

**Charles Plumier's (1646–1704) *Vespertilio maximus ex insula Sancti Vincentii*: a previously unpublished description and drawings of the Greater Bulldog Bat, *Noctilio leporinus* (Linnaeus, 1758)**

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*Abstract.*—A previously unpublished description and drawings of the Greater Bulldog Bat, *Noctilio leporinus* (Linnaeus, 1758), made by French Minim friar Charles Plumier (1646–1704) during the first (1687–1688) of three voyages of exploration to the West Indies, are described and reproduced. The earliest known depiction of this taxon, Plumier's account is compared with later descriptions, especially those of Dutch apothecary Albertus Seba (1665–1736) and Carl Linnaeus (1707–1778). Evidence is also presented to emphasize the originality and scientific accuracy of Plumier's account.

**Keywords:** Albertus Seba, Caribbean, Carl Linnaeus, Chiroptera, fishing bat, iconography, Lesser Antilles, Noctilionidae, Saint Vincent

French Minim friar Charles Plumier (1646–1704), craftsman, illustrator, and engraver, but best known for his work as a botanist, devoted the better part of his life to collecting and illustrating plants and animals (Fig. 1).<sup>1</sup> Initially trained in mathematics and the physical sciences, early contact with French and Italian botanists in Rome turned him toward natural history. Observations made during three voyages of exploration to the West Indies between 1687 and 1697<sup>2</sup> provided the foundation for an enormous body of manuscript material extant in the collec-

tions of the Bibliothèque centrale du Muséum national d'Histoire naturelle, Paris.<sup>3</sup> His surviving drawings and descriptions alone make up 39 bound volumes, containing nearly 6000 separate figures, of which about 4300 depict plants, the remainder being devoted to animals. The botanical manuscripts are rather well known (Haller 1772:12–14, Thiébaud de Berneaud 1823:lxxxiii, Planchon & Triana 1860:335–336, Triana & Planchon 1862:361–363, Urban 1898:123–130, 1920:7–8; Fournier 1932:57–59), much of the iconographic material having been published during Plumier's lifetime (Plumier 1693, 1703) and after his death (Plumier 1705, 1755–1760). In contrast, however, his drawings of animals have remained largely unobserved, those depicting fishes being the only exception (see Pietsch 2001a, b,

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<sup>1</sup> For a biography of Plumier, see Pietsch (2017:21–29).

<sup>2</sup> The start dates of Plumier's three voyages, 1687, 1689, and 1694, contrary to the slightly later dates of 1689, 1693, and 1695, respectively, which are repeated everywhere else in accounts of his life, follow Hrodej (1997:100–103) who argued convincingly for their acceptance.

<sup>3</sup> For a full account of Plumier's manuscripts, see Pietsch (2017:30–37).

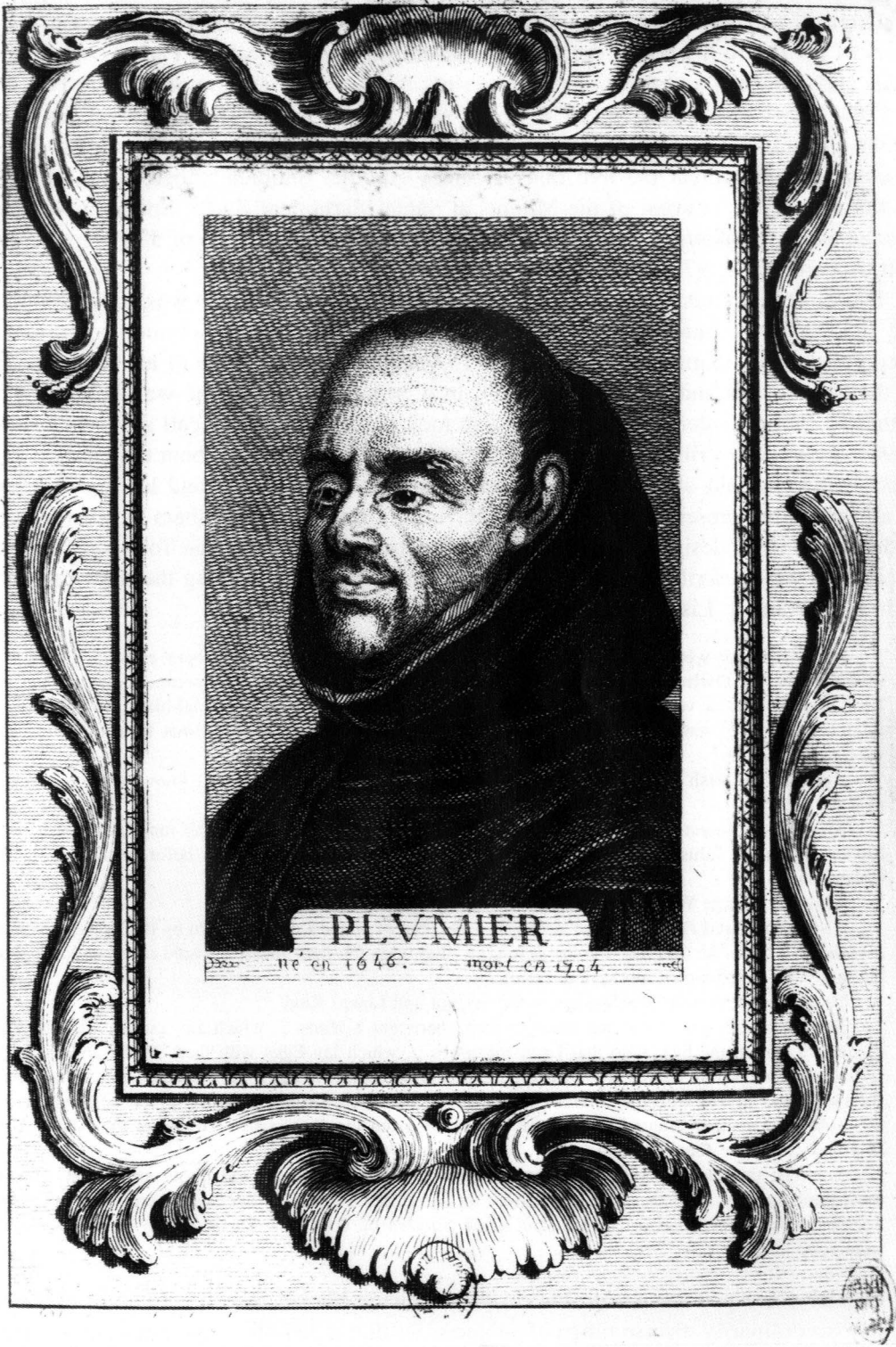


Fig. 1. Father Charles Plumier (1646–1704). Engraving by J. Blanchouse.

2017), and his influence on zoology has not been adequately explored.

Although undocumented in his published work, there is ample evidence to show that Plumier had a broad interest in animals and spent considerable time with their study. His surviving drawings, many of which are accompanied by lively, detailed descriptions, depict a surprisingly wide range of zoological taxa: molluscs (bivalves, gastropods, and chitons) are most often represented (567 drawings), followed by fishes (marine and freshwater), with 345 separate views of whole specimens, plus many more of anatomical details, including osteology as well as internal soft parts. Birds are represented by 215 drawings; amphibians and reptiles, 360 drawings (most showing anatomical details); mammals, 19 drawings; and various non-molluscan invertebrates, 46 drawings.

#### Plumier's *Vespertilio maximus*

Attention is directed here to Plumier's description and drawings of the Greater Bulldog Bat, *Noctilio leporinus* (Linnaeus, 1758),<sup>4</sup> which he observed on the Caribbean island of Saint Vincent during the first (1687–1688) of his three voyages to the West Indies (see Pietsch 2017:23–26). The Greater Bulldog Bat is a kind of fishing bat native to the Neotropical lowlands, ranging from the Pacific coast of Mexico, Cuba, and most of the Caribbean islands, and extending south through Brazil, eastern Peru, eastern Bolivia, and Paraguay, and into northern

Argentina (Gardner 2008:387). Within this broad geographic range, it is always associated with ponds, lakes, streams, rivers and their estuaries, and coastal bays and lagoons (Gardner 2008:388, Barquez et al. 2015). Considered to be the most well-studied piscivorous bat (Bloedel 1955:391, Pavan et al. 2013:211), it is known to consume insects in the same proportion as small fishes; less frequently it consumes various kinds of crustaceans and arachnids (Hood & Jones 1984:4, Brooke 1994:213–216, Pavan et al. 2013:211). It should not be confused with the morphologically similar, although somewhat smaller, Lesser Bulldog Bat, *Noctilio albiventris* Desmarest, 1818, which ranges from southern Guatemala to northern Argentina and Paraguay, including almost all of the Brazilian territory (Gardner 2008:385, Smith 2008:5, Olímpio et al. 2018:313). Although belonging to the same genus, it is primarily an insectivore that preys on insects that lie on or fly close to the water surface (Gonçalves et al. 2007:535, Smith 2008:6).

Using echolocation to detect water ripples made by potential prey (Suthers 1965:319, 1967:79; Wenstrup 1984:91, Wenstrup & Suthers 1984:75), the Greater Bulldog Bat flies toward its victim, raking the water surface with its extremely large and highly specialized feet, and gaffing prey with its massive claws (Hood & Jones 1984:4, Altenbach 1989:421). When the bat's legs leave the water, the elongate "heel bones" (calcars) are extended outward, spreading the interfemoral membrane while the knees are bent (backwards as they do in bats), thus forming a pouch that prevents the prey from falling free (Bloedel 1955:391, Schnitzler et al. 1994:339).

Calling it *Vespertilio maximus ex insula Sancti Vincentii* and citing "bouliri," the vernacular of the local inhabitants, Plumier described the bat as follows (in

<sup>4</sup> "Ornitographia Americana, quadrupedia et volatilia continens Authore R. Patra Carolo Plumier Ordinus Minimorum Provinciae Franciae et Botanico Regio," MS 27, folio 2, Bibliothèque centrale du Muséum national d'Histoire naturelle, Paris (96 pages containing images of 107 birds and three mammals (an opossum, one drawing, and two bats, eight drawings), many with numerous drawings of anatomical details, with descriptions in Latin and in French).



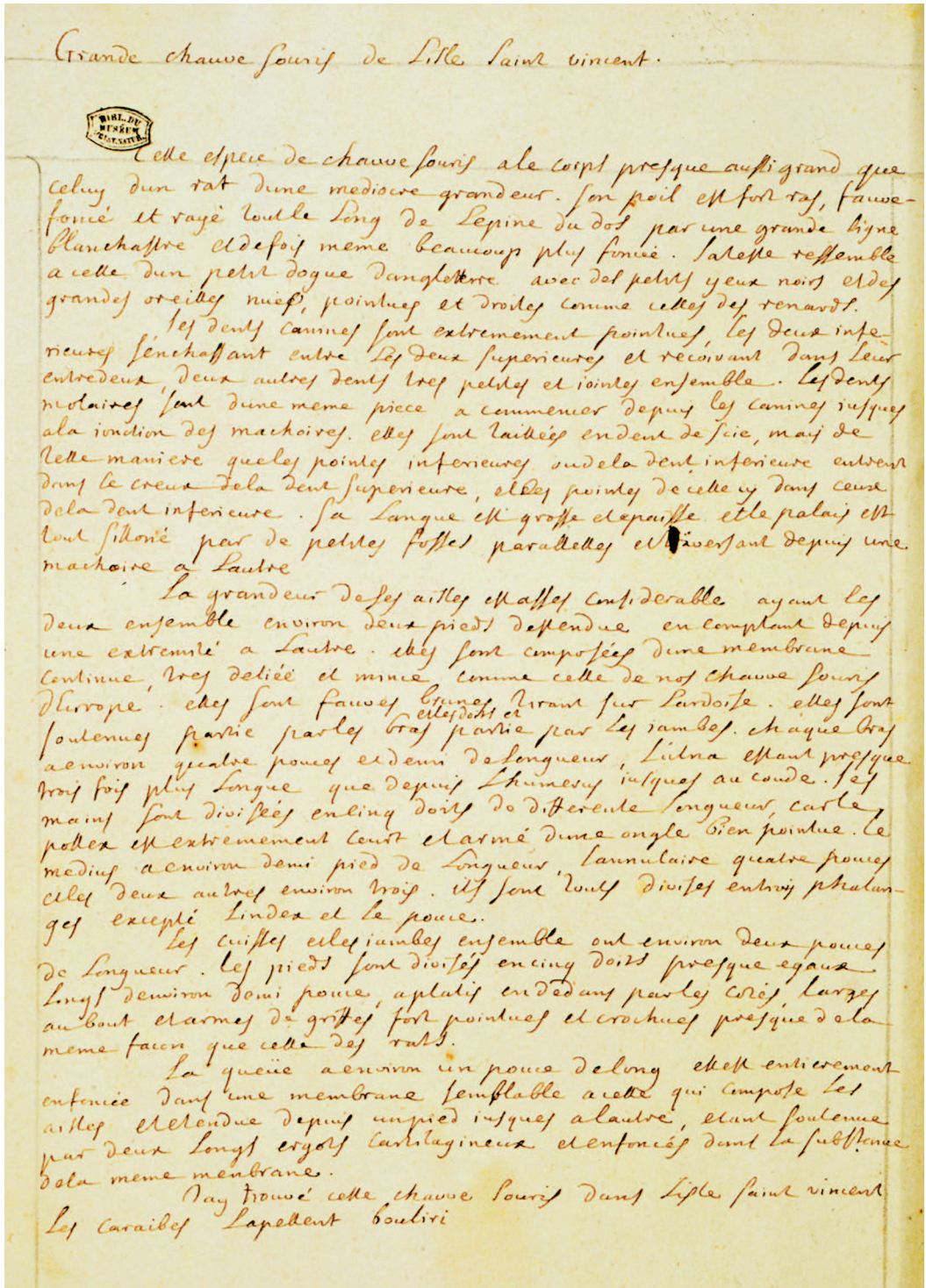


Fig. 2. Charles Plumier's description of *Vespertilio maximus ex insula Sancti Vincentii*, the Greater Bulldog Bat, *Noctilio leporinus* (Linnaeus, 1758). Plumier MS 27, folio text 2, © Muséum national d'Histoire naturelle, Paris. Used with permission.

translation from the French; for the original text, see Fig. 2):

—Large bat of the island of Saint Vincent.

This kind of bat has a body almost as big as that of a small rat. Its fur is quite short, of a dark reddish brown color, with a whitish line running down the middle of the back and at times even much darker. Its face looks like that of a small English dog, with small black eyes and long bald ears, pointed and straight like those of a fox.

The canine teeth are extremely sharp, the lower two being placed between the upper two and enclosing in between two very small teeth that are placed close together. The molars are continuous, extending from the canines to the articulation of the jaws. They are shaped in a saw-tooth pattern in such a way that the point of the lower tooth fits within the indentation of the upper tooth, and the point of the upper tooth fits within the indentation of the lower tooth. Its tongue is large and thick, and the palate is furrowed by parallel ridges crossing from one side of the jaw to the other.

Its wingspan is quite considerable, measuring about two feet from one end to the other. The wings are made of a very loose and thin membrane of skin like that of our European bats. They are of a reddish brown color, with slate hues. They are supported partly by the arms and fingers and partly by the legs. Each arm is about four and a half inches in length, the ulna being almost three times longer than from the humerus to the elbow. Its hands are divided into five fingers of different lengths, the thumb being extremely short and armed with a sharp claw. The middle finger is about half a foot in length, the ring finger four inches, and the other two are about three inches. They are all divided into three phalanges except for the index finger and the thumb.

The thighs and legs together are about two inches in length. The feet are divided into five toes of almost equal length, each about half an inch long, flattened inward on the sides, wide at their extremity, and armed with very sharp and hooked claws, almost similar to those of rats.

The tail is about an inch long and entirely embedded in a membrane similar to that which composes the wings, and extended from one foot to the other, being supported by two long cartilaginous struts embedded in the substance of the same membrane.

I found this bat on the island of Saint Vincent. The Caribbeans call it boulliri.

Plumier's drawings (Fig. 3) of his *Vespertilio maximus* include a dorsal view, with the membranes of the wings and tail

outstretched as if the animal was in flight; a dorsal, three-quarter view (with the tongue protruding), as it might look while suspended from its roost or crawling on substrate; and three details of the head, with the mouth closed and opened, and with the lips pulled back to show the teeth.

The same manuscript<sup>5</sup> contains drawings of another bat (Fig. 4), this one, labeled *Vespertilio insulae San-Dominicae, auriculis amplis, naso elato* (Bat from the island of Saint Domingue, with large ears and upturned snout) and observed by Plumier at Saint Domingue (present-day Haiti), then a French colony (1659–1804) on the Caribbean island of Hispaniola. Not so easily identified, it appears to be a fruit-eating bat, perhaps either the Cuban Fig-eating Bat, *Phyllops falcatus* (Gray, 1839) or the Jamaican Fruit Bat, *Artibeus jamaicensis* Leach, 1821. It is briefly described by Plumier as follows:

Another bat from the Island of Saint Domingue. The fur of this bat is quite short and gray like that of ordinary rats. Its wings are almost black or slate in color, and its eyes are prominent, sticking out of its head, round and black like well-polished jet. Its head is completely round, its ears are large and its nose is shriveled up by some kind of cartilaginous patch shaped almost like a *fleur-de-lis*. Its wingspan is about one foot from one extremity to the other.

I saw this animal only near [Lake] Miragoâne on the island of Saint Domingue.

Albertus Seba's *Vespertilio, Cato similis, Americanus*

The earliest published account of the Greater Bulldog Bat appeared nearly 50 years after Plumier made his observations. It was included by Albertus Seba (1665–1736) in the first volume of his *Locupletissimi rerum naturalium thesauri* ("The-saurus" for short) of 1734, the first of nine bat species or varieties for which he had specimens at the time, identified as *Ves-*

<sup>5</sup> Plumier MS 27, folio 3, Bibliothèque centrale du Muséum national d'Histoire naturelle, Paris (see footnote 4).



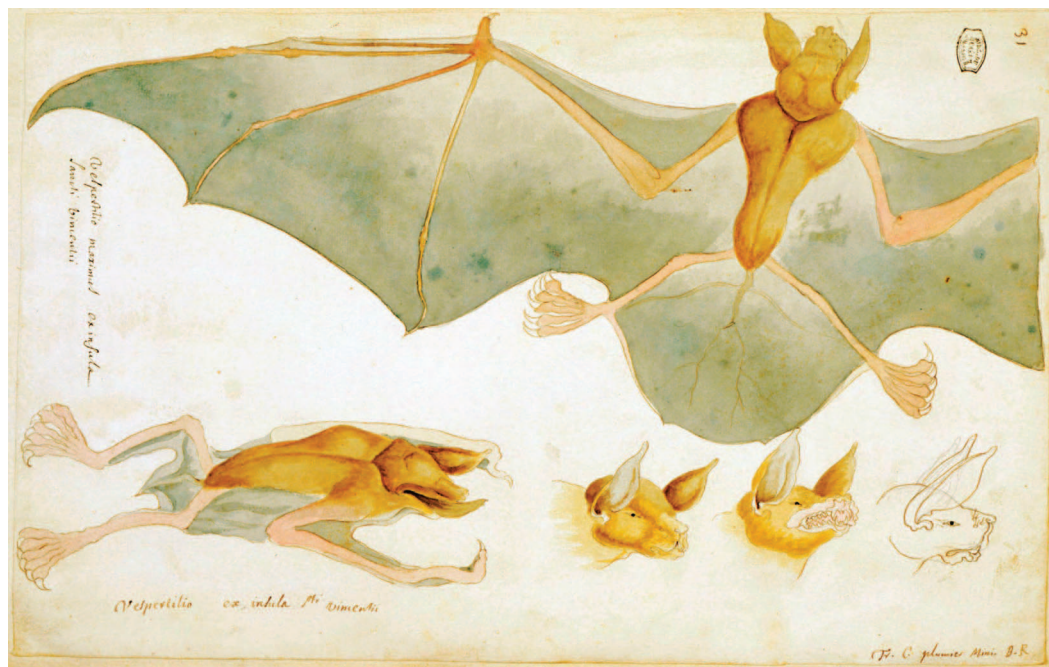


Fig. 3. Charles Plumier's drawings of *Vespertilio maxillatus ex insula Sancti Vincentii*, the Greater Bulldog Bat, *Noctilio leporinus* (Linnaeus, 1758), dorsal and three-quarter views, with profiles of the head, signed Fr. C. Plumier Mini. B. R. [Botanico Regio]. Plumier MS 27, folio 2, © Muséum national d'Histoire naturelle, Paris. Used with permission.

*pertilio*, *Cato similis*, *Americanus*, *mas* (*Chauve-Souris d'Amerique, Mâle, semblable à un petit Chat*). Seba (1734:89–90, pl. 55, fig. 1) provided a figure and a description in both Latin and French (Latin and Dutch in the Dutch edition of the same). His plate is reproduced here (Fig. 5); his description (translated from the Latin) is as follows:

As to its head, it is round as a ball, cat-like; with mouth wide imitating that of a Hare; chin hanging; teeth sharp; nostrils rounded; ears large; pelt light reddish. It was sent to us from America and shows itself as a male, and, as far as the shape of its head and body goes, it recalls a young cat, but its front feet, bordered by its wings, are rather long, in order that they suffice for extending the wings far apart; and they each end in three fingers and one thumb. The fingers consist of three extended limbs, which at the same time serve the wings. The thumb ends in a curve and a pointed claw by which the animal can affix itself securely to bodies. The tail has grown together with the wings, so that its flight is made easier by its help.

It is worthy of mention that the hind legs are split between the bones of the tibia and fibula, from the joint of the hip [sic] to the heel, keeping a perfect mutual distance, without intermediate body, so that each of these bones is clothed with its own particular covering. The hind legs are separated into five fingers [sic], armed with pointed and curved claws.

As illustrated (Fig. 5) and described by Seba (1734:90, pl. 55, fig. 1), he confused the fibula, which is very much reduced and fused to the tibia in all bats, with the “heel bone” or calcar, the name given to a spur of cartilage (sometimes calcified) arising from the inner side of the ankle and running along the outer margin of the interfemoral membrane; the calcars are especially long and narrow in species of *Noctilio* (see Schutt & Simmons 1998:2). In light of this mistake, it seems highly likely that Seba's description was based solely on the drawing rather than on the specimen itself. While blame for the error might be

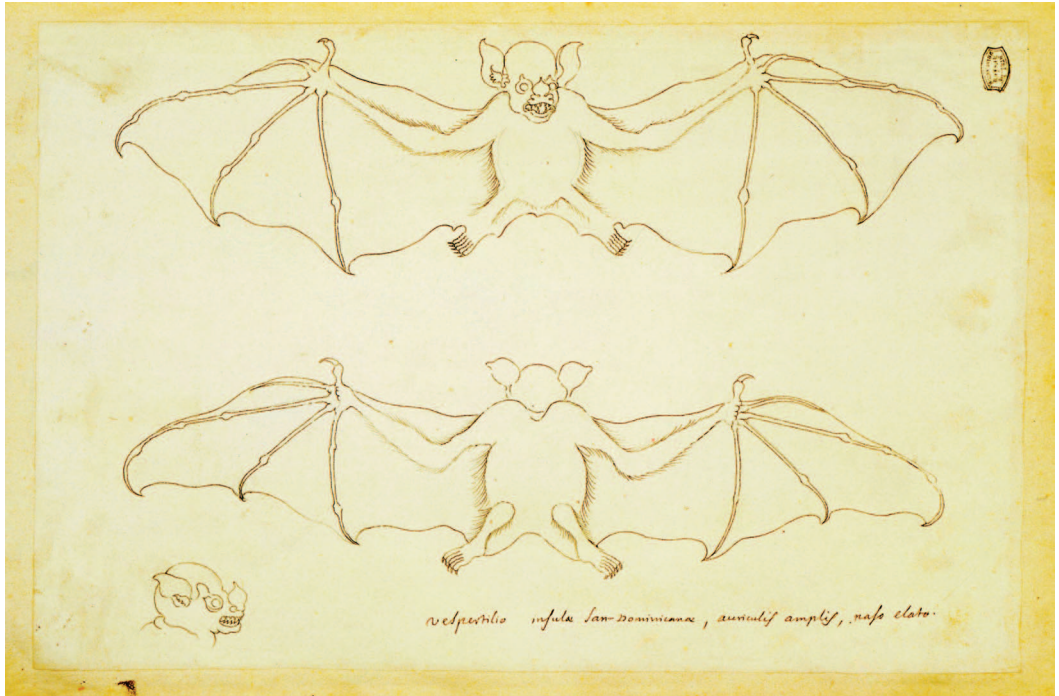


Fig. 4. *Vespertilio insulae San-Dominicanae, auriculis amplis, naso elato*, a fruit-eating bat, perhaps either the Cuban Fig-eating Bat, *Phyllops falcatus* (Gray, 1839) or the Jamaican Fruit Bat, *Artibeus jamaicensis* Leach, 1821, ventral and dorsal views, with a profile of the head, drawn by Charles Plumier. Plumier MS 27, folio 3, © Muséum national d'Histoire naturelle, Paris. Used with permission.

directed toward the artist, it appears that the responsibility lies with the author. Although many artists were engaged to illustrate the “Thesaurus,” nearly all the drawings were made under the direct supervision of Seba (Engel 1937:89, 90, 1961:120; see also Holthuis 1969:241–243, Wallach 2011:2). The descriptions that accompany the drawings are Seba’s as well, initially written by him in Dutch and subsequently translated into Latin by Hieronymus David Gaubius (1705–1780) and into French probably by Louis de Jaucourt (1704–1779).

#### Linnaeus’s *Vespertilio leporinus*

Following Seba’s (1734) account, the next reference to the Greater Bulldog Bat was published by Carl Linnaeus (1748:7) in the seventh edition of his *Systema naturae*,

under the Latin polynomial *Vespertilio caudatus, labio superiore bifido* (tailed bat, with upper lip bifurcated), with Seba’s epithet listed in synonymy. The same is repeated in *Museum S:ae R:ae M:tis Adolphi Friderici* (Linnaeus 1754:7) and yet again under *Vespertilio leporinus* in the 10th edition of *Systema naturae* (Linnaeus 1758:32), with the locality, “Habitat in America,” added. Thus, Seba’s (1734) account remains the only source for the original description of the Greater Bulldog Bat. While Linnaeus (1758) did not refer directly to a specimen, an adult male, probably from Suriname (see Thomas 1911:124, 131), in the collections of the Natural History Museum, London (NHMUK ZD 1867.4.12.339), has been shown by Thomas (1892:316; see also Carter & Dolan 1978:25–26) to have once been in the possession of Seba and survives as the sole basis for his description and









Fig. 6. The holotype of *Noctilio leporinus* (Linnaeus, 1758), NHMUK ZD 1867.4.12.339, probably from Suriname. Photos by Nemo Martin; courtesy of Roberto Portela Miguez and the Trustees of the Natural History Museum, London. Used with permission.

figure; it therefore stands as the holotype of *Noctilio leporinus* (Fig. 6).

The holotype was most likely purchased at the public auction of Seba's collection in Amsterdam (which began on 14 April 1752 and lasted for several days) by Dutch naturalist Arnout Vosmaer (1720–1799), either for his own private collection or for that of the Stadtholder of the Netherlands, Willem V, Prince of Orange (1748–1806) (Engel 1937:93, 94, 1961:120, 127, 130; Holthuis 1969:244, Bauer 2002:9, Bauer & Bell 2014:5). In 1756, much of Vosmaer's personal collection was sold and added to the Stadtholder's collection when Vosmaer formally became its director; in turn, the material (apparently including Seba's bat) was either disbursed at the auction of Vosmaer's collection in 1800 or sold in association with the later dissolution of the

Stadtholder's collection (Boeseman 1970:180, Bauer 2002:10, Bauer & Bell 2014:5). After passing through the hands of one or more private collectors, the specimen eventually ended up as one of 290 mammals in spirits, acquired in 1867 from the cabinet of Dutch naturalist Theodoor Gerard van Lidth de Jeude (1788–1863), by the Natural History Museum (NHMUK ZD 1867.4.12.324–613), where it presently resides (see Thomas 1892:309, Boeseman 1970:198).

### Summary and Conclusions

That neither Plumier nor Seba mention anything about the extraordinary foraging behavior of *Noctilio leporinus* is not surprising given that piscivory in bats

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Fig. 5. Albertus Seba's (1734) *Locupletissimi rerum naturalium thesauri*, plate 55: 1, *Vespertilio, Cato similis, Americanus* (*Chauve-Souris d'Amerique, Mâle, semblable à un petit Chat*), the Greater Bulldog Bat, *Noctilio leporinus* (Linnaeus, 1758), ventral view; 2, *Vespertilio, Americanus, vulgaris* (*Chauve souris commune d'Amerique*), Seba's Short-tailed Bat, *Carollia perspicillata* (Linnaeus, 1758), ventral view; 3, *Vespertilionis, Surinamensis, pullus* (*Le petit d'une Chauve-souris de Surinam*), unidentified, ventral views; 4, *Avis, Americana* (*Oiseau d'Amerique, nommé Acolehichi, noir & jaune*), Audubon's Oriole or Black-headed Oriole, *Icterus graduacauda* Lesson, 1839; 5, *Anguis, Americanus, elegans* (*Serpent d'Amerique, gris*), unidentified (see Wallach 2011:2).

was unknown up until the mid-nineteenth century. According to Gudger (1943:79, 1945:1), the earliest account of any bat with a diet primarily of fish was unknown before 1844. The earliest recorded observation of “fishing” in *Noctilio leporinus* was published by English zoologist and bat specialist Robert Fisher Tomes (1823–1904):

Of this species, Mr. Fraser<sup>6</sup> has forwarded several specimens, one of which has the following highly interesting note attached: “Esmeraldas, Nov. 1859; skimming the bank of the river, every now and then making a dash along, and actually striking the water, catching the minute shrimps as they pass up stream. He had a very offensive fishy smell.” This is the first recorded instance which I have met with of any species of Chiroptera being actually aquatic in its habits... Certainly I little suspected that this *Noctilio* took its food in the manner noticed by Mr. Fraser (Tomes 1860:261).

Subsequent to Tomes’s report, several additional anecdotal accounts of the fishing habits of *Noctilio leporinus* were published during the 1870s and 80s (summarized by Gudger 1945:4–8) but by the early 1890s, enough evidence had accumulated to confirm the hypothesis. Allen & Chapman (1893:206), in describing two specimens of *Noctilio leporinus* collected on Monos Islands, Trinidad, wrote that “Their stomachs contained the partially digested remains of fish; confirmation, if confirmation be needed, of the now well-known fish-eating habits of this species.”

Although obviously derived independently, Seba’s (1734:89–90) description of *Noctilio leporinus* is similar in some ways to that of Plumier, but it is about half the length and much less detailed, providing no measurements and emphasizing a similarity to a cat rather than a dog; it could quite easily suffice to describe almost any species of bat. Superficial at best, Seba’s

description accounts for only four digits in each hand, the thumb and three fingers; the index finger was somehow missed. He also erred rather badly in confusing the “heel bones” (calcars), with fibulae (as mentioned above). In comparison, Plumier’s account demonstrates exceptional observational interest and skill in providing an indication of overall size, color pattern, and texture of the fur, proportional measurements of various body parts (including wingspan, the size of the ears, the tongue, arms and legs, individual fingers and toes, and the tail), the nature of the “loose and thin” membranes that form the wings, the ridged palate, and tooth morphology, the latter foretelling the importance of this character complex to mammal identification and phylogeny, all items missing in Seba’s account. Plumier even described accurately the elongate “heel bones” (his “cartilaginous struts”) that Seba, unfortunately, mistook for fibulae.

As for the illustrations, Plumier’s drawings are arguably the most accurate and life-like depictions of a bulldog bat available in Plumier’s day and long after, only those published well over a century later are more or less comparable (e.g., see d’Orbigny 1847, pl. 9). Seba’s drawing, on the other hand, is decidedly flat and lifeless, no match for Plumier’s depiction, which, to a much greater extent, captures the true essence of the Greater Bulldog Bat.

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<sup>6</sup> Mr. Fraser is Louis Fraser (1819–c. 1884), British zoologist, natural history dealer, taxidermist, zookeeper, and long-time collector in South America for the Zoological Society of London (see Günther 1906:33).

tory Museum, London, for photography; and Hans Aili, Department of Romance Studies and Classics, Stockholm University, Stockholm, for translation of Latin. Early drafts of the manuscript were critically read by Aaron M. Bauer, Villanova University, Villanova, Pennsylvania; Roberto Portela Miguez, Vertebrate Division, the Natural History Museum, London; James W. Orr, NOAA Fisheries, Seattle, Washington; and Sharlene E. Santana, all of whom provided much-appreciated help to improve the manuscript.

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