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Review

The evolution of sanguivory in vampire bats: origins and convergences

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Abstract

Blood-feeding (sanguivory) has evolved more than two dozen times among birds, fishes, insects, arachnids, molluscs, crustaceans, and annelids; however, among mammals, it is restricted to the vampire bats. Here, the authors revisit the question of how it evolved in that group. Evidence to date suggests that the ancestors of phyllostomids were insectivorous, and that carnivory, omnivory, and nectarivory evolved among phyllostomids after vampire bats diverged. Frugivory likely also evolved after vampire bats diverged, but the phylogeny is ambiguous on that point. However, vampire bats lack any genetic evidence of a frugivorous past, and the behavioural progression from frugivory to sanguivory is difficult to envision. Thus, the most parsimonious scenario is that sanguivory evolved in an insectivorous ancestor to vampire bats via ectoparasite-eating, wound-feeding, or some combination of the two—all feeding habits found among blood-feeding birds today. Comparing vampire bats with other sanguivores, the authors find several remarkable examples of convergence. Further, it was found that blood-feeding has been ca. 50 times more likely to evolve in a vertebrate lineage than in an invertebrate one. The authors hypothesize that this difference exists because vertebrates are more likely than invertebrates to have the biochemical necessities required to assimilate the components of vertebrate blood.

Key words: blood-feeding, convergent evolution, Desmodontinae, hematophagy, sanguivory, vampire bats

Foreword

This article appears in a festschrift of the *Canadian Journal of Zoology* honouring the contributions of M. Brock Fenton to bat biology. Three decades ago, Dr. Fenton wrote a paper proposing that the vampire bats may have evolved from a wound-feeding insectivorous ancestor (Fenton 1992). That hypothesis, based on observations of other animals, was novel and would prove to be a significant contribution to the field. However, while Fenton's paper outlined predictions about fossils that might support or disprove the wound-feeding hypothesis, no such fossils have emerged. Here, with the benefit of 30 subsequent years of vampire bat research, we revisit Fenton's original question about the origins of blood-feeding in vampire bats. We (both coauthors) did our master's degrees under Dr. Fenton and had the privilege of doing fieldwork with him—including work on vampire bats. Dr. Fenton has been an inspiring mentor, collaborator, and friend throughout our careers, and we dedicate this article to him.

1. Introduction

Vampire bats are obligate sanguivores as adults, 30–40 g parasites that get all their nutrients from vertebrate blood. They are the only tetrapods that are obligate blood feeders, the only mammals that drink blood, and the only mammals that are parasites of other animals. However, the habit of blood-feeding has evolved many times in other species; so, just as selection has pushed vampires away from the typical mammalian body plan, it has also caused convergence on other blood feeders, physiologically, anatomically, and behaviourally. Here, we revisit the question of how the vampire bats evolved sanguivory, and explore the convergences with other blood-feeding animals.

1.1. A brief review of vampire bat biology

There are three species of vampire bats: the white-winged vampire bat, *Diaemus youngi* (Jentink, 1893); the hairy-legged vampire bat, *Diphylla ecaudata* Spix, 1823; and the common vampire bat, *Desmodus rotundus* (E. Geoffroy, 1810). The first two of these have physiological specializations for the blood of birds (Greenhall 1988; Hermanson and Carter 2020). *Desmodus* feed preferentially on, and have similar specializations for, the blood of mammals. All three species typically procure food by sneaking up on a much larger sleeping host, and taking blood while the host sleeps. *Diaemus* and *Diphylla* usually approach on the branches of trees in which birds roost, whereas *Desmodus* often approaches on the open ground.

To feed, vampire bats can reopen a previous bite wound, or they can prepare a new one, which can take up to 40 min—a process that includes moistening the area with saliva, shaving fur or feathers, and then biting the host (Greenhall 1972). Vampire bats lap blood that fills the divot at the site of the wound, feeding on 15–25 mL of blood (Hermanson and Carter 2020), a process facilitated by anticoagulants in their saliva. As blood is mostly water, a feeding bat must often eliminate excess water by urinating, but still finishes a meal weighing roughly 50% more than it did before it fed. After feeding, a bat flies back to its roost, where digestion and excretion continue.

Blood is low in fat, so energy from blood is physiologically difficult to store in tissues. As a result, vampires starve in ca. three days without food (Breidenstein 1982; Freitas et al. 2013). When a bat is unable to procure food, it can receive regurgitated blood from socially bonded kin and nonkin (Wilkinson 1984; Carter and Wilkinson 2013), a cooperative behaviour that was likely co-opted from maternal care, and may have shaped other aspects of their social structure and behaviour (Carter 2021).

1.2. How sanguivory evolved in bats: six hypotheses

Blood-feeding is assumed to be a synapomorphy of vampire bats (the three vampire bat species are the only members of the monophyletic subfamily Desmodontinae, within the family Phyllostomidae; Dávalos et al. 2020), but just how sanguivory first evolved has long been a source of speculation. Six hypotheses have been put forth to explain the evolutionary origins of blood-feeding in vampire bats, mostly differentiated by what food was eaten by the ancestors of vampire bats: ectoparasites, wounds, fruit, small animals, both fruit and small animals, or nectar.

1.2.1. Hypothesis 1: ectoparasite-eating

According to this hypothesis, the ancestors of vampire bats were insectivores that fed upon the invertebrate ectoparasites of large animals (e.g., biting insects and ticks). Over evolutionary time, the bats began feeding on the blood that emerged from the large animal's skin as the parasites were removed. Eventually, the bats made their own wounds, abandoning the ectoparasite prey (Gillette 1975; Turner 1975). (Note: throughout this paper, we use the term "insectivore" loosely, to mean an animal that eats any arthropods, including spiders, ticks, or mites.)

1.2.2. Hypothesis 2: wound-feeding

This hypothesis posits that sanguivory evolved as the result of insectivorous bats feeding on insects that accumulate around the wounds of large animals (Fenton 1992). From insectivory, the bats transitioned to feeding on body fluids at the injury site and then to blood. Unlike the ectoparasite-eating hypothesis, this one concerns bats feeding from wounds that they did not create themselves. The wound-feeding hypothesis includes the possibility for an intermediate step, in which bats fed upon the insect larvae (maggots) that can accumulate in wounds, but this is not a necessary step.

1.2.3. Hypothesis 3: ancestral frugivory

In this scenario, a frugivorous ancestor possessed teeth able to cut through tough fruit rinds (Slaughter 1970). That dentition became an exaptation used to bite through the tough skin of animals to procure blood.

1.2.4. Hypothesis 4: ancestral carnivory

This hypothesis is similar to the ancestral frugivory hypothesis, in that dentition that arose for one food type, in this instance small vertebrates, lent itself to biting through the skin of large animals to access blood (Ferrarezzi and Giminez 1996).

1.2.5. Hypothesis 5: ancestral omnivory

In this hypothesis, an arboreal ancestor had generalized dentition that allowed it to bite chunks of flesh from fruit and predate on small animals (Schutt 1998). A flexible hunting strategy and arboreal habits eventually brought it close enough to large animals to take bites from them, and then later to extract blood.

1.2.6. Hypothesis 6: ancestral nectarivory

This hypothesis appeared on a popular science blog (Naish 2007), and to our knowledge has not been mentioned in the refereed literature, but we mention it here for the sake of thoroughness: A nectar-feeding ancestor had dentition preadapted to liquid diets, and began feeding on the fluids at wound sites of other animals.

2. Resolving the debate: different types of evidence

To evaluate the relative likelihoods of the six hypotheses, we use phylogenetic relationships of vampire bats to those with other diet types to assess ancestral diets, and functional comparisons to other blood-feeding animals, as an indirect means of assessing the plausibility of different evolutionary scenarios. The fossil record of Desmodontinae offers little help, because the specimens uncovered thus far are from the late Pleistocene, Holocene, and early Pleistocene (Hermanson and Carter 2020), well after the evolution of sanguivory.

2.1. Phylogenetic evidence

Vampire bats are phyllostomids, a highly diversified lineage of at least 225 species (Simmons and Cirranello 2022), which spans almost every diet known among bats—carnivory, frugivory, insectivory, nectarivory, omnivory, and sanguivory. In the past, that diversity resulted in ambiguity about the diet type of the immediate ancestors to the blood-feeding desmodontines, but more recent molecular phylogenies (Shi and Rabosky 2015; Dávalos et al. 2020; López-Aguirre et al. 2022) suggest that the earliest phyllostomids were insectivorous. Species in the sister family to phyllostomids (Mormoopidae) are insectivorous, as are the first two clades to branch off from the rest of the phyllostomids (Fig. 1). The desmodontines are the next branch to diverge, and it is among the remaining phyllostomids (a clade containing eight subfamilies) that all other feeding styles arise.

In addressing what the ancestors of vampire bats ate, there are two possible interpretations of the phylogeny. The first is that desmodontines branched off from the rest of the phyllostomids before the transition from insectivory to frugivory occurred, and thus had insectivorous ancestors, supporting the ectoparasite-eating and wound-feeding hypotheses (Fig. 1, right arrow). A second possibility is that the shift from insectivory to frugivory happened before the vampire bats split off from their sister clade (Fig. 1, left arrow). If so, the ancestors of vampire bats may well have been fruit eaters, supporting the ancestral frugivory hypothesis. However, there is no genetic evidence of frugivory in vampire bats (see section 4.3, below), making the ancestral frugivory hypothesis less likely than ancestral insectivory.

The phylogeny does not support the hypotheses of ancestral carnivory, ancestral omnivory, or ancestral nectarivory, as those feeding habits arose well after desmodontines had diverged from the group. However, it is worth noting that an ancestral state reconstruction suggests that both visual and auditory systems were well developed in basal phyllostomids, which may have permitted them the behavioural flexibility to experiment with different diet types (Hall et al. 2021).

2.2. Functional evidence from other blood-feeding animals

Vampire bats share anatomical, physiological, and behavioural similarities with many other blood-feeding animals, from insects and ticks to leeches and lampreys. These trends are worth exploring in their own right, as remarkable examples of convergent evolution. However, in addition, insights from other animals also offer clues about what evolutionary sequence most likely led to sanguivory in mammals.

The closed circulatory system of vertebrates evolved more than 400 million years ago, and has been a target for parasites ever since (Mans 2011). As a result, a tremendous diversity of blood-feeding parasites has evolved. In fact, there are even blood feeders that take blood from other blood feeders: midges that resemble miniature mosquitoes, which suck blood from the engorged bellies of actual mosquitoes (Ma et al. 2013*b*).

In Table 1, we list all clades of animals known to have independently evolved sanguivory, defined narrowly for our purposes as animals that feed on vertebrate blood obtained from outside the host's body. We thus exclude blood-borne parasites, such as *Plasmodium* and *Schistosoma* (Hematozoa), blood flukes (Platyhelminthes), heartworms and hookworms (Nematoda), or larvae that feed on blood from within the flesh (some larval Diptera), which all face different selective pressures than vampire bats do. We also exclude the ingestion of blood by carnivores and scavengers as a by-product of eating flesh. However, even by our limited definition, there are still tens of thousands of blood-feeding animal species, with sanguivory having evolved independently at least 29 times (Table 1).

Our count likely underrepresents the true number of times blood-feeding has evolved, especially among arthropods, because it is difficult to know how many times sanguivory has been lost then re-evolved in a clade with many blood-feeding and nonblood-feeding species (Walter and Proctor 1999; Bradshaw et al. 2018). In Diptera, for example, blood-feeding may have evolved just 3 times, or as many as 10 times (Mans 2011).

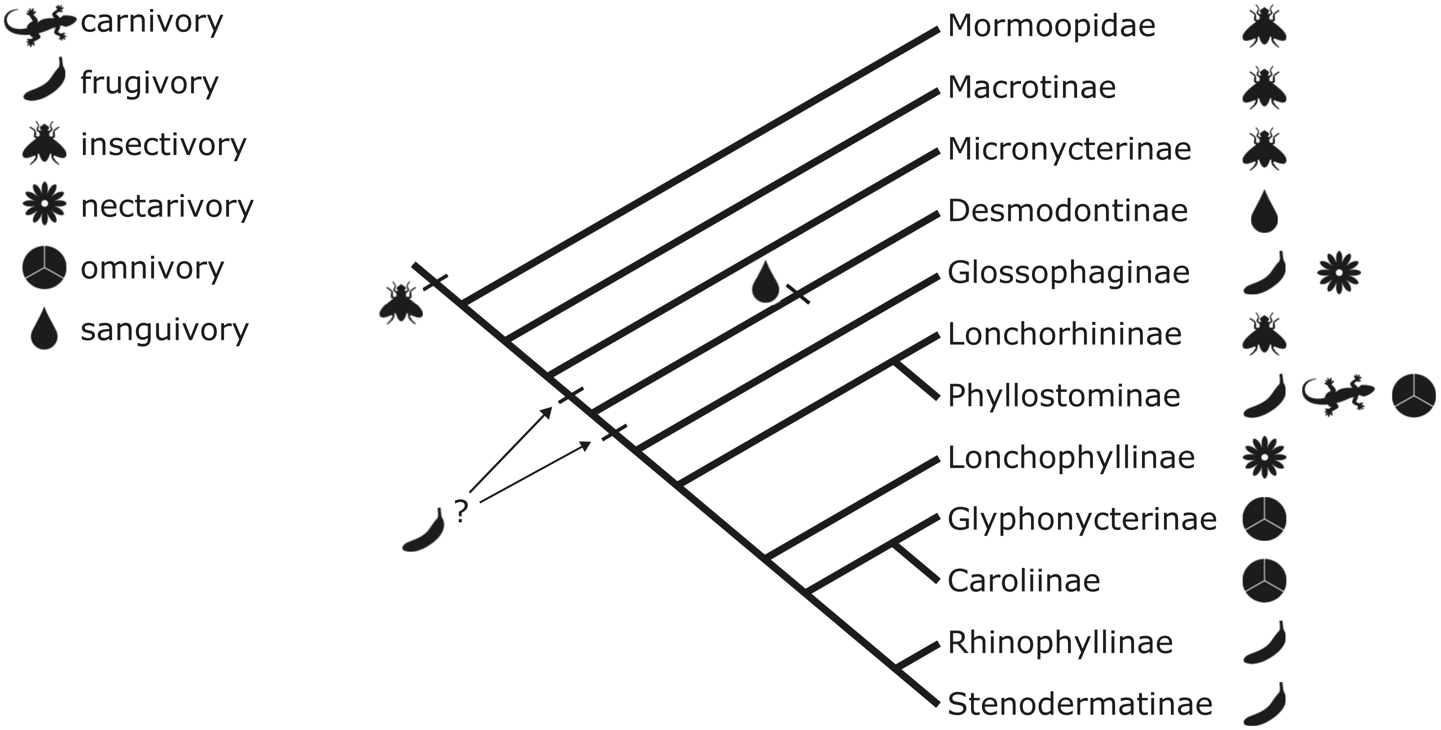
Although >14 000 insect species feed on blood (Ribeiro 1995), sanguivory has only evolved in insects ca. 16 times, and in arthropods ca. 20 times (Mans 2011; Arcà and Ribeiro 2018). This is remarkably close to the number of times sanguivory evolved in vertebrates (10 times, by our count: vampire bats, lampreys, catfishes, and seven bird clades; Table 1). Since there are many more species of insects and arthropods in the world (ca. 5.5 and 7 million, respectively; Stork 2018) than vertebrates (ca. 66 000; World Conservation Union 2014), we estimate that sanguivory has arisen at a rate roughly 50 times higher among vertebrates than among insects or arthropods. We hypothesize that this difference occurs because vertebrates' bodies already contain vertebrate blood, and are thus likely to possess biochemical tools that are effective for digesting and extracting nutrients from it. However, the increased rate at which vertebrates evolve sanguivory might alternatively reflect vertebrates being more likely to possess anatomical traits that facilitate access to blood (e.g., more powerful muscles, hard beaks or teeth, etc.).

3. The evolutionary pathway to sanguivory in other animals

Blood-feeding birds show that ectoparasite-eating and wound-feeding are both plausible on their own, and in concert. Some sanguivorous birds are ectoparasite-feeders (ground-finches, mockingbirds), others feed from wounds that they did not create themselves (sheathbills, skuas), and many do a combination of ectoparasite-eating and wound-feeding (cinclodes, caracaras, oxpeckers; Weeks 2000; Sazima and Sazima 2010; Sazima 2011). Thus, any of these three scenarios seems plausible for an ancestor to vampire bats.

In arthropods (a group for which the term "hematophagy" is typically used, rather than "sanguivory"), two different pathways are thought to have led to blood-feeding. In the first, arthropods developed close associations with vertebrates and then transitioned to blood-feeding. For example, the ancestors to some blood-feeding arthropods may have been attracted to the warm, humid, protected environment of a nest or burrow, where they fed upon organic matter (fungi, feces, etc.). For some, this diet would include dead skin and shed feathers, which could lead to seeking those food sources from the host directly. Arthropods having evolved

Fig. 1. The phylogenetic position of the vampire bats (Desmodontinae) relative to their closest relatives suggests that they evolved from an insectivorous ancestor (Shi and Rabosky 2015; Dávalos et al. 2020; López-Aguirre et al. 2022), with the transition from insectivory to frugivory in phyllostomids occurring after the desmodontines branched off (right arrow). This arrangement supports the ectoparasite-eating and/or wound-feeding hypotheses. If the shift from insectivory to frugivory in phyllostomids occurred before vampire bats branched off (left arrow), the ancestral frugivory hypothesis might be correct. However, vampire bats possess no genomic evidence of frugivory, and the transition from frugivory to sanguivory is difficult to envision.



hematophagy on this evolutionary pathway are expected to have chewing mouthparts, as in lice and mites, rather than piercing ones (Lehane 2005). This evolutionary sequence for arthropods is similar to the ancestral omnivory hypothesis proposed for bats, wherein frequent proximity to large animals leads to sanguivory (Schutt 1998).

In the second evolutionary pathway, piercing mouthparts for feeding on non-blood foods (insects or nectar, for example) were preadaptations to obtaining vertebrate blood. The plausibility of a transition from insects to blood is reflected by the hemipteran *Lyctocoris campestris* (Fabricius, 1794), which typically feeds on insects, but was also found to use its mouthparts to opportunistically take blood from sleeping humans in a student dormitory (Stys and Daniel 1957). Similarly, mosquitoes use their nectar-feeding mouthparts to obtain blood (Lehane 2005). These cases are consistent with the general idea that mouthparts can be co-opted for blood-feeding as required by the ancestral frugivory, ancestral carnivory, and ancestral nectarivory hypotheses.

The transitions to sanguivory in leeches, lampreys, and snails are less informative, as those evolutionary sequences are also not well understood. Modern leeches have two mechanisms to take blood—rhynchobdellid leeches insert a muscular proboscis into the flesh of their hosts, while arhynchobdellid leeches use sharp jaws to cut the flesh. Molecular analyses suggest that these did not evolve independently—that the ancestral leech was a blood feeder—but it is unclear what feeding style is ancestral (Siddall et al. 2016). Although the ancestral lamprey is believed to have been sanguivorous (Gill et al. 2003), its evolutionary transition to sanguivory has not, to our knowledge, been elucidated. Similarly, vampire snails have a remarkably complex feeding method—extending a long proboscis into the eye sockets of sleeping fishes—but just how that feeding style evolved is also unknown (Johnson et al. 1995).

4. Evidence for, and against, the six hypotheses

4.1. The ectoparasite-eating hypothesis

The idea that vampire bats got their start eating ectoparasites off large animals (Gillette 1975; Turner 1975) assumes an insectivorous ancestor, which is supported by phylogeny (Fig. 1). The plausibility of the ectoparasite-eating hypothesis is also supported by the observation that it parallels the evolutionary transition to sanguivory more clearly evident in several other blood-feeding animals, namely oxpeckers and ground-finches, which feed on a mix of ectoparasites

Table 1. Clades of animals in which sanguivory has independently evolved.

Count	Taxon	Number of sanguivorous species	Common name
1	Phylum Chordata Class Mammalia Order Chiroptera Family Phyllostomidae Subfamily Desmodontinae	Three: *Desmodus rotundus* *Diaemus youngi* *Diphylla ecaudata*	Vampire bats
2	Phylum Chordata Class Aves Order Passeriformes Family Buphagidae	Two: *Buphagus africanus* Linnaeus, 1766 *Buphagus erythrorynchus* (ES Stanley, 1814)	Oxpeckers
3	Phylum Chordata Class Aves Order Passeriformes Family Thraupidae	One: *Geospiza septentrionalis* Rothschild & Hartert, 1899 (sometimes considered a subspecies of *Geospiza difficilis*)	Vampire ground finch
4	Phylum Chordata Class Aves Order Passeriformes Family Furnariidae	One: *Cinclodes antarcticus* (Garnot, 1826)	Blackish cinclodes
5	Phylum Chordata Class Aves Order Charadriiformes Family Chionidae	One: *Chionis albus* (JF Gmelin, 1789)	Snowy sheathbill
6	Phylum Chordata Class Aves Order Falconiformes Family Falconidae	One: *Milvago chimachima*	Yellow-headed caracara
7	Phylum Chordata Class Aves Order Passeriformes Family Mimidae	Two: *Mimus* (*Nesomimus*) *macdonaldi*, *Mimus* (*Nesomimus*) *parvulus*	Española Mockingbird and Galápagos Mockingbird
8	Phylum Chordata Class Aves Order Charadriiformes Family Stercorariidae	One: *Stercorarius antarcticus* (R. Lesson, 1831)	Brown Skua (Antarctic Skua)
9	Phylum Chordata Infraphylum Agnatha Superclass Cyclostomata Class Hyperoartia	Though only 18 of the 40 known lamprey species feed on blood (e.g., *Petromyzon, Ichthyomyzon, Mordacia*), parasitism is the ancestral state for the family, Petromyzontidae (Gill et al. 2003)	Lampreys
10	Phylum Chordata Class Actinopterygii Order Siluriformes Family Trichomycteridae	>300 including the Candiru (*Vandellia cirrhosa* Valenciennes in Cuvier and Valenciennes, 1846)	Blood-feeding catfishes
11	Phylum Arthropoda Class Insecta Order Lepidoptera	One genus: 10 of 18 species in the genus *Calyptra* will feed on blood, at least under experimental conditions (Hill et al. 2010; Zaspel et al. 2012). "Other geometrid and pyralid moths will feed on blood oozing from wounds, or from drops of blood released from the anus of feeding mosquitoes" (Lehane 2005)	Vampire moths
12	Phylum Arthropoda Class Insecta Order Coleoptera	Unknown. "Species in which adults are ectoparasitic on mammalian hosts are found in the coleopteran groups Leptininae, Quediini, Amblyopinini and Languriidae" (Lehane 2005)	Beetles
13	Phylum Arthropoda Class Insecta Order Diptera Family Psychodidae	Roughly 600 species (Lehane 2005)	Sand flies

Table 1. (*continued*).

Count	Taxon	Number of sanguivorous species	Common name
14	Phylum Arthropoda Class Insecta Order Diptera Infraorder Culicomorpha	More than 10,000 spp. Family Culicidae (ca. 3500 species, though not all feed on blood): mosquitoes (Lehane 2005) Family Ceratopogonidae (>5000 species): blackflies, biting midges, punkies, no-see-ums Family Simuliidae (ca. 1800 species): mammal-feeding blackflies, buffalo gnats (Lehane 2005) Family Corethrellidae (ca. 100 species): frog-biting midges	Mosquitoes, blackflies, midges, buffalo gnats, etc.
15	Phylum Arthropoda Class Insecta Order Diptera Family Rhagionidae	Unknown. Most are predatory, but some feed on blood (Lehane 2005)	Snipe flies
16	Phylum Arthropoda Class Insecta Order Diptera Family Tabanidae	ca. 4300 species (Lehane 2005) Subfamily Tabaninae Subfamily Chrysopsinae	Clegs, horse flies, hippo-flies, deer flies
17	Phylum Arthropoda Class Insecta Order Diptera Family Muscidae	4200 species, but only a few feed on blood. Of the blood feeders, some have penetrating mouthparts, while others scrape through skin, or just take advantage of open wounds (Lehane 2005) e.g., *Stomoxys* spp.	Avian vampire flies (*Philornis downsi*), stableflies (*Stomoxys calcitrans*), headflies (*Hydrotaea irritans*), and *Musca planiceps*
18	Phylum Arthropoda Class Insecta Order Diptera Superfamily Hippoboscoidea	>700 spp. Family Glossinidae (22 species): including the tsetse fly, *Glossina morsitans* Westwood, 1851 Family Hippoboscidae (ca. 200 species): louse flies, including sheep keds (Lehane 2005) Family Strebilidae (ca. 239 species): strebilid batflies Family Nycteribiidae (ca. 275 spp.): nycteribiid batflies (Peterson et al. 2007; Graciolli and Dick 2018*a*, 2018*b*)	Tsetse flies, keds, batflies
19	Phylum Arthropoda Class Insecta Order Psocodea Infraorder Phthiraptera	There are ca. 5000 lice. Some sources say all feed on blood (Mans 2011), but others say not all do (Lehane 2005). Certainly, parasitism is believed to have evolved just once in the group, 100–115 mya, raising the possibility that the ancestors of lice fed on dinosaurs (de Moya et al. 2021)	Lice
20	Phylum Arthropoda Class Insecta Order Siphonaptera	ca. 2500. All ectoparasites of birds (6%) and mammals (94%)	Fleas
21	Phylum Arthropoda Class Insecta Order Hemiptera Family Cimicidae	ca. 100 species, all blood-feeding, mostly on bats, but also birds and humans (Lehane 2005)	Bedbugs
22	Phylum Arthropoda Class Insecta Order Hemiptera Family Reduviidae	138 spp: Subfamily Triatominae, most of which feed on blood (Lehane 2005)	Kissing bugs/assassin bugs
23	Phylum Arthropoda Class Insecta Order Hemiptera Family Polyctenidae	32 species (Dick and Bindokas 2007), all blood-feeding (Lehane 2005)	Bat bugs
24	Phylum Arthropoda Class Arachnida Subclass Acari Order Ixodida	ca. 900 spp. Family Ixodidae (hard ticks)—ca. 700 species Family Argasidae (soft ticks)—ca. 200 species (Guglielmone et al. 2010)	Ticks

Table 1. (*concluded*).

Count	Taxon	Number of sanguivorous species	Common name
25	Phylum Arthropoda Class Arachnida Subclass Acari Superorders Parasitiformes and Acariformes	More than 40 000 mites have been identified, but the true number is probably more than 1 000 000. Parasitic blood-feeding is widespread among mites, with multiple gains and losses of blood-feeding thought to have occurred (Walter and Proctor 1999; Van Dam et al. 2018)	Mites, chiggers
26	Phylum Arthropoda Subphylum Crustacea Class Copepoda Order Siphonostomatoida Family Pennellidae	Two species: *Pennella instructa* C.B. Wilson, 1917 *Pennella balaenopterae* Koren and Danielssen, 1877	Blood-feeding copepods
27	Phylum Arthropoda Subphylum Crustacea Class Isopoda Order Cymothoida Family Cymothoidae	11 species *Nerocila* spp.	Blood-feeding isopods
28	Phylum Mollusca Class Gastropoda Families Colubrariidae, Marginellidae, and Cancellariidae	At least six species. Best studied in *Cumia* (=*Colubraria*) spp.	Vampire snails
29	Phylum Annelida Class Clitellata Order Hirudinida	ca. 700	Leeches

Note: For some groups, sanguivory is only present in some members of the clade, but not all of them (e.g., only 18 of the 40 lamprey species feed on blood; Gill et al. 2003).

and blood, often taking both food types in a single meal. It is thus plausible that insectivorous protovampires did the same.

Ectoparasite-eating can be found in many different birds that are "cleaners", removing external parasites and organic debris, such as dead skin from large mammals. Sazima (2011) counted 101 bird species in 32 families that perform cleaning behaviour, though the majority are not known to take blood. The ubiquity of cleaning among birds suggests that it is a plausible evolutionary pathway to sanguivory for protovampire bats.

A dietary shift from insectivory to obligate sanguivory would require a period where animals fed on both, so that they could adapt physiologically to blood as a food resource over evolutionary time. The plausibility of this sequence of events is evidenced by one species of spider. While no spiders are known to feed directly on vertebrate blood, the jumping spider *Evarcha culicivora* (Wesolowska & Jackson, 2003) (Salticidae) obtains it indirectly by eating mosquitoes (Jackson et al. 2005). The spiders use the blood as a constituent for sex pheromones, and therefore preferentially hunt and eat female mosquitoes that have recently taken a blood meal (Cross et al. 2009). Similarly, vampire bat ancestors that fed upon blood-filled ectoparasites could have adapted to the blood within ticks or other prey, acquiring physiological adaptations to blood that would eventually permit obligate sanguivory.

The digestive tracts of vampire bats occasionally contain ingested insects (Arata et al. 1967; Greenhall 1972). This phenomenon has been taken as evidence supporting the ectoparasite-eating hypothesis, with the assumption insectivory is retained in vampire bats from the ancestral state (Turner 1975). Indeed, one of the insects found by Arata et al. (1967) in vampire bats was an ectoparasite. However, that study's observations of insects in the guts of 4 of 23 vampire bats may have little relevance to the origins of blood-feeding. Those insects could have been ingested accidentally, when insects were trapped in viscous blood, or during the frequent grooming and allogrooming that occurs in vampire bats (Wilkinson 1988; Carter and Leffer 2015). Since bat ectoparasites belong to phylogenetic groups not typically found on cattle or other host animals (Hemiptera: Cimicidae, Polyctenidae; Diptera: Strebilidae, Nycteribiidae; Acarina: Spinturnicidae), the source of the ectoparasite would have been clear had it been taxonomically identified. We therefore recommend that any future reports of insects in the digestive tracts of vampire bats include identification of the insects themselves.

4.2. The wound-feeding hypothesis

Like the ectoparasite-eating hypothesis, the wound-feeding hypothesis also assumes an insectivorous ancestor to vampire bats, which is phylogenetically supported. The plausibility of the wound-feeding hypothesis is also supported by its widespread occurrence in other blood-feeding animals. Wound-feeding is common among birds, such as skuas, shearwaters, and cinclodes that feed on the wounds of wounded pinnipeds (Sazima and Sazima 2010). Further, some muscid flies, such as the sheep head fly (*Hydrotaea irritans* (Fallen, 1823)), facultatively feed from the blood at wounds, though they do not make those injuries themselves (Lehane 2005).

Wound-licking is also performed by several moth species, including the blood-drinking *Calyptra* spp. (Hill et al. 2010).

4.3. The ancestral frugivory hypothesis

Slaughter (1970) first proposed the ancestral frugivory hypothesis as an explanation of how the vampire bats' sanguivorous dentition might have evolved from the dentition of a frugivorous ancestor. This rationale was motivated by morphology-based phylogenies that had desmodontines nested within a frugivorous clade—an arrangement that has since been disproved by molecular phylogenies. There is no evidence for genes associated with frugivory retained in vampire bats (Zepeda Mendoza et al. 2018), and all three species of vampire bats have lost genes associated with tasting sweet (and umami) foods (Hong and Zhao 2014).

If vampire bats supplemented their blood diets with fruit from time to time, this might be interpreted as a retained ancestral trait. Intriguingly, Trajano (1984) claimed that some *Desmodus* captured in Brazil passed feces that contained fruit, based on the atypical, greenish colour of the feces of multiple individuals, with one individual appearing to defecate seeds and fruit residues (pulp). However, this possibility requires further attention. Vampire bats in captivity, fed only blood, can sometimes exhibit lumpy, green feces when they are sick (G.G. Carter (personal observation)), and this could explain what Trajano observed. Other than that one anecdotal observation by Trajano (1984), there are no known instances of frugivory by vampire bats.

Slaughter (1970) only explained how ancestral frugivory could have led to changes in tooth shape, but why would a fruit-eating bat start biting large and dangerous animals? Slaughter did not elaborate on how such transitions would occur, only stating that this transition might have been direct or involved an intermediate stage of carnivory (ancestral carnivory hypothesis).

4.4. The ancestral carnivory hypothesis

If vampire bats evolved from a carnivorous ancestor, they would have had to evolve carnivory independently of other phyllostomids (Fig. 1). An evolutionary trajectory from carnivory to sanguivory is believed to have occurred in several arthropod taxa, such as hemipterans (Lehane 2005). In vertebrates, the carnivorous yellow-headed caracara (*Milvago chimachima* (Vieillot, 1816)) (Falconiformes) has been observed drinking blood from the wounds of capybara (Sazima and Sazima 2010), but closer examination reveals instead that this case better supports the wound-feeding or ectoparasite-eating hypothesis, because caracaras are known to feed on the wounds of, and glean ticks from, large mammals, including capybaras.

4.5. The ancestral omnivory hypothesis

The hypothesis that the ancestors to vampire bats were omnivorous envisions an arboreal ancestor taking fruit and invertebrates among the foliage, and then using its generalist dentition to bite the animals roosting there (Schutt 1998). The idea that the first vampire bats hunted arboreally is supported by the phylogeny of the vampire bats themselves (Ferrarezzi and Giminez 1996; Schutt 1998), because *Diaemus youngi* and the more basal *Diphylla ecaudata* are arboreal. However, while arboreality satisfies one assumption of the ancestral omnivory hypothesis, it does not rule out any of the other hypotheses.

An ancestral reconstruction based on cochlear and orbital sizes in phyllostomids suggests basal phyllostomids did have the sensory systems required for dietary flexibility (Hall et al. 2021). However, based on the feeding modalities of bats related to vampire bats, it appears that for desmodontines to have evolved from an omnivorous ancestor, they would have had to evolve that trait independently (Fig. 1).

The plausibility of ancestral omnivory is supported by the fact that some omnivorous birds take blood. Española Mockingbirds of Española Island, Galápagos (*Mimus macdonaldi* (Ridgway, 1890)) are omnivores, feeding on fruit, arthropods, and carrion, but they also take blood from the wounds of sea lions, marine iguanas, masked boobies, and even "twice attempted to drink blood from superficial wounds on the legs of field investigators" (Curry and Anderson 1987). *Mimus parvulus* (Gould, 1837) on nearby Santa Fe Island have also been observed drinking blood. The generalized beak shape of these omnivorous mockingbirds permits them the flexibility to drink blood, supporting the hypothesis that a generalized mammal could do the same. However, many of these wounds—certainly those on the researchers—were not made by the birds, and mockingbirds, like caracaras, are also "cleaners" of ectoparasites. Together, these facts support the ectoparasite-eating hypothesis, the wound-feeding hypothesis, or some combination of the two.

4.6. The ancestral nectarivory hypothesis

There is no clear rationale or evidence to support the ancestral nectarivory hypothesis. Although some nectar-feeding insects take blood—including mosquitoes and vampire moths—they feed by means of a proboscis that has been functionally modified into a hypodermic needle. Nectar-feeding bats lack a proboscis-like appendage and vampire bats do not obtain blood with piercing mouthparts. Nectar-feeding cannot be reasonably considered a special preadaptation to sanguivory in bats, as the ability to drink fluids is ubiquitous among mammals. Also, there is no evidence for traits or genes associated with nectarivory being retained in vampire bats (Hong and Zhao 2014; Blumer et al. 2022).

5. Noteworthy convergences of vampire bats with other blood-feeding animals

Vampire bats' sanguivory has resulted in several departures from the typical mammalian body plan, resulting in some convergences with much less closely related blood-feeding animals. Here, we review these, and organize them around the anatomical, physiological, and behavioural requirements of sanguivory.

5.1. Locating host animals

Vampire bats appear to locate food over a range of distances through some combination of olfaction, vision, echolocation, passive listening, and spatial memory (Hermanson and Carter 2020). *Desmodus* can also hear low frequencies better than most bats (Heffner et al. 2013), and can recognize individual humans by the sound of their breathing (Gröger and Wiegrebe 2006), which could help the bats find previous wounds for reopening on the same host. Vampire bats feed during the darkest part of the night, and as such can only see with their rods, having lost the colour vision present in their phyllostomid ancestors (Blumer et al. 2022).

Olfaction appears to help vampire bats to find and select their prey (Schmidt 1988; Bahlman and Kelt 2007) similar to other blood-feeding animals, including bedbugs (Harraca et al. 2010), ticks (Bunnell et al. 2011), and mosquitoes. *Aedes* mosquitoes distinguish and prefer humans over other potential hosts (Zhao et al. 2022). Ticks lack antennae, but have converged with other blood feeders in this regard, having evolved chemosensory organs at the tips of their first pair of legs (Josek et al. 2018).

5.2. Dealing with dangerous or elusive host animals

Feeding on the blood of a larger animal can be dangerous. For this reason, feeding *Desmodus* bring vibrissae on the noseleaf into contact with the skin of the host to give them a rapid means for detecting host movement and allowing a quick evasive jump if necessary (Schmidt 1988). Similar strategies to avoid host-induced injury are common among arthropod ectoparasites, such as mosquitoes (Cribellier et al. 2022). Horseflies even improve their escape performance by feeding on the darker, and warmer, locations of a host's skin, thereby increasing their own temperature-dependent muscle performance (Horváth et al. 2020). The need for rapid escape has resulted in a jumping ability and an overall terrestrial agility in *Desmodus* that exceeds that known for any other bat (Schutt et al. 1997; Riskin et al. 2006), giving them evasive abilities on par with a horsefly or deerfly.

Another way to avoid a host's aggression is to feed on it while it sleeps. This strategy is widespread among sanguivores, including bedbugs, mosquitoes, and vampire snails. *Diaemus* often avoid waking their hosts by feeding from a position adjacent to, but not directly on, the host's body, such as the underside of the branch upon which the bird is perched for the night. *Desmodus* and *Diphylla*, however, frequently feed from a position on the skin of the animal itself (Hermanson and Carter 2020).

Another challenge imposed by the long feeding times of vampire bats is the risk a host will wake up mid-feeding and run away. When this happens, *Desmodus* can use a running gait to chase after the animal without needing to take flight (Carranza and Campo 1982). The running gait of vampire bats is the only known running gait of a bat, and is the only known occurrence of a vertebrate lineage that has lost and then re-evolved the ability to run (Riskin and Hermanson 2005). The gait consists of a footfall sequence analogous to those seen in bounding squirrels, but with the roles of the forelimbs and hindlimbs reversed. The result is a gait that looks very much like "running push-ups," that is unique among tetrapods (Riskin et al. 2006).

5.3. Thermoreception

Vampire bats possess heat sensors on the noseleaf, giving them a sensitivity to infrared radiation—a signal of body temperature. No other mammal is known to have this ability. Vampire bats are presumed to use those organs to find a host's warm blood-filled capillaries near the surface of the skin. The organs are located in pits within folds of the noseleaf, and are roughly 9 °C cooler than surrounding noseleaf tissues just millimeters away (Kürten and Schmidt 1982). These thermosensitive organs of vampire bats are reminiscent of the "pit organs" found anterior to the eyes on some venomous snakes (Crotalidae; Kishida et al. 1984) used to locate the warm bodies of potential prey and to choose which part of the body to strike. Taking advantage of this, ground squirrels often heat their tails to induce a less deadly tail-oriented strike (Rundus et al. 2007). Sanguivorous mosquitoes (culidae) are also sensitive to heat, and like vampire bats, use it as a cue in the final stages of approach and landing on a host, relying on vision, olfaction, and carbon dioxide sensitivity over larger distances (Cardé 2015). This convergence of functions likely reflects the physics of heat flow—an animal's temperature is only an effective cue at short distances.

In all three groups—vampire bats, crotalid snakes, and mosquitoes—the genetic architecture that permits thermoreception of hosts and prey was co-opted from an ancestral trait that served another thermal function. Like all vertebrates, *Desmodus* has the gene *Trpv1* encoding proteins that help detect dangerously high temperatures (greater than ca. 43°C). However, *Desmodus* also expresses a unique duplicated and shortened version of the *Trpv1* gene, allowing for a much higher sensitivity roughly matching the temperature of a mammalian host's skin, ca. 30–37°C (Gracheva et al. 2011; Zepeda Mendoza et al. 2018). In snakes, it is the gene *TrpA1* that is modified for prey detection (Kang 2016), and in mosquitoes, the gene *Ir21a*, which mediates heat-avoidance across class Insecta, has been co-opted to drive heat-seeking and heat-stimulated blood-feeding (Greppi et al. 2020).

5.4. The bite

Vampire bats do not suck blood, in contrast with other blood feeders that attach to their hosts using suction, such as lamprey and leeches. For those aquatic blood feeders, the primary purpose of suction is to remain attached to the larger and faster moving host, which in the case of lamprey might even be a whale (Gill et al. 2003). Once applied, however, that suction provides the secondary benefit of a compressive force that allows the teeth to drive into the prey (Clark and Uyeno 2019). Vampire bats instead usually use the lower jaw to pinch the skin to pierce it.

The vampire bat bite itself can take several forms. The typical bite consists of a pinch between the upper and lower jaws that excises a circular divot of flesh, with diameter and depth of ca. 5 mm. A cut can also be made with a slashing slice of the upper incisors. In some instances, a "rasping" bite is made by rubbing the tongue against the skin (Greenhall 1972) similar to many hematophagous insects, including vampire moths and lice (Lehane 2005; Bänzinger 2021).

5.5. The venom (saliva)

Once bitten, a host responds with hemostasis, a process consisting of coagulation, platelet aggregation, and vasoconstriction. To feed, a sanguivore must overcome these processes. In vampire bats, that is achieved by proteins produced by the salivary glands. Bier (1932) first found that the saliva of vampire bats (but not other bats) prevented blood from clotting, and broke down existing clots. Later, Hawkey (1966) determined that this property was due to the action of salivary protein(s). With the advent of transcriptome analyses, it has now become clear that the saliva of vampire bats contains a complex cocktail of dozens, perhaps hundreds of proteins (Francischetti et al. 2013; Low et al. 2013; Ma et al. 2013a) produced by six different salivary glands in vampire bats' necks: one pair of accessory glands and two pairs (anterior and posterior) of principal submaxillary glands (Francischetti et al. 2013). The saliva of vampire bats includes proteins that directly prevent clots from forming, that break down existing clots (plasminogen activators, tissue factor pathway inhibitors, Kunitz domain proteases), and that prevent clotting indirectly by destroying host DNA that would otherwise promote clotting (DNAses). Other salivary proteins prevent platelet aggregation and vasoconstriction (lipocalins, secretoglobins, apyrases, phosphatases), inhibit the host's neutrophils and macrophages (tumor necrosis factor-α-stimulated gene 6), prevent healing of blood vessels (metalloproteases), and induce vasodilation (pituitary adenylate cyclase activating peptide and C-natriuretic peptide). Some of these proteins may also act as analgesics, reducing the likelihood of the host waking up during feeding (Francischetti et al. 2013; Low et al. 2013).

Despite their diversity, none of these proteins are unique to vampire bats. Analogues of them all can be found in the saliva of other blood-feeding animals, including biting flies (Ribeiro et al. 2010), kissing bugs (Ribeiro et al. 1993), ticks (Paesen et al. 1993; Francischetti et al. 2009), leeches (Phillips and Baker 2015), and vampire snails (Modica et al. 2018).

If a vampire bat has a cut on its lip, how does it heal? How do vampire bats not injure themselves when licking their own wounds? In leeches, the constituent proteins change over the course of a feeding event (Siddall et al. 2016). Similarly, in tick saliva, the proteins present on the first day of feeding are different from those on the last day of feeding, probably in response to different branches of the host's immune response (Francischetti et al. 2009). It is likely that vampire bats also have control over the secretion of salivary proteins, perhaps releasing them into the saliva during feeding, but not between meals. Indeed, the different salivary glands of the vampire bats express different levels of protein from one another (Francischetti et al. 2013), and this may be one mechanism by which vampire bats can avoid self-envenomation when their own wounds are healing.

5.6. Dealing with the large volume of blood ingested

Engorgement is a common feature of blood-feeding animals. *Aedes* mosquitoes drink roughly 180% of their body weight in a blood meal (Williams et al. 1983). Medicinal leeches average an increase of 890% in just 29 min (Lent and Dickinson 1987). Female ticks can increase their body weight 100-fold, or 10 000% (Kaufman 2007). Likewise, a vampire bat can gain more than 50% of its body weight in a single meal (Hermanson and Carter 2020). The stomachs of vampire bats are different from those of other mammals, having evolved to become a distensible structure that serves to store large amounts of blood, and help with absorption. Rapid diuresis (peeing) is essential for vampire bats as they feed, and is convergent with the behaviour of other blood-feeding animals. Aedes mosquitoes leak fluid out the anus while feeding, as do tsetse flies (Jones and Pilitt 1973; Gee 1975), whereas ticks force excess fluid back into the wound (Kaufman 2007).

5.7. Dealing with relatively poor nutritional value of blood

It is perhaps not surprising that as mammals, vampire bats can survive on a strict diet of blood, since blood is the fluid used by all mammals to transport the necessities of life to their own tissues. However, the dry mass and ratios of nutrients in blood make it a challenging source of food. The dry matter of blood only makes up a mass of food equal to less than 10% of body weight per day, far lower than is typical for a mammal their size (Breidenstein 1982). Blood is mostly water. For bovines, for instance, blood is ca. 78% water, and the remaining mass contains ca. 93% protein, 5% ash, 1% fat, and 1% carbohydrates (Breidenstein 1982). Chicken blood (a common food for *Diaemus* and *Diphylla*) is similarly poor in nutrients (Coen 2002). Feeding bats deal with the excess water in their food by initially producing large amounts of dilute urine, enabling them to consume as much blood as possible in a meal. As a result of that dumping of water, the blood meal becomes a concentrated, gelatinous mass in the vampire bat's stomach, as has been reported for blood-feeding invertebrates (Coen 2002). One gene expressed abundantly in the stomachs of most other mammals (*CTSE*) has been lost in vampire bats (Blumer et al. 2022), possibly reflecting a diminished role for gastric cells in acid secretion.

Many bacterial and other pathogens that would be present in typical foods are absent from blood. As a result, vampire bats appear to have lost certain mammalian defences associated with detecting spoiled or poisonous food. Taste aversion learning to avoid foods that make animals sick is widespread across animals but absent from vampire bats (Ratcliffe et al. 2003).

Proteins provide the bulk of energy obtained by bats from their blood diet, and vampire bats assimilate more than 90% of the protein they ingest (Breidenstein 1982). As proteins are broken down, urea accumulates in concentrations that would be deadly to most mammals. Vampire bats can chronically live with blood urea levels of 27–57 mmol·L^{-1}, compared with typical mammalian concentration of 2–10 mmol·L^{-1} (Breidenstein 1982). The kidneys of vampire bats then concentrate urea in urine to at least 2630 mmol·L^{-1} (Busch 1988), double the normal concentration for mice, and almost 10 times that of humans (Yang and Bankir 2005). These adaptations are convergent with those of desert-dwelling mammals (Breidenstein 1982), and are reflected by increased expression of genes associated with the disposal of excess nitrogen (*PSMA3*; Zepeda Mendoza et al. 2018). Indeed, the kidneys of vampire bats make a dramatic change in morphology when they transition from milk-feeding as juveniles to blood-feeding as adults, with associated changes in glomerular area, and overall gross anatomy that combines to produce overall "renal hypertrophy" (Ribeiro et al. 2022).

Unlike most mammals, vampire bats appear unable to store energy as fats (Breidenstein 1982). Indeed, fat is almost absent from their diet, and is assimilated at a rate of around 10% (Breidenstein 1982). A gene that helps mammals cope with excessive fat (*ERN2*) has been lost in vampire bats, since that situation never arises (Blumer et al. 2022). Gut microbes appear to play a key role in helping vampire bats hang on to what little amounts of fat they can obtain. Compared with those of nonblood-feeding bats, *Desmodus* gut microbiota have enrichment of the gene that encodes glycerol kinase, which plays an important role in fat storage (Zepeda Mendoza et al. 2018).

Blood is low in carbohydrates, so vampire bats have lower insulin levels than is typical of mammals, both immediately after feeding, and upon fasting (Freitas et al. 2013). This inhibits their ability to store energy reserves, and thus prevents access to stored sugars when starved, as would be typical of other mammals (Freitas et al. 2013). One gene associated with regulating glucose levels in the blood, *FFAR1* (free fatty acid receptor 1) has been lost in vampire bats, likely as an adaptation to ensure what little glucose is present remains in the blood, preventing hypoglycemia (Zepeda Mendoza et al. 2018; Blumer et al. 2022).

Some blood-feeding insects compensate for the low carbohydrate content of their diet by converting proteins to carbohydrates. This is known as the gluconeogenic pathway, and is used by tsetse flies (Bursell 1977), mosquitoes (Scaraffia and Wells 2003), and beetles (Gäde and Auerswald 2002). That pathway was once hypothesized as a possible source of carbohydrates for vampire bats (Coen 2002), but recently fed vampire bats have subsequently been found to have low levels of the enzyme phosphoenolpyruvate carboxykinase, which when present is a marker of gluconeogenesis activity, suggesting that gluconeogenesis is not used by vampire bats (M.B. Freitas and E.C. Pinheiro (personal communication)).

5.8. Excess iron

Blood contains relatively little free iron, but as blood is broken down during digestion, iron ions are released, presenting a significant risk to homeostasis, especially at the liver, heart, and pancreas (Zepeda Mendoza et al. 2018). Because iron is so common in the vampire bat diet, the gene *REP15* involved in cellular iron uptake in mammals, has been lost in *Desmodus* (Blumer et al. 2022). Conversely, the gene families that produce the light subunit (*FTL*) and heavy subunit (*FTH1*) of the ubiquitous vertebrate iron-storage protein, ferritin are expanded in *Desmodus* (Zepeda Mendoza et al. 2018). Excess iron is shed when ferritin-bound iron molecules are excreted into epithelial cells lining the gut, then eliminated with the feces (Morton and Wimsatt 1980). Ferritin is also used by mosquitoes to deal with excess iron, though the genes encoding the light and heavy subunits of mosquito ferritin differ from the vertebrate ones—*LCH* and *HCH*, respectively (Geiser et al. 2003; Pham and Winzerling 2010).

5.9. Gut microbiota

Vampire bats overcome the challenges of their dilute and nutrient-poor diet with the help of gut microbiota that contribute their own genes to digestion, absorption, and metabolism (Zepeda Mendoza et al. 2018), a phenomenon that is also true of blood-feeding leeches (Graf 2002; Graf et al. 2006). However, the gut microbiomes of vampire bats differ from those of other blood feeders in one respect. Because of their social behaviour, vampire bats possess a "social microbiome", which converges among groupmates via social interactions like grooming and regurgitated food sharing (Yarlagadda et al. 2021).

The vampire bat microbiome is highly adapted to periods of nutrient starvation, expressing genes associated with low nutrient availability (*LAMTOR5*, *RelA/SpoT* family protein), and genes encoding the protein guanosine pentaphosphate, which is involved in the reverse Krebs Cycle, by which some bacteria produce carbon compounds from CO_2 and H_2O (Zepeda Mendoza et al. 2018). The microbiome of vampire bats also appears to help break down urea, as the microbial genome of vampire bats expresses high levels of the gene that produces urease subunit alpha (*ureA*; Zepeda Mendoza et al. 2018).

The vampire bat microbiome, compared with those of other bats, shows an overabundance of potentially protective bacteria, such as *Amycolatopsis mediterranei*, which are known to produce antiviral compounds, protective against poxviruses and bacteriophages (Zepeda Mendoza et al. 2018). Zepeda Mendoza et al. (2018) found genomes from more than 280 microbial species in the guts of *Desmodus*, many of which are known to be pathogenic to other kinds of mammals. These include the protozoans *Acanthamoeba* and Cryptosporiidae sp., the fungus *Aspergillus*, and the bacteria *Campylobacter*, *Chlamydia*, *Helicobacter*, *Legionella*, *Mycoplasma*, and *Rickettsia*. It is unclear whether these pathogens survive in the body of *Desmodus*, or whether they are ingested from hosts, and then neutralized by the vampire immune system. One gene associated with the immune response in other mammals (RNASE7) has been lost in *Desmodus*, possibly as a reflection of the different pathogen diversity faced by sanguivores compared with other mammals (Blumer et al. 2022). Vampire bat guts contain the bacteria *Bartonella* and *Borrelia*, pathogens that are regularly transmitted by hematophagous arthropods, such as ticks, lice, fleas, and mosquitoes, and that may be a widespread consequence of drinking vertebrate blood (Zepeda Mendoza et al. 2018).

6. Conclusions

Vampire bats are unique among mammals for their blood-feeding habits, but not unique among animals. In fact, they exhibit morphological, physiological, and anatomical traits that converge with those of other blood-feeding taxa, including arthropods, leeches, and birds. The feeding habits of those other taxa thus provide indirect evidence concerning the plausibility of different hypotheses of how sanguivory evolved in vampire bats. Based on phylogeny, and on the widespread occurrences of ectoparasite-eating and wound-feeding among sanguivorous birds, we believe that sanguivory evolved in an insectivorous vampire bat ancestor by means of ectoparasite-eating (Gillette 1975; Turner 1975), wound-feeding (Fenton 1992), or a combination of these two feeding styles.

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