On bird-like mating and penile diversity in bats

Ivan Horáček
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my first encounter with topic of

bird-like mating in bats:

multiple reports in common newspapers and web media

Current Biology
Magazine
CellPress

excellent observations, perfect documentation →the most detailed record on bat mating behavior

… but conclusions

Correspondence

Mating without intromission in a bat

Nicolas J. Fasel[1,*], Jan Jeucken[2], Kseniia Kravchenko[1,3], Marcus Fritze[4,5,6], Ireneusz Ruczyński[7], Ewa Komar[7], Marharyta Moiseienko[8], Alona Shulenko[3], Anton Vlaschenko[3,9,10], Philippe Christe[1], Olivier Glaizot[1,11], and Susanne Holtze[12,*]

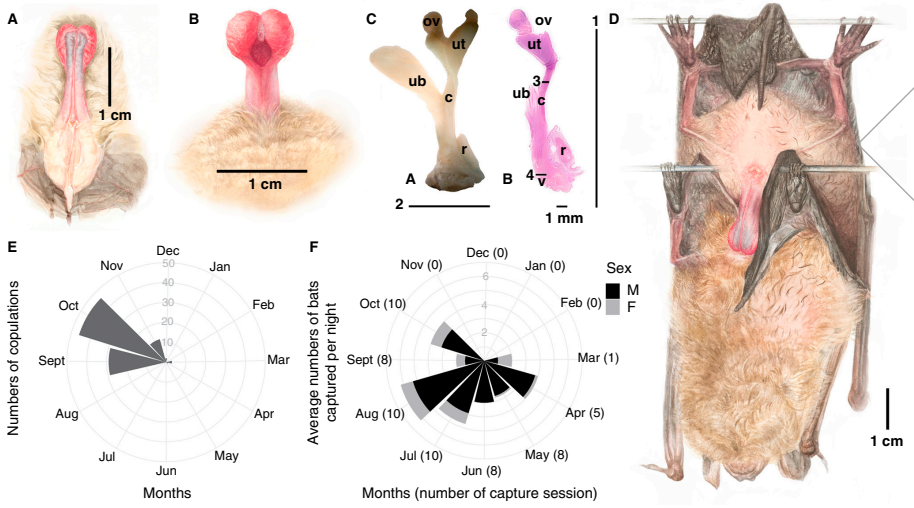
Copulatory behaviours stand as cornerstones of sexual selection, yet they remain mysterious in many species. Because of their nocturnal and elusive lifestyle, the copulatory behaviours of bats have been mostly overlooked[1]. Several aspects of bat reproduction differ from other mammals (e.g. prolonged sperm storage[2], delayed development[3]). Here, we show that in serotine bats (*Eptesicus serotinus*) the penis is used as a 'copulatory arm' rather than an intromittent organ, revealing a novel copulatory behaviour in mammals.

In the serotine bat, we observed a disproportionately large penis characterized by a heart-shaped terminal swelling. The organ constituted approximately 22% of the animal's head–body length during erection. With the erect organ seven times longer and wider than the vagina, its possible function becomes a perplexing question. Indeed, intromission might not be feasible. Instead, the motile and erect penis may be used to pass the protective tail membrane of the female to reach the vulva. However, under such conditions, the penis could not penetrate the vagina, resulting in 'contact mating' as the only option. This copulatory pattern is common in birds ('cloacal kiss'), but remains undocumented in mammals[4]. The hollow structure situated on the dorsal side of the erect penis (Figure 1B). In females, the cervix is unusually long and no more vocalisation was detected. Following copulation, the fur on the female's abdomen appeared wet, indicating the presence of semen. In the little brown bat (*Myotis lucifugus*, Brock Fenton, personal communication) and the common noctule bat (*Nyctalus noctula*, M.F., personal communication), abundant seminal fluid was found around the vulva and lower abdomen. It should be noted that the presence of ejaculation in *E. serotinus* has not been demonstrated. A vaginal swab that tests positive for sperm would still be required to prove it.

Half of the recorded copulations lasted for less than 53.0 min, but the longest event extended to 12.7 hours. No intromission was observed at any point. In addition, the erectile tissues of the penis were enlarged before the contact with the vulva and formed a shape unsuitable for intromission. The shape and the relatively small size (~1.2 mm) of the penis bone (baculum) in this species[6] suggest that it does not play any specific role in a potential intromission. The baculum of *E. serotinus* may serve to protect the urethra from compression by the erectile tissues during erection as suggested for *Eptesicus furinalis*[7].

To a degree, the female could employ the tail membrane to avoid copulation. Consequently, *E. serotinus*'s long penis might serve as a 'copulatory arm' to bypass the membrane of the female. The hollow structure observed on the dorsal side of the erect penis might serve as a suction cup and support the maintenance of the copulatory contact. Therefore, the penis' size and shape and [illegible] known to visit swarming sites, where mating events have been suggested in many bat species[10]. Data collected over twenty years of capture revealed that the peak of activity in *E. serotinus* occurs in July and August around abandoned mines (Figure 1F), similar to what was previously reported[10]. Thus, summer activity around subterranean sites occurs earlier than the peak of copulations. These gatherings might serve purposes beyond mating (e.g. information transfer or foraging).

With the caveat that sperm transfer occurs during the recorded putative copulatory events, this study reveals a novel copulatory pattern in mammals. Further investigation should focus on the role played by pre- and post-copulatory female choice as well as male competition in the evolution of this prolonged and particular mating behaviour.



Eptesicus serotinus

the primary source paper

Figure 1. Mating behaviour of *Eptesicus serotinus* does not imply intromission and summer activity around subterranean sites does not coincide with the peak of copulations.

(A) Ventral and (B) dorsal views of the erect penis. (C) Scaled digital microscopic photographs of *E. serotinus* female genital tract: (A) a formalin-fixed and (B) a HE-stained histology slide of a female genital tract. c = cervix, ov = ovary, r = rectum, ub = urinary bladder, ut = uterine horn, v = vagina. The female died on the 14th of May 2015 and was not pregnant. The scale in the lower right corner accounts for both images. [1] Length of the erect penis shaft (16.4 mm). [2] Width of the erect penis terminal swelling (7.5 mm). [3] Outer diameter of the cervix (0.7 mm) and [4] vagina (1.1 mm). (D) Copulation of an *Eptesicus serotinus* pair. The male, above on the drawing, uses its erect penis to pass by the uropatagium of the female, below on the drawing. The terminal swelling of the erect penis is firmly pressed against the vulva, without vaginal intromission. (E) Numbers of copulations merged by month. (F) Average number of bats captured at underground site per night. The numbers of capture events between 2001 and 2022 occurring during the respective months are indicated in brackets.

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SUPPLEMENTAL INFORMATION

Supplemental information including one figure, experimental procedures, acknowledgements, author contributions, Declaration of interests, Inclusion and diversity statement, and one video can be found with this article online at https://doi.org/10.1016/j.cub.2023.09.054.

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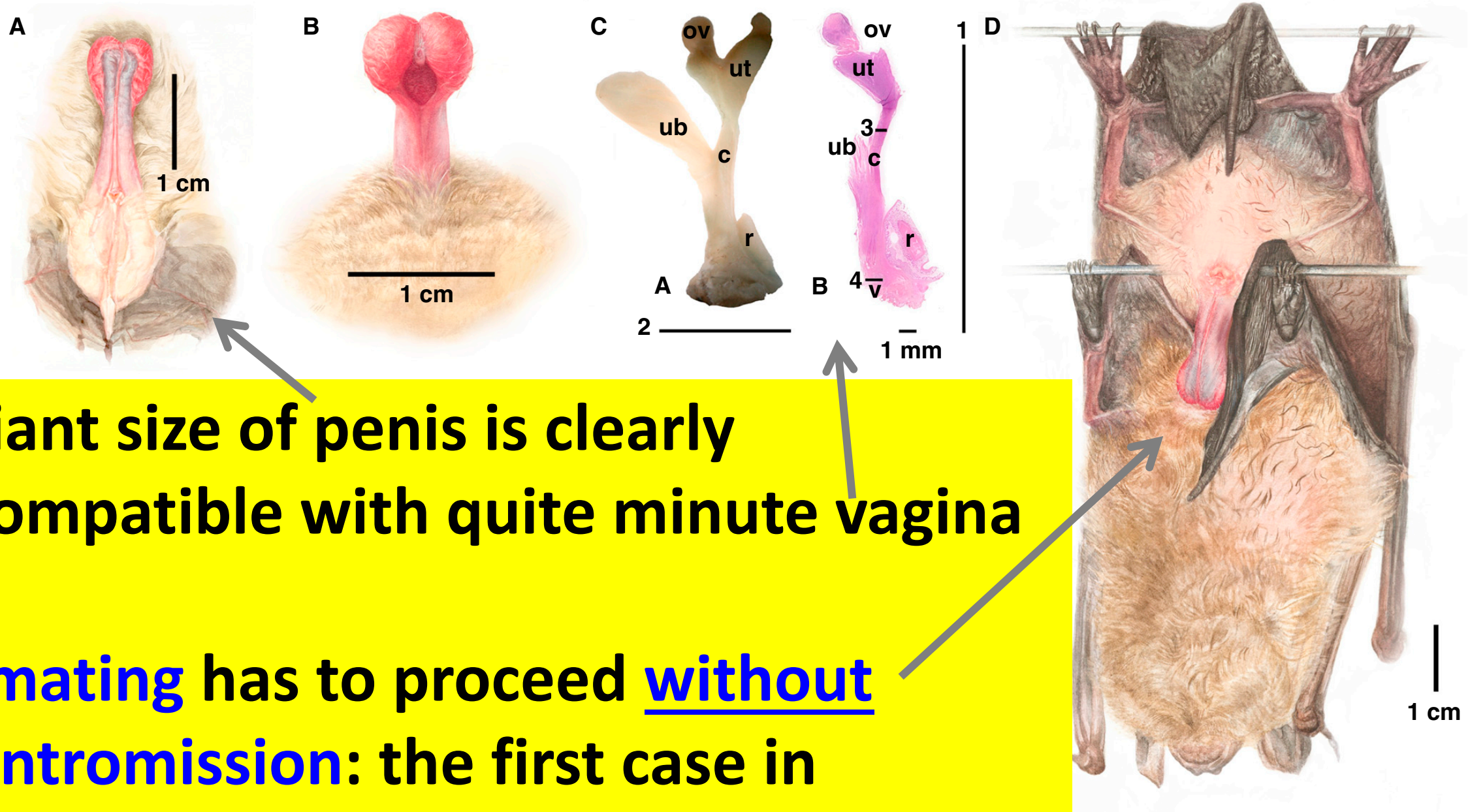

* giant size of penis is clearly incompatible with quite minute vagina

→ mating has to proceed without intromission: the first case in mammals !

Extremelly attractive issue →

an explosion of secondary references, enthusiastic comments and public interest

Nizozemský důchodce pomohl rozšifrovat záhadu obřího netopýřího penisu

ČTK/AFP

24. 11. 2023, 11:13 · Haag/Lausanne

Záhadu nepřiměřeně velkého penisu jednoho druhu netopýra se podařilo vyřešit zásluhou pozorování nizozemského penzisty. Penzistovo pozorování umožnilo týmu evropských výzkumníků

Nature:
an ultimate reference on indisputable verities!

MATING WITHOUT PENETRATION: BAT SEX IS MORE LIKE BIRD SEX

A European bat has been captured on film engaging in what seems to be an unusual reproductive strategy.

By Gayathri Vaidyanathan

Scientists have filmed what seem to be the first known instances of non-penetrative reproductive sex in mammals, in bats living in a church attic in the Netherlands and at a Ukrainian bat-rehabilitation centre. They wrote about their discovery on 20 November (N. J. Fasel *et al. Curr. Biol.* **33**, R1182–R1183; 2023).

In most mammals — the group that includes bats and humans — fertilization of eggs happens internally and gestation also takes place internally. Males are thought to have evolved penises to deliver sperm close to the eggs during sex.

Other animals use alternative methods of reproduction. For example, songbirds mate by means of a specialized opening called the cloaca, which is also used for excreting waste. Sperm is transferred from the male birds to the females when they touch their cloacas together in a 'cloacal kiss'.

"I am not aware of a mammalian species that transfers sperm" without penetration, says Mihaela Pavlíčev, an evolutionary biologist at the University of Vienna, "so this report describes a unique characteristic".

The male serotine bat (*Eptesicus serotinus*) has a penis that, when erect, is around 22% of its body length.

JOEL SARTORE/PHOTO ARK VIA NATUREPL

The study began when Nicolas Fasel, an evolutionary biologist at the University of Lausanne in Switzerland, and his colleagues noticed that the serotine bat (*Eptesicus serotinus*) has a rather large and unusual penis. When erect, it is 22% of the bat's head–body length and has a bulbous, heart-shaped tip. "We were thinking it would be really difficult for it to enter anything," he says.

"He nearly trashed an e-mail with the subject line 'Eptesicus penis' as spam before reconsidering."

The scientists would have left it at that, if not for serendipity. One day, Fasel received an e-mail with the subject line "Eptesicus penis" and a film attached. He nearly trashed it as spam before reconsidering, given the Latin species name. The e-mail was from Jan Jeucken, a bat enthusiast who is closely monitoring a population of bats that live in a church attic near his house in the Netherlands. Jeucken had made videos of bats having sex in the church from an angle that made the entire act visible. It's rare to see bat sex in the wild, let alone from directly underneath. The authors analysed 93 putative mating events that took place in this church attic, and 4 further instances at a bat-rehabilitation centre in Ukraine.

During sex, the male grasps the back of the female and bites the nape of her neck, presumably to hold on. Then he moves his erect penis around the female's tail membrane, searching for the vulva. Once this has been located, the male stays still, with the penis held firmly against the vulva. There is no penetration, but it is likely that the sperm find their way into the vagina. The longest sex act continued for 12.7 hours, but half of the recorded copulations lasted for 53 minutes or less. After mating, the fur on the female's belly appeared wet, which the researchers suggested indicates the presence of semen.

The scientists did not sample the females' wet fur to confirm whether semen was present. But Pavlíčev says that despite this, the evidence strongly suggests that the scientists' interpretation of the behaviour is correct.

A Dutch senior pensioner resolved a mystery of giant bat penis

Bird-like mating in bats

Nizozemský důchodce pomohl rozšifrovat záhadu obřího netopýřího penisu

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Záhadu nepřiměřeně velkého penisu jednoho druhu netopýra se podařilo vyřešit zásluhou pozorování nizozemského penzisty. Penzistovo pozorování umožnilo týmu evropských výzkumníků dospět k závěru, že dotyčný druh netopýra, který je rozšířen i v

... some Czech senior pensioners were shocked

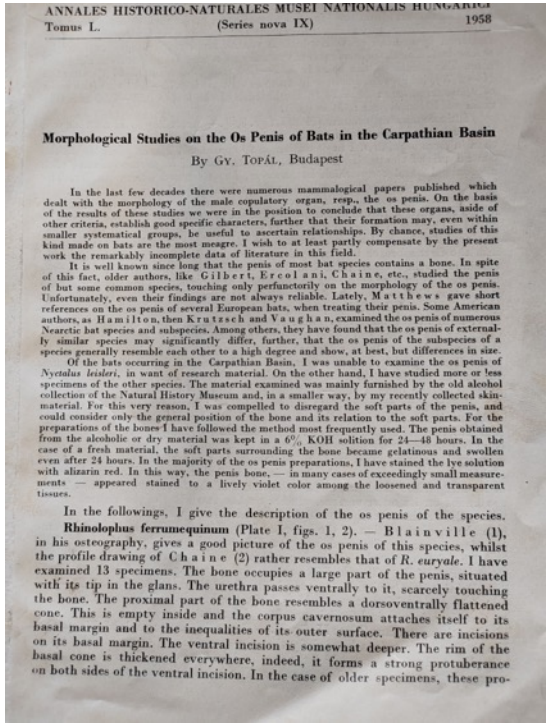
... at least those who spent years in study of bat mating biology, and topics of bat penial morphology

all normal mammals do not penetrate the delicate female's interior by a dirty hairy penis body but only by its part which is for that purpose specially designed – the *glans penis*

... hard to believe that bats make a difference

All bat clades possess glans penis,

equiped (almost in all) with baculum, which morphology is traditionally kept as important diagnostic character of particular clades.



ANNALES HISTORICO-NATURALES MUSEI NATIONALIS HUNGARICI
Tomus L. (Series nova IX) 1958

Morphological Studies on the Os Penis of Bats in the Carpathian Basin

By Gy. Topál, Budapest

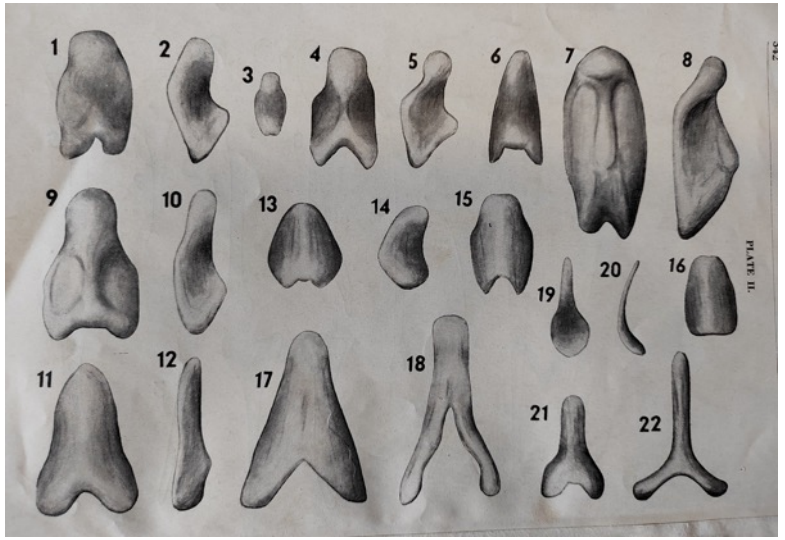
In the last few decades there were numerous mammalogical papers published which dealt with the morphology of the male copulatory organ, resp., the os penis. On the basis of the results of these studies we were in the position to conclude that these organs, aside of other criteria, establish good specific characters, further that their formation may, even within smaller systematical groups, be useful to ascertain relationships. By chance, studies of this kind made on bats are the most meagre. I wish to at least partly compensate by the present work the remarkably incomplete data of literature in this field.

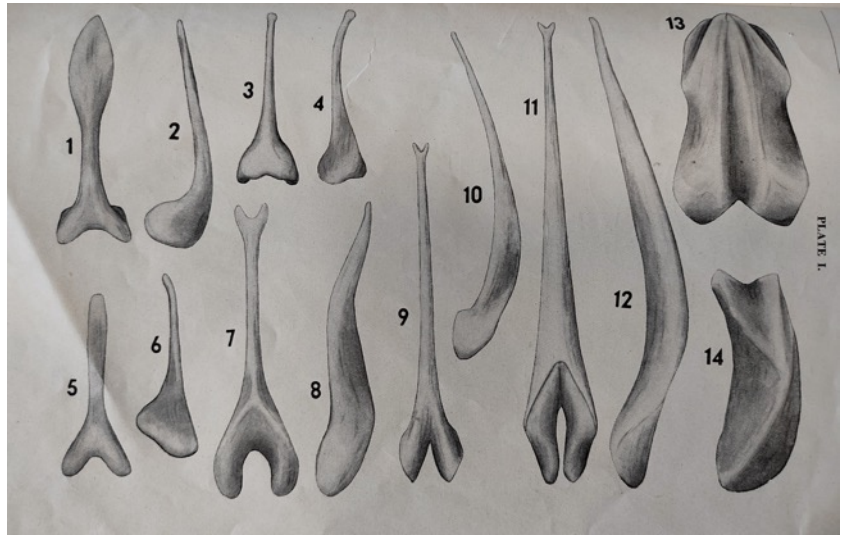
It is well known since long that the penis of most bat species contains a bone. In spite of this fact, older authors, like Gilbert, Ercolani, Chaine, etc., studied the penis of but some common species, touching only perfunctorily on the morphology of the os penis. Unfortunately, even their findings are not always reliable. Lately, Matthews gave short references on the os penis of several European bats, when treating their penis. Some American authors, as Hamilton, then Krutzsch and Vaughan, examined the os penis of numerous Nearctic bat species and subspecies. Among others, they have found that the os penis of externally similar species may significantly differ, further, that the os penis of the subspecies of a species generally resemble each other to a high degree and show, at best, but differences in size.

Of the bats occurring in the Carpathian Basin, I was unable to examine the os penis of *Nyctalus leisleri*, in want of research material. On the other hand, I have studied more or less specimens of the other species. The material examined was mainly furnished by the old alcohol collection of the Natural History Museum and, in a smaller way, by my recently collected skin-material. For this very reason, I was compelled to disregard the soft parts of the penis, and could consider only the general position of the bone and its relation to the soft parts. For the preparations of the bones I have followed the method most frequently used. The penis obtained from the alcoholic or dry material was kept in a 6% KOH solition for 24—48 hours. In the case of a fresh material, the soft parts surrounding the bone became gelatinous and swollen even after 24 hours. In the majority of the os penis preparations, I have stained the lye solution with alizarin red. In this way, the penis bone, — in many cases of exceedingly small measurements — appeared stained to a lively violet color among the loosened and transparent tissues.

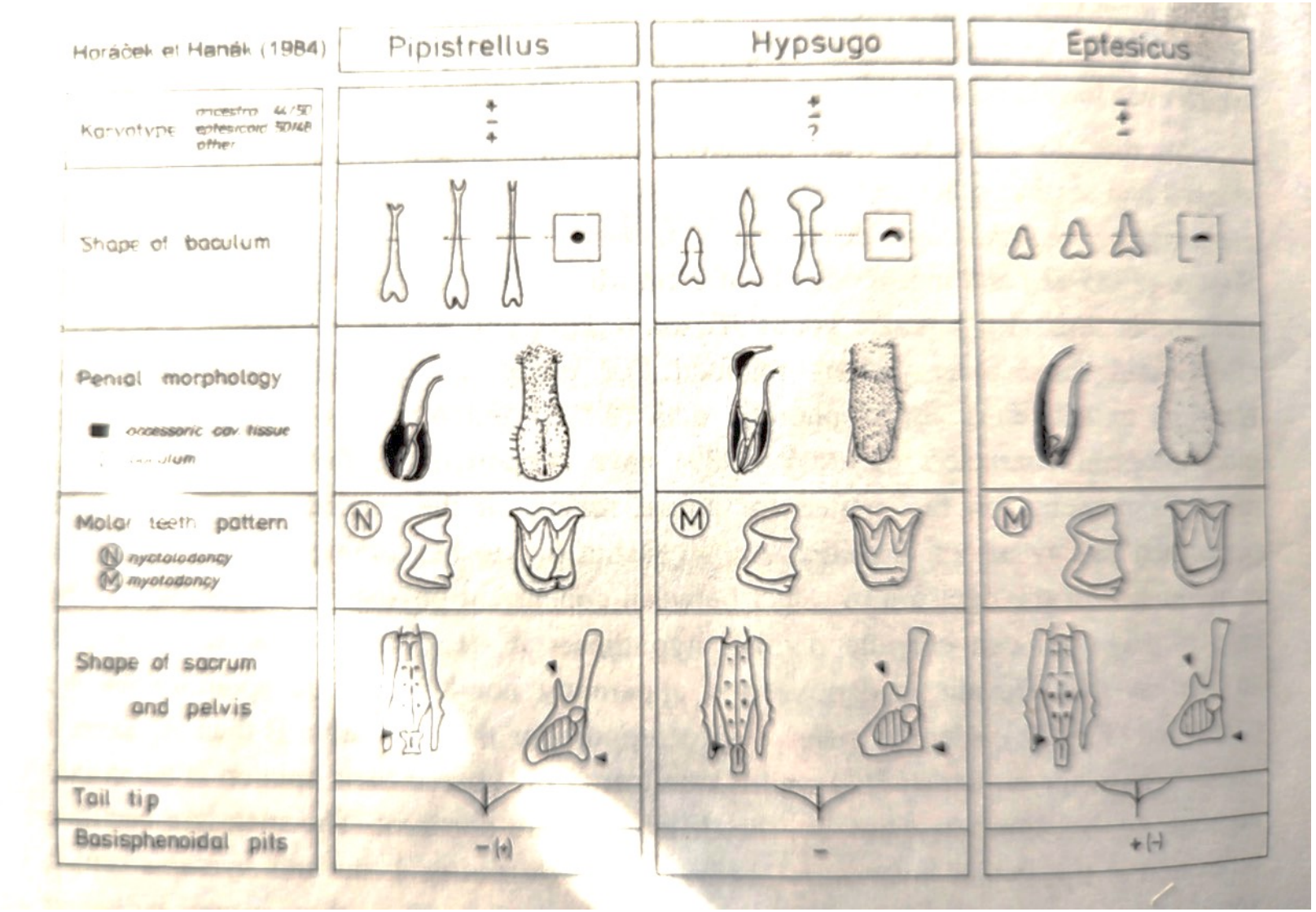
In the followings, I give the description of the os penis of the species.

Rhinolophus ferrumequinum (Plate I, figs. 1, 2). — Blainville (1), in his osteography, gives a good picture of the os penis of this species, whilst the profile drawing of Chaine (2) rather resembles that of *R. euryale*. I have examined 13 specimens. The bone occupies a large part of the penis, situated with its tip in the glans. The urethra passes ventrally to it, scarcely touching the bone. The proximal part of the bone resembles a dorsoventrally flattened cone. This is empty inside and the corpus cavernosum attaches itself to its basal margin and to the inequalities of its outer surface. There are incisions on its basal margin. The ventral incision is somewhat deeper. The rim of the basal cone is thickened everywhere, indeed, it forms a strong protuberance on both sides of the ventral incision. In the case of older specimens, these pro-



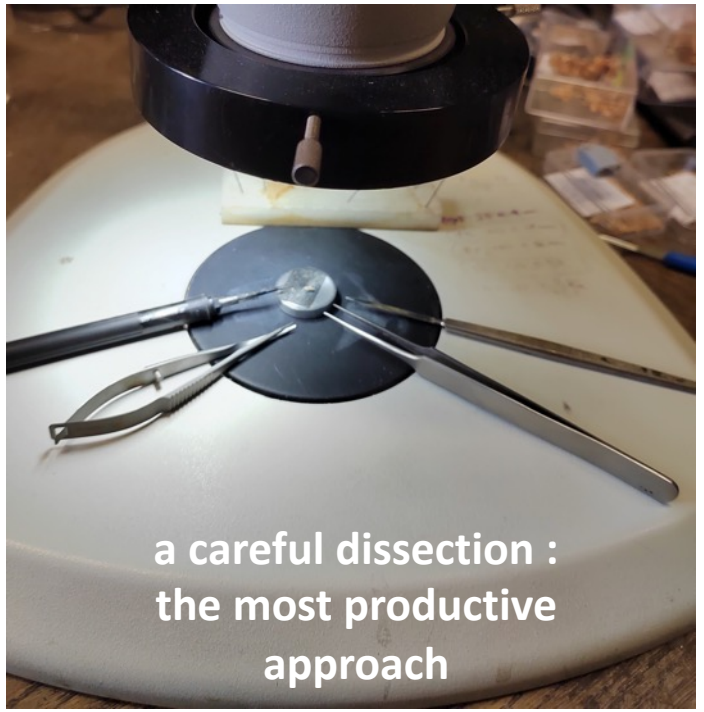


Topál (1958) – a pioneering paper on baculum diversity – one of many further studies on that topic



Horáček & Hanák (1984)

70/80': ..do soft tissues of penis (dissolved by traditional baculum preparation) provide any comparative information?



80‘: **penises of about 80 spp. dissected**

→ In all bats the penis includes:

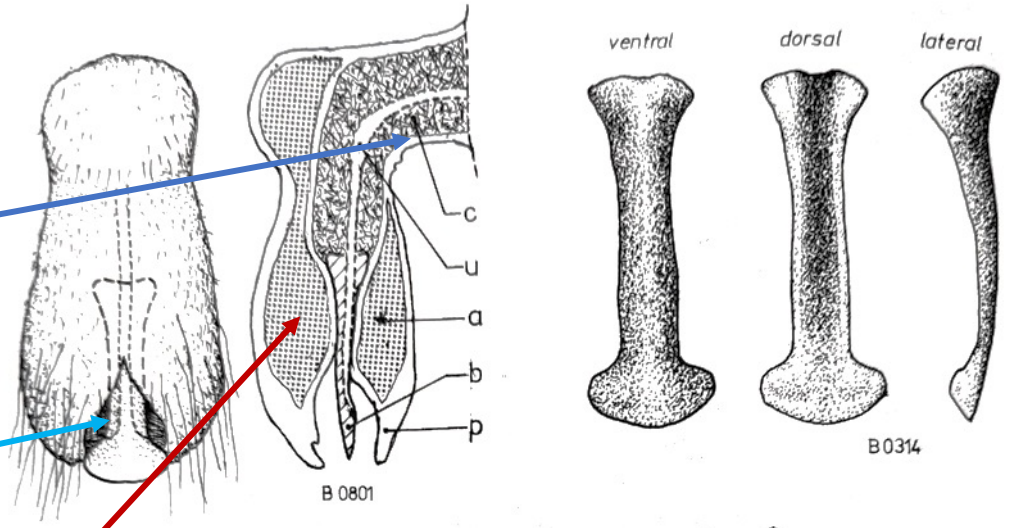
3 different types of erectile tissues :

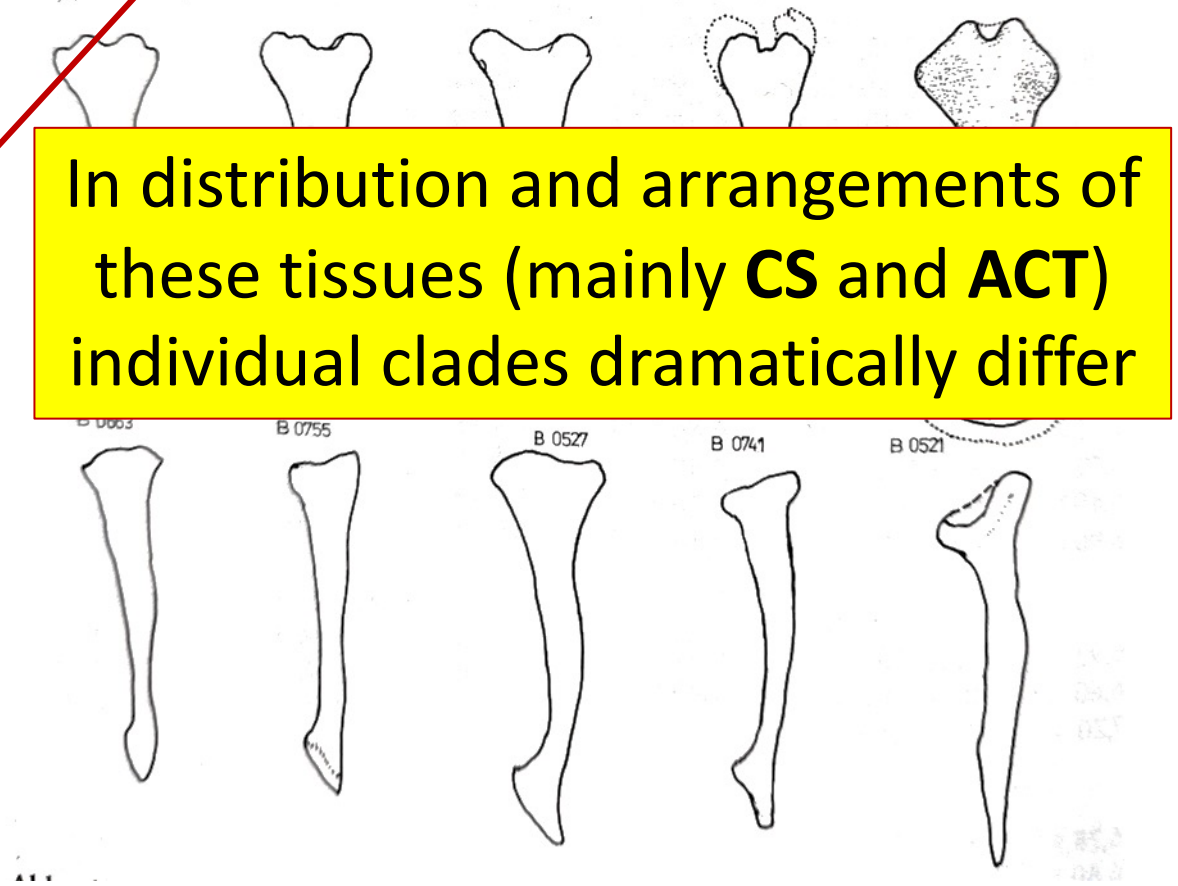
(CC) Corpora cavernosa
– central inner cone of the penis

(CS) Corpora spongiosa
along urethra nozzle and baculum in *glans penis* (disposed to *copulation lock*)

(ACT) Accessoric cavernose tissue
– in *praeputium and *subsurface layer of penis body

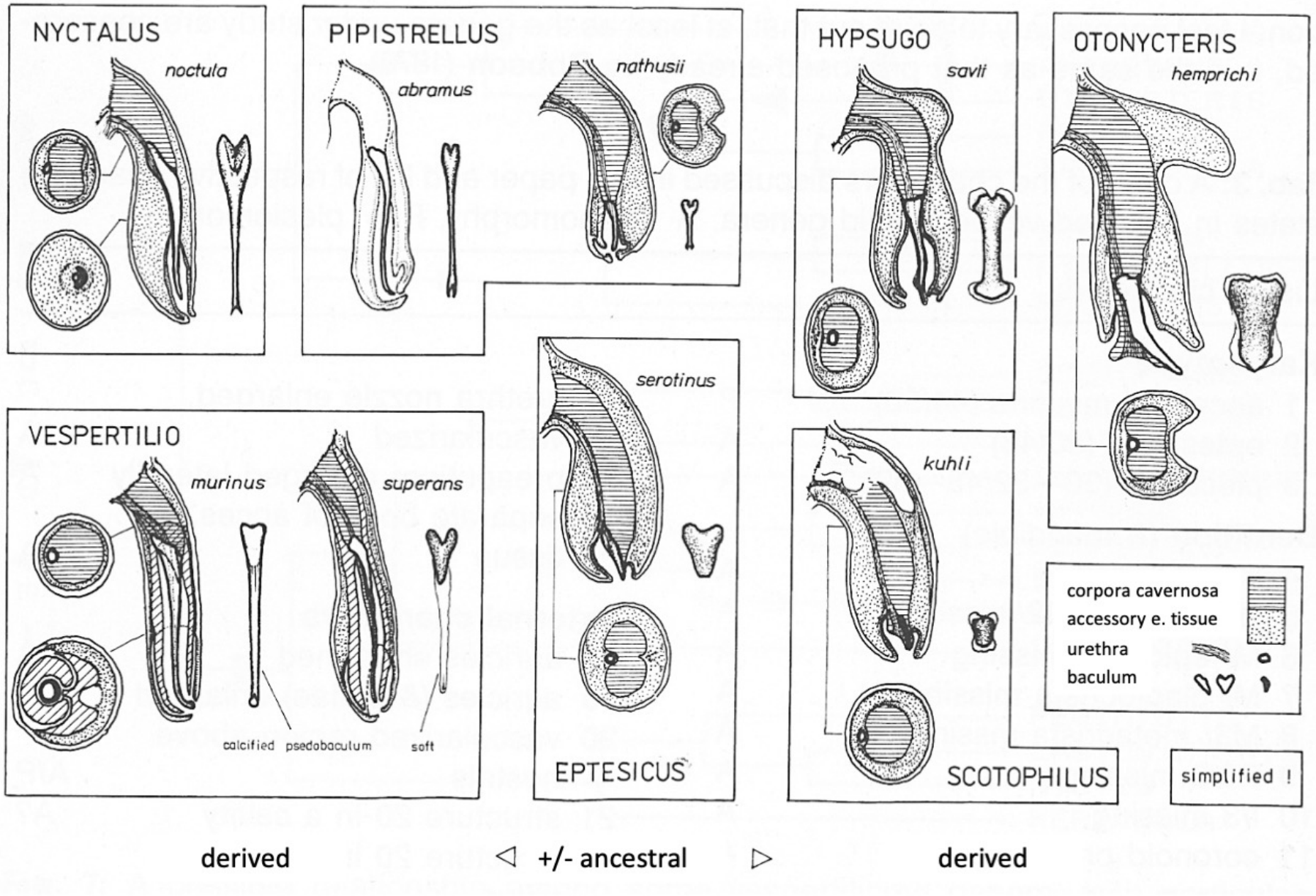
Baculum – a dorsal cover of urethra nozzle (disc, prolonged disc, stick...)





In distribution and arrangements of these tissues (mainly **CS** and **ACT**) individual clades dramatically differ

Vespertilionidae (partim)



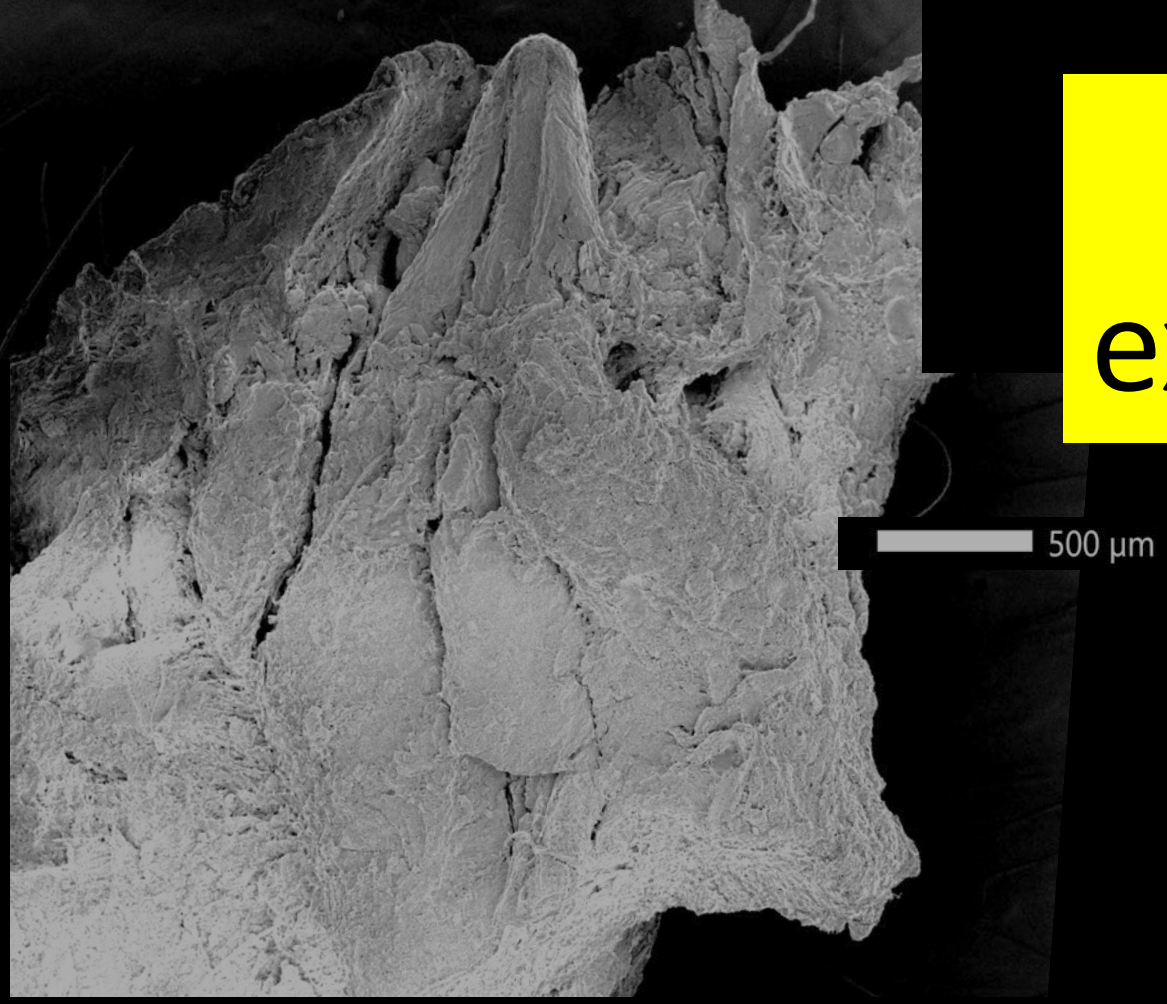
Horáček (1991)

In diversity of penile morphologies bats excessivelly exceed any mammalian order!

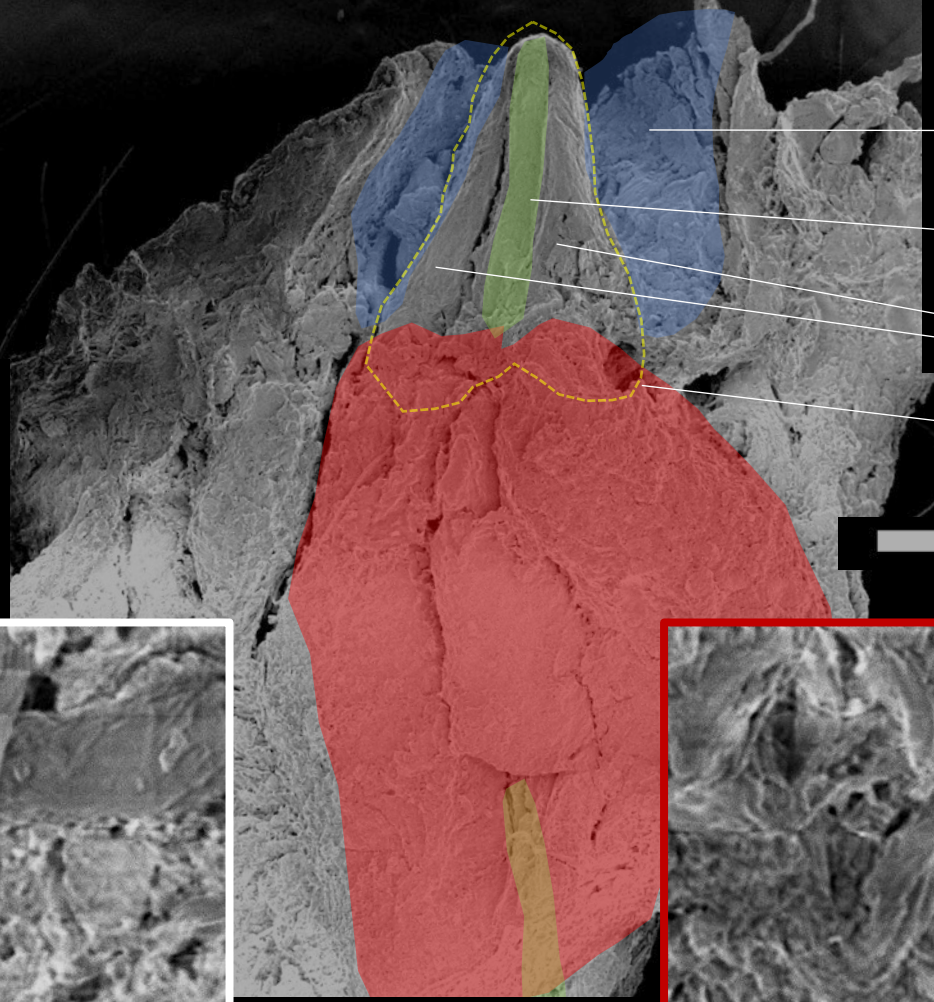
Tip of penis in
Eptesicus serotinus
(ventral view)

Few examples

Glans penis and praeputial vestibulum small (but distinct), Praaputium and subsurface body of penis infilled with accessoric cavernous tissue



Tip of penis in
Eptesicus serotinus
(ventral view)



Preputial vestibulum

Urethra

Strips of corpora spongiosa

Baculum (simple disc-like)

500 µm

Spongiose lacunes along network of longitudinal fibers with a diffuse vascularisation

10 µm

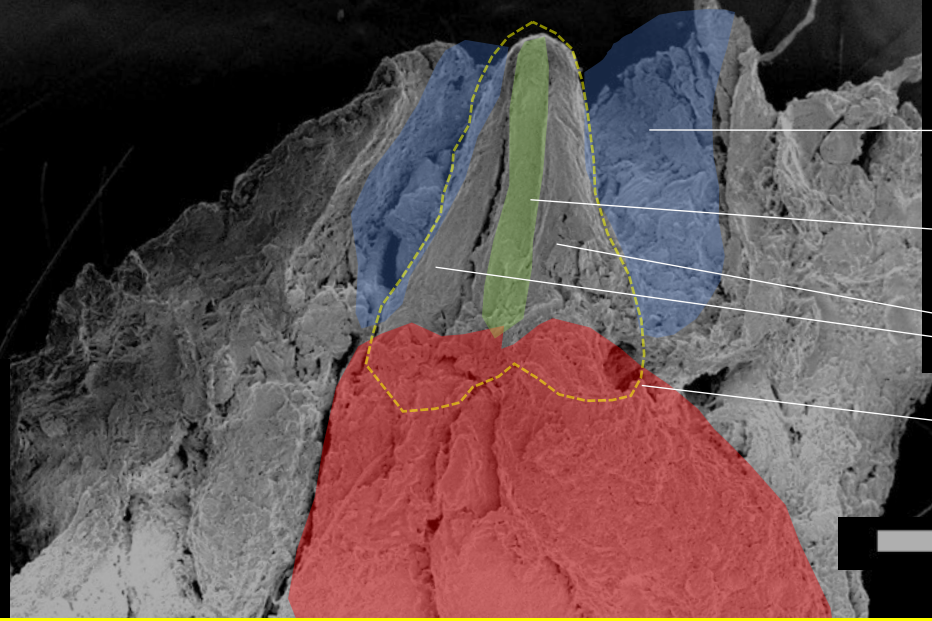
Accessoric cavernous tisseue

Corpora cavernosa

Spacious caverns of 3D arrangement
With massive vacularisation

10 µm

Tip of penis in
Eptesicus serotinus
(ventral view)



copulation proceeds by two (virtualy independent) steps:

(i) erection of *accessoric tissue* → giant penile arm with terminal praeputial disc erigating female's external genital

(ii) erection of *corpora cavernosa* and glans structures performing intromission when female tends to accept it

Spongiose lac
networ
with a d

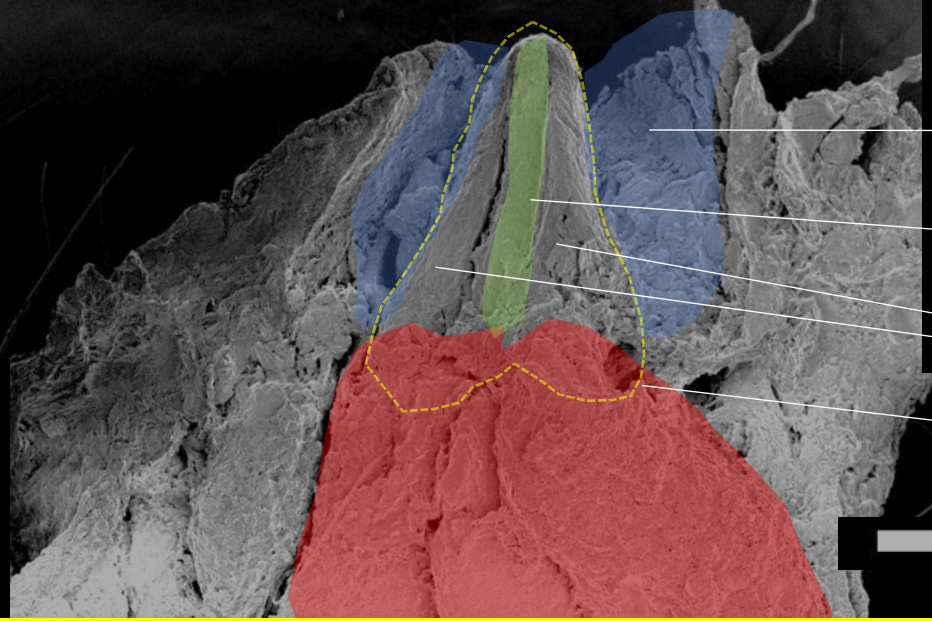
10 µm

different vascularisation with (←→) independent innervation

Spacious caverns of 3D arrangement
massive vacularisation

10 µm

functional correlates of bat penile morphology



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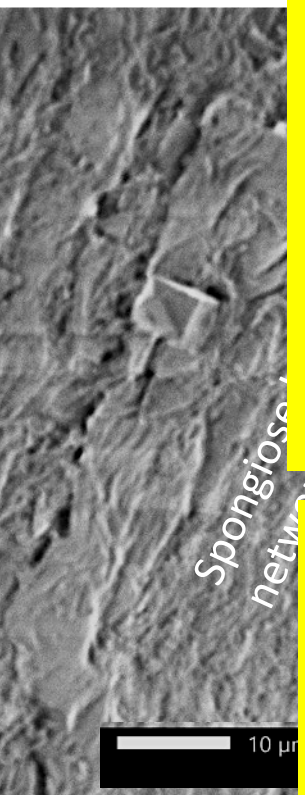
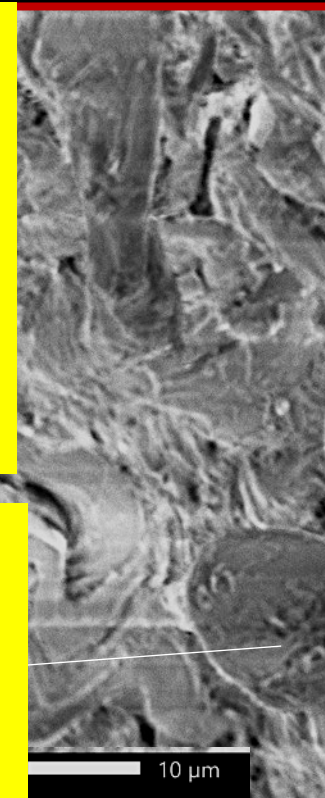
(*ii) erection of *corpora cavernosa* and glans structures performing intromission when female tends to accept it

yet, also the further step may play a serious role:

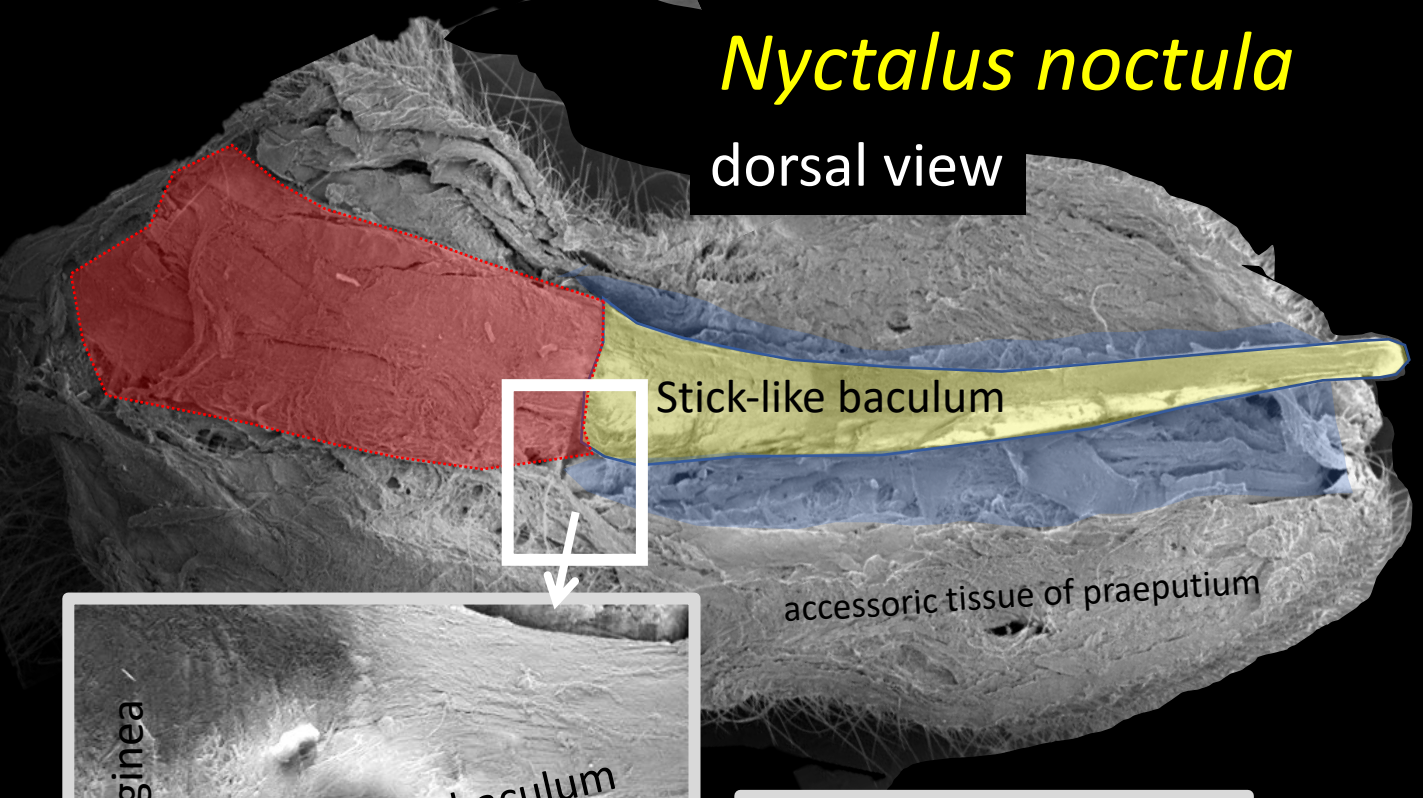
(*iii) extending vaginal pleasures performed with aid of specialised structures of *glans penis*

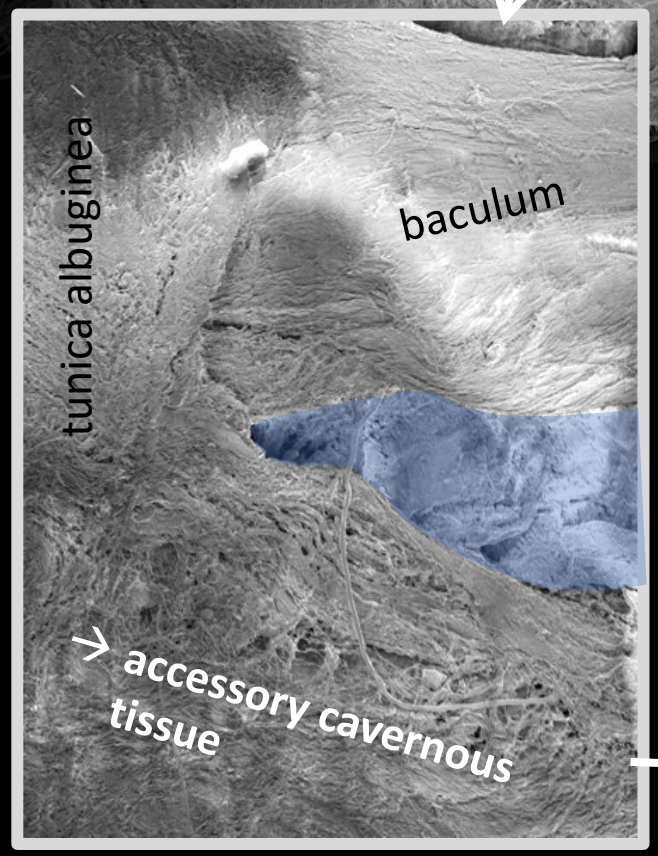


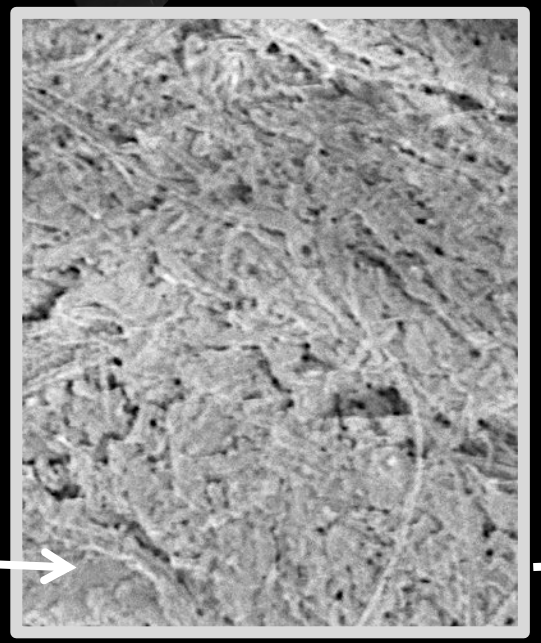


Nyctalus noctula

dorsal view







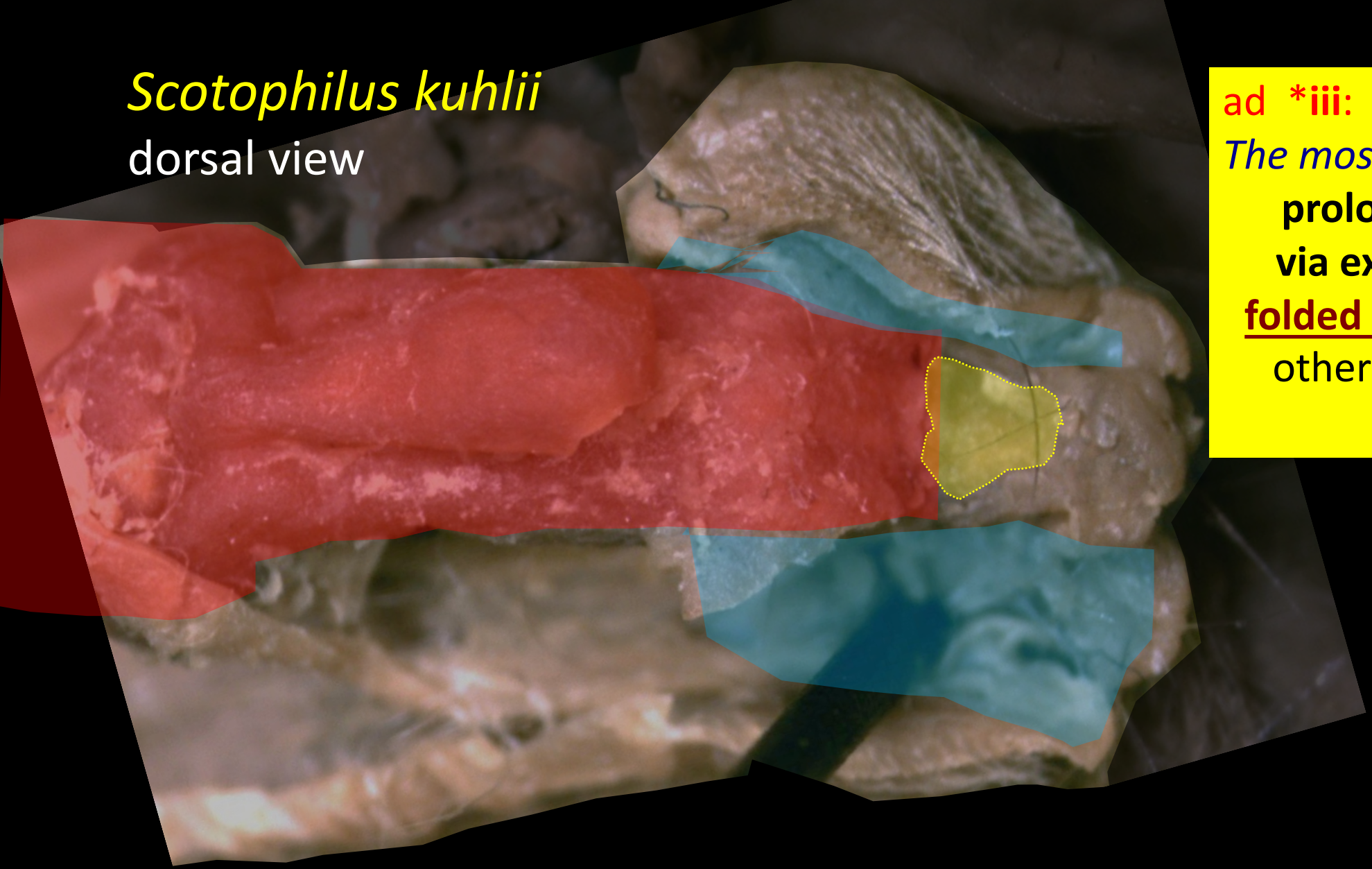
ad *iii:

The most common way:

prolonging glans penis, typically with a prolonged baculum, associated with enlarged preaputium with fibrose accessoric tissue and spatial vestibulum

the fibrose accessory cavernous tissue of praeputium is derived of tunica albuginea, i.e. supposedly separated from the accessoric tissue of penis body

Scotophilus kuhlii
dorsal view



ad ***iii**:

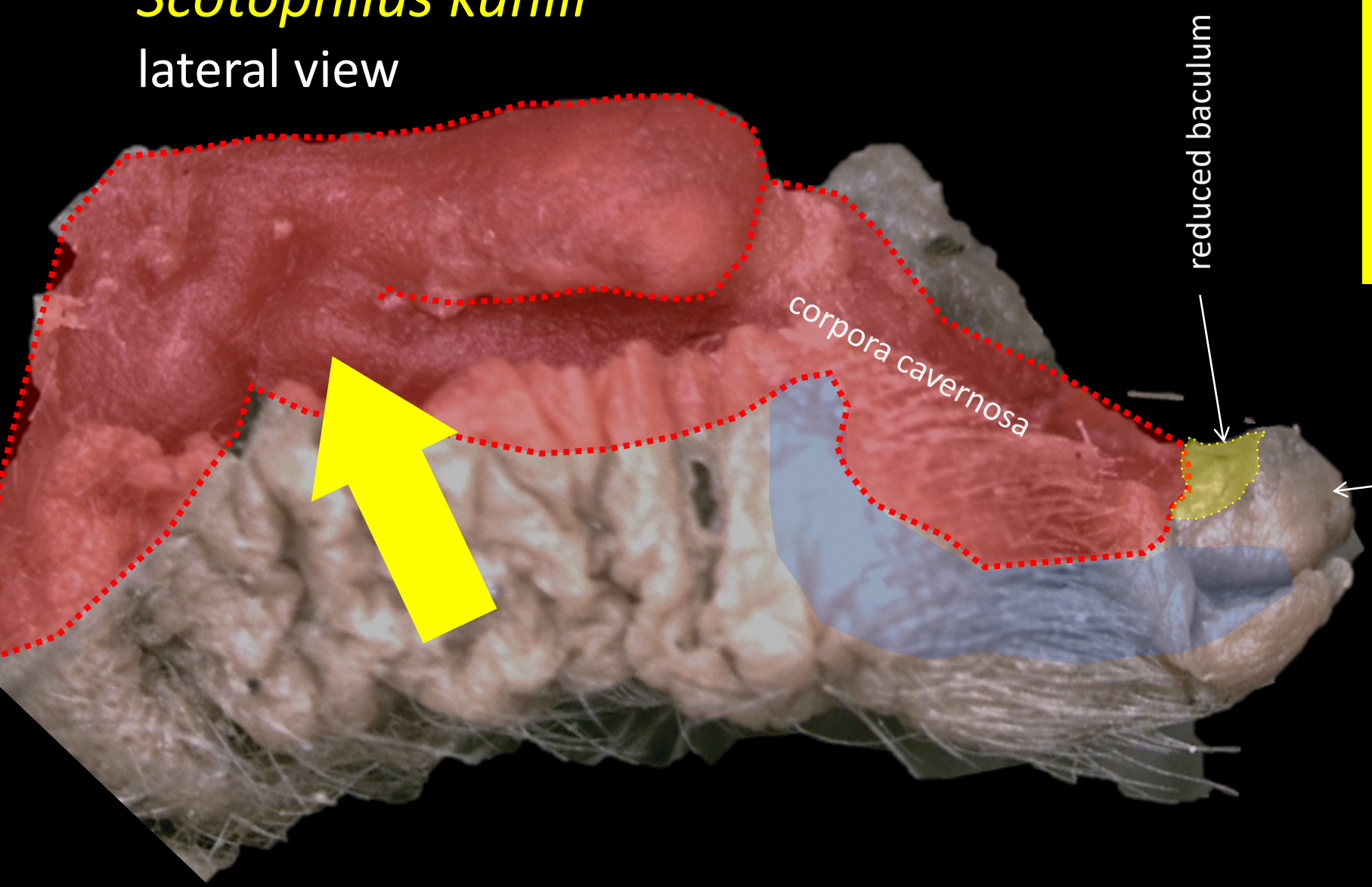
The most unique way:

prolonging (glans) penis via excessive erection of folded corpora cavernosa, other characters being in +/-ancestral state

Scotophilus kuhlii
lateral view

ad *III
The most unique way:
prolonging (glans) penis via excessive erection of folded corpora cavernosa, other characters being in +/-ancestral state

Scotophilus kuhlii
lateral view



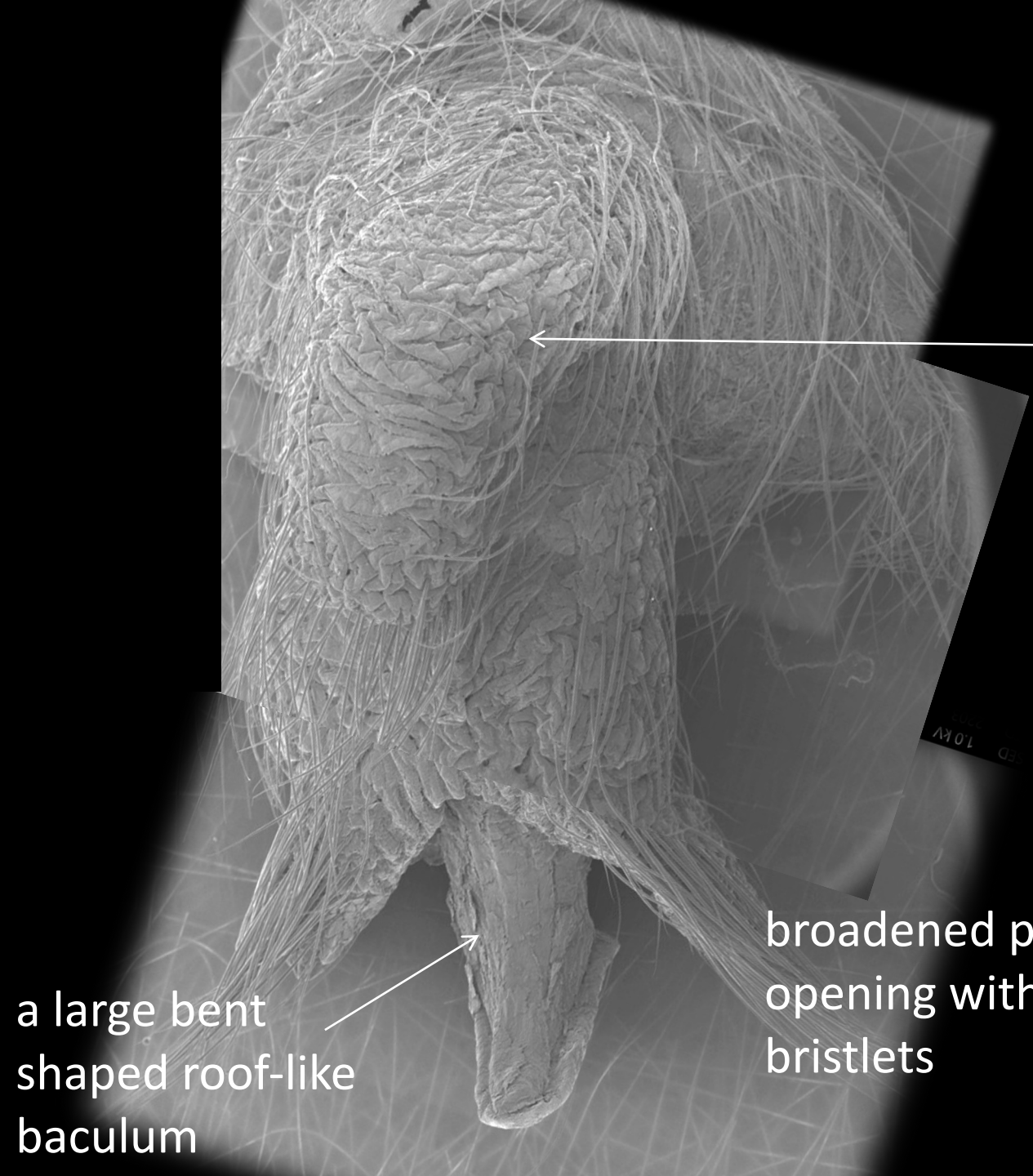
The most unique way:
prolonging (glans)penis via excessive erection of folded corpora cavernosa, other characters being in +/-ancestral state

→ ***a convergence to fibrose-vascular penises of ungulates***

Otonycteris hemprichi

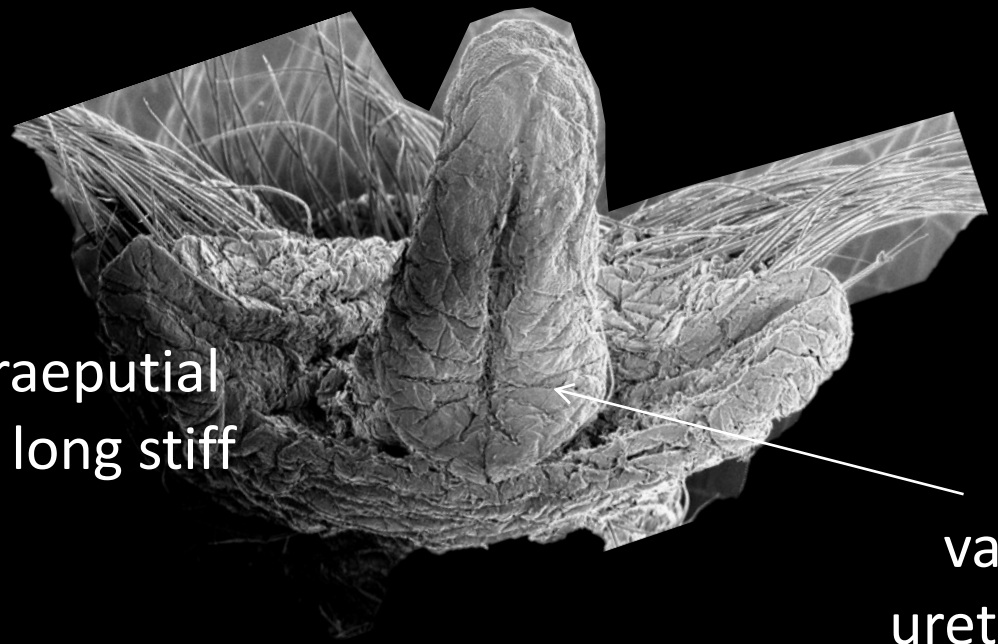
another outstanding arrangement

a separate basal body of accessoric tissue, parallel to penis



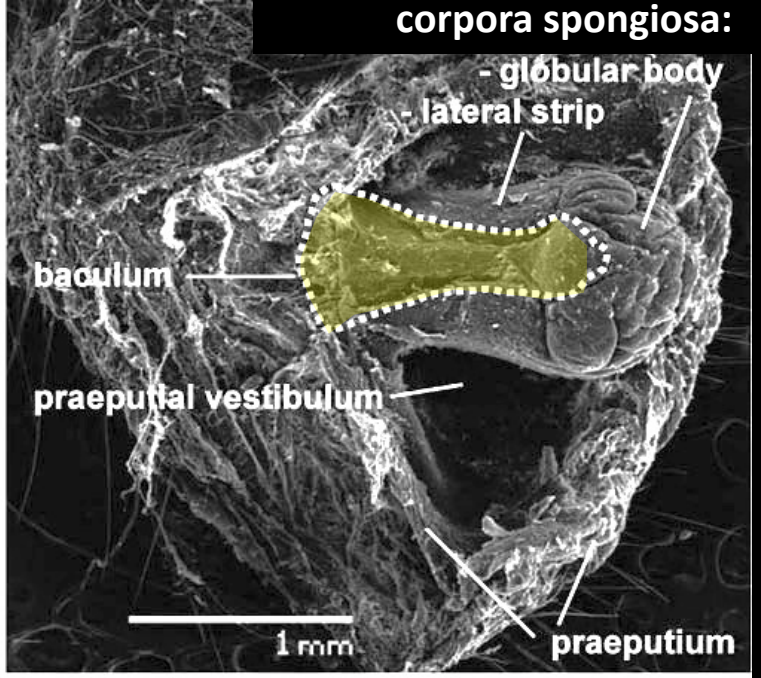
a large bent shaped roof-like baculum

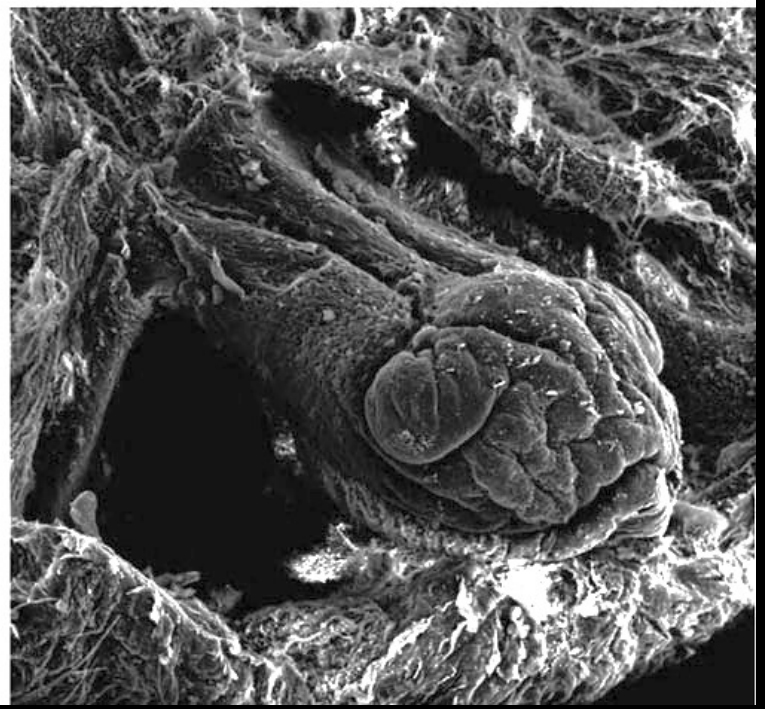
broadened praeputial opening with long stiff bristlets



enlarged vascularised urethra nozzle

Hesperostrellus hesperus





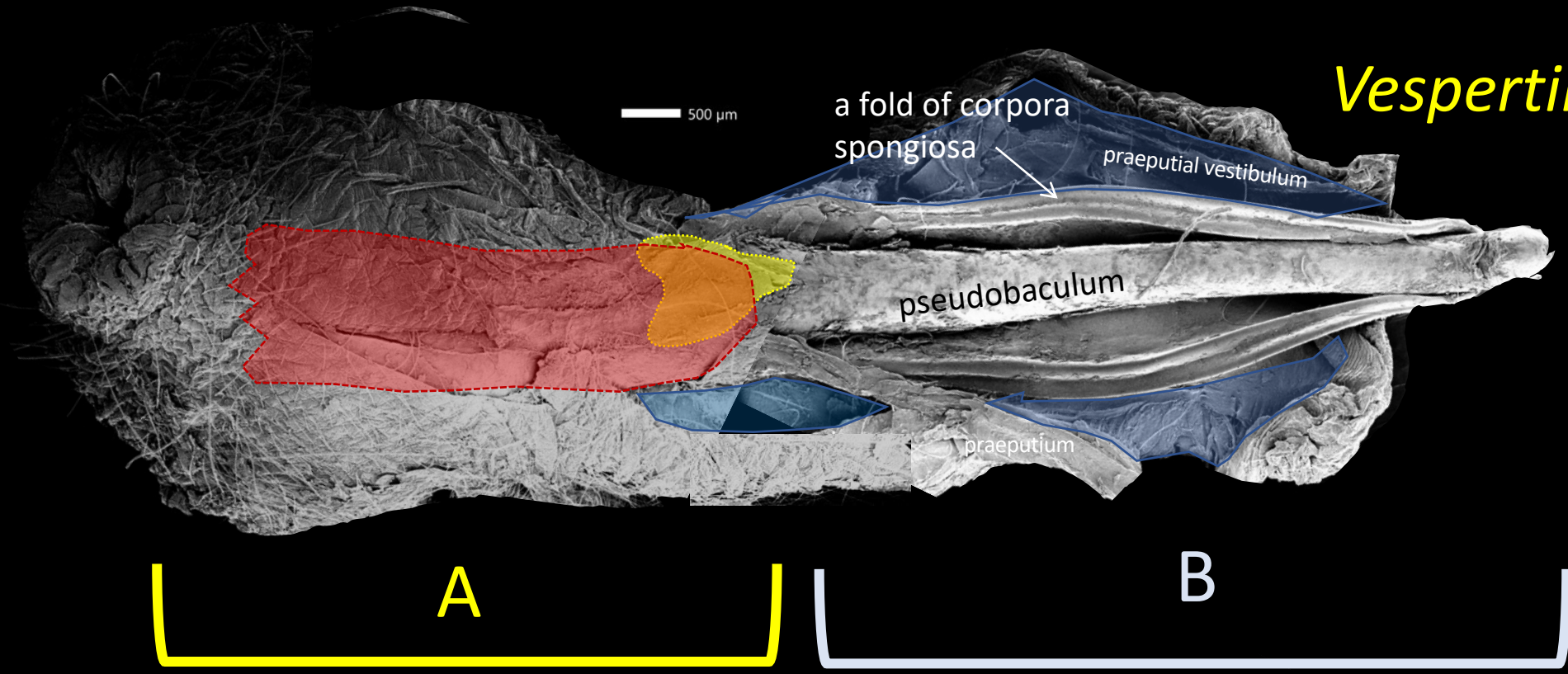
ad ***iii**:

corpora spongiosa *may play an essential role*

Glans enlarged by special modifications of corpora spongiosa (globular structures around urethra nozzle, folded coat along baculum)

– by the way: **the most robust phenotype autapomorphy of the genus**

Hoofer, van den Bussche & Horáček (2006)

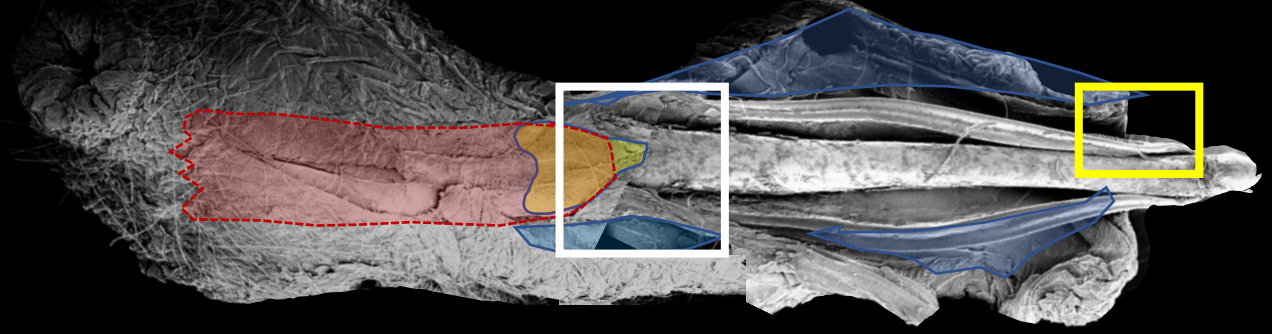


Vespertilio murinus

ventral view

ad ***iii**: - *The most derived arrangement:*

the ancestral organisation of bat penis (A) supplemented with a unique novel rearrangement of glans penis (B): hardening wall of urethra in form of pseudobaculum (either soft in *V.sinensis* or calcified in *V.murinus*) **inside folds of rigid coat of corpora spongiosa ,** along with enlarged preaputium with fibrose accessoric tissue and spatial vestibulum



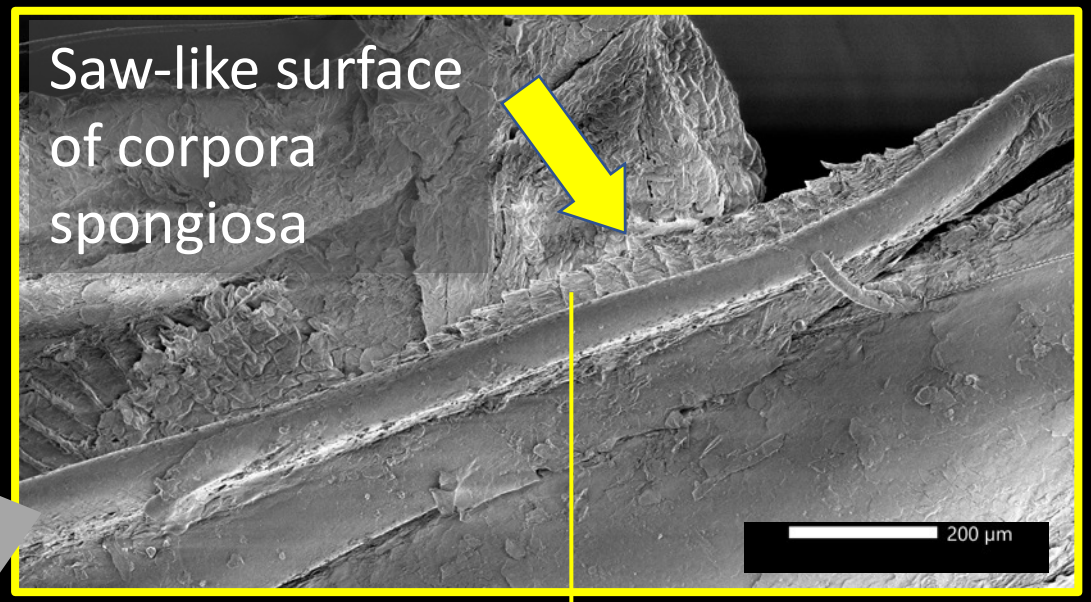
Extremelly derived strips of corpora spongiosa

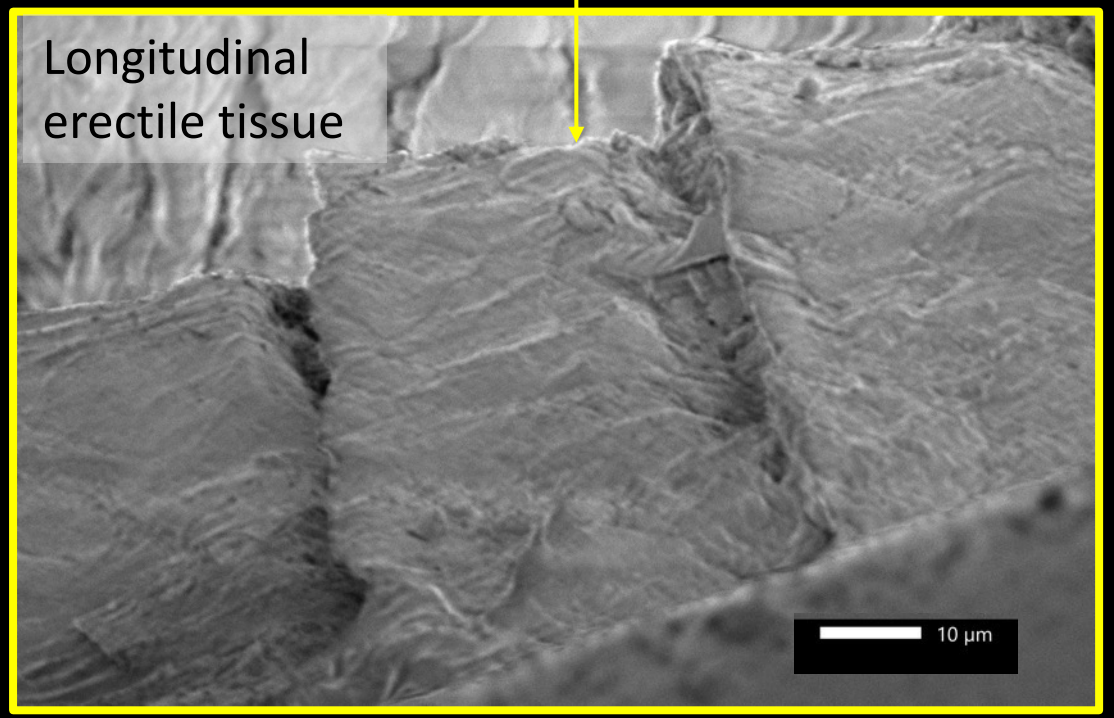
Surface cover: tunica albuginea

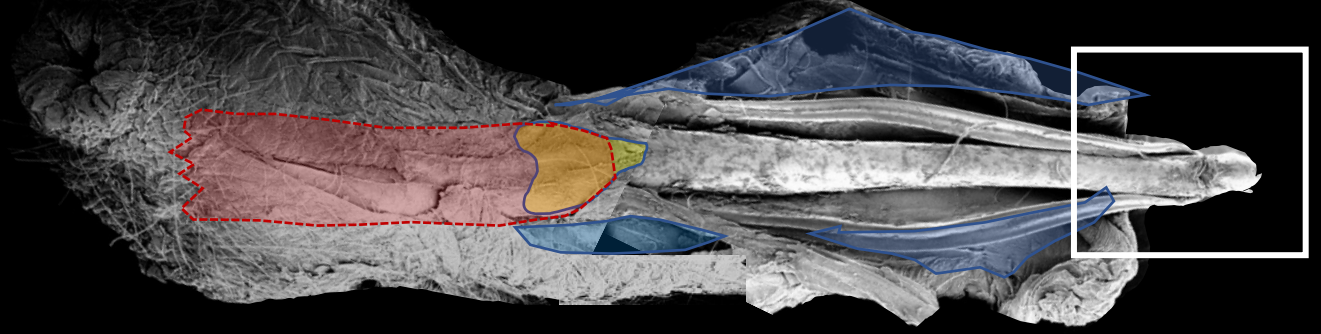
Pseudobaculum (calcified wall of urethra)

Non-calcified, vascular in *V.sinensis*

Accessory tissue of preputium





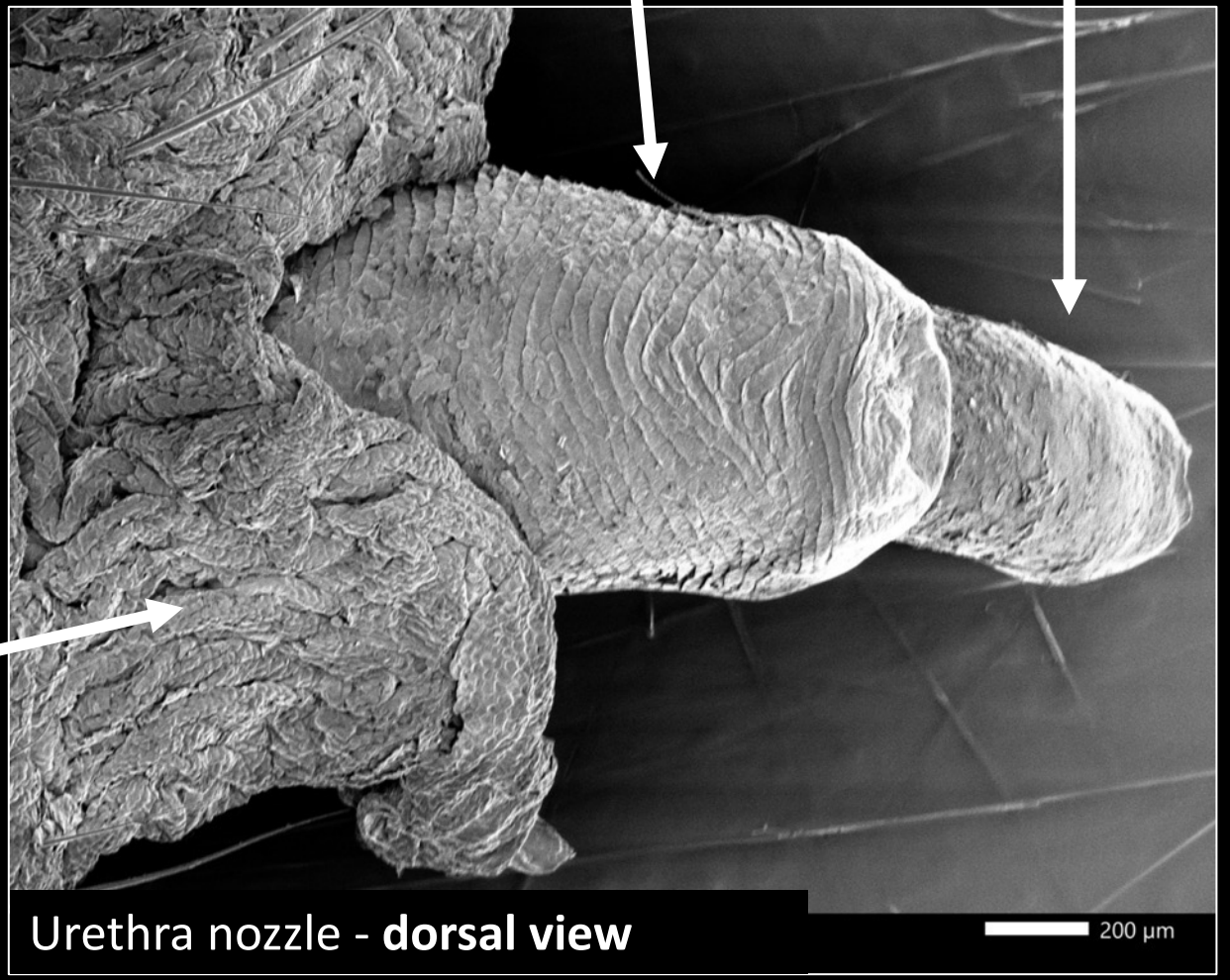


Saw-like erectile surface of corpora spongiosa

urethra

Which kind of vaginal pleasures might it exert?

Densely folded skin of praeputial opening



Why so large penile diversity
(terminating in vespertilionid bats)
?

What has been behind it ?

Why so large penile diversity
(terminating in vespertilionid bats)
?

What has been behind it ?

Constitutional invariables and constraints of being a bat

* **Virtually unconstrained mobility** and/or versatility of female's spatial behaviour → incipient role of **female choice** in mating system (much enlarged compared to non-volatile mammals)

* **Conservative drives in bat behaviour**: preference of once experienced best solutions – in roost selection, mate selection etc.) → establishing a **female's behavioral monogamy** underlined by an experience of a top male responding best to her attitudes

***Bat longevity**: under virtual female monogamy → robust increase in number of offsprings of the males responding to females' image of a top mate

The female's image of a top mate might claim (among other):

* a forced initiation of the mating **(*i)**
* prolonged stimulation of female external genitalia **(*i)**
* postponing the intromission to the stage of female's full receptivity **(*ii)**
* extraordinary vaginal pleasures **(*iii)**

For a poor male exposed to ultimate female choice it is indeed a hard task to respond it:

Yet, with incipient structural setting of bat penis morphology (three independent erectile tissues etc.), the rearrangements of penile phenotype (***i-*iii**: fixed by the above mentioned selection feedback drives) might help to respond at least some of the claims in a satisfactory way

… in short

The excessive penile diversity in bats is perhaps one of the most pertinent examples of the **Darwinian sexual selection**

Yet, the **Fisherian exposition of the sexual selection** claims to search for the female expression of the selection drives
– **the background factors patterning the female choice:**

(*) In bats, *compared to other mammals*: incipiently extended role of the ***female choice*** due to virtually unconstrained female mobility

(*) Motivation setting of female's spatial and social behaviour

***a: bats with circumannualy stable harem organisation** *(Molossus, Saccopteryx* etc.)

Females: claims for behavioral qualities of harem masters (a group integrating behavior, scent marking etc.)

→ *males:* no excessive penile morphologies

***b: bats socially identified by specific roosts** *(Miniopterus, M.blythi* etc.)

Females: cohesivity of maternity colonies and attitudes to roost companions, a limited number of male territories in a roost → *excess of demands over supply*

→ *males:* no excessive penile morphologies

***c: clades characterized by seasonal monooestry** (vespertilionids in particular **)**

Females: cohesivity of maternity colonies → sexual seggregation in breeding period (strongly selected by the Late Cenozoic increase of sesonality drives)

→ **a very strong cue needed for disrupting the primary motivation** ← memories on the top male of previous experiences

→ *males:* **a strong selection for a top male qualities** supported by excessive penile morphologies

Conclusions:

The excessive penile diversity, characterising the bats, is to be seen in context of other traits of bat biology

Then, it seems to open a novel peephole to a mysterious domain of the bat lives

Let us wish them a lot of pleasure from their penial diversities...

- Thanks for your attention