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„ Bats as inverted humans - a comparative study of pelvic morphology in Chiroptera and its implications for the human obstetric conundrum "

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Abstract

Human childbirth is difficult compared to parturition in other mammals. This is mainly due to a very tight cephalopelvic fit: humans have very large-headed neonates relative to the size of their bony pelvis. An issue long debated in anthropology concerns the failure to evolve a larger, more spacious birth canal. To shed new light on this human evolutionary question, bats (Chiroptera) were considered for comparison because they give birth to even larger neonates than humans. In order to accommodate such large young, females of all bat species possess a substantial pubic “gap” spanned by a flexible interpubic ligament instead of a pubic symphysis, enabling birth of the large fetus. The selection pressures assumed to constrain the size and flexibility of the human birth canal may not be present in bats due to their flying locomotion and particular roosting behaviour. Therefore, bats are hypothesised to be free to respond to obstetric selection and increase their pubic gap in proportion to the size of their neonate. To test this prediction, a morphometric study of pubic gap size on 273 specimens pertaining to 82 bat species was conducted. Mean adult and neonatal body mass were able to be collected for a subsample of 65 species from the literature. Contrary to expectations, no correlation between relative pubic gap size and relative neonatal body mass was found. Nevertheless, male bats rarely show a pubic gap, resulting in strong pelvic sexual dimorphism, which is evidence for sex-specific selection in female bats related to obstetrical demands.

1. Introduction

1.1 Pelvis in tetrapods and humans

When the Tetrapoda left the water and conquered terrestrial habitats, major changes of the pelvic girdle played an important role. The pelvic girdle is a ventral bony structure, often in the caudal body area, that is already present within the early Gnathostomata. There, the pelvic girdle consists of endochondral bones located within the ventral body wall, where they are loosely connected to the axial skeleton (Hyman and Wake, 1992, Fischer, 2010). Within the Tetrapoda, the pelvic girdle underwent important changes, allowing tetrapods to conquer completely new terrestrial habitats. The pelvic girdle of the Tetrapoda forms a caudal structure which consists of three bones (pubis, ischium, ilium) that are fused together in the acetabulum (Hyman and Wake, 1992, Fischer, 2010). The pubis and the ischium form the ventral part of the pelvis, while the ilium is located dorsally. Because of its dorsal position, the ilia are fused to the ribs or transverse processes of the sacral vertebrae and thus connect the pelvis to the axial skeleton. This connection is the sacroiliac joint. Overall, the pelvic girdle forms a stable structure on which new muscle attachment sites for the newly evolved hind limbs have developed. The pelvis was thus an important adaptation for locomotion on land (Hyman and Wake, 1992, Fischer, 2010). Within the Tetrapoda, the pelvis again underwent morphological changes. In mammals, for instance, a large opening, the *Foramen obturatum*, was formed from the passage of the *Nervus obturatorius* between the pubis and the ischium. Furthermore, the two pubic bones compose the pubic symphysis on the ventral side. Due to these changes the pelvis is given a frame-like structure (Hyman and Wake, 1992, Fischer, 2010). This led to new or altered muscle attachment sites and thus enabled a new type of locomotion in which the hind limbs are pulled under the trunk compared to a lateral position as in reptiles and birds (Hyman and Wake, 1992, Fischer, 2010). Moreover, the frame-like structure of the pelvis forms a natural birth canal that is limited in its size.

This restriction of the birth canal also occurs in humans. During evolution the human brain size, compared to other mammals, especially non-human primates, increased strongly in relation to the body size. This was accompanied by an increase in the neonatal brain size and therefore an increase in neonatal head size. But since the size of the birth canal is restricted by the bony pelvis, the increasing neonatal brain size caused a tight cephalopelvic fit (Rosenberg and Trevathan, 2002). However, to facilitate a successful delivery, a sexual dimorphism evolved in the pelvic area in humans, whereby women possess a wider pelvis than men. Furthermore, the release of the hormone relaxin, in combination with other hormones like estrogen, facilitates childbirth. This is done by making the compact cartilage of the joints of the pelvis, like the pubic symphysis, softer. Thereby the pelvis gets more flexible, while the neonate passes the birth canal (Schwabe et al., 1978, Kristiansson et al., 1996). Nevertheless, the tight cephalopelvic fit still makes parturition difficult and painful. In some cases, it can even occur a cephalopelvic disproportion. This means that the head (and the shoulders) of the human neonate are too large to pass through the birth canal without causing problems (Dolea and AbouZahr, 2003, Hofmeyr and Shweni, 2012, Grunstra et al., 2019). Therefore, without the help of midwives and the use of supporting methods (e.g. caesarean section, symphysiotomy) increased mother and child morbidity and mortality increases (Dolea and AbouZahr, 2003, Hofmeyr and Shweni, 2012, Say et al., 2014, Goldenberg et al., 2015).

This raises the question why women have not evolved a wider pelvis to solve or ameliorate this problem. Over time, many theories and hypotheses have been put forward on this subject. One of the most popular explanation evolved from the ideas put forth by Washburn (1960). The upright gait in hominids started approximately four million years ago (Leakey et al., 1995, Ward et al., 1999), maybe even earlier (Richmond and Jungers, 2008, Niemitz, 2010). To evolve an energy-efficient bipedal locomotion, Washburn (1960) proposed that a mediolaterally narrow pelvis would be suited best. On the other hand, the size of the brain of the genus *Homo* began to increase about 2,5 million years ago (Falk et al., 2000, Holloway et al., 2004, Holloway et al., 2009). Since the neonatal brain size is strongly correlated with the maternal brain size (Lunde et al., 2007, DeSilva and Lesnik, 2008), the neonatal head size started to get bigger in human evolution. Because of these two major events an "obstetrical dilemma" occurred in humans. In this evolutionary trade-off, a narrow pelvis for energy-efficient locomotion and a wider pelvis to give birth to neonates with an increased brain size are juxtaposed. However, recent studies show different results in terms of the pelvic width and energy-efficient bipedal locomotion. While Warrener et al. (2015) indicate that the wider pelvis of women does not cause any more energy during walking and running than that of men, Vidal-Cordasco and colleagues (2017) point out that even the pelvis in early hominids was as energy efficient as the pelvis of modern *homo sapiens*.

Another possible explanation for why the human pelvic canal is evolutionarily constrained is the pelvic floor hypothesis introduced by Abitbol (1988). He assumes that a narrower pelvis causes a stronger pelvic floor. The pelvic floor consists of four muscles, the *Musculus puborectalis*, *Musculus pubococcygeus*, *Musculus iliococcygeus* and *Musculus coccygeus* as well as their associated ligaments. Inside the pelvis the attachment points for these muscles are the pubic bones and the ischial spins (Bharucha, 2006, Bharucha et al., 2007). Hence, the pelvic floor has an oblique orientation inside the pelvic canal in both men and women (perpendicular to the long axis of the pelvic canal). Due to the upright posture in humans, gravity forces the organs towards the caudal pelvic opening.

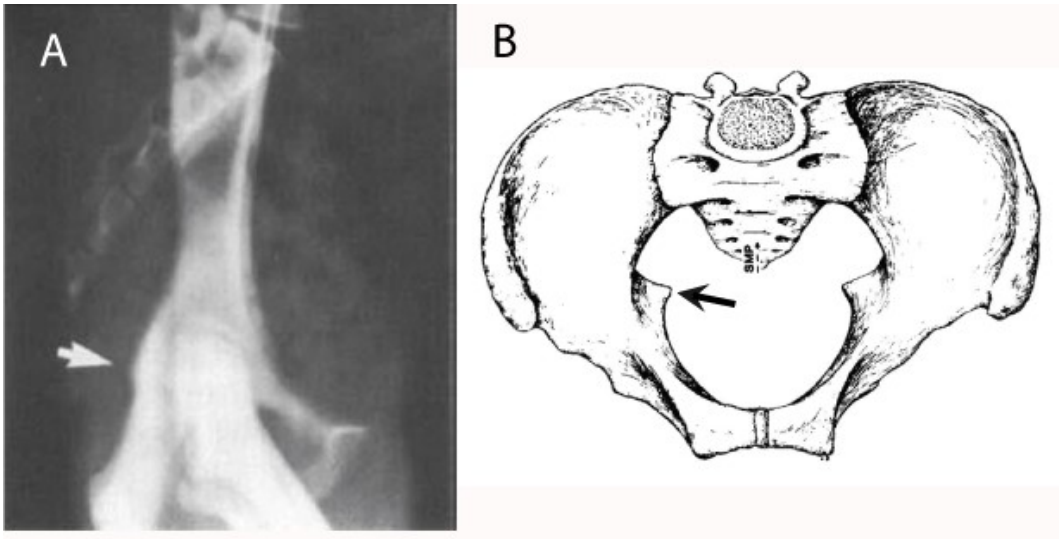

Figure 1. Figures from Abitbol (1988). A: lateral view of rhesus monkey pelvis (x-ray). B: drawing of human female pelvis, cranial view. Arrows mark position of the ischial spines.

Therefore, the pelvic floor is needed to prevent prolapse of the organs and keeps the organs inside the body. A larger pelvic canal instead would lead to a weaker pelvic floor and increases the risk of incontinence and prolapse (Sze et al., 1999, Handa et al., 2003, Brown et al., 2013). In quadrupedal mammals, the muscles of the pelvic floor are more vertical oriented and serve the lateral movement of the tail. Therefore, small ischial spines of the pelvis that are located lateral to the spine serve as muscle attachment points for the pelvic diaphragm in tailed mammals (Abitbol, 1988) (see Fig. 1). Because of the more horizontal position of the pelvic floor in humans the ischial spines are elongated, turned anteriorly and point medially to support a stronger pelvic floor. However, the new position of the ischial spines narrows the pelvic outlet even further and thus the birth canal as well (Abitbol, 1988) (Fig. 1).

Grunstra et al. (2019) pursue the approach of a comparative analysis to test existing theories about childbirth problems in humans, including the pelvic floor hypothesis. To test their assumptions, they compared the brain mass as well as the neonatal and maternal body mass between humans, non-human primates and other mammals. Among the mammals in their study bats were also considered. Because of the special pelvic morphology in bats, Grunstra and colleagues assumed that this group was well suited to test the pelvic floor hypothesis.

1.2 Bats

Bats are special in many ways and have evolved quite unique abilities among mammals. This speciose group (about 1400 species) (Wilson and Mittermeier, 2019) is the only mammalian group that evolved powered flight. Furthermore, bats are one of the few taxa that use echolocation for orientation, along with some Cetacea (Griffin, 1958, Neuweiler et al., 1980, Ketten, 1992, Teeling et al., 2016). These outstanding abilities and the resulting morphological modifications within bats have attracted the attention of many scientists and are the focus of many scientific papers.

There is another aspect of bats that is no less interesting but receives far less attention. Like in humans, female bats give birth to relatively large neonates. But unlike in humans, where the neonate makes up approximately 6% of maternal body mass, bat neonates of most species make up 20-30 % of maternal body weight. In some species they even reach 45 % of the maternal body mass (Myers, 1978, Kunz and Kurta, 1987, Hayssen and Kunz, 1996, Chaverri and Kunz, 2006). Since newborn bats do not experience the safety of a nest, as it is the case in many birds or rodents, they show high developments in some morphological aspects. As soon as the mother leaves the roosting side for foraging, the juvenile bat would no longer experience the maternal body heat and is exposed to the cooler environmental temperature. Due to the large neonatal body mass the thermal inertia of the juvenile bats increase which leads to a higher body temperature. This prevents the young bats of cooling down in the colder environment and thus ensures a better postnatal development (Fujita, 1986, Kunz and Kurta, 1987). Furthermore, the already well-developed hind limbs of newborn bats make up a significant proportion of the large neonatal body size (Brown et al., 1983, Kunz and Kurta, 1987). These well-developed hind limbs are needed to enable the baby to hold on to the mother or the roost substrate on its own shortly after birth. Otherwise they would fall on the ground, due to

the head down position of the mother during birth in most bats, what would increase the risk of an injury and predation (Foster et al., 1978, Kunz and Kurta, 1987). Due to these advantages of a higher neonatal body mass, newborn bats are larger than infants of mammals with comparable maternal size, where the neonates make up approximately 7.8 % of the maternal body mass (Kunz and Kurta, 1987). In order to deliver these large babies, female bats have evolved a particular pelvic morphology. While the pubic symphysis in the majority of adult male bats forms a ventral bony ring (or bar; technically a “synostosis”), the pubic symphysis of female bats is not fused but open (O'Connor et al., 1966, Crelin, 1969, Crelin and Newton, 1969, Chapman et al., 1994, Kofron and Chapman, 1994, Nwoha, 2000, Pelletier et al., 2017, Grunstra et al., 2019) (see Fig. 2). The resulting interpubic gap is bridged by an elastic ligament in live females (Crelin and Newton, 1969, Chapman et al., 1994, Kofron and Chapman, 1994) forming a pubic syndesmosis (a fibrous joint that is composed of two bones that are connected by a membrane or a ligament). In the outer parts, the interpubic ligament consists mainly of elastic fibers, while the core is mostly composed of collagen fibers (Crelin and Newton, 1969). Due to the elastic fibers, the interpubic ligament is able to expand to a multiple of its original length, which enables the female to increase the amount of space that is needed to give birth to the large neonate (O'Connor et al., 1966, Crelin and Newton, 1969). The female pubic symphysis is initially made of cartilage, but then transforms into an elastic interpubic ligament during sexual maturity (Crelin and Newton, 1969). As in females, the pubic symphysis in young male bats first consists of cartilage, which than, unlike in females, ossifies when the individuals mature (Crelin and Newton, 1969, Chapman et al., 1994, Nwoha, 2000). While

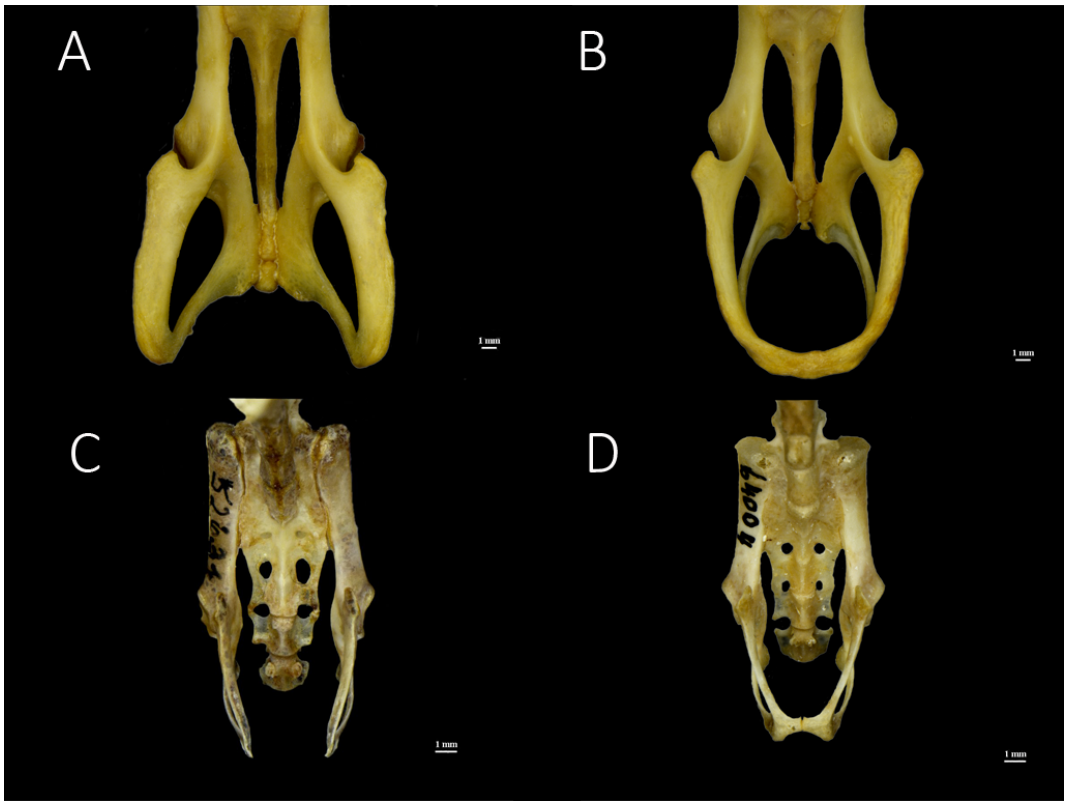

Figure 2. Male and female bat pelves of two different Chiroptera species observed in this study. A: female pelvis of *Eidolon helvum* with pubic aperture. B: male pelvis of *Eidolon helvum* with pubic symphysis. C: female pelvis of *Myotis myotis* with pubic aperture. D: male pelvis of *Myotis myotis* with pubic symphysis

this type of sexual dimorphism is not exclusive to bats – it is also found in some other small mammals like guinea pigs, some mice and rats (Ruth, 1936, Talmage, 1947, Crelin and Brightman, 1957, Crelin, 1960) or hedgehogs and tenrecs (Grunstra et al., 2019) – Chiroptera are the only large taxon that exhibits it with almost no exception. Unlike bats other small female mammals, like guinea pigs and mice, give birth to several smaller babies rather than to a single large neonate. Furthermore, the histology of the interpubic ligament of those mammals is different from that in bats, by having fibrous connective tissue instead of elastic fibers (Talmage, 1947, Crelin and Newton, 1969, Crelin, 1969). Therefore, the bat ligament is more flexible and elastic (Crelin, 1969, Crelin and Newton, 1969). Moreover, in bats the ligament remains elastic even after pregnancy and delivery, whereas in guinea pigs, for example, it never fully recovers after the first pregnancy (Talmage, 1947). The mentioned change of a cartilage symphysis into the interpubic ligament in female bats can also be found in other small mammals, such as guinea pigs (Talmage, 1947). In mice, however, the replacement does not take place until the end of the first pregnancy (Crelin, 1960, Veridiano et al., 2007). The male pubic symphysis in these small mammals, meanwhile, shows a synostosis like in bats and also originates of cartilage (Ruth, 1936, Talmage, 1947, Crelin and Newton, 1969).

In addition to these special features of the female bat pelvis and the large neonates, Grunstra et al. consider one more fact that makes bats an interesting study taxon for the pelvic floor hypothesis. Unlike most other mammals, the majority of bats spend most of their time roosting upside down (Wilson, 2015). This means that, in contrast to humans, gravity acts not in the direction of the pelvis but in the direction of the thorax. Therefore, the pressure that the abdominopelvic organs and the fetus exert on the pelvic floor is reduced in bats. Therefore, Grunstra et al. (2019) postulate that there is no significant selection pressure counteracting the obstetric selection that favours a large birth canal. Following from this, they propose that the width of the ventral pubic aperture in female bats is positively correlated with relative neonatal body mass.

1.3 Aims

The aim of this study is to test the predictions of Grunstra et al. about such a correlation between relative neonatal body mass and relative pubic aperture size in bats in the context of human pelvic evolution and the pelvic floor hypothesis. Therefore, the first hypothesis in this study states that the bat species with the relatively heaviest neonates also possess the relatively widest pelvic apertures.

Furthermore, Grunstra et al. point to a possible influence of the diet and the associated flight mode of the various bat species on the width of the pubic aperture and thus also on the strength of the pelvic floor muscles. The problem with an interpubic gap is that the muscles of the pelvic floor possess fewer muscle attachment sides because of the lack of bone in the pubic area, and the muscles therefore lose strength and stability. This would be particularly problematic for those bat species where the interpubic gap occurs very wide. Due to the decreasing strength and stability, the muscles of the pelvic floor may not be strong enough to hold abdominopelvic organs and the fetus in place during flight manoeuvres with high acceleration forces. Most insectivorous species of bat for example, hunt their prey during flight and therefore need to be highly manoeuvrable (Norberg et

al., 1987), which may lead to higher intra-abdominal pressure acting on their pelvic floor during changes in direction and velocity due to acceleration forces. Frugivorous and nectarivorous bat species, on the other hand, use a smoother and steadier flight as they do not have to hunt a moving food source (Norberg et al., 1987) and therefore may experience fewer and reduced acceleration forces during locomotion. A second aim of this study is therefore to test for an effect of different flight modes on the relationship between relative neonatal size and relative pubic gap size. Hence, the second hypothesis states that bats with a manoeuvrable flight mode possess a relatively smaller pelvic aperture as compared to frugivorous and nectarivorous species.

To test these hypotheses, morphological and morphometric analyses are carried out on the pelvis of male and female bats in the area of the pelvic canal and the pubic symphysis. Since a high number of various bat species are tested, the influence of the phylogenetic relationships among the different bat clades must be taken into account. Therefore, the above hypotheses will be tested in a phylogenetic comparative framework.

2. Material and Methods

2.1 Materials

With about 1400 species belonging to 21 taxa traditionally ranked as “families”, Chiroptera are a highly species-rich group within Mammalia (Wilson and Mittermeier, 2019). They inhabit tropical regions around the equator as well as regions with dry, temperate, and cold climate. Only in the polar regions they are not present. Due to their wide distribution, different bats species are faced with different environmental conditions and challenges. Accordingly, bats have adapted to a variety of environments, which has resulted in a vast variation of morphological, physiological, and behavioural aspects within this taxon.

From a morphological point of view, the large variation in body size among bats is most noticeable. Kitti's hog-nosed bat or bumblebee bat (*Craseonycteris thonglongyai*; Craseonycteridae), with a body weight of 1,7 to 2,0 g and a body length of 29 to 33 mm, is not only the smallest bat species but also one of the two smallest species within Mammalia, along with the Etruscan shrew (*Suncus etruscus*) (1,5 to 2 g body weight; 36 to 52 mm body length) (Hill and Smith, 1981). On the other hand, the Golden-capped Fruit bat (*Acerodon jubatus*; Pteropodidae) has a body weight of 900 to 1400 g and a body length up to 290 mm, making it one of the largest bat species, along with *Pteropus giganteus* and *Pteropus vampyrus* (Pteropodidae) (Nowak and Walker, 1994, Heaney and Roberts, 2009, Wilson and Mittermeier, 2019). Thus, in terms of body weight, the largest bat species are about 10^3 times heavier than the smallest bat species, while in terms of linear measurements there is a difference of 10^2 between the species.

In terms of physiological and behavioural aspects, Chiroptera show miscellaneous patterns of reproduction due to the different environments they inhabit. Bats in regions with temperate climate are characterized by a seasonal monestry, which is caused by seasonal food supply and an associated period of hibernation (Racey, 1982, Tuttle and Stevenson, 1982). These species give birth to only one litter per year. Although seasonal monestry is also seen in neotropical insectivorous and frugivorous bats, polyestry is observed in frugivorous and insectivorous species in the tropics as well (Racey, 1982, Tuttle and Stevenson, 1982). Polyestry can occur in two ways: On the one hand it can be continuous, meaning females give birth continuous throughout the year, as in *Desmodus rotundus* (Phyllostomidae) (Wimsatt and Trapido, 1952, Souza et al., 2018) and *Eonycteris spelaea* (Pteropodidae) (Krutzsch, 2005). On the other hand, polyestry can be bimodal like in most members of the phyllostomid clade (e.(Wilson and Mittermeier, 2019) e.g. *Artibeus lituratus*) (Tamsitt and Valdivieso, 1963, Fleming, 1973, Duarte and Talamoni, 2010). These species have two reproductive peaks per year which occur at specific times. Irrespective of these two forms of polyestry, the species that show these reproductive patterns produce two, occasionally even three, litters per year (Racey, 1982, Tuttle and Stevenson, 1982, Duarte and Talamoni, 2010).

Most bat species produce one offspring per litter, occasionally two. The number of young is restricted to the food supply in both monestry species and polyestry species (Tuttle and Stevenson, 1982). Even in tropical species, (mostly polyestric) female bats are more likely

to give birth to two young during rainy season when food supply is abundant. In the following periods the females more often bear one offspring (Tuttle and Stevenson, 1982). Nevertheless, in some species females usually give birth to twins (Tuttle and Stevenson, 1982). The majority of these species are members of the Vespertilionidae, e.g. *Lasiurus borealis* (Kunz, 1971), *Nyctalus noctla* (Gaisler et al., 1979) and *Pipistrellus nanus* (LaVal and LaVal, 1977). Apart from these vespertilionids, only two other species restricted to the pteropodids (*Epomops dobsoni* and *Pteropus rufus*) produce two young per litter (Tuttle and Stevenson, 1982). However, the size of the offspring differs between a litter with one or more young. Thus, in vespertilionids, the neonate of a litter with one offspring averages more percent of the maternal body mass than the individual young of a litter with two offspring. Yet, the litter size (body mass of all neonates) is slightly higher in a litter of twins than in a litter with only a single young in vespertilionids (Kunz and Kurta, 1987). Therefore, with increasing litter size, the neonatal body mass decreases, which is also typical for other mammal species (Millar, 1981). In terms of neonatal body mass, bat neonates are large. In relation to maternal body mass, neonatal body mass in bats averages 22.8% of maternal body mass, with *Rhinolophus cornutus* (Rhinolophidae) having one of the largest (43%) and *Pteropus poliocephalus* (Pteropodidae) one of the smallest neonates (12.2%) (Kunz and Kurta, 1987). In general, bats show a tendency for larger species to give birth to smaller young relative to maternal body mass, while smaller species bear larger neonates (Kunz and Kurta, 1987).

Furthermore, bats show different types of diet depending on their environments. In temperate regions, bats are predominantly insectivorous. Only a few species include small vertebrates into their diet, such as *Nyctalus lasiopterus* (Vespertilionidae) (Dondini and Vergari, 2000). By contrast, the diet of bats in the tropics shows greater diversity. Besides species that are predominantly insectivorous, other neotropical bats are predominantly frugivorous or nectarivorous (Pteropodidae) and feed on small vertebrates and/or insects next to fruits, nectar and pollen (Pteropodidae, most phyllostomids) (Courts, 1998, Altringham and Fenton, 2003).

As mentioned above (see introduction), flight behaviour is closely linked to diet. Species that feed predominantly on fruits and nectar either show a fairly steady flight (Pteropodidae) or have similar flight behaviour in front of flowers as hummingbirds (e.g., some phyllostomids). Species that feed predominantly on insects, conversely, show a diversity of hunting methods, such as gleaning or aerial hawking (Norberg et al., 1987).

In order to capture this large morphological, behavioural, and reproductive variation and investigate the association with pelvic form, the aim was to build a sample that was representative of the entire bat phylogeny, by capturing as many clades as possible (see Fig. 3, Tab. 1). To achieve this goal, the number of species sampled needed to be maximized rather than the number of specimens for each species. Nonetheless, the aim was to measure five specimens per sex per species to obtain reliable means. Unfortunately, the majority of bats are very small and have a very low skeletal weight to enable powered flight, making their postcranial bones very fragile. As a result, the pelvic girdle was often damaged to such an extent that the measurements of interest (see “Methods” for details) could not be taken. Furthermore, dry postcranial material of bats

(other than the forearm and shoulder girdle) is relatively scarce in museum collections. Hence, due to the lack of available, undamaged postcranial material, it was often not possible to examine five specimens per sex for each species.

Although the general aim was to represent each species by an equal number of males and females, female specimens were ultimately preferred: The main goal of this study was to investigate the association between the width of the pubic syndesmosis (pubic gap) and the relevant reproductive and flight variables, such as neonatal size and type of flight. Since only females have a pubic syndesmosis, they were of primary interest. Nonetheless, when only males were available for a given species, they were included in the sample.

Overall, 273 individuals of 82 species covering 14 "families" were examined: 126 males, 145 females, and two specimens of unknown sex. The majority of specimens (242 individuals) were from the Mammal Collection of the Natural History Museum Vienna. These included dry and wet (i.e., alcohol) specimens. In the latter case, the bony pelves were removed by an experienced taxidermist. In order to minimize the number of wet specimens from which to remove the bony pelvis (which requires partial destruction), preference was given to collect only females. The remaining specimens (31 dry specimens) were provided by other European natural history collections (the Museum für Naturkunde in Berlin, the Zoological Research Museum Alexander Koenig in Bonn, the Bavarian State Collection of Zoology in Munich and the Swedish Museum of Natural History in Stockholm) on request. The total number of specimens for each species, specified by museum accession number, sex, and type of specimen (wet or dry), is presented in table A1 in the Appendix.

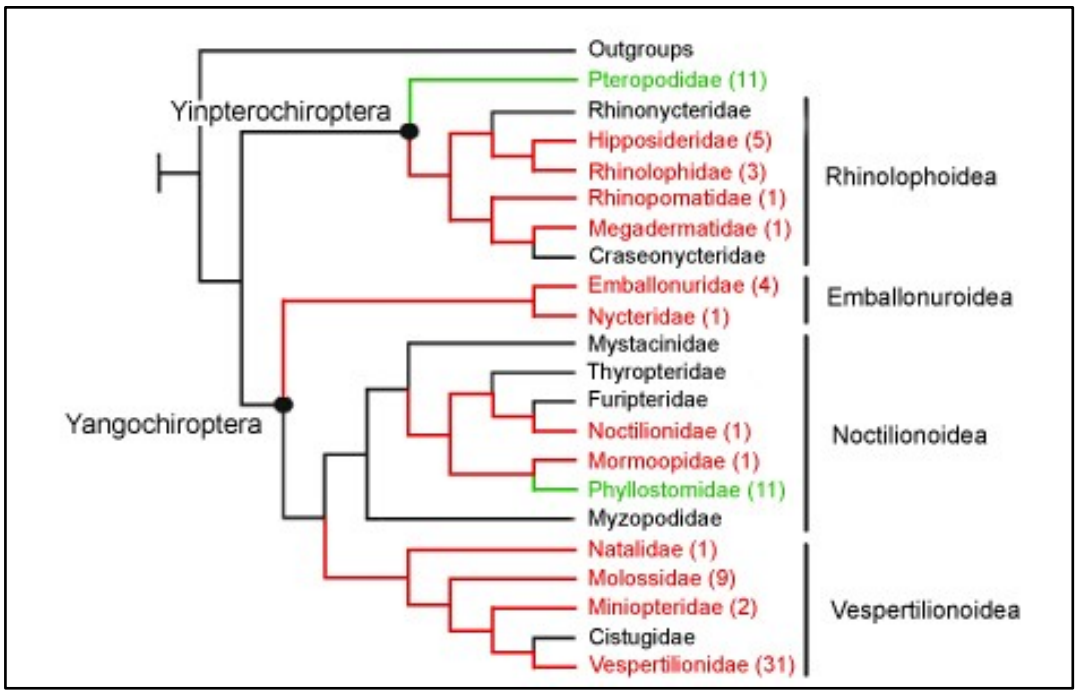

Figure 3. Bat phylogeny after Amador et al. (2018). The families represented in this study are shown in red and green. Colours indicate food preferences. Red: predominantly insectivorous. Green: predominantly frugivorous or nectarivorous. Black: groups not represented in this study. Numbers in parentheses indicate the number of species of each group sampled in this study. See also Table 1.

Table 1. Examined species. Shown are the 82 examined species and their "families" used in this study.

Yinpterochiroptera		Yangochiroptera	
Family	**Species**	**Family**	**Species**
Pteropodidae	*Cynopterus sphinx*	Emballonuridae	*Taphozous hildegardeae*
	Dobsonia moluccensis		*Taphozous longimanus*
	Eidolon dupreanum		*Taphozous melanopogon*
	Eidolon helvum		*Taphozous nudiventris*
	Eonycteris spelaea	Nycteridae	*Nycteris thebaica*
	Epomophorus labiatus	Noctilionidae	*Noctilio albiventris*
	Macroglossus minimus	Mormoopidae	*Pteronotus quadridens*
	Pteropus giganteus	Phyllostomidae	*Anoura caudifer*
	Pteropus lylei		*Anoura geoffroyi*
	Pteropus vampyrus		*Artibeus jamaicensis*
	Rousettus aegyptiacus		*Artibeus lituratus*
Rhinolophidae	*Rhinolophus clivosus*		*Brachyphylla nana*
	Rhinolophus cornutus		*Carollia perspicillata*
	Rhinolophus hipposideros		*Desmodus rotundus*
Hipposideridae	*Asellia tridens*		*Glossophaga soricina*
	Hipposideros armiger		*Macrotus waterhousii*
	Hipposideros caffer		*Phyllostomus hastatus*
	Hipposideros commersoni		*Platyrrhinus lineatus*
	Hipposideros diadema	Natalidae	*Nyctiellus lepidus*
Megadermatidae	*Megaderma lyra*	Molossidae	*Chaerephon bivittata*
Rhinopomatidae	*Rhinopoma hardwickei*		*Chaerephon plicatus*
			Molossus molossus
			Mops condylurus
			Mops demonstrator
			Mormopterus jugularis
			Otomops martiensseni
			Tadarida aegytiaca
			Tadarida brasiliensis
		Miniopteridae	*Miniopterus inflatus*
			Miniopterus schreibersii
		Vespertilionidae	*Barbastella barbastellus*
			Eptesicus furinalis
			Eptesicus nilssonii
			Eptesicus serotinus
			Euderma maculatum
			Glauconyteris argentata
			Hypsugo savii
			Myotis bechsteini
			Myotis blythii
			Myotis brandtii
			Myotis capaccinii
			Myotis daubentoni
			Myotis emarginatus
			Myotis myotis
			Myotis mystacinus

			Myotis nattereri *Neoromicia capensis* *Neoromicia nanus* *Nyctalus noctula* *Pipistrellus kuhlii* *Pipistrellus nathusii* *Pipistrellus pipistrellus* *Pipistrellus stenopterus* *Plecotus auritus* *Plecotus austriacus* *Plecotus gaisleri* *Scotoecus hirundo* *Scotophilus dinganii* *Scotophilus kuhlii* *Scotophilus nigrita* *Vespertilio murinus*

In addition to the osteological data, contextual data from the literature were collected. These include reproductive and dietary data, as well as data on flight behaviour (Table 2). They were important for investigating the association between pelvic morphology - the size of the pubic syndesmosis in particular - and the relevant reproductive and flight variables, in line with the main goal of this study.

The reproductive variables consist of adult body mass, neonatal body mass and adult forearm length. To compute the relative neonatal body mass for each species, the (absolute) adult body mass and the (absolute) neonatal body mass were required. Furthermore, species means of forearm length were collected from the literature for those species for which no skeletal specimens had associated forearms to measure.

Flight behaviour was represented by dietary (e.g., frugivore, insectivore) and wing morphology variables. Dietary variation of bats is well reflected in their type of flight. For instance, bats that hunt flying insects in the air (aerial hawking) need to be manoeuvrable and exhibit agile and acrobatic flight. Among insectivorous bats, one can distinguish between the flight of species that hunt in cluttered spaces with dense vegetation (e.g. many vespertilionids) and the flight of those that forage out in the open air (e.g. over fields or above the canopy, such as *Nyctalus noctula* and many molossids) (Norberg et al., 1987). Bats that feed on fruits, by contrast, often fly more smoothly and steadily because they do not hunt moving prey (e.g. most pteropodids and frugivorous phyllostomids; Norberg et al., 1987). Flight behaviour is also captured by wing form. Specifically, wing aspect ratio, wing loading and wing tip shape are well-established variables that characterize variation in chiropteran flight (Norberg et al., 1987). While the wing tip shape describes the shape of the wing tip, the wing aspect ratio and the wing loading characterize the shape and size of the entire wing (Norberg et al., 1987). The wing aspect ratio, A, is defined as the square of the wingspan divided by the wing area ($A = B^2/S$). A high wing aspect ratio indicates a long and rather slender wing, while a low wing aspect ratio implies a shorter and broader wing. The wing loading is the result of dividing body weight (mass multiplied by gravitational acceleration) by wing area (M*g/S) (Norberg et

al., 1987). Here, a high value indicates a narrower wing; a low value a broader wing. Taken together, this means that, for example, a bat with a high wing aspect ratio and high wing loading has long narrow wings, which is associated with a fast flight (Norberg et al., 1987). Bats with low values for both variables, on the other hand, possess short, broad wings. These bats typically have slow but manoeuvrable flight.

Table 2. Shown are the variables for which contextual data from the literature were collected, as well as the data references.

Type of Variable	Variables	References
reproductive	adult male and female body mass; neonatal body mass; litter size; forearm length	Norberg et al. (1987), Kunz & Kurta (1987), Hayssen et al. (1993), Jones et al. (2009), Fayenuwo and Halstead (1974) Kunz & Jones (2000)
dietary	frugivorous; nectarivorous; palynivorous; insectivorous; carnivorous; sanguivorous	Norberg et al. (1987), Barlow (1997)
flight behaviour	wing aspect ratio; wing loading; wing tip shape	Norberg et al. (1987)

2.2 Methods

To represent pelvic morphology, different parts of the ventral and lateral side of the pelvis were measured. On the ventral side these pelvic variables consist of the pelvic inlet, maximum pelvic width, the pelvic outlet and the pubic aperture (pubic gap; see Fig. 4). Pelvic anterior-posterior depth and pelvic height (measured in two different ways) were examined on the left lateral side of the pelvis (see Fig. 4). All these pelvic variables were chosen to determine the size and shape (mostly expressed as relative size) of the birth canal, which is limited by the bony pelvis. Furthermore, the pubic aperture was measured as the minimum width of the pubic gap. This captured the minimum amount of extra space between the pubic bones, which is traversed by the interpubic ligament during the animal's life. Note that this measurement will typically only be taken on female specimens, although male bats of some species also exhibit a pubic aperture.

Usually, the best way to collect the data for these pelvic variables would be the use of three-dimensional (3D) geometric morphometrics. Geometric morphometrics is a method of statistical analysis by which the size of a structure is separated from the shape (Mitteroecker and Gunz, 2009). For example, two identical biological structures of different size can be compared in terms of their shape. For this, homologous point locations, known as landmarks, are used to represent a structure's 3D form (size and shape) by its Cartesian coordinates (Mitteroecker and Gunz, 2009). One way to record landmark coordinates is by means of a MicroScribe. A MicroScribe (GoMeasure3D) is a portable device that allows landmarks to be manually placed on a physical object. However, due to the very small pelvic size of the bat species in the sample, it was not possible to use a MicroScribe to record 3D pelvic form without introducing substantial

measurement error. To overcome this problem, the use of a digital three-dimensional model of the bat pelvis, such as micro-CT or surface scans, would have been necessary. Using appropriate software (e.g. Amira™, Avizo™), then, landmarks can be placed digitally on virtual objects. However, micro-CT or surface scanning a high number of bat pelves, as was the case in this study (more than 250 specimens), proved too time and cost-intensive and was therefore not a viable method for this study. Moreover, at the time of data collection, insufficient 3D scans of bat pelves were freely available in public data repositories (e.g. MorphoSource).

As the use of 3D geometric morphometrics was not a feasible method for data collection and analysis, several linear measurements capturing the pelvic areas of interest were taken on high-resolution standardized photographs instead. Pictures of the pelves were taken with a Nikon SMZ25 stereomicroscope with a DS-Ri2 microscope camera-unit (see Fig. 5). In order to obtain uniform pictures of the pelves, standardised positions were used for the bat pelves. When taking pictures of the ventral side, the pelvis was fixed with the spine to the surface underneath by using Blu-Tack. The pelvis was then positioned with the inferior pubic rami parallel to the underlying surface. When pictures of the left lateral side needed to be taken, the pelvis was fixed with Blu-Tack on its right side so that the *Foramen obturatum* was parallel to the surface below. By means of the Nikon NIS-Elements BR software (Basic Research), pelvic dimensions were recorded directly on the images produced on the computer screen that was connected to the stereomicroscope.

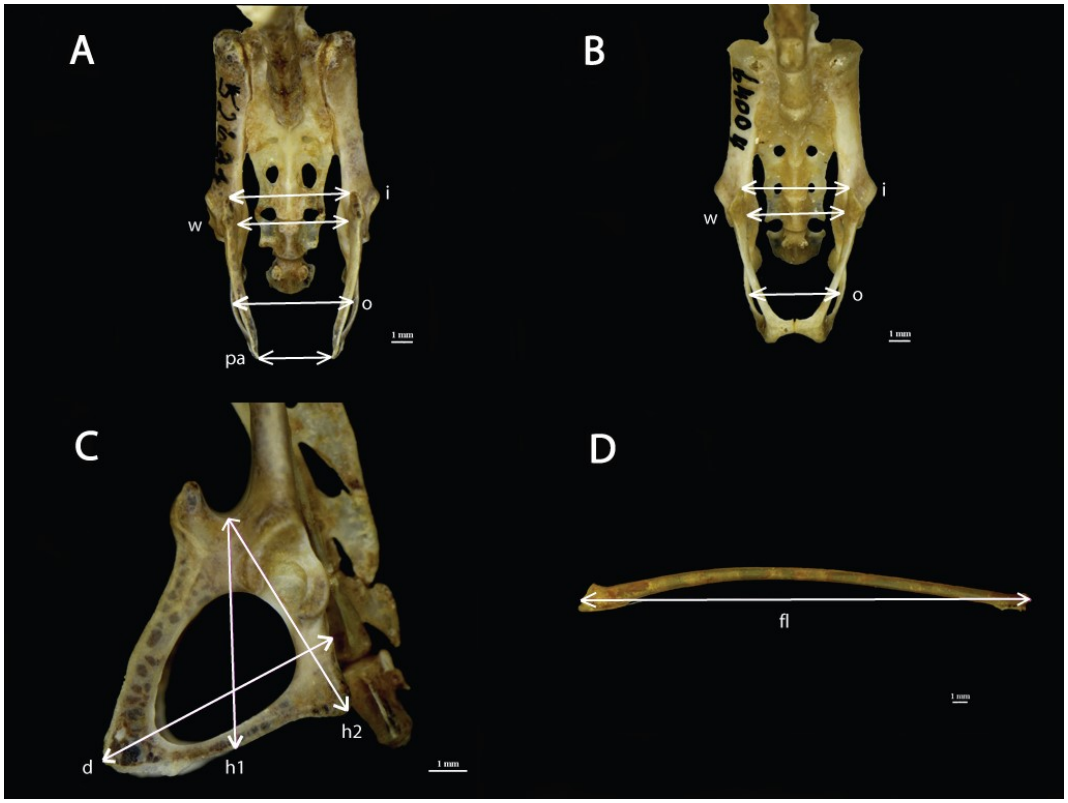

Figure 4. Pelvic and forearm measurements. A: female bat pelvis of *Myotis myotis* ventral view, i – pelvic inlet, w – maximum pelvic width, o – pelvic outlet, pa – pubic aperture. B: male bat pelvis of *Myotis myotis* ventral view, i – pelvic inlet, w – maximum pelvic width, o – pelvic outlet. C: female pelvis of *Myotis myotis* lateral view, d – pelvic anterior-posterior depth, h1 – first pelvic height, h2 – second pelvic height. D: bat forearm dorsal view, fl – forearm length

In addition to the pelvis, forearm length of each individual, if possible, was recorded to obtain a body size proxy (see Fig. 4). In bats, forearm length typically serves as a proxy for body size as it scales isometrically with body mass (Fleming, 1993). To this end, the right forearm was measured, substituted by the left when the right one was damaged or missing. Depending on the size of the forearm, its length was recorded in one of two ways. Smaller forearms were measured with the stereomicroscope, whereas some species' forearms (e.g. *Pteropus vampyrus* and other large-bodied pteropodids) were too big to be visible in their entirety under the microscope. Hence, these large forearms were measured with a sliding digital calliper (Mitutoyo NTD12-15C, Mitutoyo Corporation). Nevertheless, the position of the forearm was standardized across the two methods: it was always placed with its ventral side on the surface underneath and fixed with Blu-Tack when necessary, and the distance from the outermost part of the elbow joint to the outermost part of the wrist was measured. Both pelvis and forearm measurements were transferred to Microsoft Excel 2016™ afterwards; measurements recorded using the stereomicroscope software were input automatically.

Before the overall measuring started, a measurement error test was carried out to determine the intra-observer error. This was done by measuring 22 individuals (9 males, 13 females) belonging to 16 different species. Each specimen was measured twice at an interval of one week. Then, first, for each pelvic variable the mean across all specimens was calculated for each time point (week 1, T1, and week 2, T2). Only the values of female individuals were used for the pubic aperture measurement, since only females feature a pubic gap. Next, once these "week-specific" means were calculated the overall mean for each variable across both weeks were computed. For each specimen, the absolute deviation between T1 and T2 for each variable was determined. Therefore, the value of the second week was subtracted from the value of the first week. With the values of the absolute deviation (i.e. ignoring the sign) the average absolute deviation for each pubic variable was computed. Measurement error was then expressed as the percentage error (the mean deviation) of the mean (Tab. 3). In addition, an alternative observer error statistic, called technical measurement error (TEM) (Perini et al., 2005), was computed. Therefore, first, the absolute deviation of each specimen for each variable has been squared. Next, all squared specimen values for a variable were summed and divided by the number of specimens, which was previously multiplied by two. Last, the square root was taken from the resulting value (Perini et al., 2005). To compare the results with the results of the intra-observer error, the TEM-values were expressed as a percentage error of the overall mean. In the end, the TEM yielding comparable results for each measured variable (not shown) as the intra-observer error. As in Weinberg et all. (2005) a value of less than 5 % for the TEM and the intra-observer error is considered a good indicator of accurate measurement. The measurement error was also computed for forearm length (Tab.4).

Figure 5. Nikon SMZ25 stereomicroscope with a DS-Ri2 microscope camera unit.

Table 3. Results of pelvic intra-observer error study. Results of the intra-observer error study carried out on the seven pelvic variables in a sample of 22 specimens belonging to 16 phylogenetically diverse species[a]. Statistics are based on repeated measurements from two time points (T1 and T2). Max.=maximum

	Pubic aperture[b]	**Pelvic inlet**	**Max. pelvic width**	**Pelvic outlet**	**Pelvic antero-posterior depth**	**Pelvic height**	**Pelvic height 2**
Mean (mm)	3.619	6.271	5.211	5.249	6.300	6.612	6.930
Average absolute deviation (T1 – T2) (mm)	0.108	0.153	0.129	0.153	0.119	0.112	0.087
% error of the mean	**2.99**	**2.44**	**2.48**	**2.91**	**1.89**	**1.69**	**1.25**

[a] Pteropodidae (*Eonycteris spelaea, Epomophorus labiatus*, *Macroglossus minimus, Pteropus giganteus, Pteropus lylei, Rousettus aegyptiacus*), Rhinolophidae (*Rhinolophus clivosus*), Hipposideridae (*Asellia tridens*, *Hipposideros armiger, Hipposideros diadema*), Rhinopomatidae (*Rhinopoma hardwickei*), Vespertilionidae (*Barbastella barbastellus, Eptesicus nilssoni, Euderma maculatum, Hypsugo savii, Myotis myotis*).
[b] Females only, *N* = 13.

Table 4. Results of forearm intra-observer error study. Results of the intra-observer error study carried out on forearm length[a]. Statistics are based on repeated measurements from two time points (T1 and T2).

	Forearm length
Mean (mm)	70.012
Average absolute deviation (T1 – T2) (mm)	0.776
% error of the mean	**1.05**

[a] Based on the same sample as reported in Tab. 3, but without *Macroglossus minimus*, for which no forearm was available.

2.3 Data

To show variation patterns in the morphological variables, the data were visualized by box plots and standard deviations were compared.

2.3.1 Box plots

To visualise the variation between the specimens across the measured variables, box plots were created for each measured variable from all specimens. Measured variables include pelvic measurements as well as forearm length. The variable "forearm length" was displayed in a separate box plot due to the larger measurement values of this variable.

2.3.2 Summary statistics

For the comparison of the variation across the variables the overall mean, the overall median and the standard deviation were computed for each measured variable. Due to the sexual dimorphism between males and females in the pubic aperture and possibly other pelvic measurements, the calculation of the overall mean, the overall median and the standard deviation across all variables was carried out separately for males and females. Therefore, the mean was first calculated for each species for each sex in each variable. Then the overall mean for males and females for each variable was computed from all associated species means. Similarly, the male and female overall median for each variable was calculated from the sex-specific species means. Next, the sex-specific standard deviations were computed using the respective species' sex means for each variable. The aforementioned summary statistics were calculated across species means rather than across specimens due to the unequal sample sizes across species (e.g., the number of specimens in some species is four or more as in some vespertilionids, while in others there is only one specimen). Therefore, the sample means and the associated standard deviations would be disproportionately influenced by those species with more specimens. To avoid that, male and female summary statistics were computed from the sex-specific species means. The overall means, overall medians and standard deviations for males and females are listed in table 5 and 6.

2.4 Analyses

In the following analyses, the separation between males and females is only made with regard to sexual dimorphism. For the remaining analyses, only female specimens were used. This was done because the relationship between neonatal body mass and pubic aperture is the focus of this thesis and the pubic aperture only occurs in female bats and only females give birth to neonates. Furthermore, only the species means were used for the following analyses. The reason for this, as with the calculation of the summary statistics, is the unbalanced species sample size.

2.4.1 Sexual dimorphism

Sexual dimorphism is very common among mammals, with males usually larger in size than females (Ralls, 1977, Mori et al., 2017). Nevertheless, in some mammalian taxa, females are larger in size than males, such as in Lagomorpha and Chiroptera (Ralls, 1976,

Ralls, 1977). Commonly, sexual dimorphism in bats has been studied in relation to body size and wing size (especially wing loading) (Myers, 1978, Williams and Findley, 1979). In terms of the pelvis, clear sexual dimorphism exists in the pubic region, with the appearance of a pubic aperture in females. Otherwise, no other sexual dimorphism in the pelvic region is known or has been studied. Therefore, in this study, the pelvic measurements taken, in addition to the pubic aperture and forearm length, were tested for sexual dimorphism. The average magnitude of sex differences was computed for each measured variable. First, the male and female mean for each species for each variable was calculated. As males and females were not always present for all species in this study, only those species where measurements were taken for both sexes were considered. Second, the absolute size difference between male and female means were taken for each species per variable. At the end the overall sexual dimorphism magnitude was then determined for each measured variable. To compare the average magnitude of sex differences across the measured variables, the computed values were displayed in a bar blot.

In order to determine which sex is larger in the different pelvic variables, the previously calculated means for males and females were first log-transformed. This was necessary to provide a reasonable comparison between the variables, as the measured values for forearm length were much higher than for the pelvic variables. Afterwards the log-transformed female mean was subtracted from the log-transformed male mean for each species of each variable. When the resulting sexual dimorphism magnitude was positive, males were on average larger than females. A negative result, in contrast, meant that females were on average larger than males. The results for each variable are displayed in Fig. 10. The calculation of the sexual dimorphism magnitude for the pelvic variable “pubic aperture” could not be carried out following this protocol. An overwhelming majority of the male bats in the sample did not possess a pubic aperture, resulting in a pubic aperture value of zero. Since a log-transformation is not possible for values that are zero, the sexual dimorphism magnitude for pubic aperture could not be computed. However, due to the known strong sexual dimorphism in the pubic bone of bats in the literature and from personal observations during the data collection (see Fig. 2), it was not necessary to check in which sex the pubic opening is more prominent.

2.4.2 Principal Component Analysis

To explore the patterns of variation in pelvic morphology between the various species in this study, a principal component analysis (PCA) was performed. This was done by using the female mean for each species per variable. Due to the vast differences in body size among bats (especially between the pteropodids and most other, smaller bats), female means were log-transformed prior to the PCA. The PCA on the pelvic variables was then performed by using the software PAST (Hammer et al., 2001) . Afterwards, the first principal component (PC1) as well as the second principal component (PC2) of the PCA were plotted against the log-transformed values of the forearm length. This was done to check whether PC1 or PC2 correlates more with forearm length and therefore with body size. Moreover, patterns of variation in pelvic morphology in relation to flight behaviour were also explored by using PCA. To this end, species were classified into three groups according to their diet and associated flight behaviour. The first group, named “frugivory”,

covers all those species that feed on fruits (frugivore), nectar (nectarivore) or pollen (palynivore). Most of these species engage in slow, manoeuvrable flight to avoid obstacles, others are even able to hover. Importantly, what all these species have in common is that they feed on immobile food. Also included in the first group is the species *Desmodus rotundus*, which feeds exclusively on other animals' blood (sanguivore). Since they lick the blood of sleeping animals, their food is stationary and more or less immobile, similar to the food of frugivorous, nectarivorous and palynivorous species. The second group is called "gleaning" and includes the species that are predominantly insectivorous and which hunt their prey by slow hawking and gleaning. These species share a slow manoeuvrable flight, often in a cluttered environment. In addition, this group comprises trawling (fishing) bats and perch hunters too. The third and last group, termed "aerial hawking", covers those species that are predominantly insectivorous and which hunt their prey in open spaces. As a result, these species are characterised by fast flight and high agility but lower manoeuvrability.

2.4.3 Hypotheses Analysis

Before testing the hypotheses, it was first checked whether there is a correlation between maternal and neonatal weight, since this is the case in other mammals (Leutenegger, 1976, Martin and MacLarnon, 1985, Grunstra et al., 2019). To this end, both body mass variables were log-transformed in order to investigate the ratio of neonatal body mass to maternal weight. Therefore, neonatal body mass of the bat species used in this study was plotted against adult body mass. The same was then generated for all available bat data from the PanTHERIA database of Jones et al. (2009). The latter included a larger number of species than were surveyed in this study, enabling a comparison of the relationship among the bats in the present sample with the general chiropteran pattern.

For an accurate study between the species of different body sizes, it was important to correct the main variables pubic aperture and neonatal body mass for size for the following analyses of the hypotheses. Hence, the relative pubic aperture (relPA) as well as the relative neonatal body mass (rNBM) were calculated. Relative neonatal body mass was calculated by dividing neonatal body mass by adult body mass and multiplied by 100 for each species. The result obtained represents the percentage of adult body mass that neonates have achieved at birth. To determine the relative size of the pubic aperture, a suitable representative of body size first had to be found. As mentioned above, forearm length in bats typically serves as a proxy for body size as it scales isometrically with body mass (Fleming, 1993). However, due to the fact that not every species examined had an associated forearm to measure and the use of species means derived from the literature can be imprecise and introduce error, a body size proxy from the measured pelvic variables was chosen. The pelvic variables were selected because they were measurable for each specimen. To ascertain a good pelvic body size proxy it was investigated which variable scaled isometrically with forearm length. Isometry indicates that the relationship between, in this case, the pelvic variable and forearm length is constant across different values of body size. Such an isometric relationship was preferred because pelvic dimensions that scale allometrically with forearm length (and thus with body mass) would introduce an additional source of variation into the measure of relative pubic aperture (a ratio). This would therefore affect the interpretability of variation in relative pubic

aperture across bats. At the end of this investigation, "pelvic canal height 2" was shown to scale isometrically with forearm length, making it a suitable proxy for forearm length and thus also a useful body size proxy. Subsequently, relPA was calculated as a ratio of pubic aperture and “pelvic canal height 2”.

Another aspect that had to be considered in the analyses of the hypotheses is the phylogenetic relationship between the specimens examined. Independent data are important for a meaningful result of comparative analyses (Felsenstein, 1985). When comparing closely related species, their data (morphological data in this study) can be similar because they share a common ancestor. Therefore, the data are non-independent (Felsenstein, 1985, Pagel, 1999, Symonds and Blomberg, 2014). For this reason, to enable comparative analyses, the data must be corrected by means of a phylogenetic analysis. In order to perform phylogenetic analyses a phylogenetic tree was needed that reflects the relationships of the chiropteran species used in this study. For this purpose, several studies were compared to find the best fitting tree. In the end, the tree by Amador et al. (2018) was chosen as it covered all species examined in this study and it had the best support values for most bat families. With the software RStudio (R Core Team, 2019) this tree was then pruned to the extent that only the species used in this study were present in the tree. Although most groups had good support values, some nodes in the tree from Amador et al. unfortunately did not. Hence, the topology by Amador et al. was compared with other studies focused on specific major groups or families relevant to this study. Where these other studies had a different topology with better support values, the Amador tree was adjusted at the respective nodes using the software TreeGraph 2 (Stöver and Müller, 2010), following the tree with the better support values. As a result, minor adjustments to the Amador tree were made in the following groups and based on the following studies: Phyllostomidae (Rojas et al., 2011), Hipposideridae (Patterson et al., 2020), *Myotis* (Stadelmann et al., 2007), and non-*Myotis* Vespertilionidae (Roehrs et al., 2010). Subsequently, the tree was pruned further in RStudio so that only the species for which females were present were still contained (see Fig. 6).

2.4.4 Hypotheses Testing

To test the first hypothesis, that bat species with the relatively heaviest neonates also possess the relatively widest pelvic apertures, phylogenetically unadjusted and adjusted linear regressions were performed between relPA and rNBM. For the unadjusted linear regression, relPA was simply regressed as dependent variable on the independent variable rNBM. This was done by using RStudio. The phylogenetic regression was conducted in RStudio as well, by using the function “pgls()” in the R package “caper” (Orme et al., 2018). This function applies a phylogenetic generalized linear model (pgls) to the used data, allowing a phylogenetic regression to be performed afterwards (Symonds and Blomberg, 2014). To carry out the pgls function, the phylogenetic signal was first determined. The phylogenetic signal indicates how strong the similarities are between closely related species (Blomberg et al., 2003). The phylogenetic signal in this study is represented by Pagle’s Lambda (λ). This unit was first introduced by Pagel (Pagel, 1997) and measures the phylogenetic dependence between species in a quantitative way

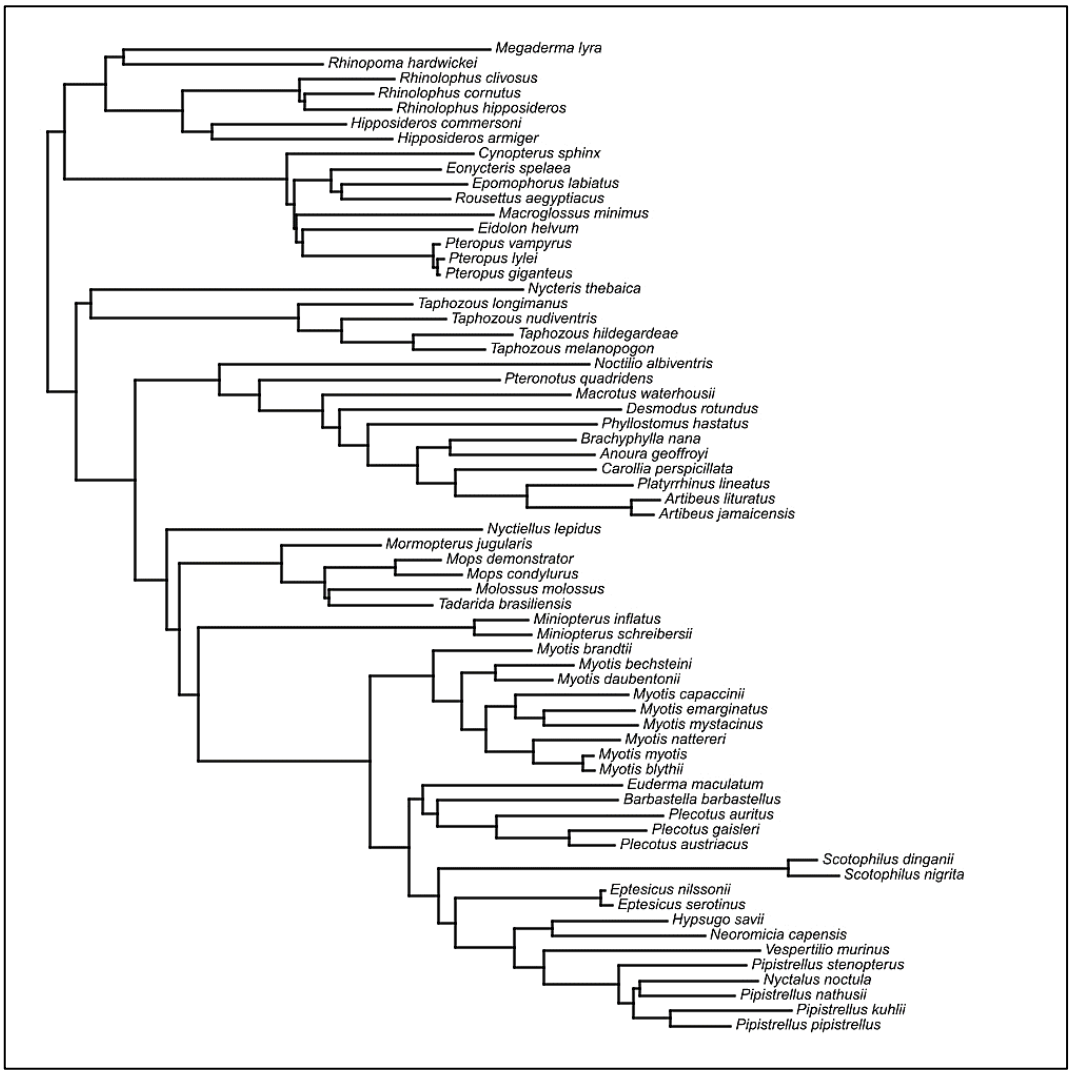

Figure 6. Phylogenetic tree of Chiroptera included in this study based on Amador et al. (2018) and adjusted following Stadelmann et al., 2007, Roehrs et al., 2010, Rojas et al., 2011 and Patterson et al., 2020. This tree was 'pruned' down to a subsample that included only the females used in the analyses.

(Kamilar and Cooper, 2013). If λ equals zero, there is no phylogenetic signal, indicating that the species evolved independently. On the other hand, a value of one shows that there is a strong phylogenetic signal which means that the data are non-independent.

The second hypothesis, that bats with a manoeuvrable flight mode possess a relatively smaller pubic aperture as compared to frugivorous and nectarivorous species, deals with additional factors that could possibly influence the width of the pubic aperture. Hence, the influence of body size and flight behaviour were also taken into account by means of an Analysis of Variance (ANOVA) and multiple regression. Since there is not a single common variable that captures flight behaviour in bats in all its complexity, separate variables were created for representing flight behaviour in this study. Classification of these variables is largely based on the work of Norberg & Rayner (1987). The first set of variables represents wing morphology, which consists of wing aspect ratio, wing loading and tip shape index. Since data for the tip shape index could only be collected for a few species from the literature, it was not used as a variable for wing morphology. Unfortunately, data for the remaining wing aspect ratio (WAR) and wing loading (WL) could not be collected for all species, resulting in missing data for various species (about

20 species). Therefore, an additional, categorical variable was constructed that represented the “flight mode”, which could be established for every species based on descriptions of relevant aspects of each species’ flight behaviour and diet published in the literature. This categorical variable (“flight mode”) was composed of three categories based on the three diet groups used for the PCA. The first category corresponds to the group “frugivory”, the second category to the group "gleaning" and the third and last category to the group "aerial hawking". In order to distinguish between the flight mode categories for a multiple regression, the species belonging to the first category were assigned the number one. Insectivorous species that hunt their prey in cluttered environments using slow and manoeuvrable flight (category two) received the number two, while species belonging to category three were given the number three.

By defining variables for flight behaviour, it was possible to carry out the multiple regressions to test hypothesis two. In these multiple regressions relPA was the dependent variable, while rNBM, the categorical variable “flight mode”, and WAR as well as WL were the predictor variables. Forearm length was used as an additional predictor (a covariate) to test for the effect of body size. The influence of the flight behaviour on the relPA size was checked in two different ways. In a first step, multiple regression was conducted to test for differences in the relationship between relPA and rNBM between the three flight mode categories using a nested model. For this purpose, the regressions of the three flight modes were compared in one regression model. In this model, differences in the slopes and intercepts of the three different regression lines indicate a different effect of rNBM on relPA and a different average relative pubic aperture size in the three flight mode groups. In addition, a multiple regression was performed using the wing morphology variables WAR and WL as a second possibility to test their influence on the relPA. Furthermore, the three flight mode categories were split to check them separately in a multiple regression. Since the focus of this thesis is on relative pubic aperture and relative neonatal body mass, an ANOVA was performed to determine if there were differences in these two variables between the flight mode categories.

To better appreciate the role that phylogeny plays in mediating the observed effects of relative neonatal body mass and the other predictors on relative pubic aperture, phylogenetic and phylogeny-unadjusted (“normal”) ANOVAs and multiple regressions were carried out and the results compared. This was done because even if phylogeny strongly mediates a functional relationship between two variables – such that the relationship disappears when phylogeny is “corrected” for – it cannot be ruled out that this relationship is not adaptive, because adaptive and phylogenetic divergence can overlap. A comparison is therefore worthwhile. Again, RStudio was used to perform the ANOVAs and the regressions. For the phylogenetic ANOVA the function “phylANOVA()” in the R package “phytools” (Revell, 2012) was used. The phylogenetic multiple regression was performed by means of the pgls function.

3. Results

3.1 Descriptive statistics

In the following the results of the descriptive statistics are presented. First, the measured variables are considered in the form of box plots and compared with each other. This is followed by a comparison of the variables between males and females to inspect sexual dimorphism.

By comparing the different pelvic variables by box plots, the laterally measured variables (“pelvic A-P depth”, “pelvic height”, “pelvic height 2”) and the ventrally measured variable “pelvic inlet” all display a median around 4.5 mm (Fig. 7). A median around 3.5 mm, on the other hand, is shown by the two remaining ventral variables (“max. pelvic width”, “pelvic outlet”). Similar observations can be made when looking at the interquartile range, which comprises the 25th to 75th percentiles of the variable data (shown by the boxes). Here, the lateral variables and the ventral variable "pelvic inlet" show a larger range (around 2 mm) than the two ventral variables “max. pelvic width” and “pelvic outlet” (around 1.5 mm) (Fig. 7). Overall, it can be seen that the highest range of variation occurs in the variable "pubic aperture".

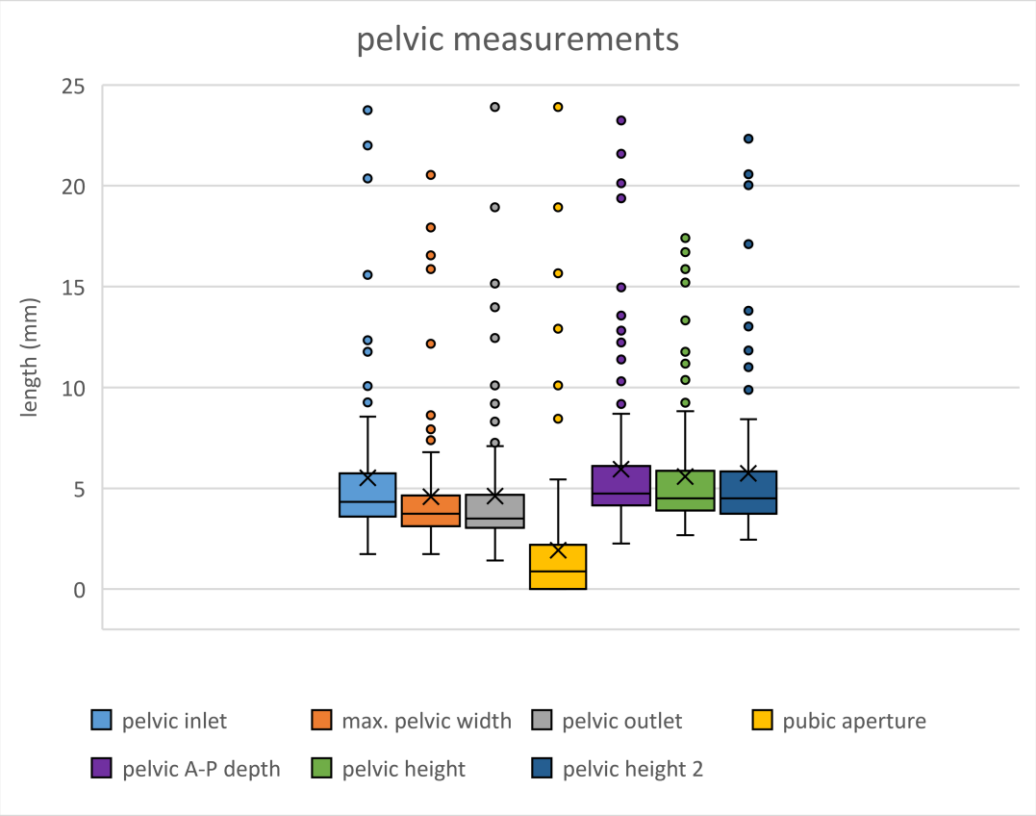

Figure 7. Boxplots and their outliers of the seven measured pelvic variables. Boxes comprise the 25th to 75th percentiles of the variable data (interquartile range). Whiskers represent the maximum and minimum that lies below 1.5 times the interquartile range from the boxes. Outliers are represented by the data that lies above 1.5 times the interquartile range from the boxes. In addition to the medians (horizontal line inside the boxes), the means are displayed, marked with an X. The variable pubic aperture does not possess a lower whisker, because males (no aperture = value of zero) and females are considered together. Max.: maximum; A-P: anterior-posterior

Because most male bats do not possess a pubic aperture, there is no lower whisker: the plot begins at zero. Since the pelvis of males was also measured in this study, the measurement value for the pubic aperture was zero for male specimens. Therefore, this variable also yields the lowest median. A common characteristic of all variables (including FA length) is the presence of six ("pubic aperture") or more positive outliers, which represent large-bodied species. These are almost exclusively data from species of the Pteropodidae. With *Hipposideros commersoni* (Hipposideridae; "pelvic inlet"; "pelvic height"; "FA length") and *Phyllostomus hastatus* (Phyllostomidae; "pelvic A-P depth"), only two species among the outliers do not belong to the Pteropodidae.

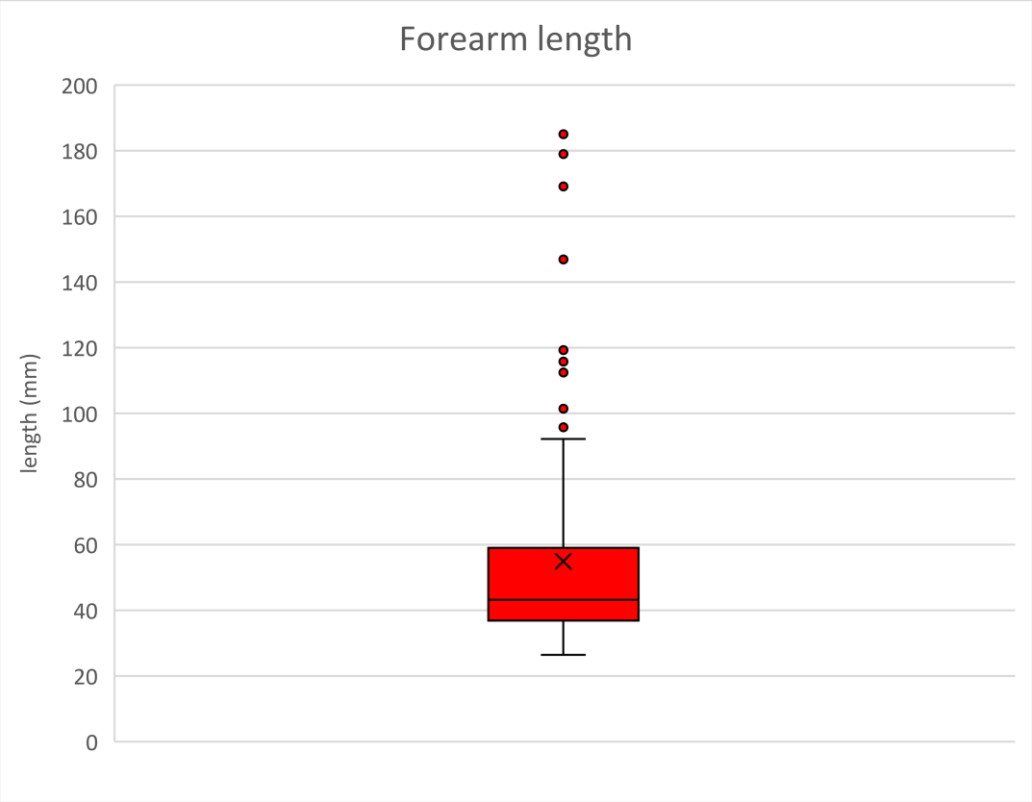

Figure 8. Boxplot and its outliers for forearm length. Box comprises the 25th to 75th percentiles of the variable data (interquartile range). Whiskers represent the maximum and minimum that lies below 1.5 times the interquartile range from the box. Outliers are represented by the data that lies above 1.5 times the interquartile range from the box. In addition to the median (horizontal line inside the box), the mean is displayed, marked with an X.

In the males, it can be seen that most pelvic variables are similarly close to each other for all three descriptive analyses. The only exception is the variable pubic aperture, which has much lower values for the overall mean, median and for the standard deviation (Table 5). This is because males of most bat species do not have a pubic aperture. Only in few species did the males exhibit a gap (*Desmodus rotundus, Cynopterus sphinx*). Because of this, the value for the overall mean is slightly higher than that of the overall median and the standard deviation is not zero (Table 5).

Table 5. Results of descriptive analyses of male bat specimens. Values are computed on the basis of sex-specific species means. Results are given in millimetres (mm). A-P: anterior-posterior; FA: forearm; M: male; max.: maximum

Variables	Overall mean M (mm)	Standard deviation M (mm)	Overall median M (mm)	N (M)
Pelvic inlet	5.47	4.21	3.95	51
Max. pelvic width	4.54	3.25	3.53	
Pelvic outlet	4.31	2.70	3.28	
Pubic aperture	0.20	0.84	0.00	
Pelvic A-P depth	6.22	4.25	4.97	50
Pelvic height	5.71	3.12	4.45	
Pelvic height 2	5.86	3.89	4.41	
FA length	57.03	35.22	41.95	43

For the females, as for the males, most variables have similar values for the overall mean, median and standard deviation (Table 6). Again, the variable “pubic aperture” shows the lowest values for the overall mean and median, although not as pronouncedly as in the males. For the standard deviation, however, pubic aperture has the highest value for all pelvic measurements (4.29 mm).

Table 6. Results of descriptive analysis of female bat specimens. Values are computed on the basis of sex-specific species means. Results are given in millimetres (mm). A-P: anterior-posterior; FA: forearm; F: female; max.: maximum

Variables	Overall mean F (mm)	Standard deviation F (mm)	Overall median F (mm)	N (F)
Pelvic inlet	5.44	3.50	4.41	67
Max. pelvic width	4.52	2.71	3.75	
Pelvic outlet	4.72	3.74	3.48	
Pubic aperture	3.08	4.29	1.53	
Pelvic A-P depth	5.69	3.18	4.70	
Pelvic height	5.44	2.74	4.51	
Pelvic height 2	5.62	3.58	4.52	
FA length	52.85	27.34	43.15	56

Comparing males and females, for the overall mean one can see that males and females differ only slightly from each other in the measured variables. The females only have a larger value for the variable “pelvic outlet” (4.72 mm vs 4.31 mm) and a substantially larger value for the variable “pubic aperture” than the males (3.08 mm vs 0.20 mm). For all other variables, the male values are higher. The same applies to the standard deviation. Here, too, only the female values for “pelvic outlet” (3.74 mm) and “pubic aperture” (4.29 mm) are higher than those of the males (2.70 mm; 0.84 mm), with the value for pubic aperture again being distinctly higher than the male value. For the overall median, by contrast, the female values are larger for almost all variables. Only for the variable "pelvic A-P depth" the value for males (4.97 mm) is higher than that for females (4.70 mm).

3.2 Sexual dimorphism

In this section the focus is on the results on sexual dimorphism within the bat pelvis across species.

Examining sexual dimorphism in the bat pelvis, Fig. 9 shows the greatest sexual dimorphism in the variables “pubic aperture” with 3.4 mm and “FA length” with 2.447 mm. With an average magnitude of 0.326 mm and 0.303 mm the two pelvic canal heights show the least sexual dimorphism, while the remaining variables do not have a value higher than 1 mm. Furthermore, in nearly all measured variables female bats are larger than males (Fig. 10, see also the medians in Tables 5 and 6). An exception is the variable "pelvic A-P depth", where the males are larger than the females. This is probably due to the presence of the ossified pubic symphysis (synostosis), which is present in males. As the pubic symphysis is resorbed in female bats during puberty, this structure is absent when the pelvis is viewed laterally, thus reducing the measurable anterior-posterior distance (pelvic A-P depth) in females.

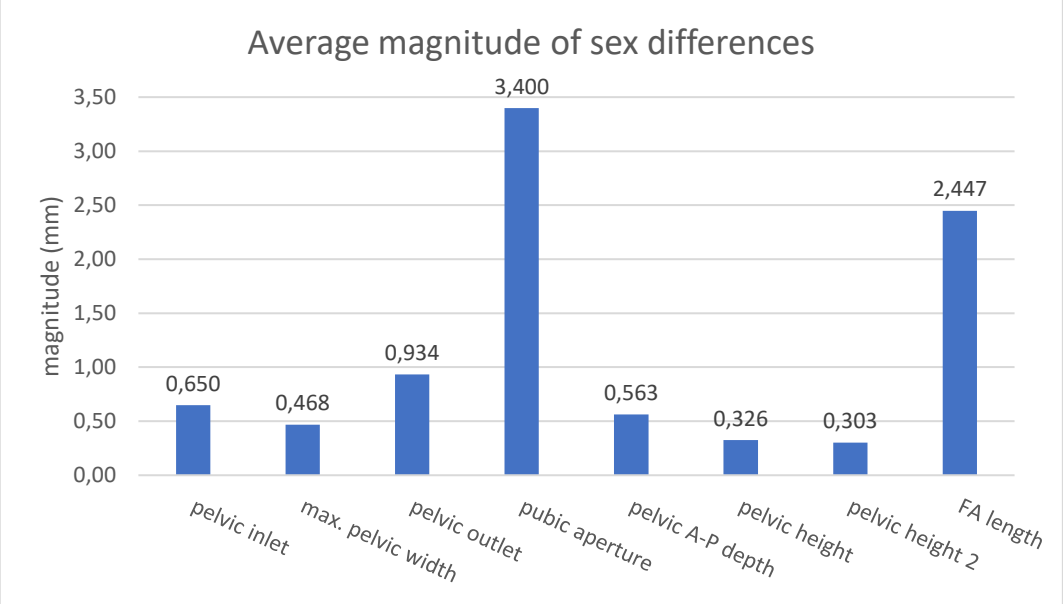

Figure 9. Comparison of the average magnitude of sex differences between the measured variables. Average magnitude was calculated for those species where measurements were taken for both sexes. Absolute size differences between male and female means were taken for each species per variable. Then overall sexual dimorphism magnitude was determined for each measured variable, by calculating the mean over species. A-P: anterior-posterior; FA: forearm; max.: maximum

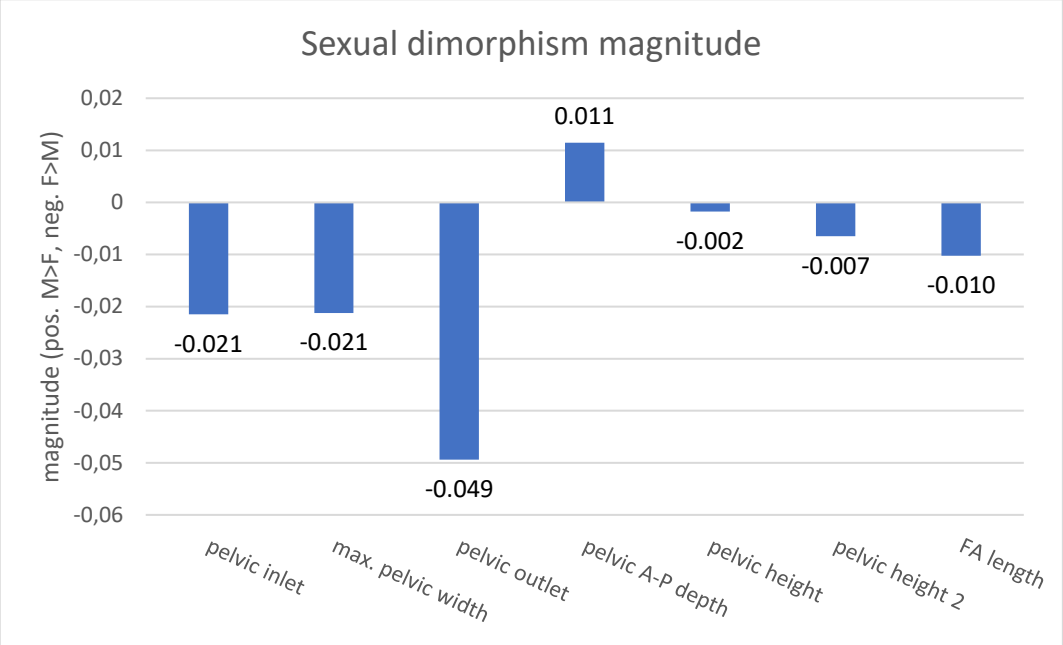

Figure 10. Comparison of the sexual dimorphism magnitude between the measured variables. The sexual dimorphism magnitude was calculated by log-transforming the means for males and females. Afterwards the log-transformed female mean was subtracted from the log-transformed male mean for each species of each variable. A positive value indicates that males are larger than females. A negative value points to females being larger than males. Due to the presence of a pubic symphysis in male bats, no measurements of pubic gap size in males could be taken (value of zero). Therefore, the variable "pubic aperture" is not shown because it could not be calculated (log-transformation is not possible for values that are zero). A-P: anterior-posterior; FA: forearm; max.: maximum

3.3 Principal Component Analysis

In the following, the results of the principal component analysis for the pelvic morphology on species level as well as in terms of flight mode are presented. For this analysis, only the log-transformed data of the female specimens were used.

The result of the principal component analysis (PCA), carried out across species, is shown in figure 15, which displays the morphospace defined by the scores of the first two principal components. Approximately 97% of the total variation of the pelvic variables is described by the first and second principal components (PC 1 and PC 2). PC 1 explains ~88% of the total variance and PC 2 describes ~9%.

All pelvic variables load positively on PC 1 (Fig. 13). This is expected given that all are linear (size) measurements and in that case PC 1 typically represents overall size (Mitteroecker et al., 2012). Variation in the pubic aperture contributes strongly to the variance captured under PC 1, with the other pelvic variables contributing more or less equally (Fig. 13). Furthermore, regressing the PC 1 scores against the log-transformed forearm length values indicates a strong positive correlation between the PC 1 and the forearm length, with a regression slope of 1.19 (Pearson p-value < 0.01) and a coefficient of determination (R^2) of 0.78 (Fig. 11). This, in addition to the PC1 loadings, implies that the PC 1 represents the overall size.

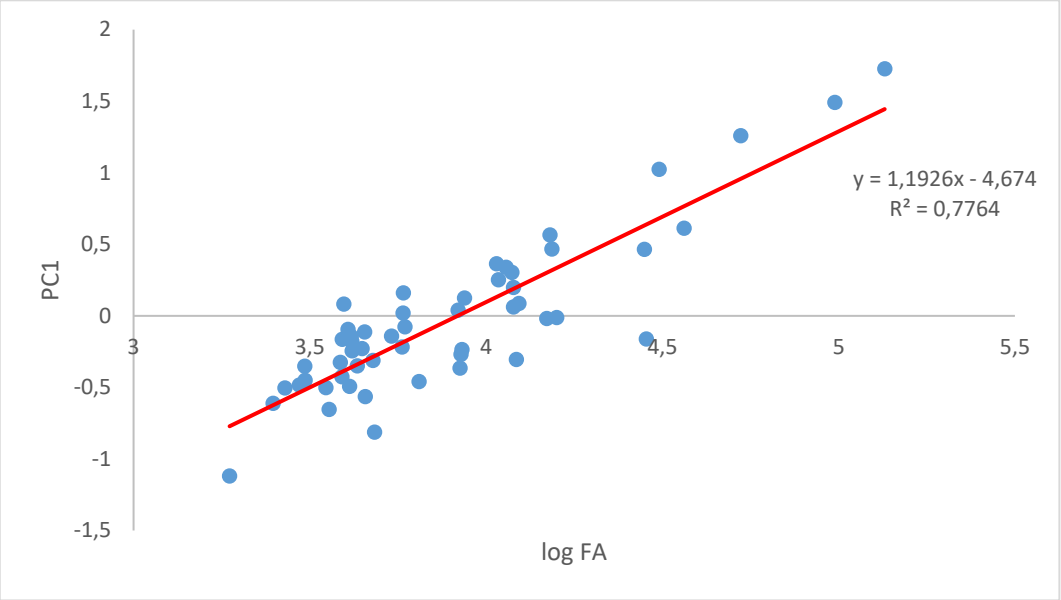

Figure 11. Simple regression of the first principal component (PC 1) scores on log-transformed forearm length. PC 1 scores derived from a principal component analysis conducted on log-transformed pelvic variables. Pearson *p*-value of the slope < 0.01

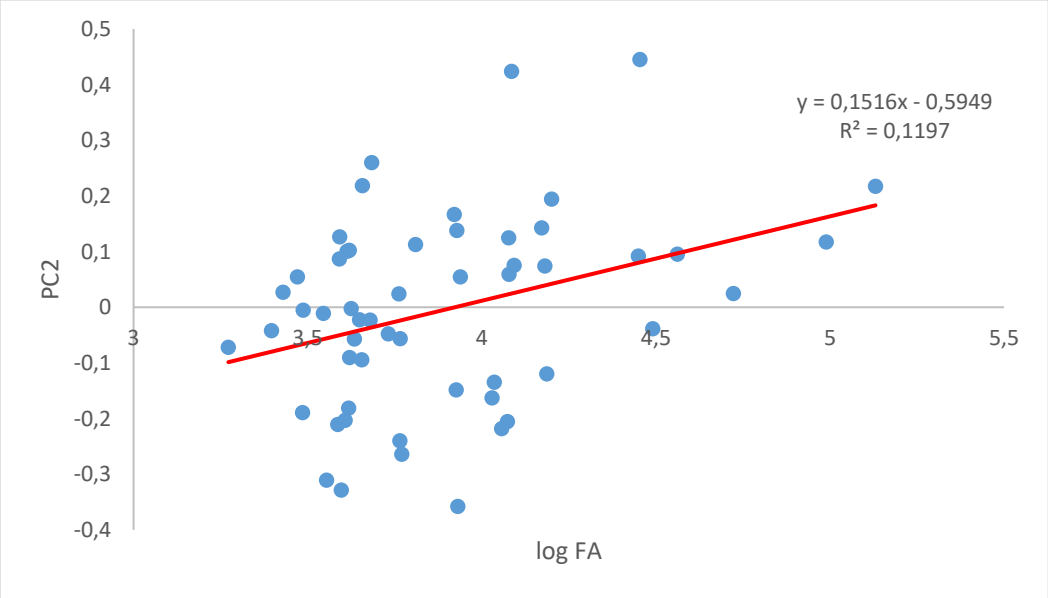

Figure 12. Simple regression of the second principal component (PC 2) scores on log-transformed forearm length. PC 2 scores derived from a principal component analysis conducted on log-transformed pelvic variables. Pearson *p*-value of the slope = 0.01

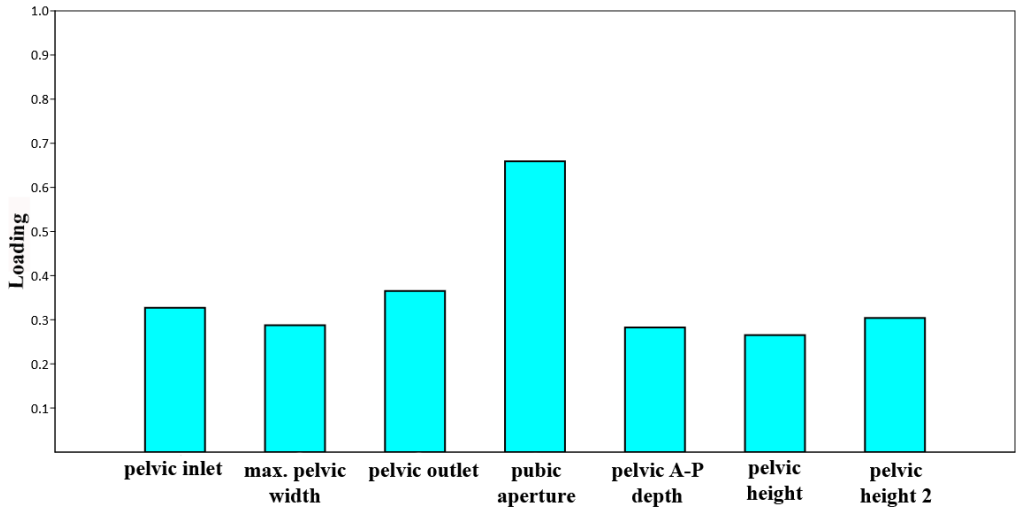

Figure 13. Loadings of the pelvic variables on the first principal component (PC 1). A-P: anterior-posterior; max.: maximum

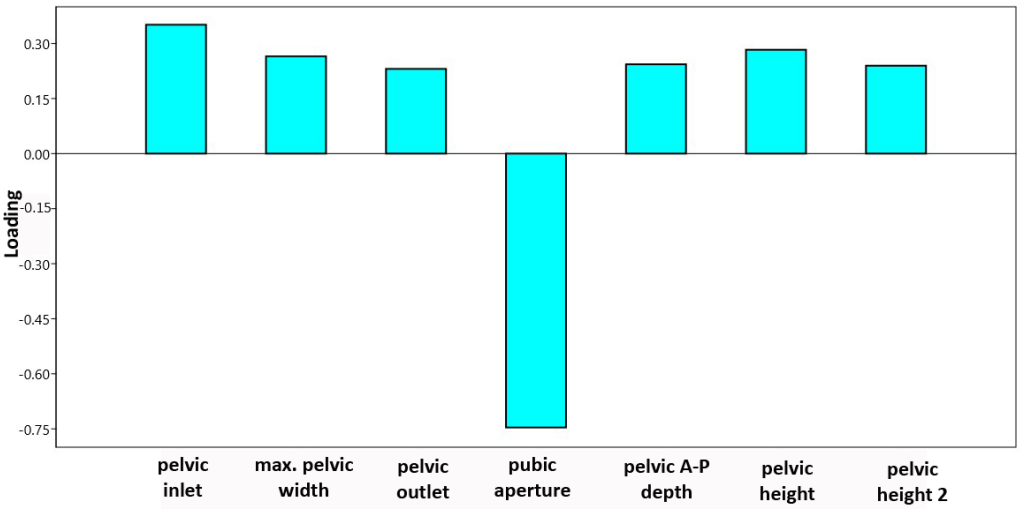

Figure 14. Loadings of the pelvic variables for the second principal component (PC 2). A-P: anterior-posterior; max.: maximum

The loading pattern of the pelvic variables on PC 2 in turn shows a contrast between the pubic aperture on the one hand and the rest of the pelvic variables on the other (Fig. 14). Since PC 1 represents overall size, and principal components are by definition orthogonal to each other (i.e. they are geometrically and statistically independent), this means that PC 2 represents relative pelvic size. In this case PC 2 describes variation among species in the size of the pubic aperture relative to the size of the other pelvic dimensions. However, a positive, yet weaker, correlation also can be seen between the PC 2 scores and the log-transformed forearm length. Despite this positive correlation, it is much weaker than the correlation between PC 1 and forearm length (slope = 0.15) and it explains less of the variation (R^2=0.12), even if it is significant (Pearson *p*-value = 0.01). Thus, PC 2 is very likely to represent relative pelvic size.

When looking at figure 15 one can see that the main differentiation among families – especially visible among the Pteropodidae, Phyllostomidae, Molossidae, Emballonuridae, Rhinolophidae and Vespertilionidae – exists along PC 1. On the right side of the PC 1 axis the pteropodids are nearly completely separate from the other families and only overlap with the Phyllostomidae, Noctilionidae and Megadermatidae (the latter two are represented by only one species). The other main groups, on the other hand, are scattered over both halves of the PC 1 axis, even though many species of these families are on the left side of the axis. Furthermore, the vespertilionids and phyllostomids overlap with all other families (excluding pteropodids and single-species families). The remaining main groups (Molossidae, Emballonuridae, Rhinolophidae) in turn do not overlap with each other but with phyllostomids and vespertilionids. Not overlapping with any of the other families are the Natalidae, Mormoopidae and Rhinopomatidae (all represented by one species), which are situated exclusively on the left side of the PC 1 axis. Moreover, along PC 2, only the emballonurids have exclusively positive PC 2 scores, while the other groups represented by multiple species exhibit both positive and negative PC scores. Nevertheless, there are fewer distinctions between the different families on the PC 2 axis than on the PC 1 axis.

Looking at the PCA in terms of diet, the three groups show a small overlap in the lower part of the PC 2 axis. Apart from that, the group “frugivores” is slightly separated from the other two groups along the PC 1 axis (Fig. 16), though some overlap remains. On the other hand, the groups “gleaners” and “aerial hawkers” overlap the most, especially on the left side of the PC 1 axis. Along PC 2, there is only poor differentiation of the three groups.

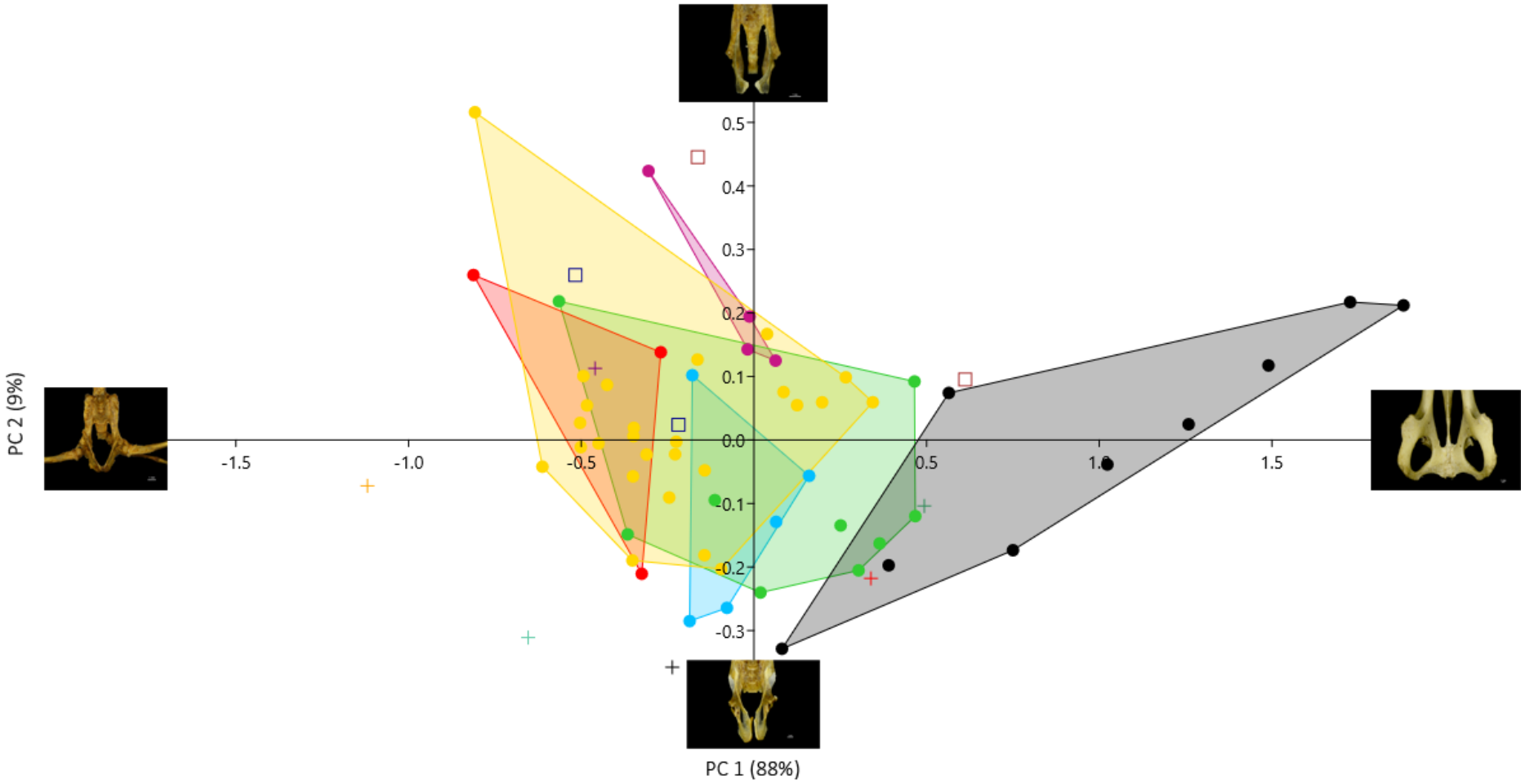

Figure 15. Morphospace of the first two principal components of the shape analysis of the bat pelvises on species level. Only log-transformed data of female specimens were used. Colours represent different families (black=Pteropodidae, blue=Molossidae, green=Phyllostomidae, purple=Emballonuridae, red=Rhinolophidae, yellow = Vespertilionidae). + symbols refer to families represented by only one species (green + symbol=Megadermatidae, bright blue + symbol=Mormoopidae, orange + symbol=Natalidae, red + symbol=Noctilionidae, purple + symbol=Nycteridae, grey + symbol=Rhinopomatidae). Square symbols stand for families represented by two species (purple square symbol=Hipposideridae, blue square symbol=Miniopteridae). Note that axes are not equally scaled, which was done for visualisation purposes. Approximately 97% of total variation of pelvic variables is described by PC 1 and PC 2. PC 1 explains ~88% of total variance, PC 2 explains ~9% of total variance.

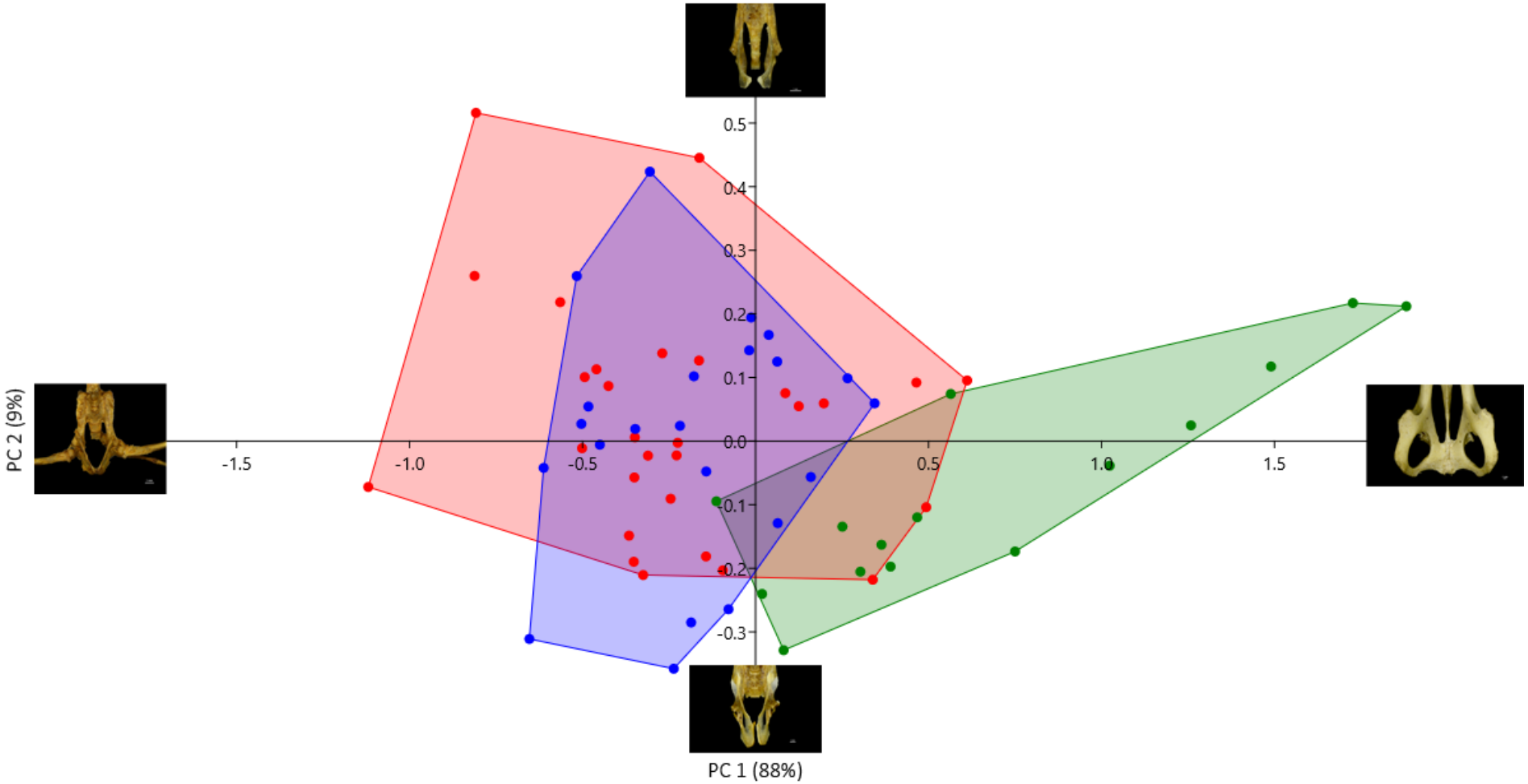

Figure 16. Morphospace of the first two principal components from the principal component analysis (PCA) of between-species variation on species level in bat pelvic morphology. Only log-transformed data of female specimens were used. Colours represent different diets and associated types of flight mode (blue = aerial hawking, green = "frugivores", red = gleaning). Approximately 97% of total variation of pelvic variables is described by PC 1 and PC 2. PC 1 explains ~88% of total variance, PC 2 explains ~9% of total variance.

3.4 Hypothesis Testing

In the following part, first the results of checking for a correlation between adult body mass and neonatal body mass are shown. Subsequently, except for the simple linear regression, only the results of the phylogenetically adjusted analyses are presented. This is due to the little difference between the phylogenetically adjusted and unadjusted models. Furthermore, the coefficient of determination (R^2) is only given for the simple regression models, since these only use one independent variable. For the multiple regression models, however, the adjusted R^2 is displayed because in these models more than one predictor variable is used, resulting in less accurate estimates of R^2.

There is a strong positive correlation between the log-transformed adult female body mass and log-transformed neonatal body mass, with a regression slope of 0.854 and a coefficient of determination of 0.95 (Fig. 17). Speaking in terms of absolute size, the biggest species have the biggest neonates. In terms of allometry, however, the allometric coefficient (α), represented by the regression slope, indicates a negative allometry ($\alpha < 1$), meaning that relative to increasing adult female body mass, the neonatal body mass decreases. A similar regression slope as for Fig. 17 can be seen when increasing the sample size by using chiropteran data from the PanTHERIA database (Fig. 18). However, the value for R^2 with 0.84 is noticeably lower than in figure 17, possibly because the exact relationship between neonatal and adult body mass differs between subgroups of chiropterans. In contrast, the regression slope of 0.9 (Fig. 18) is slightly higher than that of the previous regression. This allometric coefficient is still lower than one, again indicating a negative allometry, even though there is a positive relationship between log-transformed adult female body mass and log-transformed neonatal body mass.

When testing the first hypothesis (bat species with the relatively heaviest neonates also possess the relatively widest pelvic apertures), a simple linear regression between relative neonatal body mass (rNBM) and relative pubic aperture (relPA) yields a significant negative relationship ($F_{1;47} = 4.85$, Pearson $p = 0.033$) with a regression slope of -1.01 (95% CI = -1.91-(-0.11) and $R^2 = 0.093$ (Fig. 19, red line). Thus, the specimens of species with relatively large neonates exhibit the narrowest relative pubic aperture (relPA), while specimens of species with relatively small neonates, on the other hand, have a relatively wider pubic aperture. Furthermore, R^2 is low at 0.093, indicating that only 9 % of the variation in the relative pubic aperture is predicted by relative neonatal body mass.

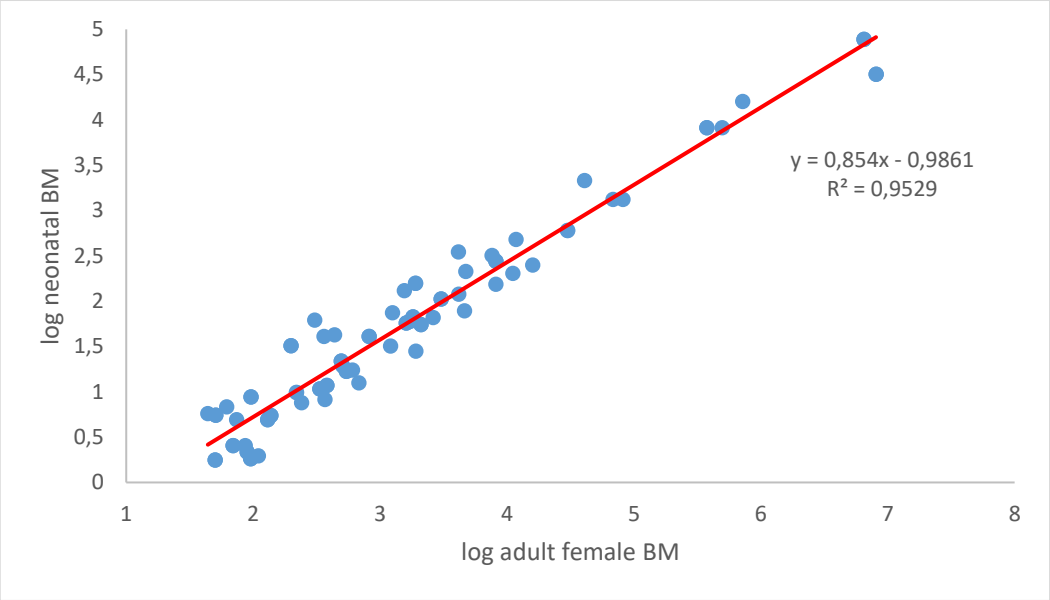

Figure 17. Regression of log-transformed neonatal body mass on log-transformed adult female body mass of bat species used in this study.

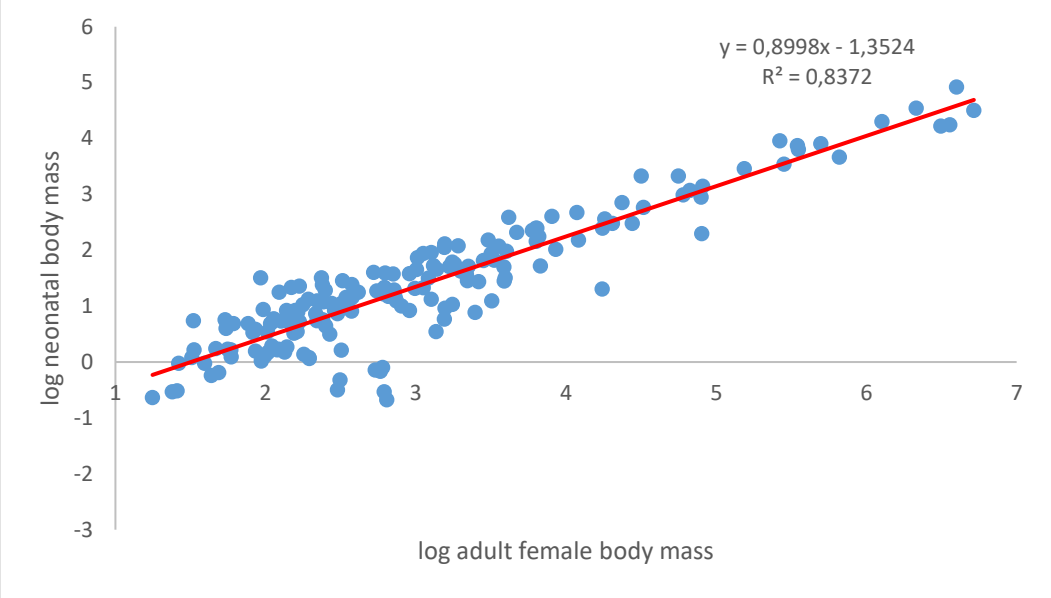

Figure 18. Regression of log-transformed neonatal body mass on log-transformed adult female body mass of bat species from the PanTheria database in addition to data from this study.

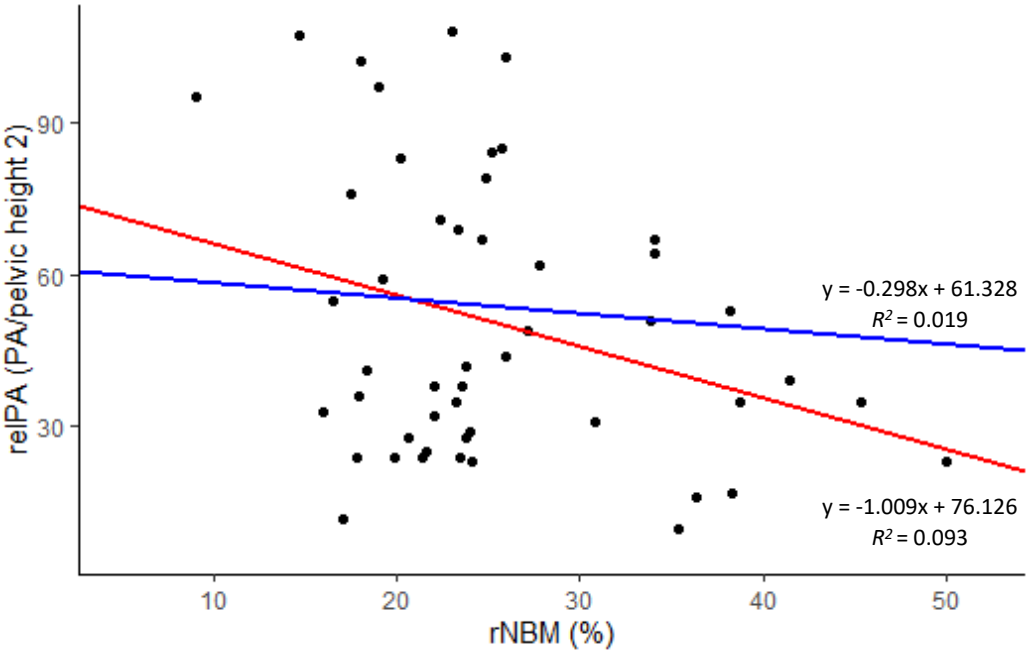

Figure 19. Phylogenetically corrected (blue line) and uncorrected (red line) regression of relative pubic aperture on relative neonatal body mass. N = 49 (for both); blue line: F1;47 = 0.886 (Pearson p = 0.351), Pagel's λ = 0.958; red line: F1;47 = 4.847 (Pearson p = 0.033)

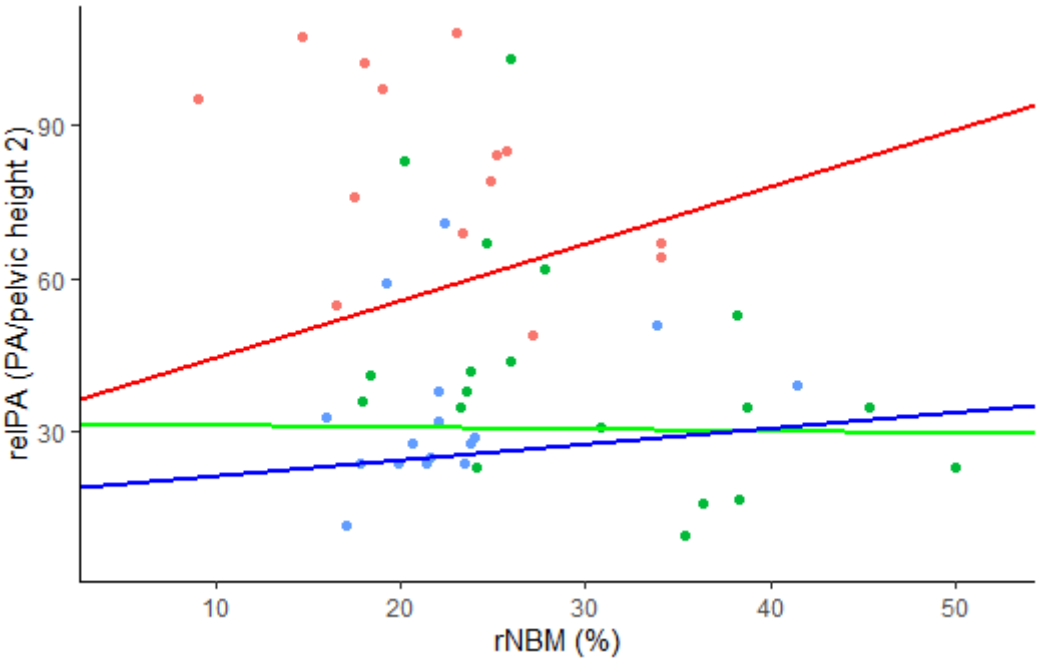

Figure 20. Phylogenetically corrected regressions between relative neonatal body mass (rNBM) and relative pubic aperture (relPA) of the three different flight modes, separated by colour (red = "frugivores", green = gleaners, blue = aerial hawkers). N = 49; Pagel's λ = 1.0

Contrary to the phylogeny-unadjusted regression model, the phylogenetic regression did not elicit a significant relationship between relative pubic aperture and relative neonatal body mass (Fig. 19, blue line). Nevertheless, as with the “normal” regression, there seems to be a slight tendency towards a negative correlation (a slope of -0.29; 95 % CI = -0.91 - 0.33). For this regression model the species with relatively heavy neonates also tend to have relatively narrower pubic apertures. However, this regression model has an even lower R^2 value (R^2 = 0.019), meaning only about 2 % of the variation in the relative pubic aperture (relPA) is predicted by relative neonatal body mass. The value of Pagel's λ needed for the phylogenetic regression is 0.958, indicating a strong phylogenetic signal within the data as it is close to one.

Testing the second hypothesis (bats with a manoeuvrable flight mode possess a relatively smaller pubic aperture) was accomplished in two ways. The first analysis of relative pubic gap size was performed in a nested model of rNBM within flight mode (as a factor variable) and FAL (forearm length) as an additional predictor. The results are displayed in table 7 and figure 20. First, it can be seen, that the relative pubic gap size gets larger with an increase in forearm length (Table 7). Comparing the intercepts of the three flight mode-specific regression lines shows different relative pubic gap sizes among the groups for the same relative neonatal size (Fig. 20). Species of flight mode one (“frugivores”) possess the widest relative pubic aperture while having relatively small neonates, whereas aerial hawking species (flight mode 3) show the narrowest relative pubic aperture. In terms of the slopes of the different flight mode groups, only flight mode two (gleaners) shows a negative slope, although not significantly (Pearson p = 0.88) (Table 7). On the other hand, the regression lines for the remaining two flight modes have a positive slope. Species from these two groups with relatively heavier neonates have a relatively wider pelvic opening, with only flight mode one showing a statistically significant positive increase (slope = 1.115; 95% CI = 0.108 - 2.122). The overall regression model shows a significant p-value (0.002), with a moderate adjusted R^2 of ca. 0.3 (Table 7). This shows that 30 % of the variation in relPA is explained by the factor variable “flight mode” and the predictor FAL.

The second way of testing the second hypothesis was to test the possible influence of wing morphology on the relative pubic aperture. However, the results displayed in table 8 do not show any significant effects of relative neonatal body mass, nor of wing aspect ratio (WAR) or wing loading (WL), on relative pubic aperture. The only significant effect is shown for the forearm length (FAL). Thus, due to the influence of forearm length, there is a significant p-value of 0.02 for the overall regression model, which, as for the flight mode model, also has a low adjusted R^2 value (Table 8).

Table 7. Results of the (phylogenetically adjusted) nested multiple regression model using flight modes as predictors. FAL: forearm length; df: degrees of freedom; flight mode 1: "frugivores"; flight mode 2: gleaners; flight mode 3: aerial hawkers; N = 49; Pagel's λ = 1.0

	FAL	flight mode 1		flight mode 2		flight mode 3	
		intercept	slope	intercept	slope	intercept	slope
relPA	0.333**	33.337	1.115*	31.663*	-0.032	18.289	0.315
Std. Error	(± 0.108)	(± 20.237)	(± 0.514)	(± 14.469)	(± 0.215)	(± 23.121)	(± 0.851)
R^2				0.385			
Adjusted R^2				0.297			
Residual Std. Error				53.07 (df = 42)			
F				4.372** (df = 7; 42)			

*p<0.05; **p<0.01

Table 8. Results of the phylogenetically adjusted multiple regression model using wing morphology variables as predictors. FAL: forearm length; WL: wing loading; WAR: wing aspect ratio; df: degrees of freedom; N = 40; Pagel's λ = 0.948

	relPA
rNBM	-0.361
Std. Error	(± 0.306)
WL	-1.134
Std. Error	(± 0.883)
WAR	-5.172
Std. Error	(± 3.369)
FAL	0.567*
Std. Error	(± 0.265)
Intercept	87.386**
Std. Error	(± 27.525)
R^2	0.278
Adjusted R^2	0.195
Residual Std. Error	45.19 (df = 35)
F	3.364** (df = 4; 35)

*p<0.05; **p<0.01

Examining the three different flight modes separately, it can be seen that, other than in the nested model, all three flight modes have a positive correlation between rNBM and relPA. However, only for the flight mode "frugivores" (flight mode one) the value for rNBM is significant (Table 9). Moreover, the adjusted R^2 for the whole regression model for the first flight mode (non-insectivorous species) is 0.473, which is higher than those of the remaining two (Table 9). In addition, with a Pearson *p*-value of 0.01, only the regression model of the non-insectivorous species is significant, while the other two are not.

Of the performed ANOVAs only the phylogenetic ANOVA is presented here, as for the multiple regressions, since the phylogenetically unadjusted and adjusted ANOVAs yielded the same results.

After performing the ANOVA for relative pubic aperture size, it can be seen that the width of the relative pubic aperture differs between the three types of flight mode (Table 10). Specifically, the relative size of the pubic gap of non-insectivorous species differs significantly from insectivorous species (gleaners and aerial hawkers). On the other hand, there is no significant distinction between the different flight modes of insectivorous species. Unlike the ANOVA for relative pubic gap size, there are no significant differences between the three flight mode groups in relative neonatal body mass (Table 11).

Table 9. Results of the phylogenetic multiple regressions for the three flight modes separately. FAL: forearm length

	relPA		
	frugivores	gleaners	hawkers
rNBM	1.382*	0.068	0.115
Std. Error	(± 0.495)	(± 0.354)	(± 0.775)
log (FAL)	35.314**	22.768	13.667
Std. Error	(± 11.028)	(± 18.252)	(± 19.557)
Intercept	-100.336	-44.739	-12.959
Std. Error	(± 53.363)	(± 81.575)	(± 82.990)
Pagel's λ	1.000	1.000	1.000
N	14	19	16
R^2	0.554	0.137	0.036
Adjusted R^2	0.473	0.029	-0.112
Residual Std. Error	48.31 (df = 11)	64.92 (df = 16)	43.01 (df = 13)
F	6.834* (df = 2; 11)	1.27 (df = 2; 16)	0.246 (df = 2; 13)
p-value	0.012	0.308	0.786

*p<0.05; **p<0.01

Table 10. Results of phylogenetically adjusted ANOVA in terms of relative pubic aperture.*

	Sum^2	Mean^2	$F_{2;63}$
between groups	23376.63	11688.314	31.234 (p = 0.008)
within groups	23575.49	374.214	

* Post hoc tests revealed that frugivores are significantly different from gleaners and aerial hawkers (*Pearson* p = 0.027 in both cases). No other significant group differences were detected.

Table 11. Results of phylogenetically adjusted ANOVA in terms of relative neonatal body mass.

	Sum^2	Mean^2	$F_{2;46}$
between groups	624.901	312.450	5.165 (p = 0.257)
within groups	2782.776	60.495	

4. Discussion

This study was conducted to test the pelvic floor hypothesis (Abitbol, 1988, Grunstra et al., 2019) of human pelvic evolution. The hypothesis assumes that a narrower or smaller bony pelvis yields a stronger and more supportive pelvic floor. A strong pelvic floor is necessary in humans, especially in women, to resist the pressure of abdominopelvic organs and a possible fetus from above and to hold them in place. If the pelvis were wider or larger in all dimensions – despite being beneficial for childbirth - the muscles, ligaments, and connective tissue of the pelvic floor would be rendered "weaker" and, according to the hypothesis, be compromised in their supportive capacity. As a result, especially women would be increasingly predisposed to developing incontinence and pelvic organ prolapse (Grunstra et al., 2019, Pavličev et al., 2020, Stansfield et al., 2021). Therefore, the size of the human female bony pelvis is constrained by the stability and strength of the pelvic floor and thus is limited in becoming wider to facilitate the birth of large-headed neonates. Bats, on the other hand, bear even larger neonates than humans. The pubic gap and the associated interpubic ligament in female bats have long been thought to enable them to give birth to offspring that are typically very large relative to maternal body size (O'Connor et al., 1966, Crelin, 1969, Crelin and Newton, 1969, Chapman et al., 1994, Kofron and Chapman, 1994, Nwoha, 2000, Grunstra et al., 2019). However, the presence of a pubic gap likely also means a less stable and supportive pelvic floor, as a ventrally "open" pelvis entails fewer or smaller attachment sites for the muscles of the pelvic floor. Perhaps bats were able to afford such structural differences in pelvic anatomy and evolve an "open" pelvis, because the vast majority of bat species hang upside down a considerable portion of the day. Hence, their pelvic floor does not suffer from high organ pressure as the weight of the organs is directed towards the thorax. Furthermore, bats are considerably smaller-bodied than humans, and due to positive allometric scaling of organ mass with pelvic floor surface area across large differences in body size, smaller species experience relatively lower forces on their pelvic floor muscles from their abdominal organs compared to larger-bodied taxa. With functional demands that constrain pelvic size or prevent the pelvic from "opening" removed, bats may have been able to freely respond to obstetric selection. Hence, the expectation was that the larger the neonate, the larger the pubic gap (and the 'weaker' the pelvic floor) would be. This study on bats was designed as a test of the pelvic floor hypothesis by checking for a relationship between the width of the pubic aperture in female bat pelves and the size of the neonates (both relative to adult female body size).

4.1 Simple linear regression

The results obtained in the present study, however, were not able to offer conclusive and robust support for the pelvic floor hypothesis. One of the main tasks was to test if chiropteran species with a relatively wider pubic aperture also give birth to relatively heavier neonates. In order to address this, linear phylogenetically adjusted and unadjusted regressions between relative pubic aperture and relative neonatal body mass were carried out. However, simple, bivariate regressions revealed an unexpected result. Contrary to the expectation of a positive relationship between the two variables, the results surprisingly showed a negative relationship (Fig. 19, red line) when phylogeny was not taken into account. Thus, not the species with relatively heavier neonates – which are

presumably also larger in linear dimensions - but the species with relatively smaller neonates possess relatively wider pubic apertures. When the phylogenetic relatedness among the species was taken into account statistically, no relationship between relative neonatal size and relative pubic aperture size was found (Fig. 19, blue line). These findings suggest that the relative width of the pubic aperture has not evolved in response to relative neonatal size across bats. Given these initial results from simple linear regressions, additional predictors were investigated by means of multiple regressions to find out if other relevant factors might influence pubic aperture width and potentially mediate the relationship with neonatal size. In these analyses, forearm length in particular proved to be a statistically significant additional predictor of relative pubic aperture size in all multiple regressions. This was not a surprising result, as the width of the pubic aperture increases with body size, of which forearm length is a proxy. Apart from that only one multiple regression model yielded another statistically significant predictor other than forearm length. In the multiple regression that was performed as a nested model and that used three different flight modes as additional predictors (next to forearm length), the flight mode categorised as "frugivore" proved to be a statistically significant predictor too. Furthermore, there were no differences between phylogenetically adjusted and unadjusted multiple regression models. Thus, phylogeny does not appear to be a strong driver of pubic aperture variation, unlike in the linear regression model. Considering now the multiple regression models related to the first hypothesis, only the nested model showed a statistically significant positive relationship between the relative size of the neonates and the relative width of the pubic aperture, particularly for species included in the “frugivorous” group (Fig. 20). This indicates that the first hypothesis (the larger the offspring is at birth relative to adult female body size, the larger the relative size of the pubic aperture) has been supported in the category “frugivores”, but not in insectivorous species (gleaners and aerial hawkers). Further support is provided by the analysis of relative neonatal body mass and relative pubic aperture size in the three flight mode groups separately. Here, only the “frugivorous” group (flight mode 1) shows a positive, statistically significant relationship between relative neonatal body mass and relative pubic aperture size (Table 9).

4.2 Multiple regressions

The phylogenetically adjusted multiple regressions were also used to test the second hypothesis that bats with a manoeuvrable flight mode possess a relatively smaller pelvic aperture as compared to frugivorous and nectarivorous species. The multiple regression using common wing morphology parameters (wing loading, wing aspect ratio) as additional predictors showed different results than the nested model using different flight modes representing different types of diet. Thus, the wing morphology variables did not show any statistically significant influence on pubic aperture size. By contrast, the nested model yielded a statistically significant result in terms of the size of the pubic aperture. Differences in intercept in this phylogenetic multiple regression showed that frugivores, nectarivores, and other non-insectivorous bats have, as a group, a relatively wider pubic aperture at equal relative neonatal body mass compared to the two insectivorous groups (gleaners and aerial hawkers). This result was verified by comparing the three flight mode groups in terms of the width of the relative pubic aperture by means of an ANOVA. This showed that the "frugivorous" group was statistically significantly different from the two

insectivorous groups in having relatively larger pubic apertures. As mentioned above, the group of "frugivores" were non-insectivorous species, which are less manoeuvrable than insectivorous species due to their food preference. Overall, the results of the two different multiple regression models suggest that the way in which flight behaviour influences pubic morphology is not captured well by the wing morphology variables wing loading and wing aspect ratio. Instead, the pubic morphology is apparently influenced by the flight mode in relation to diet. On the other hand, it should also be considered that the division into dietary categories may represent differences among bats other than differences in flight, which are not considered in this study. Nevertheless, the second hypothesis seemed to be confirmed.

Differences between different flight modes within insectivorous bats were also investigated, with the idea that fast aerial hawkers (flight mode 3) would experience the highest acceleration forces on their skeleton, including the pelvis, and therefore would have the smallest pubic apertures relative to their body size. However, gleaners and aerial hawkers could not be statistically differentiated in terms of relative pubic gap size. Therefore, the difference that exists between the two insectivores‘ flight modes in terms of acceleration forces might be so small that the effect of acceleration forces on the width of the pubic aperture is not observable. Alternatively, differences in pelvic morphology between insectivorous bats have little to do with differences in acceleration.

A possible explanation why species of the “frugivorous” group showed a wider pubic gap might be related to the flight behaviour and functional demands on pelvic morphology associated with this type of diet. The “frugivorous” group includes species that are frugivorous, nectarivorous, palynivorous or sanguivorous. All these species have in common that they feed on immobile food and therefore do not need to be highly manoeuvrable during flight. Insectivorous bats (and those that feed on vertebrates), in contrast, hunt on living, moving prey that they catch in the air or from surfaces. Hence, they typically need to be more manoeuvrable (gleaners) and agile (aerial hawkers) (Norberg et al., 1987). Due to the lower manoeuvrability of the “frugivorous” species, they probably experience fewer or lower acceleration forces, and therefore lower intra-abdominal pressures act on their bony pelvis and pelvic floor during flight. This may have enabled these species to widen the pubic gap over the course of evolution to give birth to large neonates, unlike insectivorous bat species.

Another explanation, at least for the absolutely and relatively large pubic aperture of most pteropodids (old world fruit bats), is the presence of large eyes. Unlike most chiropteran species, pteropodids rely on visual rather than auditory cues for their orientation in a three-dimensional space, in addition to a good sense of smell (Raghuram et al., 2009, El-Mansi et al., 2020). Associated with that is a large brain due to large visual centers and large olfactory bulbs (Jones and MacLarnon, 2004). This leads to the highest degree of encephalization among bats (average encephalization quotient of 1.2) (Wilson and Mittermeier, 2019). Hence, in comparison to other bats, neonatal pteropodids are born with relatively large eyes, which in most pteropodids are already open after birth (Wilson and Mittermeier, 2019). Thus, large eyes, which demand large eye sockets, and a large brain in neonatal pteropodids likely imply a relatively large neonatal skull that requires

more space at birth. This could then explain the wider pubic gap within the Pteropodidae. Unfortunately, no data on neonatal bat skull size was available to test this hypothesis.

In summary, however, the non-existing relationship between the width of the relative pubic aperture and the relative neonatal body mass within bats shown in the phylogenetically corrected linear regression suggests that the size of the neonate in general has no influence on the size of the pubic gap. More simply said, the widening of the pubic gap does not seem to be related to, or at least adapted to, the birth of large neonates. Even the addition of further possibilities for influencing the pubic gap like flight behaviour did not show any clear results. It should be considered that even if the ANOVA between the three flight mode groups yielded statistically significant results between "frugivorous" species and insectivorous species, there is no relationship between the width of the relative pubic aperture and the neonatal body mass in insectivorous species, as their slopes tend towards zero (Table 9). This is important as the majority of chiropteran species belong to the insectivorous group (Wilson and Mittermeier, 2019). Furthermore, although the relationship between relative pubic aperture and relative neonatal body mass is statistically significant in "frugivores", the result is not very strong, with a regression slope close to one (Table 9).

4.3 Error consideration

Moreover, it must be taken into account that possible sources of noise could have influenced the results and obscured, to some extent, any functional signals present in the morphological data. First, sample sizes were often small as some species were represented by a single individual (*Anoura caudifer*, Phyllostomidae; *Hipposideros caffer*, Hipposideridae; *Mormopterus jugularis*, Mormoopidae; *Eonycteris spelaea*, Pteropodidae; *Nycteris thebaica*, Nycteridae). Measurements from single specimens may therefore not have yielded reliable mean values for the pelvic variables for these species. Another error source might be the within-species variability regarding the width of the pubic aperture. This variability in female pubic aperture width was not only detectable in the measured data but was also clearly visible during the measurements, whereas in the male specimens there was no or only very little variability (males of *Desmodus rotundeus* and *Cynopterus sphinx* showed an “open” pelvis).

Furthermore, unlike other mammals of the same size, bats live quite long (Jürgens and Prothero, 1987). During their long lives, female bats can give birth to many young across multiple pregnancies, which likely causes the pubic aperture to widen slightly with each pregnancy and birth, without reverting back to the previous condition. In humans, for example, it is well known that in women all pelvic dimensions increase with increasing age (Huseynov et al., 2016, Auerbach et al., 2018). Changes in pelvic morphology after birth that differ from the pre-partum condition can also be observed in other mammals. In mice and cows, observations showed a change in the size of the pelvic bones, which were larger in females that were parous than in nulliparous females (Schutz et al., 2009), and a general increase in the size of the pelvic area in females that had given birth to many offspring (Johanson and Berger, 2003). Moreover, in pocket gophers (Geomyidae, Rodentia), the female pubic symphysis is lost through bone resorption, resulting in a wider pubic symphysis in older individuals with multiple parturitions than in younger with fewer

births (Hisaw, 1925). Bone resorptions occur in female mice (*Mus musculus*) too. Here, pregnant mice that give birth show some kind of ligament between pubic bones instead of a pubic symphysis due to bone resorption (Gardner, 1936, Crelin, 1960). However, Gardner (1936) was also able to demonstrate that in older virgin female mice, despite the pubic symphysis still being present, the pubic bones were thinner than in males of the same age owing to decalcification. The possibility that female bats also undergo repeated bone resorption at the pubic bones, cumulatively widening their pubic gaps, complicates the determination of a species' representative pubic gap size. All these findings of other studies suggest that structural changes in the pelvis may also occur in female bats after each birth, although these may be different in bats due to their different pelvic morphology. Therefore, older female individuals that have given birth to many young may have a wider pubic aperture than younger female bats that have given birth to fewer young. It was unfortunately not known nor possible to determine the age of the individuals and the number of pregnancies and young they had given birth to among the museum specimens. Not knowing the age and number of births may therefore have affected the outcome of this study to some extent. Lastly, there might be a difference in the width of the pubic gap between dry specimens and specimens from alcohol. In dry specimens, the loss of moisture may have caused the two pubic bones in female bats to move slightly further apart from each other, thus extending the width of the pubic gap. Unfortunately, no literature is known to the author that can confirm or refute this as a reasonable possibility. However, if true, then the increase in the distance between the pubic bones was probably very small and the influence on this study's results are likely marginal, though they should be kept in mind.

4.4 Obstetric adaptation

Despite the lack of a positive relationship between relative pubic aperture width and relative neonatal body mass, the pubic aperture is nonetheless likely an obstetric adaptation in female bats. Support for this suggestion comes from the strong sexual dimorphism in the pubic region of bats, which was clearly visible when measuring the specimens. The analyses of sexual dimorphism showed that, in relation to the pelvic variables, the greatest sexual dimorphism was for the pubic aperture, and females had a considerably wider pubic gap on average than males, since most males did not have a pubic aperture at all. Furthermore, the sexual dimorphism is much more likely to be an obstetric than an ecological adaption. If it were an ecological adaptation, the two sexes would have to be exposed to different ecological conditions (Lande, 1980). Another possibility is that both sexes are exposed to the same ecological conditions but show different gene expression (Lande, 1980). Since the same genes are probably expressed in male and female bats and both sexes live in the same habitats with the same ecological conditions, sexual dimorphism through ecological adaptation can be ruled out. Given that only female bats give birth to offspring and that the pelvis shows obstetrical adaptations only in females, it is much more likely that, as in other mammals, a sex-specific selection acts that leads to a sexual dimorphism in the pelvic region (Grunstra et al., 2019, Pavličev et al., 2020). Previous studies also argued that the sexual dimorphism of the pelvis in bats is birth-related. Kofron and Chapman (1994), Chapman (1994) as well as Nwoha (2000) observed pelvic sexual dimorphism in pteropodids, as documented also in this study, in

which the females had very wide pubic apertures bridged by an interpubic ligament. They too assume a strong benefit for the birth of large neonates.

Crelin and Newton (1969) pointed out even more clearly the use of the pubic gap and the pubic ligament for the birth of large neonates. They studied the structure of the pubic ligament in female free-tailed bats (*Tadarida brasiliensis*) and the width of the pelvic canal that was necessary to give birth to their young. They concluded that depending on the size of the neonate, the interpubic ligament can expand by up to 15 times its normal length and thus the pubic aperture would expand by a multiple to enable the neonate to pass through the bony birth canal. In other female mammals, similar structural changes occur to widen the pelvis to ensure the birth of many or large young. The sacroiliac-joints in sheep (Bassett and Phillips, 1955) and the pubic symphysis in mice and humans (Crelin et al., 1957, Schwabe et al., 1978, Kristiansson et al., 1996), for example, become more flexible due the influence of hormones already during pregnancy and especially during birth to widen the pelvis. Moreover, guinea pigs also have a pubic gap that is bridged by flexible collagen fibres to provide more space for large neonates during birth (Talmage, 1947). The findings of obstetric adaptation from these studies therefore further strengthen the notion of a birth-related adaptation of the pelvis through the presence of a pubic aperture and an interpubic ligament in female bats. Still, the suggestion that the presence of a pubic aperture and an expandable pubic ligament enable the large neonates to pass *through* the bony pelvic birth canal seems to make sense only in pteropodids and other bat species with a very wide pubic opening. In these species the pubic aperture should be wide enough to support the birth of large neonates. However, it has to be noted that these species with the relatively widest pubic aperture have, in contrast, the relatively smallest neonates, as shown in this study. This combination should therefore simplify the birth process. In contrast, the situation is different for species with relatively narrower pubic apertures. These species possess relatively heavier and thus larger neonates. In these species – which likely make up the majority of Chiroptera, it is rather unlikely that the neonate would actually fit *through* the bony pelvis. There is little visual documentation of the size of a neonate in comparison with the pelvis it is, or needs to be, delivered through. But the few available documentations show the large discrepancy between fetal size and pelvic size (Fig. 21), raising strong doubts that the fetus would fit through the pelvis despite the pubic gap and the presence of an elastic interpubic ligament. Crelin and Newton (1969) suggested that widening of the pubic opening occurs when the pelvic bones move apart during parturition. However, this seems rather unlikely since this would require the pelvic bones to be flexible so as to achieve the width of the pubic aperture needed for parturition. But the bones probably could not withstand such high bending stresses and would break. Alternatively, a high degree of mobility of the sacroiliac joints would presumably be necessary. But again, the extra space necessary to enable the neonate to pass through the pelvis according to Crelin and Newton (1969) is probably unachievable by the mobility of the sacroiliac joints. It seems unlikely that the sacroiliac joints could provide the mobility required to widen the pubic aperture to a multiple, as they are closely connected to the sacrum and thus restricted in their degree of movement (Neuweiler, 2000). Nevertheless, a slight, hormonally induced mobility of the sacroiliac joints, although probably not of major importance at birth, could help to facilitate the birth of large neonates, similar to other mammalian species (Bassett and Phillips, 1955, Crelin et al., 1957, Schwabe et al., 1978, Kristiansson et al., 1996). Yet, if

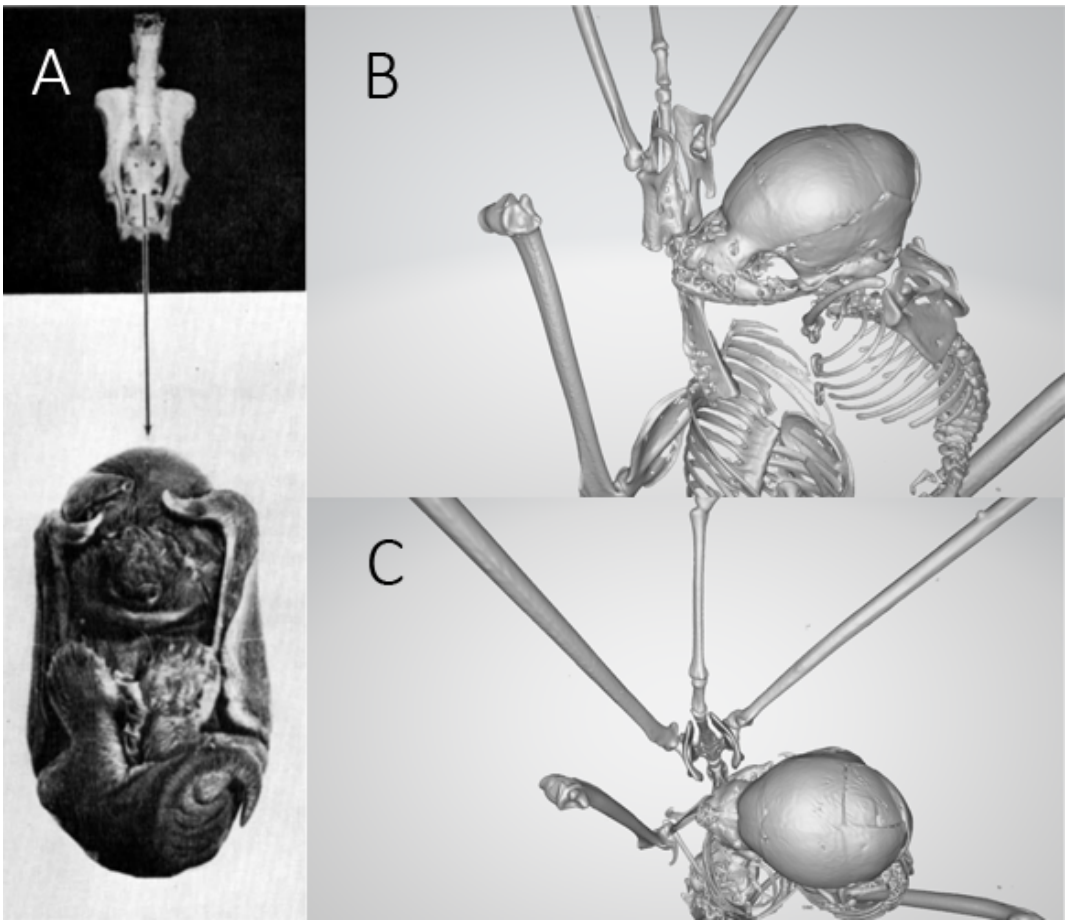

Figure 21.Pelvic-neonate-disproportion. A: Figure from Crelin (1969) showing the pelvis of a female *Tadarida brasiliensis* and its associated neonate in size ratio. Average adult body mass = 12.61 g, average neonatal body mass = 3.19 g (Jones et al., 2009); B and C: three-dimensional CT scan of a pregnant *Amorphochilus schnablii* female and her fetus in ventrolateral (B) and caudal view (C). The fore- and hindlimbs were partially (female) or completely (fetus) removed through segmentation in order to provide an unobstructed view of the maternal pelvis and fetal body. The disproportion between the size of the mother's pelvis or the width of the pubic aperture and the size of the skull of the fetus can clearly be seen. The CT scan was provided by the Yale Peabody Museum of Natural History (US), specimen number YPM MAM 005693, and downloaded from MorphoSource. Adult and fetal body masses are not known for this mother-offspring specimen. Average adult body mass for *A. schnablii* is estimated to be 3-5 g (Blessing, 2002)

the joints could provide the necessary mobility, this would presuppose a strong relaxation of the joints, which would then probably require a high amount of relaxin and other hormones to be released during pregnancy and birth to make the pubic joints flexible (Bassett and Phillips, 1955, Crelin et al., 1957, Schwabe et al., 1978, Kristiansson et al., 1996). Such a high amount of relaxin would presumably not only result in a destabilisation of the pelvic girdle as it would lose its stiffness. Rather, it would probably lead to the relaxation of all body joint, since such a high amount of relaxin would not only target specific joints. This would have the consequence that the female's overall mobility would be impaired, so the bat might no longer be able to hunt properly, which would eventually result in starvation and death. If only the sacroiliac joints were affected by relaxin, still a solution would have to be found to stabilise the pelvic girdle. To resolve the destabilisation of the pelvic girdle and still benefit from highly mobile sacroiliac joints, additional or thicker muscles could stabilise the pelvis in the area of the sacroiliac joints. However, no literature is known to the author that describe such additional or thickened muscles. Furthermore, more muscle tissue would mean more weight for the bat to carry

during flight, which is presumably unlikely since bats underwent a loss of body weight during their evolution to save energy costs and to enable powered flight (Rayner, 2008).

Assuming that the presence of a pubic opening and an interpubic ligament is related to parturition, how do these two things support the birth of large neonates if not through substantial lateral pelvic expansion? One possibility is the ventral expansion of the interpubic ligament. In bat species with a relatively very wide pubic aperture (as seen in flying foxes) the ventral expansion of the ligament could be enough to provide the neonate with the required space to fit *through* the pelvic birth canal (Kofron and Chapman, 1994). However, in bat species where the pubic aperture is relatively narrow, ventral expansion of the interpubic ligament would likely still not be sufficient to allow passage of the fetus between the left and right pubic bone (see Fig. 21), especially as the fetuses in these species also tend to be relatively larger than those in other bat species. A possible alternative birth mechanism could be a ventral bypass of the bony pelvis by the fetus, along the pubic aperture. To make this feasible, the vaginal portion of the birth canal would have to be led ventrally past the bony pelvis. During labour, then, the ligament would expand widely to let the neonate pass through the soft tissue of the birth canal, which itself does not run through, but rather alongside, the lower pelvis. In moles, for example, the pelvis and particularly the pelvic outlet is narrowed to such an extinct due to their burrowing lifestyle that the digestive and urogenital tracts are unable to pass through it (Slonaker, 1920, Starck, 1995). To get the required space these tracts are bypassing the pelvis ventrally (Slonaker, 1920, Starck, 1995). Even though moles have a different way of life than bats (burrowing vs. flying), the relocation of the urogenital tract outside the pelvis in moles shows that this could also be a possibility in bats. However, the ventral bypass of the birth canal to pass the pelvis in bats would require the vaginal opening to be more ventral to the pelvis instead of caudal. Unfortunately, the author is not aware of any literature describing the location of the vaginal opening. To investigate this proposed explanation ideas for further studies are given in the outlook below.

4.5 Comparison with shoulder girdle

Bats have long been the focus of many studies because they have evolved unique abilities among mammals. Due to their ability for powered flight, their wings and shoulder girdle in particular have been one of the main topics of bat research (Vaughan, 1970b, Vaughan and Bateman, 1970, Norberg et al., 1987, Neuweiler, 2000, Assis et al., 2011, Marinello and Bernard, 2014, Gaudioso et al., 2020, Lopez Aguirre et al., 2020). The chiropteran front limbs and shoulder girdle have undergone several evolutionary modifications to enable bats to perform powered flight. For example, the metacarpal bones of the metacarpus and the phalanges of the bat digits lengthened to span the dactylopatagium and plagiopatagium to form the wings (Vaughan, 1970, Neuweiler, 2000). In addition, the position of the scapula and its morphology, as well as that of the clavicle, changed compared to that in other mammals, which enabled the ability for powered flight (Vaughan, 1970, Neuweiler, 2000). When looking at the individual components of the shoulder girdle, one notices a high degree of diversity in the morphology of the scapula (Vaughan, 1970b, Gaudioso et al., 2020). In bats, dorsoventral movements of the pectoral girdle and front limbs are of more importance than the anteroposterior movements in terrestrial mammals, thus creating the necessary wing beat for powered flight in bats (Vaughan, 1970b). Therefore, some of the strongest and most important flight muscles in

bats attach predominantly to the large surface of the scapula and are thus closer to the body's centre of mass, which also enables aerodynamically efficient flight (Vaughan, 1970a, Vaughan and Bateman, 1970, Assis et al., 2011). Due to the different diets and associated flight modes of the bats, it was thought that this had an influence on the flight musculature and morphology of the scapula, resulting in differences between bat species (Vaughan, 1970, Vaughan and Bateman, 1970, Assis et al., 2011). Recent studies, however, found that the morphology of the flight apparatus of bats and especially the morphology of the scapula is not primarily driven by diet and flight mode but by phylogeny (Marinello and Bernard, 2014, Gaudioso et al., 2020, Lopez Aguirre et al., 2020).

In comparison with the shoulder girdle and forelimbs, the chiropteran pelvis has received markedly less scientific attention. The present study showed that morphological diversity between different bat species is also evident in the pelvis and especially in the width of the pubic aperture (see Fig. 22). The results of the principal component analysis show, first and foremost, an increase in pelvic size with increasing absolute body size. The species with the largest pelvis and therefore with the absolutely widest pubic aperture are represented by the large-bodied pteropodids (Fig. 15). The main axis of variation among chiropteran pelvic size is thus strongly associated with variation in overall body

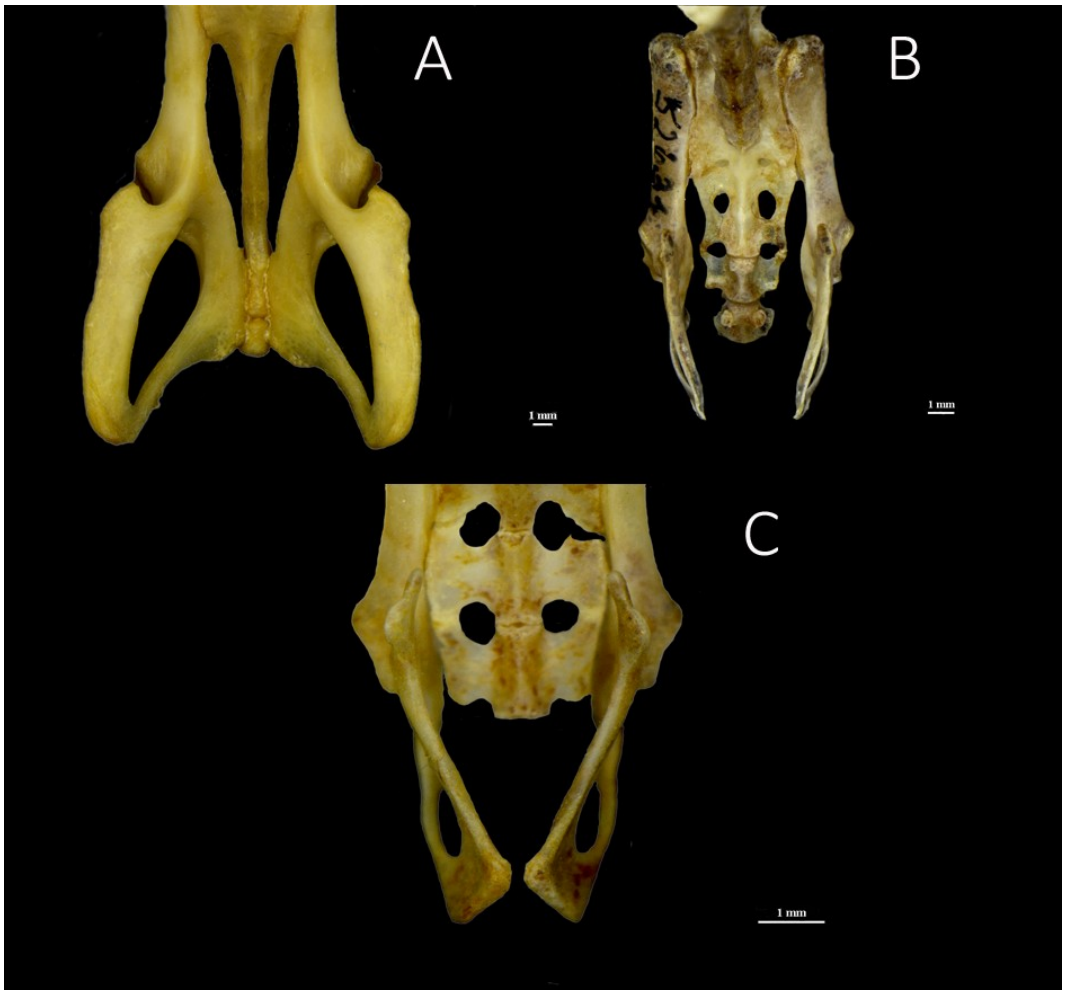

Figure 22. Ventral view of the female pelvis of three different species. A: *Eidolon helvum*; B: *Pipistrellus pipistrellus*; C: *Myotis myotis*. Pictures were taken during pelvic measurements in this study.

size, which was to be expected. In contrast, the second principal component (PC 2) represents the width of the pubic aperture relative to the other pelvic variables (and all relative to overall body size, which is represented by PC 1). Along this axis, differences between species, families and dietary groups were less pronounced. It was not the large pteropodids that had the widest pubic aperture relative to other pelvic variables, but smaller species from the emballonurid and vespertilionid families. Given the results of the PCA regarding diet and, more importantly, the results of the multiple regressions, it was thought that diet and flight mode had an influence on pelvic morphology, particularly on the width of the pubic aperture. Yet, when considering the phylogenetic signal for pelvic dimensions, there is a moderately strong influence of phylogeny on linear pelvic dimensions. Studies on the flight apparatus in bats, i. e. scapula (Gaudioso et al., 2020) and wings (Marinello and Bernard, 2014, Lopez Aguirre et al., 2020), similarly found strong phylogenetic signals and less clear ecological patterns, although the present study of linear dimensions is not directly comparable to the shape of the wing and shoulder girdle bones.

4.6 Comparison with birds

When it comes to studies on the flight of bats, comparisons with birds are often made. Since one of the hypotheses of this study included the suggestion that the flight mode of the bat might have an effect on the width of the pubic aperture, it is worthwhile to compare the pelvis of bats with the pelvis of birds. Like bats, birds evolved powered flight, and both taxa had to overcome the same challenges, such as weight limits and the development of wings being capable for flight. In terms of the pelvis, similarities appear in both taxa with regard to the pubic bones of the pelvis. Both birds and bats do not have a pubic symphysis that connects the pubic bones, instead there is a gap between them. But in bats this pubic gap only applies to the females, leading to a sexual dimorphism in this taxon with respect to pelvic morphology. Sexual dimorphism in the avian pelvis, though, has not been studied in a comparative context so far. Only in some parrots a visual sexual dimorphism occurs in a way that the pelvis, as its whole, is wider in females (Welty and Baptista, 1988). The pubic gap, however, seems to occur in bird regardless of sex. Furthermore, the pubic gap in bats is bridged by the interpubic ligament, whereas in birds no such ligament or other structures extend between the pubic bones. At least, as far as the author is aware, no such structure is mentioned in the literature. The morphology of the pelvic region in birds differs even further from that in bats. The most noticeable morphological difference is the presence of the synsacrum in birds: the lumbar, sacral and caudal vertebrae are fused into one unit, which is in turn firmly fused with the bones of the pelvic girdle (Fig. 23). In birds, the synsacrum serves to support weight (Hughes, 2014, Anten-Houston et al., 2017) and stabilise the body during flight (Kaiser, 2010). Furthermore, it provides various attachment sites for the muscles of the hindlimbs (Kaiser, 2010, Anten-Houston et al., 2017). Unlike in bats, the hindlimbs in birds are also used for terrestrial and aquatic locomotion. Due to the loss of the pubic symphysis egg size in extant birds, contrary to their ancestors, is not restricted to the size of a bony birth canal anymore (Dyke and Kaiser, 2010, Deeming and Mayr, 2018). Yet, a comparison between female bats and birds in terms of the use of a pubic gap to assist in the birth of large offspring is difficult, because bats give birth to live offspring while birds lay eggs.

Nevertheless, the function of a pubic gap as an obstetric adaptation might be the same in bats and birds.

Whether the presence of a pubic gap in bats is an obstetric adaptation or not might also be shown by comparing Sauropsida and mammals. In the Sauropsida (reptiles and birds), a stable pelvic girdle is of great importance as propulsion is done by the hind limbs and therefore a stable pelvis plays an important role in ensuring propulsion (Fischer, 2010). To provide this stability, the pubic bones of the pelvis are connected via the pelvic symphysis. However, the presence of this symphysis restricts the space through which the eggs can pass during reproduction, limiting the maximum size of the eggs (Deeming and Mayr, 2018). This space restriction of the bony pelvic canal by a symphysis can also be found in fossil Theropoda skeletons, which leads to the assumption that the size of eggs was also limited in dinosaurs (Dyke and Kaiser, 2010, Deeming and Mayr, 2018). In the extinct theropods‘ descendants, the birds, however, the pubic symphysis was lost in the course of evolution, leading to a ventral opening of the pelvis. Although, as mentioned above, this pubic gap occurs in both male and female birds, it mainly assists females to lay larger eggs, which are less restricted in size by the ventral opening of the pelvis (Shatkovska et al., 2018). A similar pattern can be seen within mammals. Many mammals have a ventrally closed pelvis with a pubic symphysis. Nevertheless, in many mammals there is an altered pelvic morphology in females, which is thought to facilitate the birth of young and thus leads to sexual dimorphism in the pelvic region. In primates in particular, obstetric adaptations, such as a widened female pelvis and hormone-induced increased mobility of the pelvic joints during pregnancy and birth, enable the birth of young with particularly large heads (Ankel-Simons, 2000, Grunstra et al., 2019, Fischer et al., 2021). In some primate species, such as chimpanzees, these obstetric adaptations enable a more or less uncomplicated birth (Schultz, 1949, Leutenegger, 1974, Rosenberg, 1992, Fischer et al., 2021). In other primates, such as humans, gibbons or macaques, birth is difficult despite the obstetric adaptations, because the size of the neonate has reached the maximum size and is limited by the size of the pelvic outlet (Schultz, 1949, Leutenegger, 1974, Ankel-Simons, 2000, Fischer et al., 2021). As mentioned earlier in this study, bats also give birth to large young. Similar to birds, the loss of the pelvic symphysis and the ventral opening of the pelvis probably remove the space limitation of the pelvis in bats, which probably limits the size of the young much less than in primates, for example. However, like in this study, in birds no positive correlation between relative eggs size and relative pelvic size could be found (Shatkovska et al., 2018). Nevertheless, the presence of a pubic gap is probably sufficient for relative offspring size to increase in bats and birds, which probably makes the pubic aperture an obstetric adaptation in itself. Thus, the width of the pubic aperture itself could no longer correlate with offspring size or egg size, which in turn could explain the non-existent relationships between the relative pubic aperture width and the relative neonatal body size in the results of the simple phylogenetically corrected regression in this study.

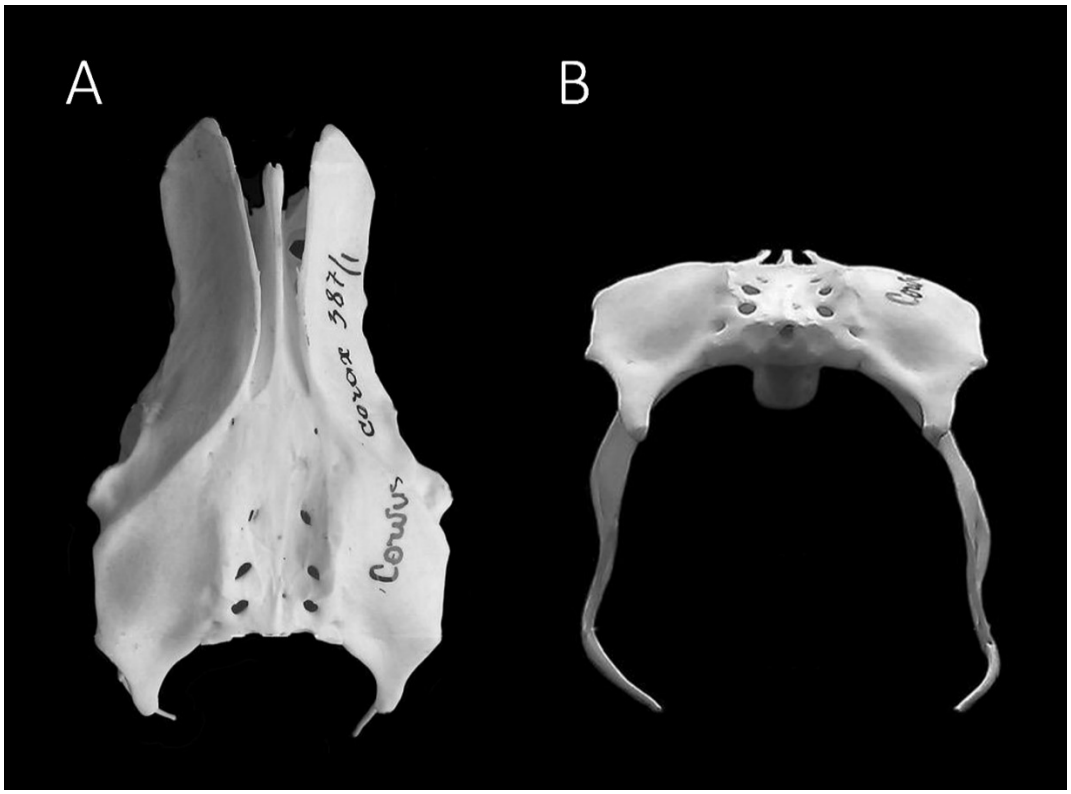

Figure 23. Synsacrum and pelvic girdle of *Corvus corax*. Edited image from Shatkovska et al. (2018). A: dorsal view. B: caudal view. The absence of a pubic symphysis and the ventral opening of the pelvis are clearly visible.

In addition to the presence of a pubic gap in bats and birds some further structural similarities in the pelvis can also be found at least between large pteropodids and birds. In pteropodids, the ilium fuses completely with the vertebrae of the sacrum, which makes the pelvic girdle more rigid (Neuweiler, 2000). This stiffness of the pelvic girdle, similar to the synsacrum stiffened by bone fusion in birds, could serve to keep the spine and hindlimbs stable in the air during flight. Due to their larger average body mass compared to other bat species, pteropodids are less likely to use flapping flight, which is typical of bats in general (Panyutina et al., 2015). Here, the wings are not moved vertically to the body as in birds, but obliquely. However, this type of flight demands much energy, especially for larger bat species such as many pteropodids (Panyutina et al., 2015). To fly as energy-efficiently as possible, pteropodids therefore use gliding (Pennycuick, 1971) or soaring (Lindhe-Norberg et al., 2000, Thomson et al., 2002), similar to birds (Panyutina et al., 2015). Smaller bat species can also glide and incorporate this into their flight behaviour, which known as undulating flight (Thomas et al., 1990, Panyutina et al., 2015). However, the gliding here occurs less frequently and for a shorter period of time. To enable a long glide, the body must be kept as stable and straight in the air as possible. Thus, the pelvic girdle in pteropodids, which is stiffened by the fusion of the ilium and sacrum, could help to do exactly that. However, the complete fusion of these bones in pteropodids results in the loss of the cartilaginous sacroiliac joints. This prevents a possible hormone induced movement of the sacroiliac joints in female pteropodids during birth. In birds, the presence of a synsacrum could lead to sufficient stabilisation of the pelvic girdle so that the loss of the pubic symphysis could be compensated for. Due to the increased stiffness of the dorsal pelvis as a result of the fusion of the ilium and sacrum, this could also have been the case in pteropodids, allowing them to develop a large ventral pubic symphysis. Even though this pubic gap results in a loss of structural support, the

stiffened dorsal pelvis may be able to compensate for that loss. The development of the clearly visible large pubic gap therefore could be a compensation of the loss of the sacroiliac mobility to facilitate the birth of large neonates. In non-pteropodid species, on the other hand, according to Neuweiler (2000,) the ilium is "fused" with the sacrum up to the position of the acetabulum so that movements of the sacroiliac joint are no longer possible. In accordance to own observations when taking the measurements: a tight connection between ilium and sacrum that constrains or restricts the mobility of the sacroiliac joint strongly was obvious. Yet, the author of the present study is not assuming a fusion of the two bones in this area, since a hormonally induced mobility of the sacroiliac joint during birth, even if to a low extent, can still be considered supportive during birth. A fusion of ilium and sacrum, on the other hand, would completely exclude this obstetric adaptation. Since this obstetric adaptation occurs in many other female mammals, a complete immobility of the sacroiliac joint through fusion is rather unlikely.

Furthermore, the absence of a sacroiliac joint due to bone fusion would possibly constrain movements of the tail. The tail in bats increases manoeuverability in flight and is connected for this purpose to the caudal wing membrane (uropatagium) that spans between the hindlimbs (Norberg et al., 1987). The length of the tail varies in bats and is not present in every species. For example, most pteropodids and frugivorous phyllostomids lack a tail (Norberg et al., 1987). By contrast, in most insectivorous bats, especially vespertilionids, the tail plays an important role in hunting prey. Not only does it increase the manoeuverability needed to hunt prey in cluttered environments, but it also enables the bats to catch their prey with the uropatagium (Webster and Griffin, 1962, Norberg et al., 1987). To do this, the tail bends ventrally, turning the uropatagium into a pouch with which to catch the prey (Webster and Griffin, 1962). As mentioned above, fusion of the ilium and sacrum would limit the mobility of the tail, so that, apart from the loss of improved manoeuverability in flight, ventral bending of the tail would be restricted or impossible in insectivorous species. But to afford a moveable tail, the dorsal pelvis is presumably not fused but rather tightly connected to the sacrum. It may thus be that insectivorous bats, and presumably especially those with large uropatagia and long tails, cannot “afford” to increase pelvic rigidity dorsally in order to open the pelvis more ventrally. This assumption needs to be tested by future studies.

4.7 Outlook

The results in this study revealed no relationship between the relative pubic aperture size and the relative neonatal body mass in bats, which was surprisingly unexpected. Nevertheless, the pubic aperture in female bats is thought to be an obstetric adaptation. In some species, however, the pubic gap appears to be too small to provide the necessary space for the large foetus. A possible alternative birth mechanism could be a ventral bypass of the bony pelvis by the fetus, along the pubic aperture. To make this feasible, the vaginal portion of the birth canal would have to be led ventrally past the bony pelvis. To test this, CT scans of whole-body specimens with stained soft tissues, for example, would enable the position of the vaginal opening as well as the location of the vaginal birth canal relative to the pelvis to be examined in female bats. In addition, a comparison between pregnant and non-pregnant females would shed light on whether any morphological reconfiguration takes place during pregnancy. Furthermore, an

examination of the sacroiliac joints with a focus on their mobility would be interesting. X-rays or CT scans of pregnant and non-pregnant females preserved in alcohol could be taken. A possible gap between the ilium and sacrum, as well as its width, could provide information about the mobility of the sacroiliac joint in pregnant females. In addition, results in this study showed a positive correlation between relative pubic aperture size and relative neonatal body mass in species that feed on immobile food. However, as these results were not very robust, further investigations would be interesting to clarify the influence of diet and associated flight mode in these species on the width of the pubic gap.

5. Conclusion

The tight cephalopelvic fit in humans makes childbirth difficult and can lead to increased maternal and infant mortality when medical intervention is not available. What factors have prevented an enlargement of the female pelvis during human evolution, therefore maintaining a relatively difficult and risky birth of large neonates in our species, has been the focus of many scientific studies. One possible explanation is the pelvic floor hypothesis, which states that a narrower pelvis causes a stronger pelvic floor. Due to the upright posture and mode of locomotion in humans, gravity forces the organs towards the caudal pelvic opening, which is spanned by the pelvic floor muscles. Therefore, the human pelvic floor plays a crucial role in preventing prolapse of the organs and the fetus in women and keeping them inside the body. A larger pelvic canal instead would lead to a less supportive pelvic floor and increases the risk of incontinence and prolapse. To test this hypothesis, the pelvis of different female Chiroptera species was examined in detail in this study, as within this taxon particularly large neonates are born and females have a ventral opening of the pelvis due to the loss of the pelvic symphysis, which presumably offers less structural support to the pelvic floor muscles. But since bats spend a lot of time roosting upside down, there is less abdominal organ pressure on the pelvic floor, which may have enabled the evolutionary expansion and “opening up” of the pelvis in female bats to ease the parturition of their large young.

The aim of this study was therefore to test for a correlation between relative neonatal body mass and relative pubic aperture size in bats in the context of human pelvic evolution and the pelvic floor hypothesis. Instead of an expected positive correlation, the results of the analyses surprisingly showed no clear relationship between relative neonatal body mass and relative pubic aperture size. There was even a slightly negative correlation (i.e., species that give birth to relatively heavier fetuses tend to have relatively smaller pubic gaps) when phylogeny was not taken into account. However, a positive relationship between the two variables did seem to exist in species that feed on immobile food, although this result was not very robust. Therefore, with regard to the pelvic floor hypothesis in humans, no conclusive evidence could be obtained in favour of it in this study. Regarding bats, it seems that the width of the pubic gap depends on other, as yet unknown factors than those examined in this study. Which factors these are should be investigated in future studies.

Nonetheless, although no clear relationship between relative neonatal body mass and relative pubic aperture size in bats was observed in this study, the presence of the ventral pubic gap in female bats is presumably an obstetric adaptation for the birth of particularly large young. Evidence for this can be found in the sexual dimorphism in the pelvic region of almost all Chiroptera species, which very likely is the result of sex-specific selection in female bats related to obstetrical demands. Furthermore, similar pubic gap structures can be found in the pelvis of other female mammals, where they develop, for example, during pregnancy in response to sex steroids and pregnancy hormones.

More studies of the pelvis in bats are necessary to shed further light on the factors that influence the variation in the width of the pubic gap and thus the facilitation of the birth of large neonates in bats. These findings may in turn help to better understand the evolutionary and developmental influences that limit pelvic width in humans and effect the cephalopelvic fit in women.

References

ABITBOL, M. M. 1988. Evolution of the ischial spine and of the pelvic floor in the hominoidea. *American Journal of Physical Anthropology,* 75**,** 53-67.

AMADOR, L. I., MOYERS ARÉVALO, R. L., ALMEIDA, F. C., CATALANO, S. A. & GIANNINI, N. P. 2018. Bat Systematics in the Light of Unconstrained Analyses of a Comprehensive Molecular Supermatrix. *Journal of Mammalian Evolution,* 25**,** 37-70.

ANKEL-SIMONS, F. 2000. *Primate Anatomy: An Introduction*, Academic Press.

ASSIS, A. B. D., DOS SANTOS, K. R. P., NETO, E. D. S. & LANGGUTH, A. 2011. Morphology of the musculature of the arm and shoulder girdle in Mormoopidae, Phyllostomidae and Noctilionidae (Mammalia, Chiroptera). *Revista Nordestina de Biologia,* 20**,** 27-45.

AUERBACH, B. M., KING, K. A., CAMPBELL, R. M., CAMPBELL, M. L. & SYLVESTER, A. D. 2018. Variation in obstetric dimensions of the human bony pelvis in relation to age-at-death and latitude. *American Journal of Physical Anthropology,* 167**,** 628-643.

BHARUCHA, A. E. 2006. Pelvic floor: anatomy and function. *Neurogastroenterology & Motility,* 18**,** 507-519.

BHARUCHA, A. E., BLANDON, R. E., LUNNISS, P. J. & SCOTT, S. M. 2007. Anatomy and Physiology of Continence. *In:* RATTO, C., DOGLIETTO, G. B., LOWRY, A. C., PÅHLMAN, L. & ROMANO, G. (eds.) *Fecal Incontinence: Diagnosis and Treatment.* Milano: Springer Milan.

BLESSING, S. 2002. *"Amorphochilus schnablii" (On-line), Animal Diversity Web.* [Online]. Available:https://animaldiversity.org/accounts/Amorphochilus_schnablii/ [Accessed].

BLOMBERG, S. P., GARLAND, T., JR. & IVES, A. R. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution,* 57**,** 717-745.

BROWN, K. M., HANDA, V. L., MACURA, K. J. & DELEON, V. B. 2013. Three-dimensional shape differences in the bony pelvis of women with pelvic floor disorders. *International Urogynecology Journal,* 24**,** 431-439.

BROWN, P. E., BROWN, T. W. & GRINNELL, A. D. 1983. Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. *Behavioral Ecology and Sociobiology,* 13**,** 287-298.

CHAPMAN, A., HALL, L. S. & BENNETT, M. B. 1994. Sexual dimorphism in the pelvic girdle of Australian flying foxes. *Australian journal of zoology,* 42**,** 261-265.

CHAVERRI, G. & KUNZ, T. H. 2006. Reproductive biology and postnatal development in the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae). *Journal of Zoology,* 270**,** 650-656.

CRELIN, E. S. 1960. The Development of Bony Pelvic Sexual Dimorphism in Mice. *Annals of the New York Academy of Sciences,* 84**,** 481.

CRELIN, E. S. 1969. Interpubic ligament: elasticity in pregnant free-tailed bat. *Science,* 164**,** 81-82.

CRELIN, E. S. & BRIGHTMAN, M. W. 1957. The pelvis of the rat: Its response to estrogen and relaxin. *The Anatomical Record,* 128**,** 467-483.

CRELIN, E. S. & NEWTON, E. V. 1969. The pelvis of the free-tailed bat: Sexual dimorphism and pregnancy changes. *The Anatomical Record,* 164**,** 349-357.

DEEMING, C. D. & MAYR, G. 2018. Pelvis morphology suggests that early Mesozoic birds were too heavy to contact incubate their eggs. *Journal of Evolutionary Biology,* 31**,** 701-709.

DESILVA, J. M. & LESNIK, J. J. 2008. Brain size at birth throughout human evolution: A new method for estimating neonatal brain size in hominins. *Journal of Human Evolution,* 55**,** 1064-1074.

DOLEA, C. & ABOUZAHR, C. 2003. Global burden of obstructed labour in the year 2000. *World Health Organization***,** 1-17.

DUARTE, A. P. G. & TALAMONI, S. A. 2010. Reproduction of the large fruit-eating bat *Artibeus lituratus* (Chiroptera: Phyllostomidae) in a Brazilian Atlantic forest area. *Mammalian Biology,* 75**,** 320-325.

DYKE, G. J. & KAISER, G. W. 2010. Cracking a developmental constraint: egg size and bird evolution. *Records of the Australian Museum,* 62**,** 207-216.

FALK, D., REDMOND, J. C., GUYER, J., CONROY, C., RECHEIS, W., WEBER, G. W. & SEIDLER, H. 2000. Early hominid brain evolution: a new look at old endocasts. *Journal of Human Evolution,* 38**,** 695-717.

FELSENSTEIN, J. 1985. Phylogenies and the Comparative Method. *The American Naturalist,* 125**,** 1-15.

FISCHER, B., GRUNSTRA, N. D. S., ZAFFARINI, E. & MITTEROECKER, P. 2021. Sex differences in the pelvis did not evolve de novo in modern humans. *Nature Ecology & Evolution,* 5**,** 625-630.

FISCHER, M. S. 2010. Bewegungsapparat: Postcraniales Skelett und Muskulatur. *In:* WESTHEIDE, W. & RIEGER, G. (eds.) *Spezielle Zoologie: Teil 2: Wirbel- oder Schädeltiere.* Heidelberg: Spektrum Akademischer Verlag, 49-68.

FLEMING, T. H. 1993. Plant-visiting bats. *American Scientist,* 81**,** 460-460.

FOSTER, G. W., HUMPHREY, S. R. & HUMPHREY, P. P. 1978. Survival Rate of Young Southeastern Brown Bats, Myotis austroriparius, in Florida. *Journal of Mammalogy,* 59**,** 299-304.

FUJITA, M. S. 1986. *A latitudinal comparison of growth and development in the little brown bat, Myotis lucifugus, with implications fore geographic variation in adult morphology.* PhD., Boston University.

GAISLER, J., HANAK, V. & DUNGEL, J. 1979. A Contribution to the population ecology of *Nyctalus noctula* (MAMMALIA: CHIROPTERA).

GARDNER, W. U. 1936. Sexual dimorphism of the pelvis of the mouse, the effect of estrogenic hormones upon the pelvis and upon the development of scrotal hernias. *American Journal of Anatomy,* 59**,** 459-483.

GAUDIOSO, P. J., MARTÍNEZ, J. J., BARQUEZ, R. M. & DÍAZ, M. M. 2020. Evolution of scapula shape in several families of bats (Chiroptera, Mammalia). *Journal of Zoological Systematics and Evolutionary Research,* 58**,** 1374-1394.

GOLDENBERG, R. L., MCCLURE, E. M., BOSE, C. L., JOBE, A. H. & BELIZÁN, J. M. 2015. Research results from a registry supporting efforts to improve maternal and child health in low and middle income countries. *Reproductive Health,* 12**,** 54.

GRIFFIN, D. R. 1958. *Listening in the dark: The acoustic orientation of bats and men,* Oxford, England, Yale Univer. Press.

GRUNSTRA, N. D. S., ZACHOS, F. E., HERDINA, A. N., FISCHER, B., PAVLIČEV, M. & MITTEROECKER, P. 2019. Humans as inverted bats: A comparative approach to the obstetric conundrum. *American Journal of Human Biology,* 31**,** e23227.

HAMMER, Ø., HARPER, D. A. T. & RYAN, P. D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica,* 4**,** 9.

HANDA, V. L., PANNU, H. K., SIDDIQUE, S., GUTMAN, R., VANROOYEN, J. & CUNDIFF, G. 2003. Architectural differences in the bony pelvis of women with and without pelvic floor disorders. *Obstetrics & Gynecology,* 102**,** 1283-1290.

HAYSSEN, V. & KUNZ, T. H. 1996. Allometry of Litter Mass in Bats: Maternal Size, Wing Morphology, and Phylogeny. *Journal of Mammalogy,* 77**,** 476-490.

HEANEY, L. R. & ROBERTS, T. E. 2009. *New perspectives on the long-term biogeographic dynamics and conservation of Philippine fruit bats*.

HISAW, F. L. 1925. The influence of the ovary on the resorption of the pubic bones of the pocket gopher, Geomys bursarius (Shaw). *Journal of Experimental Zoology,* 42**,** 411-441.

HOFMEYR, G. J. & SHWENI, P. M. 2012. Symphysiotomy for feto-pelvic disproportion. *Cochrane Database of Systematic Reviews*.

HOLLOWAY, R. L., BROADFIELD, D. C., SCHWARTZ, J. H., TATTERSALL, I. & YUAN, M. S. 2004. *Brain Endocasts-The Paleoneurological Evidence*, Wiley-Liss.

HOLLOWAY, R. L., SHERWOOD, C. C., HOF, P. R. & RILLING, J. K. 2009. Evolution of the brain in humans–Paleoneurology. *Encyclopedia of neuroscience***,** 1326-1334.

HUSEYNOV, A., ZOLLIKOFER, C. P. E., COUDYZER, W., GASCHO, D., KELLENBERGER, C., HINZPETER, R. & PONCE DE LEÓN, M. S. 2016. Developmental evidence for obstetric adaptation of the human female pelvis. *Proceedings of the National Academy of Sciences,* 113**,** 5227-5232.

HYMAN, L. H. & WAKE, M. H. 1992. *Hyman's comparative vertebrate anatomy*, University of Chicago Press.

JOHANSON, J. M. & BERGER, P. J. 2003. Birth Weight as a Predictor of Calving Ease and Perinatal Mortality in Holstein Cattle1. *Journal of Dairy Science,* 86**,** 3745-3755.

JONES, K. E., BIELBY, J., CARDILLO, M., FRITZ, S. A., O'DELL, J., ORME, C. D. L., SAFI, K., SECHREST, W., BOAKES, E. H., CARBONE, C., CONNOLLY, C., CUTTS, M. J., FOSTER, J. K., GRENYER, R., HABIB, M., PLASTER, C. A., PRICE, S. A., RIGBY, E. A., RIST, J., TEACHER, A., BININDA-EMONDS, O. R. P., GITTLEMAN, J. L., MACE, G. M. & PURVIS, A. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology,* 90**,** 2648-2648.

JÜRGENS, K. D. & PROTHERO, J. 1987. Scaling of maximal lifespan in bats. *Comparative biochemistry and physiology. A, Comparative physiology,* 88**,** 361-367.

KAMILAR, J. M. & COOPER, N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 368**,** 20120341.

KETTEN, D. R. 1992. The Marine Mammal Ear: Specializations for Aquatic Audition and Echolocation. *In:* WEBSTER, D. B., POPPER, A. N. & FAY, R. R. (eds.) *The Evolutionary Biology of Hearing.* New York, NY: Springer New York.

KOFRON, C. P. & CHAPMAN, A. 1994. Reproduction and sexual dimorphism of the West African fruit bat, *Epomops buettikoferi*, in Liberia. *African Journal of Ecology,* 32**,** 308-316.

KRISTIANSSON, P., SVÄRDSUDD, K. & VON SCHOULTZ, B. 1996. Serum relaxin, symphyseal pain, and back pain during pregnancy. *American Journal of Obstetrics and Gynecology,* 175**,** 1342-1347.

KUNZ, T. H. 1971. Reproduction of Some Vespertilionid Bats in Central Iowa. *The American Midland Naturalist,* 86**,** 477-486.

KUNZ, T. H. & KURTA, A. Size of bats at birth and maternal investment during pregnancy. Symposia of the Zoological Society of London, 1987. 79-106.

LANDE, R. 1980. Sexual Dimorphism, Sexual Selection, and Adaptation in Polygenic Characters. *Evolution,* 34**,** 292-305.

LAVAL, R. K. & LAVAL, M. L. 1977. Reproduction and Behavior of the African Banana Bat, *Pipistrellus nanus*. *Journal of Mammalogy,* 58**,** 403-410.

LEAKEY, M. G., FEIBEL, C. S., MCDOUGALL, I. & WALKER, A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature,* 376**,** 565-571.

LEUTENEGGER, W. 1974. Functional aspects of pelvic morphology in simian Primates. *Journal of Human Evolution,* 3**,** 207-222.

LEUTENEGGER, W. 1976. Allometry of neonatal size in eutherian mammals. *Nature,* 263**,** 229-230.

LOPEZ AGUIRRE, C., HAND, S., KOYABU, D., TU, V. & WILSON, L. 2020. Phylogeny and foraging behaviour shape modular morphological variation in bat humeri. *Journal of Anatomy,* 238.

LUNDE, A., MELVE, K. K., GJESSING, H. K., SKJÆRVEN, R. & IRGENS, L. M. 2007. Genetic and Environmental Influences on Birth Weight, Birth Length, Head Circumference, and Gestational Age by Use of Population-based Parent-Offspring Data. *American Journal of Epidemiology,* 165**,** 734-741.

MARINELLO, M. M. & BERNARD, E. 2014. Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. *Canadian Journal of Zoology,* 92.

MARTIN, R. D. & MACLARNON, A. M. 1985. Gestation period, neonatal size and maternal investment in placental mammals. *Nature,* 313**,** 220-223.

MILLAR, J. S. 1981. Pre-Partum Reproductive Characteristics of Eutherian Mammals. *Evolution,* 35**,** 1149-1163.

MITTEROECKER, P., GUNZ, P., NEUBAUER, S. & MÜLLER, G. 2012. How to Explore Morphological Integration in Human Evolution and Development? *Evolutionary Biology,* 39**,** 536-553.

MORI, E., MAZZA, G. & LOVARI, S. 2017. Sexual dimorphism. *Encyclopedia of Animal Cognition and Behavior (J. Vonk, and T. Shakelford, Eds). Springer International Publishing, Switzerland***,** 1-7.

MYERS, P. 1978. Sexual Dimorphism in Size of Vespertilionid Bats. *The American Naturalist,* 112**,** 701-711.

NEUWEILER, G. 2000. *The biology of bats*, Oxford University Press on Demand.

NEUWEILER, G., BRUNS, V. & SCHULLER, G. 1980. Ears adapted for the detection of motion, or how echolocating bats have exploited the capacities of the mammalian auditory system. *The Journal of the Acoustical Society of America,* 68**,** 741-753.

NIEMITZ, C. 2010. The evolution of the upright posture and gait—a review and a new synthesis. *Naturwissenschaften,* 97**,** 241-263.

NORBERG, U. M., RAYNER, J. M. V. & LIGHTHILL, M. J. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences,* 316**,** 335-427.

NOWAK, R. M. & WALKER, E. P. 1994. *Walker's bats of the world*, JHU Press.

NWOHA, P. U. 2000. Sex differences in the bony pelvis of the fruit-eating bat, *Eidolon helvum*. *Folia morphologica,* 59**,** 291-295.

O'CONNOR, W. B., CAIN, G. D. & ZARROW, M. X. 1966. Elongation of the Interpubic Ligament in the Little Brown Bat (*Myotis lucifugus*). *Proceedings of the Society for Experimental Biology and Medicine,* 123**,** 935-937.

ORME, D., FRECKLETON, R., THOMAS, G., PETZOLDT, T., FRITZ, S., ISAAC, N. & PEARSE, W. 2018. The caper package: comparative analysis of phylogenetics and evolution in R. *R package version,* 5**,** 1-36.

PAGEL, M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta,* 26**,** 331-348.

PAGEL, M. 1999. Inferring the historical patterns of biological evolution. *Nature,* 401**,** 877-884.

PATTERSON, B. D., WEBALA, P. W., LAVERY, T. H., AGWANDA, B. R., GOODMAN, S. M., KERBIS PETERHANS, J. C. & DEMOS, T. C. 2020. Evolutionary relationships and population genetics of the Afrotropical leaf-nosed bats (Chiroptera, Hipposideridae). ZooKeys 929: 117–161.

PAVLIČEV, M., ROMERO, R. & MITTEROECKER, P. 2020. Evolution of the human pelvis and obstructed labor: new explanations of an old obstetrical dilemma. *American Journal of Obstetrics and Gynecology,* 222**,** 3-16.

PELLETIER, M., STOETZEL, E., COCHARD, D. & LENOBLE, A. 2017. Sexual dimorphism in the pelvis of Antillean fruit-eating bat (*Brachyphylla cavernarum*) and its application to a fossil accumulation from the Lesser Antilles. *Geobios,* 50**,** 311-318.

R CORE TEAM 2019. R: A language and environment for statistical computing. *In:* TEAM, R. C. (ed.).

RACEY, P. A. 1982. Ecology of Bat Reproduction. *In:* KUNZ, T. H. (ed.) *Ecology of Bats.* Boston, MA: Springer US.

RALLS, K. 1976. Mammals in Which Females are Larger Than Males. *The Quarterly Review of Biology,* 51**,** 245-276.

RALLS, K. 1977. Sexual Dimorphism in Mammals: Avian Models and Unanswered Questions. *The American Naturalist,* 111**,** 917-938.

REVELL, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution,* 3**,** 217-223.

RICHMOND, B. G. & JUNGERS, W. L. 2008. Orrorin tugenensis Femoral Morphology and the Evolution of Hominin Bipedalism. *Science,* 319**,** 1662-1665.

ROEHRS, Z. P., LACK, J. B. & VAN DEN BUSSCHE, R. A. 2010. Tribal phylogenetic relationships within Vespertilioninae (Chiroptera: Vespertilionidae) based on mitochondrial and nuclear sequence data. *Journal of Mammalogy,* 91**,** 1073-1092.

ROJAS, D., VALE, Á., FERRERO, V. & NAVARRO, L. 2011. When did plants become important to leaf-nosed bats? Diversification of feeding habits in the family Phyllostomidae. *Molecular Ecology,* 20**,** 2217-2228.

ROSENBERG, K. & TREVATHAN, W. 2002. Birth, obstetrics and human evolution. *BJOG: An International Journal of Obstetrics & Gynaecology,* 109**,** 1199-1206.

ROSENBERG, K. R. 1992. The evolution of modern human childbirth. *American Journal of Physical Anthropology,* 35**,** 89-124.

RUTH, E. B. 1936. Metamorphosis of the pubic symphysis. II. The guinea pig. *The Anatomical Record,* 67**,** 69-79.

SAY, L., CHOU, D., GEMMILL, A., TUNÇALP, Ö., MOLLER, A.-B., DANIELS, J., GÜLMEZOGLU, A. M., TEMMERMAN, M. & ALKEMA, L. 2014. Global causes of maternal death: a WHO systematic analysis. *The Lancet Global Health,* 2**,** e323-e333.

SCHULTZ, A. H. 1949. Sex differences in the pelves of primates. *American Journal of Physical Anthropology,* 7**,** 401-424.

SCHUTZ, H., DONOVAN, E. R. & HAYES, J. P. 2009. Effects of parity on pelvic size and shape dimorphism in Mus. *Journal of Morphology,* 270**,** 834-842.

SCHWABE, C., STEINETZ, B., WEISSE, G., SEGALOFF, A., MCDONALD, J. K., O'BYRNE, E., HOCHMAN, J., CARRIERE, B. & GOLDSMITH, L. 1978. Relaxin. *In:* GREEP, R. O. (ed.) *Proceedings of the 1977 Laurentian Hormone Conference.* Boston: Academic Press.

SHATKOVSKA, O. V., GHAZALI, M., MYTIAI, I. S. & DRUZ, N. 2018. Size and shape correlation of birds' pelvis and egg: Impact of developmental mode, habitat, and phylogeny. *Journal of Morphology,* 279**,** 1590-1602.

SLONAKER, J. R. 1920. Some morphological changes for adaptation in the mole. *Journal of Morphology,* 34**,** 334-373.

STADELMANN, B., LIN, L. K., KUNZ, T. H. & RUEDI, M. 2007. Molecular phylogeny of New World Myotis (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution,* 43**,** 32-48.

STANSFIELD, E., KUMAR, K., MITTEROECKER, P. & GRUNSTRA, N. D. S. 2021. Biomechanical trade-offs in the pelvic floor constrain the evolution of the human birth canal. *Proceedings of the National Academy of Sciences,* 118**,** e2022159118.

STARCK, D. 1995. Lehrbuch der Speziellen Zoologie. Wirbeltiere. Teil 5: Säugetiere. Gustav Fischer Verlag, Jena.

STÖVER, B. C. & MÜLLER, K. F. 2010. TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics,* 11**,** 7.

SYMONDS, M. R. E. & BLOMBERG, S. P. 2014. A Primer on Phylogenetic Generalised Least Squares. *In:* GARAMSZEGI, L. Z. (ed.) *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice.* Berlin, Heidelberg: Springer Berlin Heidelberg.

SZE, E. H., KOHLI, N., MIKLOS, J. R., ROAT, T. & KARRAM, M. M. 1999. Computed tomography comparison of bony pelvis dimensions between women with and without genital prolapse. *Obstetrics & Gynecology,* 93**,** 229-232.

TALMAGE, R. V. 1947. Changes produced in the symphysis pubis of the guinea pig by the sex steroids and relaxin. *The Anatomical Record,* 99**,** 91-113.

TEELING, E. C., JONES, G. & ROSSITER, S. J. 2016. Phylogeny, Genes, and Hearing: Implications for the Evolution of Echolocation in Bats. *In:* FENTON, M. B., GRINNELL, A. D., POPPER, A. N. & FAY, R. R. (eds.) *Bat Bioacoustics.* New York, NY: Springer New York.

TUTTLE, M. D. & STEVENSON, D. 1982. Growth and Survival of Bats. *In:* KUNZ, T. H. (ed.) *Ecology of Bats.* Boston, MA: Springer US.

VAUGHAN, T. A. 1970a. The muscular system. *Biology of bats.*

VAUGHAN, T. A. 1970b. The skeletal system. *Biology of bats.*

VAUGHAN, T. A. & BATEMAN, G. C. 1970. Functional Morphology of the Forelimb of Mormoopid Bats. *Journal of Mammalogy,* 51**,** 217-235.

VERIDIANO, A. M., GARCIA, E. A., PINHEIRO, M. C., NISHIMORI, F. Y., TOLEDO, O. M. S. & JOAZEIRO, P. P. 2007. The mouse pubic symphysis as a remodeling system: morphometrical analysis of proliferation and cell death during pregnancy, partus and postpartum. *Cell and Tissue Research,* 330**,** 161-167.

VIDAL-CORDASCO, M., MATEOS, A., ZORRILLA-REVILLA, G., PRADO-NÓVOA, O. & RODRÍGUEZ, J. 2017. Energetic cost of walking in fossil hominins. *American Journal of Physical Anthropology,* 164**,** 609-622.

WARD, C., LEAKEY, M. & WALKER, A. 1999. The new hominid species Australopithecus anamensis. *Evolutionary Anthropology: Issues, News, and Reviews,* 7**,** 197-205.

WARRENER, A. G., LEWTON, K. L., PONTZER, H. & LIEBERMAN, D. E. 2015. A wider pelvis does not increase locomotor cost in humans, with implications for the evolution of childbirth. *PloS one,* 10**,** e0118903.

WASHBURN, S. L. 1960. Tools and Human Evolution. *Scientific American,* 203**,** 62-75.

WEBSTER, F. A. & GRIFFIN, D. R. 1962. The role of the flight membranes in insect capture by bats. *Animal Behaviour,* 10**,** 332-340.

WEINBERG, S. M., SCOTT, N. M., NEISWANGER, K. & MARAZITA, M. L. 2005. Intraobserver error associated with measurements of the hand. *American Journal of Human Biology,* 17**,** 368-371.

WELTY, J. C. & BAPTISTA, L. 1988. *The Life of Birds,* New York, Saunders College Publishing.

WILLIAMS, D. F. & FINDLEY, J. S. 1979. Sexual Size Dimorphism in Vespertilionid Bats. *The American Midland Naturalist,* 102**,** 113-126.

WILSON, D. E. 2015. *Bats in question: the Smithsonian answer book*, Smithsonian Institution.

WILSON, D. E. & MITTERMEIER, R. A. (eds.) 2019. *Handbook of the Mammals of the World. Vol. 9. Bats,* Barcelona: Lynx Edicions.

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Appendix

Zusammenfassung

Die Geburt beim Menschen ist komplizierter im Vergleich zu anderen Säugetieren. Dies liegt vor allem an der Größe des Schädels des Neugeborenen, welcher, im Verhältnis zur Größe des mütterlichen, knöchernen Beckens, sehr groß ist und nur schwer durch dieses passt. In der Anthropologie wird seit langem darüber diskutiert, warum sich daher kein größerer und breiterer Geburtskanal entwickelt hat. Um diese spezielle Frage der menschlichen Evolution besser zu verstehen, wurden Fledermäuse (Chiroptera) als Vergleich herangezogen, welche noch größere Neugeborene zur Welt bringen als der Mensch. Um die Geburt eines solch großen Fötus zu ermöglichen, besitzen die Weibchen aller Fledermausarten eine "Schamlücke", die von einem flexiblen Ligament anstelle einer Schambeinfuge überspannt wird. Es wird vermutet, dass der Selektionsdruck, der die Größe und Flexibilität des menschlichen Geburtskanals einschränkt, bei Fledermäusen aufgrund ihrer fliegenden Fortbewegung und ihres besonderen Rastverhaltens nicht vorhanden ist. Daher könnten Fledermäuse frei auf die geburtshilfliche Selektion reagieren und ihre Schamlücke im Verhältnis zur Größe ihres Neugeborenen vergrößern. Um diese Annahme zu überprüfen, wurde eine morphometrische Studie zur Größe der Schamlücke an 273 Exemplaren von 82 Fledermausarten durchgeführt. Das durchschnittliche adulte und neonatale Körpergewicht konnte für eine Teilstichprobe von 65 Arten aus der Literatur ermittelt werden. Entgegen den Erwartungen wurde keine Korrelation zwischen der relativen Größe der Schamlücke und dem relativen Körpergewicht der Neugeborenen festgestellt. Dennoch weisen männliche Fledermäuse nur selten eine Schamlücke auf, was zu einem starken Sexualdimorphismus im Beckenbereich führt, der auf eine geschlechtsspezifische Selektion bei weiblichen Fledermäusen im Zusammenhang mit geburtshilflichen Anforderungen hindeutet.

Table A1 List of used specimens. Listed are the specimens used in this study, derived from various institutions. Shown are the respective institutions, inventory numbers, *sex* and the type of preservation of the specimens.

Musuem/Collection	Family	Species	Inventory number	Sex	Typ of preservation (alcohol or dry)
Museum für Naturkunde Berlin	Emballonuridae	*Taphozous nudiventris*	ZMB_Mam_15030	female	dry
	Phyllostomidae	*Desmodus rotundus*	ZMB_Mam_85670	female	dry
		Glossophaga soricina	ZMB_Mam_85644	male	dry
		Phyllostomus hastatus	ZMB_Mam_108269	male	dry
	Pteropodidae	*Dobsonia moluccensis*	ZMB_Mam_8516	female	dry
		Dobsonia moluccensis	ZMB_Mam_8514	male	dry
	Rhinolophidae	*Rhinolophus cornutus*	ZMB_Mam_50080	female	dry
		Rhinolophus cornutus	ZMB_Mam_50081	male	dry
Zoological Research Museum Alexander Koenig Bonn	Emballonuridae	*Taphozous nudiventris*	ZFMK MAM 96.545	female	dry
	Phyllostomidae	*Desmodus rotundus*	ZFMK MAM 79.172	male	dry
	Pteropodidae	*Eidolon dupreanum*	ZFMK MAM 1978.0529	male	dry
		Rousettus aegyptiacus	ZFMK MAM 1994-0502-s	male	dry
		Rousettus aegyptiacus	ZFMK MAM 2010.214	male	dry
Bavarian State Collection of Zoology Munich	Hipposideridae	*Hipposideros caffer*	1904/206	male	dry
		Hipposideros diadema	1987/70	male	dry
		Hipposideros diadema	1987/69	male	dry
		Hipposideros diadema	1987/68	male	dry
	Molossidae	*Mops condylurus*	1987/128	male	dry
	Phyllostomidae	*Carollia perspicillata*	1972/8	male	dry
		Phyllostomus hastatus	2011/283	male	dry

		Phyllostomus hastatus	2011/282	male	dry
		Tadarida brasiliensis	598450	female	dry
	Phyllostomidae	*Anoura caudifer*	584107	male	dry
		Carollia perspicillata	597427	male	dry
		Carollia perspicillata	597436	unknown	dry
		Carollia perspicillata	20075190	female	dry
		Desmodus rotundus	582270	female	dry
		Desmodus rotundus	590416	female	dry
		Desmodus rotundus	640419	female	dry
		Phyllostomus hastatus	584113	female	dry
Natural History Museum Vienna	Emballonuridae	*Taphozous hildegardae*	NMW 32233	female	dry
		Taphozous longimanus	NMW 19120	female	alcohol
		Taphozous melanopogon	NMW 19123	male	alcohol
	Hipposideridae	*Asellia tridens*	NMW 27959	male	dry
		Asellia tridens	NMW 27953	male	dry
		Hipposideros armiger	NMW 42887	female	dry
		Hipposideros armiger	NMW 42888	male	dry
		Hipposideros commersoni	NMW 32351	female	dry
		Hipposideros diadema	NMW 29893	male	dry
	Megadermatidae	*Megaderma lyra*	NMW 21395	female	dry
	Miniopteridae	*Miniopterus inflatus*	NMW 32805	female	dry
		Miniopterus inflatus	NMW 32807	male	dry
		Miniopterus schreibersii	NMW 27905	male	dry

		Miniopterus schreibersii	NMW 27907	female	dry
		Miniopterus schreibersii	NMW 27908	female	dry
		Miniopterus schreibersii	NMW 28765	female	dry
		Miniopterus schreibersii	NMW 28761	male	dry
	Molossidae	*Chaerephon bivittata*	NMW 32508	female	dry
		Chaerephon bivittata	NMW 32509	male	dry
		Chaerephon plicatus	NMW 42861	male	dry
		Chaerephon plicatus	NMW 29896	male	dry
		Chaerephon plicatus	NMW 27415	female	alcohol
		Chaerophon plicatus	NMW 42860	female	dry
		Molossus molossus	NMW 27436	female	dry
		Molossus molossus	NMW 22695	female	alcohol
		Mops condylurus	NMW 64109	female	alcohol
		Mops demonstrator	NMW 30788	female	dry
		Mormopterus jugularis	NMW 27421	female	dry
		Otomops martiensseni	NMW 32507	male	dry
		Tadarida aegytiaca	NMW 18166	male	dry
	Mormoopidae	*Pteronotus quadridens*	NMW 49206	female	alcohol
		Pteronotus quadridens	NMW49217	female	alcohol
		Pteronotus quadridens	NMW49221	female	alcohol
	Natalidae	*Nyctiellus lepidus*	NMW 49604	female	alcohol
	Noctilionidae	*Noctilio albiventris*	NMW 19597	female	alcohol
	Nycteridae	*Nycteris thebaica*	NMW 10322	female	alcohol
	Phyllostomidae	*Anoura geoffroyi*	NMW 10836	unkown	alcohol
		Artibeus lituratus	NMW 28730	female	alcohol
		Artibeus jamaicensis	NMW 49596	female	alcohol

		Carollia perspicillata	NMW 73595	female	alcohol
		Brachyphylla nana	NMW 49404	female	alcohol
		Brachyphylla nana	NMW 49408	female	alcohol
		Macrotus waterhousii	NMW 49403	female	alcohol
		Phyllostomus hastatus	NMW 30744	female	alcohol
		Platyrrhinus lineatus	NMW 30760	female	alcohol
	Pteropodidae	*Cynopterus sphinx*	NMW 39319	male	dry
		Cynopterus sphinx	NMW 21391	male	dry
		Cynopterus sphinx	NMW 40394	female	dry
		Cynopterus sphinx	NMW 63028	male	dry
		Eidolon helvum	NMW 41486	female	dry
		Eidolon helvum	NMW 41511	female	dry
		Eidolon helvum	NMW 41484	male	dry
		Eidolon helvum	NMW 41485	female	dry
		Eonycteris spelaea	NMW 39390	female	dry
		Epomophorus labiatus	NMW 32688	female	dry
		Macroglossus minimus	NMW 40398	male	dry
		Macroglossus minimus	NMW 61440	female	alcohol
		Pteropus giganteus	NMW 63182	female	dry
		Pteropus giganteus	NMW 67988	female	dry
		Pteropus giganteus	NMW 68554	male	dry
		Pteropus giganteus	NMW 63183	female	dry
		Pteropus giganteus	NMW 68513	male	dry
		Pteropus lylei	NMW 36301	female	dry
		Pteropus vampyrus	NMW 1615	female	dry
		Pteropus vampyrus	NMW 957	male	dry

		Rousettus aegyptiacus	NMW 20834	female	dry
		Rousettus aegyptiacus	NMW 20839	female	dry
		Rousettus aegyptiacus	NMW 20835	female	dry
		Rousettus aegyptiacus	NMW 20836	male	dry
		Rousettus aegyptiacus	NMW 20837	male	dry
		Rousettus aegyptiacus	NMW 20840	male	dry
	Rhinolophidae	*Rhinolophus clivosus*	NMW 32266	female	dry
		Rhinolophus hipposideros	NMW 34319	female	dry
		Rhinolophus hipposideros	NMW 52276	male	dry
		Rhinolophus hipposideros	NMW 52235	female	dry
		Rhinolophus hipposideros	NMW 52737	male	dry
		Rhinolophus hipposideros	NMW 52744	male	dry
		Rhinolophus hipposideros	NMW 52741	female	dry
	Rhinopomatidae	*Rhinopoma hardwickei*	NMW 28691	female	dry
		Rhinopoma hardwickei	NMW 28690	female	dry
	Vespertilionidae	*Barbastella barbastellus*	NMW 64095	male	dry
		Barbastella barbastellus	NMW 36101	male	dry
		Barbastella barbastellus	NMW 53501	female	dry
		Barbastella barbastellus	NMW 56230	male	dry
		Barbastella barbastellus	NMW 52218	female	dry
		Barbastella barbastellus	NMW 52325	male	dry
		Barbastella barbastellus	NMW 52217	female	dry
		Eptesicus furinalis	NMW 66059	male	dry
		Eptesicus nilssonii	NMW 53322	female	dry
		Eptesicus nilssonii	NMW 61556	female	dry
		Eptesicus nilssonii	NMW 30028	female	dry

		Eptesicus nilssonii	NMW 50734	male	dry
		Eptesicus nilssonii	NMW 52216	male	dry
		Eptesicus nilssonii	NMW 53457	female	dry
		Eptesicus nilssonii	NMW 61560	female	dry
		Eptesicus nilssonii	NMW 36110	male	dry
		Eptesicus nilssonii	NMW 51447	male	dry
		Eptesicus serotinus	NMW 15711	female	dry
		Eptesicus serotinus	NMW 57233	female	dry
		Eptesicus serotinus	NMW 29406	female	dry
		Eptesicus serotinus	NMW 36103	male	dry
		Eptesicus serotinus	NMW 36104	male	dry
		Eptesicus serotinus	NMW 51018	female	dry
		Eptesicus serotinus	NMW 34316	female	dry
		Eptesicus serotinus	NMW 52805	male	dry
		Eptesicus serotinus	NMW 52817	male	dry
		Eptesicus serotinus	NMW 64042	male	dry
		Euderma maculatum	NMW 61755	female	dry
		Glauconyteris argentata	NMW 32739	male	dry
		Hypsugo savii	NMW 43657	female	dry
		Hypsugo savii	NMW 66482	female	dry
		Hypsugo savii	NMW 66936	female	dry
		Hypsugo savii	nicht inv. KS 09/75	male	dry
		Myotis bechsteini	NMW 52852	male	dry
		Myotis bechsteini	NMW 52329	female	dry
		Myotis bechsteini	NMW 66140	male	dry
		Myotis bechsteini	NMW 9290	male	dry

		Myotis bechsteini	NMW 52225	female	dry
		Myotis blythii	NMW 23385	female	dry
		Myotis blythii	NMW 65181	male	dry
		Myotis blythii	NMW 61484	male	dry
		Myotis blythii	NMW 28000	female	dry
		Myotis brandtii	NMW 66519	male	dry
		Myotis brandtii	NMW 65241	female	dry
		Myotis brandtii	NMW 30396	male	dry
		Myotis brandtii	NMW 62674	female	dry
		Myotis capaccinii	NMW 30343	male	dry
		Myotis capaccinii	NMW 15715	female	dry
		Myotis daubentoni	NMW 52344	female	dry
		Myotis daubentoni	NMW 52344	male	dry
		Myotis daubentoni	NMW 50981	male	dry
		Myotis daubentoni	NMW 51502	male	dry
		Myotis daubentoni	NMW 50977	female	dry
		Myotis daubentoni	NMW 34219	male	dry
		Myotis daubentoni	NMW 29048	male	dry
		Myotis daubentoni	NMW 29046	female	dry
		Myotis daubentoni	NMW 30401	female	dry
		Myotis daubentoni	NMW 29464	female	dry
		Myotis emarginatus	NMW 57203	female	dry
		Myotis emarginatus	NMW 58149	female	dry
		Myotis emarginatus	NMW 58150	female	dry
		Myotis emarginatus	NMW 36982	female	dry
		Myotis emarginatus	NMW 61488	male	dry

		Myotis emarginatus	NMW 9117	female	dry
		Myotis emarginatus	NMW 52323	male	dry
		Myotis emarginatus	NMW 53486	male	dry
		Myotis emarginatus	NMW 69932	male	dry
		Myotis myotis	NMW 50723	female	dry
		Myotis myotis	NMW 52631	female	dry
		Myotis myotis	NMW 52632	female	dry
		Myotis myotis	NMW 52630	female	dry
		Myotis myotis	NMW 52645	female	dry
		Myotis myotis	NMW 64061	male	dry
		Myotis myotis	NMW 64004	male	dry
		Myotis myotis	NMW 25162	male	dry
		Myotis myotis	NMW 64006	male	dry
		Myotis myotis	NMW 67021	male	dry
		Myotis myotis	NMW 52641	female	dry
		Myotis myotis	NMW F1311	female	dry
		Myotis mystacinus	NMW 51012	female	dry
		Myotis mystacinus	NMW 52713	male	dry
		Myotis mystacinus	NMW 58145	female	dry
		Myotis mystacinus	NMW 58146	female	dry
		Myotis mystacinus	NMW 65230	female	dry
		Myotis mystacinus	NMW 66471	male	dry
		Myotis mystacinus	NMW 52727	male	dry
		Myotis mystacinus	NMW 66142	male	dry
		Myotis nattereri	NMW 52338	male	dry

		Myotis nattereri	NMW 69831	male	dry
		Myotis nattereri	NMW 61653	male	dry
		Myotis nattereri	NMW 57200	female	dry
		Myotis nattereri	NMW 71932	female	dry
		Myotis nattereri	NMW 66579	female	dry
		Myotis nattereri	NMW 15149	male	dry
		Myotis nattereri	NMW 69191	female	dry
		Neoromicia capensis	NMW 18164	female	dry
		Neoromicia nanus	NMW 32716	male	dry
		Neoromicia nanus	NMW 32718	male	dry
		Nyctalus noctula	NMW 42212	male	dry
		Nyctalus noctula	NMW 72318	male	dry
		Nyctalus noctula	NMW 70101	female	dry
		Nyctalus noctula	NMW 27528	male	dry
		Nyctalus noctula	NMW 12066	male	dry
		Nyctalus noctula	NMW 66945	female	dry
		Nyctalus noctula	NMW 66946	female	dry
		Nyctalus noctula	NMW 66947	female	dry
		Pipistrellus kuhlii	NMW 66528	male	dry
		Pipistrellus kuhlii	NMW 64081	male	dry
		Pipistrellus kuhlii	NMW 69867	female	dry
		Pipistrellus kuhlii	NMW 69862	female	dry
		Pipistrellus kuhlii	NMW 68354	male	dry
		Pipistrellus kuhlii	NMW 66479	female	dry
		Pipistrellus kuhlii	NMW 66916	male	dry

		Pipistrellus kuhlii	NMW 43654	female	dry
		Pipistrellus nathusii	NMW 71821	male	dry
		Pipistrellus nathusii	NMW 52331	male	dry
		Pipistrellus nathusii	NMW 61506	male	dry
		Pipistrellus nathusii	NMW 64019	male	dry
		Pipistrellus nathusii	NMW 52749	female	dry
		Pipistrellus nathusii	NMW 52333	female	dry
		Pipistrellus nathusii	NMW 61735	female	dry
		Pipistrellus nathusii	NMW 51131	female	dry
		Pipistrellus pipistrellus	NMW 63017	male	dry
		Pipistrellus pipistrellus	NMW 52797	female	dry
		Pipistrellus pipistrellus	NMW 53382	male	dry
		Pipistrellus pipistrellus	NMW 61498	female	dry
		Pipistrellus pipistrellus	NMW 50907	male	dry
		Pipistrellus pipistrellus	NMW 34303	female	dry
		Pipistrellus pipistrellus	NMW 68935	male	dry
		Pipistrellus pipistrellus	NMW 69857	female	dry
		Pipistrellus stenopterus	NMW 40266	female	dry
		Pipistrellus stenopterus	NMW 40268	female	dry
		Plecotus auritus	NMW 55548	female	dry
		Plecotus auritus	NMW 50533	female	dry
		Plecotus auritus	NMW 50532	female	dry
		Plecotus auritus	NMW 50531	female	dry
		Plecotus auritus	NMW 50526	male	dry
		Plecotus auritus	NMW 50482	male	dry

		Plecotus auritus	NMW 50478	male	dry
		Plecotus auritus	NMW 43658	male	dry
		Plecotus austriacus	NMW 52235	female	dry
		Plecotus austriacus	NMW 69312	male	dry
		Plecotus austriacus	NMW 34243	male	dry
		Plecotus austriacus	NMW 34248	male	dry
		Plecotus austriacus	NMW 36129	male	dry
		Plecotus austriacus	NMW 69326	female	dry
		Plecotus austriacus	NMW 69304	female	dry
		Plecotus austriacus	NMW 52238	female	dry
		Plecotus gaisleri	NMW 30143	female	dry
		Scotoecus hirundo	NMW 32727	male	dry
		Scotoecus hirundo	NMW 32728	male	dry
		Scotophilus dinganii	NMW 32782	female	dry
		Scotophilus kuhlii	NMW 40402	male	dry
		Scotophilus kuhlii	NMW 28486	male	dry
		Scotophilus nigrita	NMW 32793	female	dry
		Scotophilus nigrita	NMW 32794	female	dry
		Vespertilio murinus	NMW 69843	male	dry
		Vespertilio murinus	NMW 69847	male	dry
		Vespertilio murinus	NMW 69851	male	dry
		Vespertilio murinus	NMW 29396	female	dry
		Vespertilio murinus	NMW 29455	female	dry
		Vespertilio murinus	NMW 66930	female	dry

Table A2 Pelvic measurements of specimens from the Museum für Naturkunde in Berlin. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Pteropodidae	*Dobsonia moluccensis*	1	23.09.2019	1	ZMB_Mam_8516	2	1	9.35	7.804	7.599	0	10.891	10.573	10.986	if female than still with ligament
	Dobsonia moluccensis	2	04.10.2019	1	ZMB_Mam_8514	4	1	11.138	8.121	10.784	0	11.874	11.797	12.693	
Phyllostomidae	*Anoura caudifer*	3	23.09.2019	1	ZMB_Mam_85633	1	1	/	/	/	/	/	/	/	mounted, chest covers pelvis
	Desmodus rotundus	4	23.09.2019	1	ZMB_Mam_85670	2	1	5.01	4.288	4.878	4.42	4.874	5.552	6.125	left iliopubic eminence broken
	Glossophaga soricina	5	23.09.2019	1	ZMB_Mam_85644	1	1	3.949	3.158	3.086	0	3.847	3.917	3.741	right iliopubic eminence broken; leg covers lateral view
	Glossophaga soricina	6	23.09.2019	1	ZMB_Mam_90000	1	1	/	/	/	/	/	/	/	mounted, only dorsal view possible
	Phyllostomus hastatus	7	23.09.2019	1	ZMB_Mam_108269	1	1	7.49	5.793	5.764	0	8.044	6.751	7.579	left iliopubic eminence broken
	Phyllostomus hastatus	8	04.10.219	1	ZMB_Mam_85621	4	1	/	/	/	/	/	/	/	pelvis broken
Rhinolophidae	*Rhinolophus cornutus*	9	23.09.2019	1	ZMB_Mam_50080	2	1	3.752	2.501	2.646	0.374	2.685	3.67	3.614	chest covers pelvis
	Rhinolophus cornutus	10	23.09.2019	1	ZMB_Mam_50081	1	1	3.403	2.392	1.836	0	2.87	3.673	3.898	right iliopubic eminence broken
	Rhinolophus cornutus	11	23.09.2019	1	ZMB_Mam_50082	1	1	/	/	/	/	/	/	/	chest covers pelvis; articulated limbs prevent lateral measuring
	Rhinolophus cornutus	12	23.09.2019	1	ZMB_Mam_50083	1	1	/	/	/	/	/	/	/	chest covers pelvis; articulated limbs prevent lateral measuring
Emballonuridae	*Taphozous nudiventris*	13	23.09.2019	1	ZMB_Mam_15030	2	1	5.017	3.091	2.894	0.351	5.225	4.716	4.934	left iliopubic eminence; with ligament

Table A3 Forearm measurements of specimens from the Museum für Naturkunde in Berlin. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown (?)	Right forearm length linear (mm)	Comments
Pteropodidae	*Dobsonia moluccensis*	1	23.09.2019	1	ZMB_Mam_8516	2	1	101.42	measured with calliper
	Dobsonia moluccensis	2	04.10.2019	1	ZMB_Mam_8514	4	1	/	no forearm
Phyllostomidae	*Anoura caudifer*	3	23.09.2019	1	ZMB_Mam_85633	1	1	36.164	measured with microscope
	Desmodus rotundus	4	23.09.2019	1	ZMB_Mam_85670	2	1	/	no forearm
	Glossophaga soricina	5	23.09.2019	1	ZMB_Mam_85644	1	1	34.862	measured with microscope
	Glossophaga soricina	6	23.09.2019	1	ZMB_Mam_90000	1	1	35.746	measured with microscope
	Phyllostomus hastatus	7	23.09.2019	1	ZMB_Mam_108269	1	1	/	no forearm
	Phyllostomus hastatus	8	04.10.219	1	ZMB_Mam_85621	4	1	/	no forearm
Rhinolophidae	*Rhinolophus cornutus*	9	23.09.2019	1	ZMB_Mam_50080	2	1	39.795	measured with microscope
	Rhinolophus cornutus	10	23.09.2019	1	ZMB_Mam_50081	1	1	40.531	measured with microscope
	Rhinolophus cornutus	11	23.09.2019	1	ZMB_Mam_50082	1	1	37.311	measured with microscope
	Rhinolophus cornutus	12	23.09.2019	1	ZMB_Mam_50083	1	1	38.459	measured with microscope
Emballonuridae	*Taphozous nudiventris*	13	23.09.2019	1	ZMB_Mam_15030	2	1	62	measured with calliper

Table A4 Pelvic measurements of specimens from the Zoological Research Museum Alexander Koenig in Bonn. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Pteropodidae	*Eidolon dupreanum*	1	12.06.2019	1	ZFMK MAM 1978.0529	1	3	12.589	8.256	9.259	0	13.571	11.856	13.808	
	Rousettus aegyptiacus	2	12.06.2019	1	ZFMK MAM 1994-0502-s	1	1	10.467	7.571	8.802	0	13.193	10.733	10.973	
	Rousettus aegyptiacus	3	12.06.2019	1	ZFMK MAM 2010.214	1	1	9.51	7.582	7.992	0	12.919	10.967	10.493	
Phyllostomidae	*Desmodus rotundus*	4	12.06.2019	1	ZFMK MAM 79.172	1	1	3.255	2.61	3.276	1.996	5.422	5.014	5.886	both iliopubic eminence broken, both pubic bones slightly broken
Emballonuridae	*Taphozous nudiventris*	5	12.06.2019	1	ZFMK MAM 96.545	3	1	7.86	4.961	5.208	2.605	6.97	6.466	6.761	

Table A5 Forearm measurements of specimens from the Zoological Research Museum Alexander Koenig in Bonn. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Pteropodidae	*Eidolon dupreanum*	1	12.06.2019	1	ZFMK MAM 1978.0529	1	1	119.24	measured with calliper; right forearm broken -> used left one
	Rousettus aegyptiacus	2	12.06.2019	1	ZFMK MAM 1994-0502-s	1	1	89.46	measured with calliper
	Rousettus aegyptiacus	3	12.06.2019	1	ZFMK MAM 2010.214	1	1	89.14	measured with calliper
Phyllostomidae	*Desmodus rotundus*	4	12.06.2019	1	ZFMK MAM 79.172	1	1	47.22	measured with calliper
Emballonuridae	*Taphozous nudiventris*	5	12.06.2019	1	ZFMK MAM 96.545	3	1	71.4	measured with calliper

Table A6 Pelvic measurements of specimens from the Bavarian State Collection of Zoology in Munich. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Phyllostomidae	*Phyllostomus hastatus*	1	28.03.2019	1	2011/283	1	1	6.239	5.31	4.79	0	9.885	7.734	9.216	left iliopubic eminence is broken
	Phyllostomus hastatus	2	28.03.2019	2	2011/282	4	1	6.777	5.599	5.241	0	9.607	6.796	8.473	right leg still linked to pelvis -> depth and length measured on the right side
	Carollia perspicillata	3	28.03.2019	1	1972/8	1	1	3.987	4.042	4.082	1.325	6.327	4.955	4.271	spine covers pelvis -> measurements of a slightly different angel; pelvis is asymmetric
Molossidae	*Mops condylurus*	4	28.03.2019	1	1987/128	4	1	5.343	4.575	4.165	0	6.029	6.292	5.504	left iliopubic eminence is broken; right pubic is broken
Hipposideridae	*Hipposideros diadema*	5	28.03.2019	1	1987/70	4	1	6.521	5.29	4.992	0	5.955	13,672/ 7,975	11,424/ 5,858	two measurements of length
	Hipposideros diadema	6	28.03.2019	1	1987/69	4	1	6.24	5.048	5.236	0	5.249	14,022/ 8,994	12,627/ 7,714	two measurements of length
	Hipposideros diadema	7	28.03.2019	1	1987/68	1	1	6.612	5.159	4.973	0	5.493	14,113/ 9,209	12,84/ 8,01	two measurements of length
	Hipposideros caffer	8	28.03.2019	1	1904/206	4	1	2.888	2.371	2.479	0				depth and length not measurable (pubic badly broken)

Table A7 Forearm measurements of specimens from the Bavarian State Collection of Zoology in Munich. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Phyllostomidae	*Phyllostomus hastatus*	1	28.03.2019	1	2011/283	1	1	82.98	measured with callipers
	Phyllostomus hastatus	2	28.03.2019	2	2011/282	4	1		no forearm
	Carollia perspicillata	3	28.03.2019	1	1972/8	1	1	40.04	fingers still linked with forearm -> measured with callipers
Molossidae	*Mops condylurus*	4	28.03.2019	1	1987/128	4	1		no forearm
Hipposideridae	*Hipposideros diadema*	5	28.03.2019	1	1987/70	4	1		no forearm
	Hipposideros diadema	6	28.03.2019	1	1987/69	4	1		no forearm
	Hipposideros diadema	7	28.03.2019	1	1987/68	1	1		no forearm
	Hipposideros caffer	8	28.03.2019	1	1904/206	4	1		no forearm

Table A8 Pelvic measurements of specimens from the Swedish Museum of Natural History in Stockholm. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Phyllostomidae	*Anoura caudifer*	1	13.09.2019	1	584107	4	1	3.844	2.594	2.32	0	4.162	3.546	3.09	legs still linked with pelvis
	Anoura caudifer	2	13.09.2019	1	605414	4	1								chest covers pelvis
	Carollia perspicillata	3	13.09.2019	1	597427	4	1	3.098	2.266	2.414	0	4.944	3.945	3.879	symphysis slightly broken
	Carollia perspicillata	4	13.09.2019	1	597436	5	1	4.118	3.276	3.287	0.774	5.911	4.704	4.073	legs still linked to pelvis
	Carollia perspicillata	5	17.09.2019	1	597466	3	1								chest covers pelvis
	Carollia perspicillata	6	17.09.2019	1	20075190	2	3	4.863	3.758	2.808	1.712	5.582	4.382	4.136	
	Carollia perspicillata	7	17.09.2019	1	20125436	2	1								spine covers pelvis
	Desmodus rotundus	8	17.09.2019	1	582270	2	1	2.499	2.098	3.03	0.408	4.936	5.362	6.015	whole skeleton except head and legs
	Desmodus rotundus	9	17.09.2019	1	590416	2	1	4.365	3.02	3.763	3.673	6.453	6.07	6.835	
	Desmodus rotundus	10	17.09.2019	1	640419	2	1	5.759	3.763	5.452	5.452	5.697	5.558	6.541	left iliopubic eminence broken
	Phyllostomus hastatus	11	17.09.2019	1	584113	2	1	7.327	5.388	5.405	2.679	8.873	7.323	8.31	
Mollosidae	*Tardarida brasiliensis*	12	17.09.2019	1	590263	1	1	3.668	3.183	3.216	0	4.549	4.28	4.123	
	Tardarida brasiliensis	13	17.09.2019	1	598450	2	1	4.285	3.348	3.187	2.724	4.043	3.935	3.948	

Table A9 Forearm measurements of specimens from the Swedish Museum of Natural History in Stockholm. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Phyllostomidae	*Anoura caudifer*	1	13.09.2019	1	584107	4	1	33.284	measured with microscope; left arm
	Anoura caudifer	2	13.09.2019	1	605414	4	1	38.66	measured with calliper -> unable to measure with microscope because of linked fingers
	Carollia perspicillata	3	13.09.2019	1	597427	4	1	38.5	measured with calliper -> unable to measure with microscope because of linked fingers
	Carollia perspicillata	4	13.09.2019	1	597436	5	1	40.23	measured with microscope; left arm
	Carollia perspicillata	5	17.09.2019	1	597466	3	1	40.23	measured with microscope; left arm
	Carollia perspicillata	6	17.09.2019	1	20075190	2	3	38.425	measured with microscope
	Carollia perspicillata	7	17.09.2019	1	20125436	2	1	41.279	measured with microscope
	Desmodus rotundus	8	17.09.2019	1	582270	2	1	55.65	measured with calliper
	Desmodus rotundus	9	17.09.2019	1	590416	2	1	59.84	measured with calliper
	Desmodus rotundus	10	17.09.2019	1	640419	2	1	57.67	measured with calliper
	Phyllostomus hastatus	11	17.09.2019	1	584113	2	1	87.14	measured with calliper
Mollosidae	*Tardarida brasiliensis*	12	17.09.2019	1	590263	1	1	40.656	measured with microscope
	Tardarida brasiliensis	13	17.09.2019	1	598450	2	1	43.38	measured with calliper

Table A10 Pelvic measurements of species from the family Pteropodidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Pteropodidae	*Cynopterus sphinx*	1	12.06.2019	1	39319	1	1	6.143	4.848	6.376	5.297	7.715	7.02	6.43	box 1. TL.
	Cynopterus sphinx	2	12.06.2019	1	21391	1	1	5.18	3.413	4.914	3.045	6.47	6.027	6.249	box 1. TL.; labelled with 47 g
	Cynopterus sphinx	3	12.06.2019	1	40394	2	1	7.332	4.985	7.086	8.451	8.529	7.908	7.831	box 2.TL.; left pubic bone broken
	Cynopterus sphinx	4	12.06.2019	1	63028	1	1	5.276	4.058	7.961	7.961	7.223	6.025	6.243	box 2.TL.
	Eidolon helvum	5	12.06.2019	1	41486	2	1	13.295	9.579	14.594	14.594	12.575	12.25	13.32	box Sudan; labelled with 314 g
	Eidolon helvum	6	12.06.2019	1	41511	2	1	9.853	8.009	8.754	10.117	10.446	10.436	12.054	box 41511; right iliopubic eminence broken
	Eidolon helvum	7	15.07.2019	1	41484	1	1	12.336	8.627	8.299	0	14.96	11.774	13.029	box 41484
	Eidolon helvum	8	15.07.2019	1	41485	2	1	12.172	9.386	14.017	14.017	13.668	11.869	14.388	box 41485
	Macroglossus minimus	9	17.09.2019	1	61440	2	1	3.606	3.16	3.963	3.963	4.703	4.646	4.683	from alcohol
	Pteropus giganteus	10	04.07.2019	1	63182	2	1	20.022	14.136	12.517	12.517	24.091	17.12	22.903	box o.FO.
	Pteropus giganteus	11	04.07.2019	1	67988	2	1	19.562	15.534	20.434	20.434	16.484	13.805	18.142	box o.FO. TG Schönbrunn
	Pteropus giganteus	12	04.07.2019	1	68554	1	1	24.704	20.258	18.462	0	27.076	17.521	21.845	box o.F. TG Schönbrunn

	Pteropus giganteus	13	04.07.2019	1	63183	2	1	21.524	17.932	23.851	23.851	17.572	14.67	19.029	box transparent o.FO.
	Pteropus vampyrus	14	13.09.2019	1	1615	2	1	20.484	17.94	23.902	23.902	20.128	17.408	22.327	
	Pteropus vampyrus	15	13.09.2019	1	957	1	1	23.754	20.541	13.97	0	21.583	16.709	20.572	
	Rousettus aegyptiacus	16	04.07.2019	1	20834	2	1	11.447	8.638	10.64	10.64	10.549	9.346	10.04	box transparent; labelled with 137g
	Rousettus aegyptiacus	17	04.07.2019	1	20839	2	1	9.658	7.028	10.337	10.337	9.671	9.083	9.395	box transparent; left iliopubic eminence slightly broken; labelled with 135g
	Rousettus aegyptiacus	18	04.07.2019	1	20835	2	1	9.119	6.498	9.316	9.316	10.725	9.323	10.182	box transparent; labelled with 138g
	Rousettus aegyptiacus	19	04.07.2019	1	20836	1	1	9.688	7.453	7.564	0	12.235	10.045	10.69	box transparent; ladled with 149g; pictures at "test" file
	Rousettus aegyptiacus	20	04.07.2019	1	20837	1	1	11.307	8.757	8.886	8.886	12.661	10.437	11.855	box transparent; labelled with 156g
	Rousettus aegyptiacus	21	04.07.2019	1	20840	1	1	10.953	8.299	9.057	0	13.111	10.812	11.004	box transparent; labelled with 163g

Table A11 Forearm measurements of species from the family Pteropodidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Pteropodidae	*Cynopterus sphinx*	1	12.06.2019	1	39319	1	1		no forearm
	Cynopterus sphinx	2	12.06.2019	1	21391	1	1		no forearm
	Cynopterus sphinx	3	12.06.2019	1	40394	2	1		no forearm
	Cynopterus sphinx	4	12.06.2019	1	63028	1	1	61.33	measured with calliper
	Eidolon helvum	5	12.06.2019	1	41486	2	1		both forearms broken
	Eidolon helvum	6	12.06.2019	1	41511	2	1	105.22	measured with calliper
	Eidolon helvum	7	15.07.2019	1	41484	1	1	115.71	measured with calliper
	Eidolon helvum	8	15.07.2019	1	41485	2	1	119.61	measured with calliper
	Macroglossus minimus	9	17.09.2019	1	61440	2	1	36.482	measured with microscope
	Pteropus giganteus	10	04.07.2019	1	63182	2	1	184.02	measured with calliper; calliper too short -> measured in two steps
	Pteropus giganteus	11	04.07.2019	1	67988	2	1	154.22	measured with calliper
	Pteropus giganteus	12	04.07.2019	1	68554	1	1	202.81	measured with calliper; calliper too short -> measured in two steps
	Pteropus giganteus	13	04.07.2019	1	63183	2	1		no forearm
	Pteropus vampyrus	14	13.09.2019	1	1615	2	1		no forearm
	Pteropus vampyrus	15	13.09.2019	1	957	1	1	178.97	measured with calliper; calliper too short -> measured in two steps
	Rousettus aegyptiacus	16	04.07.2019	1	20834	2	1	89.11	measured with calliper
	Rousettus aegyptiacus	17	04.07.2019	1	20839	2	1	88.38	measured with calliper
	Rousettus aegyptiacus	18	04.07.2019	1	20835	2	1	90.17	measured with calliper
	Rousettus aegyptiacus	19	04.07.2019	1	20836	1	1	87.2	measured with calliper
	Rousettus aegyptiacus	20	04.07.2019	1	20837	1	1	92.38	measured with calliper
	Rousettus aegyptiacus	21	04.07.2019	1	20840	1	1	90.77	measured with calliper

Table A12 Pelvic measurements of species from the families Rhinolophidae, Megadermatidae and Hipposideridae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Rhinolophidae	*Rhinolophus hipposideros*	1	15.07.2019	1	34319	2	1	4.337	3.443	3.205	1.947	2.687	3.891	3.523	box NÖ 1.TL.
	Rhinolophus hipposideros	2	15.07.2019	1	52276	1	1	3.451	2.53	2	0	2.083	3.811	3.573	box NÖ 2.TL.; both iliopubic eminences broken
	Rhinolophus hipposideros	3	15.07.2019	1	52235	2	1	4.517	3.142	3.028	1.777	2.501	3.844	3.4	box NÖ 2.TL.
	Rhinolophus hipposideros	4	15.07.2019	1	52737	1	1	3.87	2.599	2.365	0	2.463	3.866	3.219	box NÖ 2.TL.; right iliopubic eminence slightly broken
	Rhinolophus hipposideros	5	15.07.2019	1	52744	1	1	3.67	2.647	2.027	0.481	2.255	3.473	3.27	box NÖ 2.TL.
	Rhinolophus hipposideros	6	15.07.2019	1	52741	2	1	3.919	2.7	2.422	1.65	1.936	3.662	3.264	box NÖ 2.TL.
Megadermatidae	*Megaderma lyra*	7	16.07.2019	1	21395	3	1	8.383	5.91	6.393	5.135	5.938	5.906	4.968	box Indien; right pubic bone broken
Hipposideridae	*Hipposideros commersoni*	8	16.07.2019	1	32351	2	1	9.258	6.796	7.251	4.401	5.866	17,755; 10,368	14,077; 7,126	box Kenya 2.TL.; two different measurements of high and length

Table A13 Forearm measurements of species from the families Rhinolophidae, Megadermatidae and Hipposideridae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Rhinolophidae	*Rhinolophus hipposideros*	1	15.07.2019	1	34319	2	1	36.482	measured with microscope
	Rhinolophus hipposideros	2	15.07.2019	1	52276	1	1	35.569	measured with microscope
	Rhinolophus hipposideros	3	15.07.2019	1	52235	2	1	37.306	measured with microscope
	Rhinolophus hipposideros	4	15.07.2019	1	52737	1	1	35.127	measured with microscope
	Rhinolophus hipposideros	5	15.07.2019	1	52744	1	1	36.187	measured with microscope
	Rhinolophus hipposideros	6	15.07.2019	1	52741	2	1	34.509	measured with microscope
Megadermatidae	*Megaderma lyra*	7	16.07.2019	1	21395	3	1		no forearm
Hipposideridae	*Hipposideros commersoni*	8	16.07.2019	1	32351	2	1	95.71	measured with calliper

Table A14 Pelvic measurements of species from the families Emballonuridae and Natalidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Emballonuridae	*Taphozous longimanus*	1	18.09.2019	1	19120	2	1	5.824	4.35	4.392	1.792	6.608	5.758	5.36	from alcohol; right iliopubic eminence broken
	Taphozous melanopogon	2	18.09.2019	1	19123	4	1	6.23	3.99	3.722	0.616	5.484	5.396	5.181	from alcohol
Natalidae	*Nyctiellus lepidus*	3	18.09.2019	1	49604	3	1	2.006	1.74	1.422	0.419	2.297	2.682	2.446	from alcohol; left iliopubic eminence broken

Table A15 Forearm measurements of species from the families Emballonuridae and Natalidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Emballonuridae	*Taphozous longimanus*	1	18.09.2019	1	19120	2	1	58.98	measured with calliper
	Taphozous melanopogon	2	18.09.2019	1	19123	4	1	59.49	measured with calliper
Natalidae	*Nyctiellus lepidus*	3	18.09.2019	1	49604	4	1	26.373	measured with microscope

Table A16 Pelvic measurements of species from the families Mormoopidae, Noctilionidae and Nycteridae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Mormoopidae	*Pteronotus quadridens*	1	18.07.2019	1	49206	2	1	2.566	2.451	2.328	1.456	3.315	2.787	3.058	alcohol; both iliopubic eminence broken
	Pteronotus quadridens	2	19.07.2019	1	49217	2	1	1.645	2.223	1.921	1.067	3.367	2.935	3.32	alcohol
	Pteronotus quadridens	3	19.07.2019	1	49221	2	1	0.993	2.072	1.755	1.224	3.548	2.63	3.147	alcohol; left iliopubic eminence broken
Noctilionidae	*Noctilio albiventris*	4	19.07.2019	1	19597	2	1	5.808	4.547	4.87	4.87	5.844	4.496	5.871	alcohol
Nycteridae	*Nycteris thebaica*	5	19.07.2019	1	10322	2	1	3.836	4.116	2.114	0.851	4.014	4.857	3.771	alcohol

Table A17 Forearm measurements of species from the families Mormoopidae, Noctilionidae and Nycteridae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Mormoopidae	*Pteronotus quadridens*	1	18.07.2019	1	49206	2	1	34.097	measured with microscope
	Pteronotus quadridens	2	19.07.2019	1	49217	2	1	35.068	measured with microscope
	Pteronotus quadridens	3	19.07.2019	1	49221	2	1	35.746	measured with microscope
Noctilionidae	*Noctilio albiventris*	4	19.07.2019	1	19597	2	1	57.78	measured with calliper
Nycteridae	*Nycteris thebaica*	5	19.07.2019	1	10322	2	1	45.14	measured with calliper

Table A18 Pelvic measurements of species from the family Phyllostomidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Phyllostomidae	*Anoura geoffroyi*	1	18.09.2019	1	10836	5	1	4.725	3.118	2.24	0.602	4.419	4.098	3.714	from alcohol
	Artibeus lituratus	2	17.07.2019	1	28730	2	1	7.549	4.637	5.091	5.091	6.601	6.196	6.683	from alcohol
	Artibeus jamaicensis	3	18.09.2019	1	49596	2	1	6.457	5.133	4.683	4.683	5.589	5.569	5.575	from alcohol
	Carollia perspicillata	4	18.09.2019	1	73595	2	1	3.846	3.621	3.445	2.518	4.985	4.254	4.188	from alcohol
	Brachyphylla nana	5	16.07.2019	1	49404	2	1	6.059	4.625	4.227	4.227	5.687	5.496	5.687	from alcohol
	Brachyphylla nana	6	17.07.2019	1	49408	2	1	5.426	4.53	3.776	3.299	6.277	5.348	5.501	from alcohol
	Macrotus waterhousii	7	17.07.2019	1	49403	2	1	2.352	2.967	2.978	1.465	3.634	4.51	4.237	from alcohol; right iliopubic eminence broken
	Phyllostomus hastatus	8	18.09.2019	1	30744	2	1	6.743	5.247	5.798	4.286	8.507	7.427	8.512	from alcohol
	Platyrrhinus lineatus	9	18.07.2019	1	30760	2	1	4.579	3.094	3.17	3.17	4.566	4.688	4.988	from alcohol; left iliopubic eminence broken

Table A19 Forearm measurements of species from the family Phyllostomidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Phyllostomidae	*Anoura geoffroyi*	1	18.09.2019	1	10836	5	1	38.749	measured with microscope
	Artibeus lituratus	2	17.07.2019	1	28730	2	1	65.8	measured with calliper
	Artibeus jamaicensis	3	18.09.2019	1	49596	2	1	56.23	measured with calliper
	Carollia perspicillata	4	18.09.2019	1	73595	2	1	37.365	measured with microscope
	Brachyphylla nana	5	16.07.2019	1	49404	2	1	56.67	measured with calliper
	Brachyphylla nana	6	17.07.2019	1	49408	2	1	56.46	measured with calliper
	Macrotus waterhousii	7	17.07.2019	1	49403	2	1	50.72	measured with calliper
	Phyllostomus hastatus	8	18.09.2019	1	30744	2	1	83.99	measured with calliper
	Platyrrhinus lineatus	9	18.07.2019	1	30760	2	1	43.148	measured with microscope; measured left forearm

Table A20 Pelvic measurements of species from the families Molossidae and Miniopteridae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Molossidae	*Chaerephon bivittata*	1	10.05.2019	1	32508	3 (but labelled with m)	1	4.575	3.869	3.644	0	5.13	5.047	5.055	box Kenia
	Chaerephon bivittata	2	10.05.2019	1	32509	1	1	5.301	4.191	3.933	0	5.393	5.373	5.573	box Kenia
	Chaerephon plicatus	3	10.05.2019	1	42861	1	1	4.479	3.562	3.308	0	4.457	4.087	4.015	box Thailand
	Chaerephon plicatus	4	10.05.2019	1	29896	4	1	4.278	3.204	3.173	0	4.716	4.362	3.99	box Malaysia; right iliopubic eminence broken
	Chaerephon plicatus	5	18.09.2019	1	27415	2	1	5.213	3.481	3.544	1.714	4.261	4.374	4.42	from alcohol
	Molossus molossus	6	10.05.2019	1	27436	2	4	5.17	3.9	3.522	0	4.579	4.593	4.49	box Haiti; labelled with 12 g
	Molossus molossus	7	18.07.2019	1	22695	2	1	4.788	4.277	3.822	1.547	4.527	4.982	4.559	alcohol; pubic aperture might be closed; pelvis quite damaged -> estimations about outlet average and pubic aperture
	Mops condylurus	8	19.07.2019	1	64109	2	1	5.287	4.348	4.288	2.842	5.385	5.885	5.582	alcohol
	Mops demonstrator	9	10.05.2019	1	30788	2	1	4.45	3.879	4.192	2.759	5.019	5.116	4.796	box Sudan

	Mormopterus jugularis	10	10.05.2019	1	27421	2	1	3.506	3.086	3.058	2.48	3.492	3.918	3.759	box Madagaskar; left iliopubic eminence broken
	Otomops martiensseni	11	10.05.2019	1	32507	1	1	6.867	5.297	4.833	0	6.965	6.469	6.058	box Kenia
	Tadarida aegytiaca	12	10.05.2019	1	18166	1	1	4.658	3.746	3.982	0	3.751	4.603	4.561	box south Africa
Miniopteridae	*Miniopterus inflatus*	13	10.05.2019	1	32805	3 (but labelled with m)	1	3.808	3.654	3.286	0.87	5.15	4.071	4.209	box Kenia 2.TL.
	Miniopterus inflatus	14	10.05.2019	1	32807	1	1	3.357	3.179	2.9	0.69	5.132	4.168	4.151	box Kenia 2.TL.; left pubic bone broken
	Miniopterus schreibersii	15	10.05.2019	1	27905	1	1	3.523	3.653	2.995	0	5.435	4.543	4.505	box Marokko 1. TL:
	Miniopterus schreibersii	16	12.06.2019	1	27907	2	1	3.24	3.36	2.903	0.301	5.195	4.482	4.19	box Marokko 1: TL.; right iliopubic eminence broken
	Miniopterus schreibersii	17	12.06.2019	1	27908	2	1	3.675	3.89	3.019	1.32	5.326	4.429	4.157	box Marokko 1. TL: right pubic bone damaged
	Miniopterus schreibersii	18	12.06.2019	1	28765	2	1	3.924	3.992	3.128	1.456	5.881	4.471	4.483	box Ö; left iliopubic eminence slightly broken
	Miniopterus schreibersii	19	12.06.2019	1	28761	1	1	3.629	3.788	3.128	0	5.52	4.34	4.373	box Ö

Table A21 Forearm measurements of species from the families Molossidae and Miniopteridae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Molossidae	*Chaerephon bivittata*	1	10.05.2019	1	32508	3 (but labelled with m)	1	46.58	measured with callipers
	Chaerephon bivittata	2	10.05.2019	1	32509	1	1		no forearm
	Chaerephon plicatus	3	10.05.2019	1	42861	1	1	43.771	measured with microscope
	Chaerephon plicatus	4	10.05.2019	1	29896	4	1	40.131	measured with microscope
	Chaerephon plicatus	5	18.09.2019	1	27415	2	1	46.48	measured with calliper
	Molossus molossus	6	10.05.2019	1	27436	2	4	36.787	measured with microscope
	Molossus molossus	7	18.07.2019	1	22695	2	1	37.836	measured with microscope
	Mops condylurus	8	19.07.2019	1	64109	2	1	43.18	measured with microscope
	Mops demonstrator	9	10.05.2019	1	30788	2	1		no forearm
	Mormopterus jugularis	10	10.05.2019	1	27421	2	1		no forearm
	Otomops martiensseni	11	10.05.2019	1	32507	1	1	66.66	measured with callipers
	Tadarida aegytiaca	12	10.05.2019	1	18166	1	1	45.57	measured with callipers
Miniopteridae	*Miniopterus inflatus*	13	10.05.2019	1	32805	3 (but labelled with m)	1		no forearm
	Miniopterus inflatus	14	10.05.2019	1	32807	1	1		no forearm
	Miniopterus schreibersii	15	10.05.2019	1	27905	1	1	43.311	measured with microscope
	Miniopterus schreibersii	16	12.06.2019	1	27907	2	1	43.18	measured with microscope
	Miniopterus schreibersii	17	12.06.2019	1	27908	2	1	43.869	measured with microscope
	Miniopterus schreibersii	18	12.06.2019	1	28765	2	1	42.197	measured with microscope
	Miniopterus schreibersii	19	12.06.2019	1	28761	1	1	41.607	measured with microscope

Table A22 Pelvic measurements of species from the family Vespertilionidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number (NMW)	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Vespertilionidae	*Barbastella barbastellus*	1	22.03.2019	1	64095	1	1	3.987	3.758	3.264	0	4.568	3.915	3.626	box OÖ
	Barbastella barbastellus	2	22.03.2019	1	36101	1	1	4.152	3.822	3.048	0	4.6	3.773	3.816	box STMK
	Barbastella barbastellus	3	22.03.2019	1	53501	2	3	4.135	3.756	3.173	0.236	4.514	3.736	3.737	box STMK; left iliopubic eminence broken; symphysis slightly open
	Barbastella barbastellus	4	22.03.2019	1	56230	1	1	4.187	4.002	3.286	0	4.397	3.814	3.74	box STMK
	Barbastella barbastellus	5	22.03.2019	1	52218	2	1	4.339	3.98	3.609	1.868	4.479	3.725	3.97	box S
	Barbastella barbastellus	6	01.04.2019	1	52325	1	1	3.982	3.644	2.825	0	4.45	3.725	3.707	box NÖ
	Barbastella barbastellus	7	01.04.2019	1	52217	3	1	4.447	3.981	3.242	0.592	4.535	3.881	4.032	box NÖ
	Eptesicus furinalis	8	22.03.2019	1	66059	1	1	3.408	3.603	3.501	0	4.956	3.723	4.117	
	Eptesicus nilssonii	9	22.03.2019	1	53322	2	1	3.963	3.644	3.705	0.481	4.286	4.108	4.267	box NÖ
	Eptesicus nilssonii	10	25.03.2019	1	61556	2	1	3.533	3.66	3.542	1.678	4.289	3.997	3.96	box NÖ
	Eptesicus nilssonii	11	25.03.2019	1	30028	2	1	3.66	3.446	3.533	2.098	4.52	4.533	4.322	box STMK
	Eptesicus nilssonii	12	25.03.2019	1	50734	1	1	3.659	3.386	3.523	0	4.17	4.227	4.116	box STMK
	Eptesicus nilssonii	13	25.03.2019	1	52216	1	1	3.757	3.572	3.845	0	4.051	4.136	4.187	box STMK; symphysis slightly broken

	Eptesicus nilssonii	14	25.03.2019	1	53457	2	1	4.069	3.767	3.972	0.459	4.333	4.228	4.299	box STMK
	Eptesicus nilssonii	15	01.04.2019	1	61560	2	1	3.517	3.312	3.42	1.662	4.201	4.235	4.063	box STMK
	Eptesicus nilssonii	16	01.04.2019	1	36110	1	1	3.808	3.49	3.736	0	4.106	4.084	4.108	box OÖ
	Eptesicus nilssonii	17	03.04.2019	1	51447	1	1	3.88	3.449	3.31	0	4.283	4.113	3.957	box OÖ
	Eptesicus serotinus	18	01.04.2019	1	15711	2	1	5.247	5.278	4.727	1.875	5.163	5.277	5.655	box Jugos.; 21g
	Eptesicus serotinus	19	01.04.2019	1	57233	2	1	4.738	4.901	4.53	1.518	5.447	5.709	5.899	box OÖ; pelvis is asymmetric
	Eptesicus serotinus	20	01.04.2019	1	29406	2	1	4.754	4.322	3.947	0.546	4.944	4.913	5.28	box NÖ 1.TL.; right pubic slightly broken
	Eptesicus serotinus	21	01.04.2019	1	36103	1	1	4.842	4.769	4.818	0	5.308	5.15	5.311	box NÖ 1. TL.
	Eptesicus serotinus	22	01.04.2019	1	36104	1	1	5.004	4.799	4.773	0	5.893	5.729	5.936	box NÖ 1. TL.
	Eptesicus serotinus	23	01.04.2019	1	51018	2	1	5.926	5.474	5.474	0.614	5.924	5.7	6.068	box NÖ 1. TL.
	Eptesicus serotinus	24	01.04.2019	1	34316	3	1	5.939	5.721	4.838	3.223	5.54	5.657	5.806	box NÖ 1. TL.
	Eptesicus serotinus	25	01.04.2019	1	52805	1	1	5.46	5.255	4.311	0	5.383	5.437	5.111	box NÖ 2. TL.
	Eptesicus serotinus	26	01.04.2019	1	52817	1	1	5.107	5.059	4.879	0	5.322	5.339	5.33	box BGLD 1. TL.
	Eptesicus serotinus	27	01.04.2019	1	64042	1	1	5.05	4.936	4.642	0	5.766	5.817	5.796	box B 2. TL.
	Glauconyteris argentata	28	01.04.2019	1	32739	1	1	3.992	3.776	2.969	0	5.243	4.13	3.704	box Kenia 1.TL.
	Hypsugo savii	29	03.04.2019	1	43657	2	1	3.797	3.524	3.117	1.015	3.713	3.526	3.794	box KTN; left pubic slightly damaged -> depth measurements on right side
	Hypsugo savii	30	03.04.2019	1	66482	2	1	3.71	3.397	2.928	0.732	3.696	3.128	3.22	box Österr.; left iliopubic eminence broken

	Hypsugo savii	31	03.04.2019	1	nicht inv. KS 09/75	1	5	3.266	2.509	1.684	0.11	2.799	2.74	2.763	box Österr.; pelvis not linked to spine; pelvis got broken
	Myotis bechsteini	32	03.04.2019	1	52852	1	1	3.894	3.562	3.425	0	4.826	4.604	4.176	box OÖ
	Myotis bechsteini	33	03.04.2019	1	52329	2	1	3.521	3.122	3.255	1.065	4.481	4.311	4.112	box OÖ; right iliopubic eminence broken; pubic bones at aperture broken
	Myotis bechsteini	34	03.04.2019	1	66140	1	1	3.952	3.581	3.454	0	4.491	4.365	3.993	box NÖ 2.TL.
	Myotis bechsteini	35	03.04.2019	1	9290	1	1	4.008	3.383	2.624	0	4.542	4.305	3.727	box W,B; right iliopubic eminence broken
	Myotis bechsteini	36	03.04.2019	1	52225	2	1	3.695	3.337	3.03	1.535	4.429	4.06	3.906	box Ktn
	Myotis blythii	37	10.04.2019	1	23385	2	1	4.71	4.579	4.798	2.15	6.438	5.909	6.023	box Zypern
	Myotis blythii	38	10.04.2019	1	65181	1	1	4.721	4.83	4.589	0	6.185	5.876	5.668	box NÖ
	Myotis blythii	39	10.04.2019	1	61484	1	1	4.48	4.428	4.21	0	6.036	5.66	5.413	box NÖ
	Myotis blythii	40	10.04.2019	1	28000	2	1	4.887	4.737	4.478	1.843	6.062	5.654	5.454	box Marokko
	Myotis brandtii	41	10.04.2019	1	66519	1	1	3.123	2.979	2.774	0	3.915	3.639	3.292	box NÖ, W
	Myotis brandtii	42	10.04.2019	1	65241	3	1	3.079	3.055	3.089	0.703	3.844	3.515	3.519	box K, St
	Myotis brandtii	43	10.04.2019	1	30396	1	1	2.962	2.577	2.337	0	3.774	3.758	3.59	box V
	Myotis brandtii	44	10.04.2019	1	62674	2	1	3.266	2.903	2.747	1.193	4.016	3.422	3.224	box Slowak.
	Myotis capaccinii	45	10.04.2019	1	30343	1	1	3.484	2.82	2.888	0	4.974	3.912	3.617	box Slowenien, left iliopubic eminence slightly broken

	Myotis capaccinii	46	10.04.2019	1	15715	2	1	3.888	3.049	2.928	0	4.741	3.884	3.799	box Kroatien; iliopubic bone broken; labelled as female but symphysis closed
	Myotis daubentoni	47	10.04.2019	1	52344	2	1	3.275	2.794	2.938	0.41	4.642	3.925	3.718	box NÖ 1.TL.
	Myotis daubentoni	48	10.04.2019	1	52344	1	1	2.632	2.294	2.49	0	3.758	3.444	3.355	box NÖ 1.TL.; outlet is estimated
	Myotis daubentoni	49	10.04.2019	1	50981	1	1	3.173	3.002	2.835	0	4.561	3.876	3.682	box NÖ 1.TL.
	Myotis daubentoni	50	10.04.2019	1	51502	1	1	2.817	2.568	2.957	0	4.456	4.053	3.782	box NÖ 1.TL.
	Myotis daubentoni	51	10.04.2019	1	50977	2	1	3.204	2.999	3.327	0.952	4.852	4.072	3.97	box NÖ 1.TL.
	Myotis daubentoni	52	10.04.2019	1	34219	1	1	3.904	3.056	2.731	0	4.518	4.069	3.67	box NÖ 1.TL.
	Myotis daubentoni	53	10.04.2019	1	29048	1	1	3.063	2.535	2.955	0	4.499	3.872	3.656	box NÖ 1.TL.
	Myotis daubentoni	54	12.04.2019	1	29046	2	1	3.423	2.817	2.928	0.452	4.643	4.066	3.703	box Steiermark
	Myotis daubentoni	55	12.04.2019	1	30401	2	1	3.577	3.09	3.15	1.024	4.731	4.261	3.715	box Voralberg
	Myotis daubentoni	56	12.04.2019	1	29464	2	1	3.446	2.971	3.287	0.717	4.606	4.193	3.936	box Voralberg
	Myotis emaginatus	57	12.04.2019	1	57203	2	1	3.645	3.286	3.184	0.973	4.875	3.816	3.75	box OÖ
	Myotis emaginatus	58	12.04.2019	1	58149	2	1	4.5	3.767	3.777	2.303	4.668	3.598	3.648	box OÖ
	Myotis emaginatus	59	12.04.2019	1	58150	2	1	4.289	3.941	4.197	2.313	4.47	3.463	3.574	box OÖ
	Myotis emaginatus	60	12.04.2019	1	36982	2	1	3.275	2.815	2.974	0.982	4.485	3.787	3.762	box NÖ
	Myotis emaginatus	61	12.04.2019	1	61488	1	1	3.858	3.159	2.78	0	4.285	3.421	3.679	box NÖ

	Myotis emaginatus	62	12.04.2019	1	9117	2	1	3.44	2.835	3.009	0.768	4.403	3.639	3.71	box W; labelled with 8,2 g; too much tissue on the left side -> pubic length measured on the right side
	Myotis emaginatus	63	12.04.2019	1	52323	1	1	3.442	2.894	2.825	0	4.531	3.427	3.578	box ST
	Myotis emaginatus	64	12.04.2019	1	53486	1	3	3.991	3.288	3.21	0	4.29	3.445	3.731	box KTN
	Myotis emaginatus	65	12.04.2019	1	69932	1	1	3.269	2.957	3.006	1.464	4.426	4.008	3.692	
	Myotis myotis	66	12.04.2019	1	50723	2	1	4.104	3.941	3.449	0.542	5.829	5.778	5.6	box NÖ PB Gmünd
	Myotis myotis	67	25.04.2019	1	52631	2	1	5.545	5.315	5.72	3.29	6.737	5.998	5.929	box NÖ PB Korneuburg
	Myotis myotis	68	25.04.2019	1	52632	2	1	5.046	4.781	4.625	1.843	6.656	6.023	5.981	box NÖ PB Korneuburg, left iliopubic eminence broken
	Myotis myotis	69	25.04.2019	1	52630	2	1	5.095	4.998	4.938	1.831	6.417	5.881	5.527	box NÖ PB Korneuburg, left iliopubic eminence broken
	Myotis myotis	70	25.04.2019	1	52645	2	1	4.338	4.428	4.483	0.346	6.178	5.779	5.938	box NÖ PB Mödlingen
	Myotis myotis	71	25.04.2019	1	64061	1	1	5.12	5.03	4.658	0	6.664	6.159	5.743	box NÖ PB Mödlingen
	Myotis myotis	72	25.04.2019	1	64004	1	1	4.868	4.413	4.39	0	6.083	5.888	5.614	box BGLD PB Güssing 1. TL
	Myotis myotis	73	25.04.2019	1	25162	1	1	5.802	5.502	5.106	0	6.928	6.272	6.144	box NÖ PB Neunkirchen; labelled with 22,5g
	Myotis myotis	74	25.04.2019	1	64006	1	1	4.71	4.48	4.529	0	6.293	5.954	5.844	box B PB Jennersdorf
	Myotis myotis	75	25.04.2019	1	67021	1	1	5.468	4.926	4.432	0.169	6.421	5.898	5.849	box B PB Jennersdorf; left iliopubic eminence slightly broken

	Myotis mystacinus	76	25.04.2019	1	51012	2	1	3.303	3.115	3.279	1.447	3.905	3.254	2.956	box OÖ PB Steyr-Land 1.TL.; right iliopubic eminence slightly broken
	Myotis mystacinus	77	25.04.2019	1	52713	1	1	2.792	2.702	2.681	0	3.481	3.143	3.138	box OÖ PB Steyr-Land 1.TL.
	Myotis mystacinus	78	25.04.2019	1	58145	2	1	2.778	2.833	2.904	1.519	3.776	3.618	3.455	box OÖ PB Steyr-Land 1.TL.
	Myotis mystacinus	79	25.04.2019	1	58146	2	1	3.167	3.112	3.064	1.836	3.592	3.432	3.205	box OÖ PB Steyr-Land 1.TL.
	Myotis mystacinus	80	25.04.2019	1	65230	2	1	3.159	3.116	3.056	1.669	3.655	3.521	3.403	box NÖ PB Scheibbs
	Myotis mystacinus	81	25.04.2019	1	66471	1	1	2.035	2.131	2.07	0	3.195	3.111	3.085	box NÖ PB Scheibbs; right iliopubic eminence broken
	Myotis mystacinus	82	25.04.2019	1	52727	1	1	3.063	2.62	2.635	0	3.863	3.248	3.226	box Wien; right iliopubic eminence broken
	Myotis mystacinus	83	25.04.2019	1	66142	1	1	2.671	2.612	2.465	0	3.774	2.997	2.9	box NÖ PB Baden, Mödling; right iliopubic eminence broken
	Myotis nattereri	84	25.04.2019	1	52338	1	1	3.433	3.151	3.116	0	4.369	3.824	3.603	box OÖ 1. Teil
	Myotis nattereri	85	25.04.2019	1	69831	1	1	4.097	3.223	3.053	0	4.566	3.842	3.591	box OÖ 1. Teil; strange right iliopubic eminence
	Myotis nattereri	86	26.04.2019	1	61653	1	1	3.321	3.236	3.38	0	4.448	4.006	3.425	box OÖ 1. Teil
	Myotis nattereri	87	26.04.2019	1	57200	2	1	3.022	3.288	3.159	1.139	4.809	4.287	3.72	box OÖ 1. Teil
	Myotis nattereri	88	26.04.2019	1	71932	2	1	3.472	3.321	3.097	1.785	4.422	3.967	3.818	box OÖ 2. Teil
	Myotis nattereri	89	26.04.2019	1	66579	2	1	2.911	2.766	2.68	1.207	4.632	4.251	3.61	box NÖ 1. Teil
	Myotis nattereri	90	26.04.2019	1	15149	1	1	3.077	2.918	2.723	0	4.548	3.927	3.562	box NÖ 1. Teil

	Myotis nattereri	91	26.04.2019	1	69191	2	1	3.485	3.33	3.022	1.062	4.42	3.818	3.381	box NÖ 2. Teil; pubic bone at symphysis broken; lateral picture + measurements of the right side
	Neoromicia capensis	92	26.04.2019	1	18164	2	1	3.818	3.51	3.476	1.156	4.185	3.414	3.787	box Südafr.; labelled as Eptesicus capensis
	Neoromicia nanus	93	26.04.2019	1	32716	1	1	2.781	2.613	2.497	0	3.415	2.887	2.991	box Kenia; labelled with Pipistrellus nanus
	Neoromicia nanus	94	26.04.2019	1	32718	1	1	2.592	2.539	2.232	0	3.208	2.918	2.805	box Kenia; labelled with Pipistrellus nanus
	Nyctalus noctula	95	26.04.2019	1	42212	1	5	4.761	3.756	3.696	0	5.508	5.351	5.048	box Ungarn
	Nyctalus noctula	96	26.04.2019	1	72318	1	1	5.178	4.93	4.901	0	6.394	6.578	6.094	box BRD
	Nyctalus noctula	97	26.04.2019	1	70101	2	1	4.833	4.792	4.724	1.87	6.185	5.942	5.557	box o.F.
	Nyctalus noctula	98	26.04.2019	1	27528	1	1	5.157	4.774	4.786	0	5.953	5.893	5.713	box NÖ PB Krems/D. 1. TL.; labelled with 19g
	Nyctalus noctula	99	26.04.2019	1	12066	1	1	4.755	4.889	4.984	0	6.31	6.571	6.15	box NÖ PB Krems/D. 1. TL.; labelled with 23g
	Nyctalus noctula	100	26.04.2019	1	66945	2	1	4.753	4.63	4.26	1.024	6.5	6.198	5.589	box W 2. Bez.
	Nyctalus noctula	101	26.04.2019	1	66946	2	1	5.149	5.12	4.301	1.477	6.241	6.374	5.911	box W 2. Bez.
	Nyctalus noctula	102	26.04.2019	1	66947	2	1	5.515	5.208	4.974	2.004	6.237	5.865	5.452	box W 2. Bez.
	Pipistrellus kuhlii	103	26.04.2019	1	66528	1	1	2.494	2.684	2.882	0	3.621	3.178	3.399	box Österr.: B
	Pipistrellus kuhlii	104	26.04.2019	1	64081	1	1	2.868	2.944	2.966	0	3.704	3.157	3.396	box Österr.: B
	Pipistrellus kuhlii	105	03.05.2019	1	69867	2	1	3.51	3.322	3.014	0.334	4.052	3.79	3.787	box W
	Pipistrellus kuhlii	106	03.05.2019	1	69862	2	1	3.554	3.313	3.125	1.062	3.932	3.545	3.75	box W

	Pipistrellus kuhlii	107	03.05.2019	1	68354	1	1	3.253	3.071	2.944	0	3.675	3.217	3.373	box W; right iliopubic eminence broken
	Pipistrellus kuhlii	108	03.05.2019	1	66479	2	1	3.275	3.306	2.672	1.075	3.901	3.621	3.73	box W; pubic bone at symphysis damaged
	Pipistrellus kuhlii	109	03.05.2019	1	66916	1	1	3.411	3.205	3.053	0	4.277	3.642	3.744	box W
	Pipistrellus kuhlii	110	03.05.2019	1	43654	2	1	3.099	3.176	2.885	0.916	4.054	3.49	3.522	box KT
	Pipistrellus nathusii	110	03.05.2019	1	71821	1	1	2.562	3.008	2.865	0	4.457	4.193	3.653	box OÖ
	Pipistrellus nathusii	111	03.05.2019	1	52331	1	1	2.732	2.853	2.732	0	4.411	4.767	3.757	box OÖ
	Pipistrellus nathusii	112	03.05.2019	1	61506	1	1	2.881	3.114	2.993	0	4.555	4.24	3.614	box NÖ
	Pipistrellus nathusii	113	03.05.2019	1	64019	1	1	2.919	3.106	2.883	0	3.866	4.195	3.317	box NÖ
	Pipistrellus nathusii	114	03.05.2019	1	52749	2	1	2.83	2.955	2.687	0.366	4.125	4.033	4.046	box NÖ
	Pipistrellus nathusii	115	03.05.2019	1	52333	2	1	2.774	2.825	2.645	1.207	3.786	3.602	3.442	box NÖ
	Pipistrellus nathusii	116	03.05.2019	1	61735	2	1	3.437	3.41	3.401	1.116	4.019	3.694	3.565	box W 1. Teil
	Pipistrellus nathusii	117	03.05.2019	1	51131	2	1	3.134	3.168	2.903	0.848	3.856	3.642	3.542	box W 1. Teil
	Pipistrellus pipistrellus	117	03.05.2019	1	63017	1	1	2.729	2.502	2.452	0	3.637	2.935	2.908	box Griechenland
	Pipistrellus pipistrellus	118	03.05.2019	1	52797	2	1	2.747	2.681	2.328	1.11	3.532	3.307	3.436	box NÖ PB Amstetten
	Pipistrellus pipistrellus	119	03.05.2019	1	53382	1	1	2.448	2.593	2.631	0	3.642	3.015	3.222	box NÖ PB Amstetten
	Pipistrellus pipistrellus	120	08.05.2019	1	61498	2	1	3.134	2.7	2.065	0.747	3.555	3.379	3.595	box NÖ PB Zwettl 1.TL.; left iliopubic eminence broken; asymmetric pelvis
	Pipistrellus pipistrellus	121	08.05.2019	1	50907	1	1	2.985	2.852	2.51	0	3.737	3.244	3.337	box NÖ PB Zwettl 1.TL.

	Pipistrellus pipistrellus	122	08.05.2019	1	34303	2	1	2.619	2.627	2.355	0.699	3.758	3.309	3.506	box NÖ PB Zwettl 1.TL.
	Pipistrellus pipistrellus	123	03.05.2019	1	68935	1	1	2.396	2.531	2.384	0	3.578	3.328	3.234	box W 1. Teil
	Pipistrellus pipistrellus	124	06.05.2019	1	69857	2	1	2.667	2.55	2.33	0.385	3.761	3.368	3.238	box Wien 2. Teil
	Pipistrellus stenopterus	125	08.05.2019	1	40266	2	1	4.821	4.494	4.084	1.351	5.305	4.722	4.657	box N-Sumatra
	Pipistrellus stenopterus	126	08.05.2019	1	40268	2	1	5.21	4.217	3.419	1.177	5.213	4.282	4.298	box N-Sumatra
	Plecotus auritus	127	06.05.2019	1	55548	2	1	5.063	4.354	4.046	3.198	3.962	3.762	3.693	box Ktn 2.TL.
	Plecotus auritus	128	06.05.2019	1	50533	2	1	4.289	3.51	3.005	1.722	3.872	3.772	3.612	box Ktn 2.TL.
	Plecotus auritus	129	06.05.2019	1	50532	3	1	3.742	3.185	3.039	0.462	4.029	3.798	3.71	box Ktn 2.TL.
	Plecotus auritus	130	06.05.2019	1	50531	2	1	3.739	3.459	3.757	2.499	4.124	3.812	3.804	box Ktn 2.TL.
	Plecotus auritus	131	06.05.2019	1	50526	1	1	3.981	3.374	3.008	0	4.056	4.003	3.794	box Ktn 2.TL.
	Plecotus auritus	132	06.05.2019	1	50482	1	1	4.245	3.65	3.435	0	4.148	3.843	3.66	box OÖ 1.TL.
	Plecotus auritus	133	06.05.2019	1	50478	1	1	3.677	3.29	3.224	0	4.37	3.98	3.807	box OÖ 1.TL.
	Plecotus auritus	134	06.05.2019	1	43658	1	1	3.733	3.32	3.375	0	4.234	3.821	3.769	box Ktn 1.TL.
	Plecotus austriacus	135	06.05.2019	1	52235	2	1	3.974	3.86	3.8	2.831	4.101	3.94	3.809	box NÖ PB Horn; asymmetric pelvis
	Plecotus austriacus	136	06.05.2019	1	69312	1	1	3.8	3.324	3.245	0	4.164	3.956	3.627	box NÖ PB Horn
	Plecotus austriacus	137	06.05.2019	1	34243	1	1	3.777	3.382	3.39	0	4.454	4.08	3.995	box NÖ PB Horn
	Plecotus austriacus	138	06.05.2019	1	34248	1	1	3.75	3.433	3.202	0	4.458	3.864	3.736	box NÖ PB Horn
	Plecotus austriacus	139	06.05.2019	1	36129	1	1	3.831	3.438	3.081	0	4.414	3.911	3.68	box NÖ PB Horn

	Plecotus austriacus	140	06.05.2019	1	69326	2	1	3.45	3.45	3.179	1.818	4.324	4.027	3.829	box B PB Güssing 1. Teil
	Plecotus austriacus	141	06.05.2019	1	69304	2	4	3.89	3.356	3.019	0.165	4.197	3.769	3.82	box B PB Neusiedl/S.
	Plecotus austriacus	142	06.05.2019	1	52238	2	4	3.899	3.364	3.101	0.576	4.304	4.04	3.879	box B PB Neusiedl/S.
	Plecotus gaisleri	143	08.05.2019	1	30143	2	1	3.81	3.271	3.048	0.796	3.989	3.668	3.494	box Libyen
	Scotoecus hirundo	144	08.05.2019	1	32727	1	1	4.35	4.278	4.237	0	5.728	5.246	4.814	box Kenya
	Scotoecus hirundo	145	08.05.2019	1	32728	1	1	4.289	3.91	4.063	0	5.176	4.709	4.672	box Kenya
	Scotophilus dinganii	146	08.05.2019	1	32782	2	1	6.203	5.661	5.69	2.517	6.932	5.631	6.232	box Kenia, Südafrika
	Scotophilus kuhlii	147	08.05.2019	1	40402	1	1	4.8	4.78	4.35	0	6.472	5.296	5.821	box N-Sumatra
	Scotophilus kuhlii	148	08.05.2019	1	28486	1	1	6.142	4.79	4.596	0	6.707	5.534	5.854	box Java 2. TL.
	Scotophilus nigrita	149	08.05.2019	1	32793	2	1	6.757	6.271	6.437	3.071	6.905	5.622	6.184	box Kenya
	Scotophilus nigrita	150	08.05.2019	1	32794	2	1	6.817	5.89	5.697	3.011	6.548	5.658	5.879	box Kenya
	Vespertilio murinus	151	08.05.2019	1	69843	1	1	3.785	3.45	3.17	0	4.052	3.85	4.305	box OÖ
	Vespertilio murinus	152	08.05.2019	1	69847	1	1	3.425	3.373	3.151	0	4.444	4.071	4.48	box OÖ
	Vespertilio murinus	153	10.05.2019	1	69851	1	1	3.917	3.571	3.319	0	4.349	3.898	4.336	box OÖ
	Vespertilio murinus	154	10.05.2019	1	29396	2	1	3.808	3.337	3.031	0.338	4.527	4.006	4.373	box Wien 1. TL., left pubic bone broken at symphysis
	Vespertilio murinus	155	10.05.2019	1	29455	2	1	3.879	3.431	3.254	2.163	4.09	3.958	4.325	box Wien 1. TL.
	Vespertilio murinus	156	10.05.2019	1	66930	2	1	4.127	4.077	3.897	1.498	5.285	4.806	4.858	box W 3. TL.

Table A23 Forearm measurements of species from the family Vespertilionidae from the Mammal Collection of the Natural History Museum Vienna. All measurements are taken in millimetres.

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Right forearm length linear (mm)	Comments
Vespertilionidae	*Barbastella barbastellus*	1	22.03.2019	1	64095	1	1	37.607	measured with microscope
	Barbastella barbastellus	2	22.03.2019	1	36101	1	1	36.56	measured with microscope
	Barbastella barbastellus	3	22.03.2019	1	53501	2	3	38.133	measured with microscope; no right forearm -> used left one
	Barbastella barbastellus	4	22.03.2019	1	56230	1	1	36.06	measured with microscope
	Barbastella barbastellus	5	22.03.2019	1	52218	2	1	37.772	measured with microscope
	Barbastella barbastellus	6	01.04.2019	1	52325	1	1	37.181	measured with microscope
	Barbastella barbastellus	7	01.04.2019	1	52217	3	1	37.279	measured with microscope
	Eptesicus furinalis	8	22.03.2019	1	66059	1	1		no forearm
	Eptesicus nilssonii	9	22.03.2019	1	53322	2	1	39.279	measured with microscope
	Eptesicus nilssonii	10	25.03.2019	1	61556	2	1	38.197	measured with microscope
	Eptesicus nilssonii	11	25.03.2019	1	30028	2	1	39.115	measured with microscope
	Eptesicus nilssonii	12	25.03.2019	1	50734	1	1		no forearm
	Eptesicus nilssonii	13	25.03.2019	1	52216	1	1	39.873	measured with microscope
	Eptesicus nilssonii	14	25.03.2019	1	53457	2	1	37.41	measured with microscope
	Eptesicus nilssonii	15	01.04.2019	1	61560	2	1	36.525	measured with microscope
	Eptesicus nilssonii	16	01.04.2019	1	36110	1	1	37.542	measured with microscope
	Eptesicus nilssonii	17	03.04.2019	1	51447	1	1	39.443	measured with microscope
	Eptesicus serotinus	18	01.04.2019	1	15711	2	1		no forearm; with body mass
	Eptesicus serotinus	19	01.04.2019	1	57233	2	1	52.13	measured with callipers
	Eptesicus serotinus	20	01.04.2019	1	29406	2	1		no forearm
	Eptesicus serotinus	21	01.04.2019	1	36103	1	1	48.49	measured with callipers
	Eptesicus serotinus	22	01.04.2019	1	36104	1	1	51.02	measured with callipers

	Eptesicus serotinus	23	01.04.2019	1	51018	2	1	54.05	measured with callipers
	Eptesicus serotinus	24	01.04.2019	1	34316	3	1	50.57	measured with callipers
	Eptesicus serotinus	25	01.04.2019	1	52805	1	1	52.09	measured with callipers
	Eptesicus serotinus	26	01.04.2019	1	52817	1	1	49.25	measured with callipers
	Eptesicus serotinus	27	01.04.2019	1	64042	1	1	50.35	measured with callipers
	Glauconyteris argentata	28	01.04.2019	1	32739	1	1		no forearm
	Hypsugo savii	29	03.04.2019	1	43657	2	1	30.433	measured with microscope
	Hypsugo savii	30	03.04.2019	1	66482	2	1	33.869	measured with microscope
	Hypsugo savii	31	03.04.2019	1	nicht inv. KS 09/75	1	1	24.673	measured with microscope
	Myotis bechsteini	32	03.04.2019	1	52852	1	1	41.87	measured with microscope; right forearm broken -> used left one
	Myotis bechsteini	33	03.04.2019	1	52329	2	1	41.118	measured with microscope
	Myotis bechsteini	34	03.04.2019	1	66140	1	1	40.361	measured with microscope
	Myotis bechsteini	35	03.04.2019	1	9290	1	1	39.74	measured with microscope
	Myotis bechsteini	36	03.04.2019	1	52225	2	1	38.131	measured with microscope
	Myotis blythii	37	10.04.2019	1	23385	2	1	58.87	measured with callipers
	Myotis blythii	38	10.04.2019	1	65181	1	1	52.99	measured with callipers
	Myotis blythii	39	10.04.2019	1	61484	1	1	51.09	measured with callipers
	Myotis blythii	40	10.04.2019	1	28000	2	1	60.94	measured with callipers
	Myotis brandtii	41	10.04.2019	1	66519	1	1	33.125	measured with microscope
	Myotis brandtii	42	10.04.2019	1	65241	3	1	34.893	measured with microscope
	Myotis brandtii	43	10.04.2019	1	30396	1	1		no forearm
	Myotis brandtii	44	10.04.2019	1	62674	2	1	34.394	measured with microscope
	Myotis capaccinii	45	10.04.2019	1	30343	1	1	36.365	measured with microscope
	Myotis capaccinii	46	10.04.2019	1	15715	2	1		no forearm
	Myotis daubentoni	47	10.04.2019	1	52344	2	1	37.213	measured with microscope

	Myotis daubentoni	48	10.04.2019	1	52344	1	1		both forearms broken
	Myotis daubentoni	49	10.04.2019	1	50981	1	1	34.332	measured with microscope
	Myotis daubentoni	50	10.04.2019	1	51502	1	1	35.217	measured with microscope
	Myotis daubentoni	51	10.04.2019	1	50977	2	1	36.276	measured with microscope
	Myotis daubentoni	52	10.04.2019	1	34219	1	1	33.743	measured with microscope
	Myotis daubentoni	53	10.04.2019	1	29048	1	1	33.657	measured with microscope
	Myotis daubentoni	54	12.04.2019	1	29046	2	1		no forearm
	Myotis daubentoni	55	12.04.2019	1	30401	2	1		no forearm
	Myotis daubentoni	56	12.04.2019	1	29464	2	1		no forearm
	Myotis emaginatus	57	12.04.2019	1	57203	2	1	39.345	measured with microscope
	Myotis emaginatus	58	12.04.2019	1	58149	2	1	38.426	measured with microscope
	Myotis emaginatus	59	12.04.2019	1	58150	2	1	37.508	measured with microscope
	Myotis emaginatus	60	12.04.2019	1	36982	2	1	36.217	measured with microscope
	Myotis emaginatus	61	12.04.2019	1	61488	1	1	36.6	measured with microscope
	Myotis emaginatus	62	12.04.2019	1	9117	2	1		no forearm
	Myotis emaginatus	63	12.04.2019	1	52323	1	1	36.896	measured with microscope
	Myotis emaginatus	64	12.04.2019	1	53486	1	3	35.482	measured with microscope
	Myotis emaginatus	65	12.04.2019	1	69932	1	1	35.216	measured with microscope
	Myotis myotis	66	12.04.2019	1	50723	2	1	55.92	measured with callipers
	Myotis myotis	67	25.04.2019	1	52631	2	1	60.04	measured with callipers; right forearm broken -> used left one
	Myotis myotis	68	25.04.2019	1	52632	2	1	58.45	measured with callipers
	Myotis myotis	69	25.04.2019	1	52630	2	1	58.28	measured with callipers
	Myotis myotis	70	25.04.2019	1	52645	2	1	58.45	measured with callipers
	Myotis myotis	71	25.04.2019	1	64061	1	1	54.39	measured with callipers
	Myotis myotis	72	25.04.2019	1	64004	1	1	58.93	measured with callipers

	Myotis myotis	73	25.04.2019	1	25162	1	1	58.6	measured with callipers
	Myotis myotis	74	25.04.2019	1	64006	1	1	54.8	measured with callipers
	Myotis myotis	75	25.04.2019	1	67021	1	1	59.52	measured with callipers
	Myotis mystacinus	76	25.04.2019	1	51012	2	1	32.847	measured with microscope
	Myotis mystacinus	77	25.04.2019	1	52713	1	1	31.819	measured with microscope
	Myotis mystacinus	78	25.04.2019	1	52713	2	1	33.079	measured with microscope
	Myotis mystacinus	79	25.04.2019	1	58146	2	1	32.025	measured with microscope
	Myotis mystacinus	80	25.04.2019	1	65230	2	1	32.59	measured with microscope
	Myotis mystacinus	81	25.04.2019	1	66471	1	1	32.436	measured with microscope
	Myotis mystacinus	82	25.04.2019	1	52727	1	1	32.437	measured with microscope
	Myotis mystacinus	83	25.04.2019	1	66142	1	1	34.286	measured with microscope
	Myotis nattereri	84	25.04.2019	1	52338	1	1	38.22	measured with microscope
	Myotis nattereri	85	25.04.2019	1	69831	1	1	36.629	measured with microscope
	Myotis nattereri	86	26.04.2019	1	61653	1	1	39.044	measured with microscope
	Myotis nattereri	87	26.04.2019	1	57200	2	1	38.455	measured with microscope
	Myotis nattereri	88	26.04.2019	1	71932	2	1	37.63	measured with microscope
	Myotis nattereri	89	26.04.2019	1	66579	2	1	37.866	measured with microscope
	Myotis nattereri	90	26.04.2019	1	15149	1	1		no forearm
	Myotis nattereri	91	26.04.2019	1	69191	2	1	37.542	measured with microscope
	Neoromicia capensis	92	26.04.2019	1	18164	2	1		no forearm
	Neoromicia nanus	93	26.04.2019	1	32716	1	1		no forearm
	Neoromicia nanus	94	26.04.2019	1	32718	1	1		no forearm
	Nyctalus noctula	95	26.04.2019	1	42212	1	5	44.459	measured with microscope
	Nyctalus noctula	96	26.04.2019	1	72318	1	1		both forearms broken
	Nyctalus noctula	97	26.04.2019	1	70101	2	1	51.36	measured with callipers; right forearm broken -> used left one

	Nyctalus noctula	98	26.04.2019	1	27528	1	1	49.31	measured with callipers
	Nyctalus noctula	99	26.04.2019	1	12066	1	1	51.14	measured with callipers
	Nyctalus noctula	100	26.04.2019	1	66945	2	1	50.84	measured with callipers; right forearm broken -> used left one
	Nyctalus noctula	101	26.04.2019	1	66946	2	1	49.51	measured with callipers; right forearm broken -> used left one
	Nyctalus noctula	102	26.04.2019	1	66947	2	1	50.07	measured with callipers
	Pipistellus kuhlii	103	26.04.2019	1	66528	1	1	31.255	measured with microscope
	Pipistellus kuhlii	104	26.04.2019	1	64081	1	1	29.621	measured with microscope
	Pipistellus kuhlii	105	03.05.2019	1	69867	2	1	32.538	measured with microscope
	Pipistellus kuhlii	106	03.05.2019	1	69862	2	1	32.487	measured with microscope
	Pipistellus kuhlii	107	03.05.2019	1	68354	1	1	29.661	measured with microscope
	Pipistellus kuhlii	108	03.05.2019	1	66479	2	1	33.13	measured with microscope
	Pipistellus kuhlii	109	03.05.2019	1	66916	1	1	31.716	measured with microscope
	Pipistellus kuhlii	110	03.05.2019	1	43654	2	1	32.435	measured with microscope
	Pipistellus nathusii	110	03.05.2019	1	71821	1	1		no forearm
	Pipistellus nathusii	111	03.05.2019	1	52331	1	1	32.487	measured with microscope
	Pipistellus nathusii	112	03.05.2019	1	61506	1	1	29.428	measured with microscope
	Pipistellus nathusii	113	03.05.2019	1	64019	1	1	30.302	measured with microscope
	Pipistellus nathusii	114	03.05.2019	1	52749	2	1	32.127	measured with microscope; right forearm broken -> used left one
	Pipistellus nathusii	115	03.05.2019	1	52333	2	1	29.454	measured with microscope
	Pipistellus nathusii	116	03.05.2019	1	61735	2	1	30.354	measured with microscope
	Pipistellus nathusii	117	03.05.2019	1	51131	2	1	31.485	measured with microscope
	Pipistellus pipistellus	117	03.05.2019	1	63017	1	1	28.754	measured with microscope
	Pipistrellus pipistrellus	118	03.05.2019	1	52797	2	1	28.777	measured with microscope; right forearm broken -> used left one
	Pipistrellus pipistrellus	119	03.05.2019	1	53382	1	1	28.207	measured with microscope

	Pipistrellus pipistrellus	120	08.05.2019	1	61498	2	1	30.945	measured with microscope
	Pipistrellus pipistrellus	121	08.05.2019	1	50907	1	1	30.045	measured with microscope
	Pipistrellus pipistrellus	122	08.05.2019	1	34303	2	1	29.814	measured with microscope
	Pipistrellus pipistrellus	123	03.05.2019	1	68935	1	1	27.956	measured with microscope
	Pipistrellus pipistrellus	124	06.05.2019	1	69857	2	1	27.523	measured with microscope
	Pipistrellus stenopterus	125	08.05.2019	1	40266	2	1	36.57	measured with microscope
	Pipistrellus stenopterus	126	08.05.2019	1	40268	2	1	36.011	measured with microscope
	Plecotus auritus	125	06.05.2019	1	55548	2	1	37.336	measured with microscope
	Plecotus auritus	126	06.05.2019	1	50533	2	1	36.164	measured with microscope
	Plecotus auritus	127	06.05.2019	1	50532	3	1	36.918	measured with microscope
	Plecotus auritus	128	06.05.2019	1	50531	2	1	37.159	measured with microscope
	Plecotus auritus	129	06.05.2019	1	50526	1	1	36.217	measured with microscope
	Plecotus auritus	130	06.05.2019	1	50482	1	1	36.423	measured with microscope; only left forearm available
	Plecotus auritus	131	06.05.2019	1	50478	1	1	37.365	measured with microscope
	Plecotus auritus	132	06.05.2019	1	43658	1	1	36.923	measured with microscope
	Plecotus austriacus	133	06.05.2019	1	52235	2	1	36.865	measured with microscope
	Plecotus austriacus	134	06.05.2019	1	69312	1	1	35.981	measured with microscope
	Plecotus austriacus	135	06.05.2019	1	34243	1	1	36.482	measured with microscope
	Plecotus austriacus	136	06.05.2019	1	34248	1	1	36.835	measured with microscope
	Plecotus austriacus	137	06.05.2019	1	36129	1	1	37.246	measured with microscope
	Plecotus austriacus	138	06.05.2019	1	69326	2	1	37.63	measured with microscope
	Plecotus austriacus	139	06.05.2019	1	69304	2	4	36.482	measured with microscope
	Plecotus austriacus	140	06.05.2019	1	52238	2	4	37.424	measured with microscope
	Plecotus gaisleri	143	08.05.2019	1	30143	2	1	37.071	measured with microscope
	Scotoecus hirundo	144	08.05.2019	1	32727	1	1		no forearm
	Scotoecus hirundo	145	08.05.2019	1	32728	1	1		no forearm

	Scotophilus dinganii	146	08.05.2019	1	32782	2	1		no forearm
	Scotophilus kuhlii	147	08.05.2019	1	40402	1	1	46.97	measured with callipers
	Scotophilus kuhlii	148	08.05.2019	1	28486	1	1	50.45	measured with callipers
	Scotophilus nigrita	149	08.05.2019	1	32793	2	1		no forearm
	Scotophilus nigrita	150	08.05.2019	1	32794	2	1		no forearm
	Vespertilio murinus	151	08.05.2019	1	69843	1	1	38.985	measured with microscope
	Vespertilio murinus	152	08.05.2019	1	69847	1	1	41.344	measured with microscope
	Vespertilio murinus	153	10.05.2019	1	69851	1	1	42.951	measured with microscope; right forearm broken -> used left one
	Vespertilio murinus	154	10.05.2019	1	29396	2	1	41.738	measured with microscope; right forearm broken -> used left one
	Vespertilio murinus	155	10.05.2019	1	29455	2	1	39.771	measured with microscope; right forearm broken -> used left one
	Vespertilio murinus	156	10.05.2019	1	66930	2	1	43.705	measured with microscope; right forearm broken -> used left one

Table A24 Remeasurements of 5 Specimens whose first measurements were not accurate. All measurements are taken in millimetres. ant.-post.=anterior-posterior; Max.=maximum

Family	Species	Specimen no.	Date	Taxonomy (1 = correct, 2 = unsure, 3 = incorrect)	Inventory number	Sex (1=M, 2=F, 3=suspect F because open, 4= suspected male, 5=unknown)	Age (1=adult, 2=juvenile, 3=suspected adult, 4=suspected juvenile, 5=unknown)	Inlet (mm)	Max. pelvic width (mm)	Outlet average (inside, outside) (mm)	Pubic aperture (mm)	Depth of birth canal length (mm) (ant.-post.)	Birth canal hight (mm)	Birth canal hight 2 (mm)	Comment
Miniopteridae	*Miniopterus inflatus*	1	24.10.2019	1	NMW 32805	2	1	3.874	3.624	3.276	0.661	5.233	4.114	4.218	box Kenia 2. Teil
Molossidae	*Chaerophon plicatus*	1	24.10.2019	1	NMW 42860	2	1	/	/	/	/	4.612	4.23	4.111	Pelvis to broken to measure it frontal, only lateral measurements possible
	Tardarida brasiliensis	1	24.10.2019	1	598450	2	1	4.311	3.321	3.115	2.839	3.995	3.957	3.971	Stockholm sample
Phyllostomidae	*Desmodus rotundus*	1	24.10.2019	1	582270	2	1	2.517	2.481	2.994	0.421	5.063	5.202	5.891	Stockholm sample
Vespertilionidae	*Myotis capaccinii*	1	24.10.2019	1	NMW 15715	2	5	3.899	3.002	2.887	0	4.725	3.978	3.87	box Kroatien; iliopubic bone broken; labelled as female but symphysis closed