diffusible Iodine-Based Contrast-Enhanced Computed Tomography (diceCT): An Emerging Tool for Rapid, High-Resolution, 3-D Imaging of Metazoan Soft Tissues." *Journal of Anatomy* 228: 889–909. https://doi.org/10.1111/joa.12449.

Griffin, D. R., D. C. Dunning, D. A. Cahlander, and F. A. Webster. 1962. "Correlated Orientation Sounds and Ear Movements of Horseshoe Bats." *Nature* 196: 1185–1186.

Håkansson, J., L. Jakobsen, A. Hedenström, and L. C. Johansson. 2017. "Body Lift, Drag and Power Are Relatively Higher in Large Eared Than in Small-Eared Bat Species." *Journal of the Royal Society Interface* 14: 20170455. https://doi.org/10.1098/rsif.2017.0455.

Holland, R. A., and D. A. Waters. 2005. "Echolocation Signals and Pinnae Movement in the Fruitbat Rousettus Aegyptiacus." *Acta Chiropterologica* 7: 83–90. https://doi.org/10.3161/1733-5329(2005)7[83:ESAPMI]2.0.CO;2.

Holland, R. A., D. A. Waters, and J. M. V. Rayner. 2004. "Echolocation Signal Structure in the Megachiropteran Bat *Rousettus aegyptiacus* (Geoffroy 1810)." *Journal of Experimental Biology* 207: 4361–4369.

Huber, E. 1922. "Über das Muskelgebeit des Nervus facialis beim Hund, nebst allgemeinen Betrachtungen über die Facialis-Muskulatur." *Morphologisches Jahrbuch* 52: 1–110.

Huber, E. 1923. "Über das Muskelgebeit des Nervus facialis beim Hund, nebst allgemeinen Betrachtungen über die Facialis-Muskulatur." *Morphologisches Jahrbuch* 52: 353–414.

Huber, E. 1924–1925. "Der M. mandibulo-auricularis, nebst Bemerkungen über die Ohrmuschel und das Scutulum der Säugetiere. Zur Wertschätzung der Innervationsverhaltnisse bei vergleichend-morphologischen Muskelunter-suchungen." *Anatomischer Anzeiger* 59: 353–379.

Huber, E. 1930a. "Evolution of Facial Musculature and Cutaneous Field of Trigeminus, Part I." *Quarterly Review of Biology* 5: 133–188.

Huber, E. 1930b. "Evolution of Facial Musculature and Cutaneous Field of Trigeminus, Part II." *Quarterly Review of Biology* 5: 389–437.

Huber, E. 1931. *Evolution of Facial Musculature and Facial Expression*. Baltimore: Johns Hopkins University Press.

Hutcheon, J. M., and J. A. W. Kirsch. 2006. "A Moveable Face: Deconstructing the Microchiroptera and a New Classification of Extant Bats." *Acta Chiropterologica* 8: 1–10.

ICVGAN (International Committee on Veterinary Gross Anatomical Nomenclature). 2017. *Nomina Anatomica Veterinaria*, 6th ed. Columbia MO: World Association of Veterinary Anatomists.

Johansson, L. C., J. Håkansson, L. Jakobsen, and A. Hedenström. 2016. "Ear-Body Lift and a Novel Thrust Generating Mechanism Revealed by the Complex Wake of Brown Long-Eared Bats (*Plecotus auritus*)." *Scientific Reports* 6: 24886. https://doi.org/10.1038/srep24886.

Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. "A Phylogenetic Supertree of the Bats (Mammalia: Chiroptera)." *Biological Reviews* 77: 223–259. https://doi.org/10.1017/S1464793101005899.

Kainer, R. A. 1993. "Clinical Anatomy of the Equine Head." *Veterinary Clinics of North America. Equine Practice* 9: 1–23. https://doi.org/10.1016/S0749-0739(17)30413-3.

Keeley, B. W., A. Keeley, and P. Houlahan. 2018. "Ridge Number in Bat Ears Is Related to Both Guild Membership and Ear Length." *PLoS One* 13, no. 7: e0200255.

Keeley, B. W., and A. T. H. Keeley. 2021. "Acoustic Wave Response to Groove Arrays in Model Ears." *PLoS One* 16, no. 11: e0260020. https://doi.org/10.1371/journal.pone.0260020.

Klindtworth, M., G. Wendl, K. Klindtworth, and H. Pirkelmann. 1999. "Electronic Identification of Cattle With Injectable Transponders." *Computers and Electronics in Agriculture* 24: 65–79.

Kneepkens, A. F. L. M., and A. A. Macdonald. 2010. "Cranial Muscles of the Sulawesi Babirusa (*Babyrousa celebensis*)." *Anatomia Histologia Embryologia* 39: 120–137.

Kushnir, Y., G. S. Marwitz, Y. Shilo-Benjamini, and J. Milgram. 2018. "Description of a Regional Anaesthesia Technique for the Dorsal Cranium in the Dog: A Cadaveric Study." *Veterinary Anaesthesia and Analgesia* 45: 684–694.

Lamb, N. P., and P. B. Sawin. 1963. "Morphogenetic Studies of the Rabbit. XXXIII. Cartilages and Muscles of the External Ear as Affected by the Dachs Gene (Da)." *American Journal of Anatomy* 113: 365–388.

Ma, J., and R. Müller. 2011. "A Method for Characterizing the Biodiversity in Bat Pinna as a Basis for Engineering Analysis." *Bioinspired Biomimetics* 6: e026008.

May, D. S. N. 1970. *The Anatomy of the Sheep*. Brisbane, Australia: University of Queensland Press.

Medvedeva, G. A. 1989. "Evolutionary Tendencies in Development of Auricle Musculature in Bats." In *European Bat Research*, edited by V. Hanák, I. Horáĉek, and J. Gaisler, 49–60. Praha: Charles University Press.

Minkoff, E. C., P. Mikkelsen, W. A. Cunningham, and K. W. Taylor. 1979. "The Facial Musculature of the Opossum (*Didelphis virginiana*)." *Journal of Mammalogy* 60: 46–57.

Mogdans, J., J. Ostwald, and H.-U. Schnitzler. 1988. "The Role of Pinna Movement for the Localization of Vertical and Horizontal Wire Obstacles in the Greater Horseshoe Bat, *Rhinolopus ferrumequinum*." *Journal of the Acoustical Society of America* 84: 1676–1679.

Müller, R. 2004. "A Numerical Study of the Role of the Tragus in the Big Brown Bat." *Journal of the Acoustical Society of America* 116: 3701–3712. https://doi.org/10.1121/1.1815133.

Müller, R. 2010. "Numerical Analysis of Biosonar Beamforming Mechanisms and Strategies in Bats." *Journal of the Acoustical Society of America* 128: 1414–1425.

Müller, R., H. Lu, and J. R. Buck. 2008. "Sound-Diffracting Flap in the Ear of a Bat Generates Spatial Information." *Physical Review Letters* 100: 108701.

Nojiri, T., L. A. B. Wilson, C. López-Aguirre, et al. 2021. "Embryonic Evidence Uncovers Convergent Origins of Laryngeal Echolocation in Bats." *Current Biology* 31: 1353–1365.e3.

Obrist, M. K., M. B. Fenton, J. L. Eger, and P. A. Schlegel. 1993. "What Ears Do for Bats: A Comparative Study of Pinna Sound Pressure Transformation in Chiroptera." *Journal of Experimental Biology* 180: 119–152.

Pedersen, S. C. 1993. "Cephalometric Correlates of Echolocation in the Chiroptera." *Journal of Morphology* 218: 85–98.

Pedersen, S. C. 1995. "Cephalometric Correlates of Echolocation in the Chiroptera II: Fetal Development." *Journal of Morphology* 225: 107–123.

Pedersen, S. C., and R. Müller. 2013. "Noseleaves & Nasal Emission." In *Bat Evolution, Ecology, & Conservation*, edited by R. Adams and S. Pedersen, 2–91. New York: Springer Press.

Pedersen, S. C., and D. W. Timm. 2012. "Cephalometry & Evolutionary Constraint in Bats." In *Evolutionary History of Bats: Fossils, Molecules & Morphology*, edited by G. Gunnell and N. Simmons, 470–499. New York: Cambridge University Press.

Pye, J. D., M. Flinn, and A. Pye. 1962. "Correlated Orientation Sounds and Ear Movements of Horseshoe Bats." *Nature* 196: 1186–1188.

Pye, J. D., and L. H. Roberts. 1970. "Ear Movements in a Hipposiderid Bat." *Nature* 225: 285–286.

Qiu, P., and R. Müller. 2020. "Variability in the Rigid Pinna Motions of Hipposiderid Bats and Their Impact on Sensory Information Encoding." *Journal of the Acoustical Society of America* 147: 469–479.

Raghunath Rao, K., and J. Ben-Arie. 1996. "Optimal Head Related Transfer Functions for Hearing and Monaural Localization in Elevation: A Signal Processing Design Perspective." *IEEE Transactions on Biomedical Engineering* 43: 1093–1105.

Reighard, J., and H. S. Jennings. 1902. *Anatomy of the Cat*. NY: Henry Holt and Co.

Schneider, H. 1961. "Die Ohrmuskulatur von *Asellia tridens* Geoffr. (Hipposideridae) und *Myotis myotis* Borkh. (Vespertilionidae) (Chiroptera)." *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie* 79: 93–122.

Schneider, H., and F. P. Möhres. 1960. "Die Ohrbewegungen der Hufeisenfledermäuse (Chiroptera, Rhinolophidae) und der Mechanismus des Bildhörens." *Zeitschrift für Vergleichende Physiologie* 44: 1–40.

Schoeman, M. C., and S. M. Goodman. 2012. "Vocalizations in the Malagasy Cave-Dwelling Fruit Bat, *Eidolon dupreanum*: Possible Evidence of Incipient Echolocation?" *Acta Chiropterologica* 14: 409–416. https://doi.org/10.3161/150811012X661729.

Sharsher, A., S. Ali, R. Rashed, and B. E. Abedellaah. 2020. "Ultrasound Imaging of Tympanic Bulla and the Surrounding Structures in Donkey (*Equus asinus*)." *Journal of Current Veterinary Research* 2: 21–27.

Shojaeipour, A., G. Falzon, P. Kwan, N. Hadavi, F. C. Cowley, and D. Paul. 2021. "Automated Muzzle Detection and Biometric Identification via Few-Shot Deep Transfer Learning of Mixed Breed Cattle." *Agronomy* 11: 2365.

Simmons, N. B., and J. H. Geisler. 1998. "Phylogenetic Relationships of Icaronycteris, Archaeonycteris, *Hassianycteris*, and *Palaeochiropteryx* to Extant Bat Lineages, With Comments on the Evolution of Echolocation and Foraging Strategies in Microchiroptera." *Bulletin of the American Museum of Natural History* 235: 1–182.

Simmons, N. B., K. L. Seymour, J. Habersetzer, and G. F. Gunnell. 2008. "Primitive Early Eocene Bat From Wyoming and the Evolution of Flight and Echolocation." *Nature* 451: 818–821. https://doi.org/10.1038/nature06549.

Simmons, N. B., K. L. Seymour, J. Habersetzer, and G. F. Gunnell. 2010. "Inferring Echolocation in Ancient Bats." *Nature* 466: E8. https://doi.org/10.1038/nature09219.

Sisson, S. 1914. *The Anatomy of the Domestic Animals*. Philadelphia and London: WB Saunders Co.

Sisson, S. 1975. "Equine Digestive System." In *The Anatomy of the Domestic Animals*, edited by R. Getty, 5th ed. Philadelphia: W. B. Sounders Co.

Snipes, C. C. G., and R. T. Carter. 2021. "The Hyoid as a Sound Conducting Apparatus in Laryngeally Echolocating Bats." *Journal of Anatomy* 240: 1020–1033.

Springer, M. S., E. C. Teeling, O. Madsen, M. J. Stanhope, and W. W. de Jong. 2001. "Integrated Fossil and Molecular Data Reconstruct Bat Echolocation." *Proceedings of the National Academy of Sciences of the United States of America* 98: 6241–6246.

Teeling, E. C., O. Madsen, R. A. Van Den Bussche, W. W. de Jong, M. J. Stanhope, and M. S. Springer. 2002. "Microbat Paraphyly and the Convergent Evolution of a Key Innovation in Old World Rhinolophoid Microbats." *Proceedings of the National Academy of Sciences of the United States of America* 99: 1431–1436.

Thiagavel, J., C. Cechetto, S. E. Santana, L. Jakobsen, E. J. Warrant, and J. M. Ratcliffe. 2018. "Auditory Opportunity and Visual Constraint Enabled the Evolution of Echolocation in Bats." *Nature Communications* 9: 98. https://doi.org/10.1038/s41467-017-02532-x.

Usui, K., E. R. Khannoon, and M. Tokita. 2022. "Facial Muscle Modification Associated With Chiropteran Noseleaf Development: Insights Into the Developmental Basis of a Movable Rostral Appendage in Mammals." *Developmental Dynamics* 251: 1368–1379.

Usui, K., T. Yamamoto, E. R. Khannoon, and M. Tokita. 2024. "Musculoskeletal Morphogenesis Supports the Convergent Evolution of Bat Laryngeal Echolocation." *Proceedings Biological Sciences* 291: 20232196. https://doi.org/10.1098/rspb.2023.2196.

Vanderelst, D., H. Peremans, N. A. Razak, E. Verstraelen, and G. Dimitriadis. 2015. "The Aerodynamic Cost of Head Morphology in Bats: May be not as Bad as it Seems." *PLoS One* 10, no. 3: e0118545. https://doi.org/10.1371/journal.pone.0118545.

Vaughan, T. A. 1966. "Morphology and Flight Characteristics of Molossid Bats." *Journal of Mammalogy* 47: 249–260.

Veselka, N., D. D. McErlain, D. W. Holdsworth, et al. 2010. "A Bony Connection Signals Laryngeal Echolocation in Bats." *Nature* 463: 939–942.

Walker, V. A., H. Peremans, and J. C. T. Hallam. 1998. "One Tone, Two Ears, Three Dimensions: A Robotic Investigation of Pinnae Movements Used by Rhinolophid and Hipposiderid Bats." *Journal of the Acoustical Society of America* 104: 569–579.

Wang, X., and R. Müller. 2009. "Pinna-Rim Skin Folds Narrow the Sonar Beam in the Lesser False Vampire Bat (*Megaderma spasma*)." *Journal of the Acoustical Society of America* 126: 3311–3318.

Wiedersheim, R. 1895. *The Structure of Man, an Index to His Past History*. London: Macmillan and Co.

Wohlgemuth, M. J., N. B. Kothari, and C. F. Moss. 2016. "Action Enhances Acoustic Cues for 3-D Target Localization by Echolocating Bats." *PLoS Biology* 14, no. 9: e1002544. https://doi.org/10.1371/journal.pbio.1002544.

Yin, X., and R. Müller. 2019. "Fast-Moving Bat Ears Create Informative Doppler Shifts." *Proceedings of the National Academy of Science of the United States of America* 116: 12270–12274.

Yin, X., P. Qiu, L. Yang, and R. Müller. 2017. "Horseshoe Bats and Old World Leaf-Nosed Bats Have Two Discrete Types of Pinna Motions." *Journal of the Acoustical Society of America* 141: 3011–3017.

Zhang, S., Y. Liu, J. Tang, L. Ying, and R. Müller. 2019. "Dynamic Relationship Between Noseleaf and Pinna in Echolocating Hipposiderid Bats." *Journal of Experimental Biology* 222: jeb210252. https://doi.org/10.1242/jeb.210252.

Zherebtsova, O. V. 2012. "The Auricle Muscles in the Relict Rodent *Laonastes aenigmamus* (Rodentia: Diatomyidae)." *Proceedings of the Zoological Institute RAS* 316: 273–281.

Zhuang, Q., W.-X. Zhai, F.-X. Wang, and R.-W. Kong. 2023. "Antitragus Suppresses Fundamental Harmonic Pulse in a Horseshoe Bat, *Rhinolophus sinicus*." *Acoustics Australia* 51: 107–113. https://doi.org/10.1007/s40857-022-00278-1.