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A new study on the structure and function of the adhesive organs of the Old World sucker-footed bat (Myzopoda: Myzopodidae) of Madagascar

Abstract Both species of Madagascar's endemic sucker-footed bats (*Myzopoda aurita* and *M. schliemanni*) have a pair of adhesive discs on the wrists and ankles with a complex anatomy. Until recently, it was not known how these organs provided the means for *Myzopoda* to cling to smooth vertical surfaces. Recent experiments (Riskin & Racey 2010) with living animals have shown that the pads function by wet adhesion. Here we present details on the anatomy of these specialized structures and present new morphological data, which support the experimental results.

Keywords *Myzopoda*, adhesive organs, wet adhesion, functional anatomy, Madagascar

Running Title Adhesive organs of Old World sucker-footed bat *Myzopoda*

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Introduction

The adhesive discs of *Myzopoda aurita* MILNE-EWARDS et GRANDIDIER, 1878 and the newly described *M. schliemanni* GOODMAN, RAKOTONDRAPARANY AND KOFOKY, 2007, both endemic to Madagascar, have been cited in the literature as extraordinary anatomical structures (see for example MILNE-EDWARDS & GRANDIDIER 1878, DOBSON 1878, MILLER 1907, KOOPMAN 1994, STARCK 1995, SCHLIEMANN & GOODMAN 2003, KULZER 2005). These discs are small complex organs having developed as skin accessories on the ventral side of the thumb and on the planta pedis (Fig. 1, Fig. 2). Even though known for over 150 years, the anatomy of these organs has been studied only once (SCHLIEMANN 1970), based on older specimens in the Zoologisches Museum Hamburg, which had been preserved in alcohol for nearly 100 years. Considering the age of this material, the quality for histological examination was excellent, although the study was confined to light microscopy. At the time of the 1970 publication, it was assumed that members of the genus were very rare, with less than 20 specimens preserved in the world's natural history museums. Further, nothing was known about the biology of these bats and several ideas were advanced on how the adhesive discs function and their use in nature (SCHLIEMANN 1970, 1971, THEWISSEN & ETNIER 1995).

In the meantime, the discovery of a second species of *Myzopoda* (GOODMAN et al. 2007) largely coincided with renewed interest in these enigmatic animals, their unique adhesive organs, and their biology. The question on how these organs function has been recently answered based on field experiments (RISKIN & RACEY 2010). Further, since the analysis of the structure of the adhesive organs by SCHLIEMANN (1970) new preserved material, suitable for ultrastructural studies, has become available.

The aim of the present study is a new assessment of the anatomy of the adhesive organs of *Myzopoda*, in this case using ultrastructure in combination with light microscopy. The results of this analysis provide a structural link between the morphology of the adhesive organs and recent field observations of living *Myzopoda* using these adhesive discs (RISKIN & RACEY 2010).

Fig. 1 *Myzopoda aurita* clinging to a leaf surface by its adhesive organs. The discs of the forelimb are ventral of the proximal phalange of the thumb. Photo courtesy of JON RUSS.

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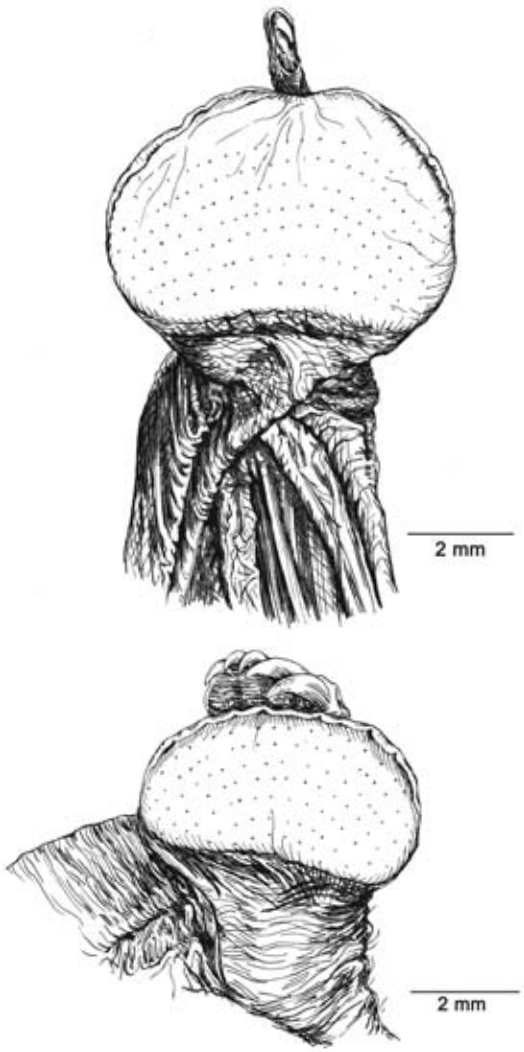

Fig. 2 Ventral views of the adhesive organs of *Myzopoda aurita*, above adhesive organ of the left forelimb, below adhesive organ of the left hindlimb. Note the openings of the glands of the organs, arranged in transverse rows. Drawing by A. Scholz.

Materials and methods

The material employed in this study comprises adhesive organs of 10 specimens of *Myzopoda.* Five of them, all males of the recently discovered species *M. schliemanni*, were obtained in 2005 in the Province of Mahajanga, Forêet d'Andranomanintsy, 24.5 km north of Besalampy (Goodman et al. 2007). One adhesive disc of the forelimb and one of the hindlimb of each of these individuals was preserved in a 2.5% aq. formaldehyde/glutaraldehyde solution, with a 0.1 M sodium cacodylate buffer and at a pH of

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7.4. Adhesive organs of two specimens were prepared for transmission electron microscopy, while the discs of one animal were used for scanning electron microscopy – standard procedures were used for both methods.

Furthermore, preparations of the discs of five different specimens of *Myzopoda aurita* from the collection of the Zoologisches Museum Hamburg, which included three males and two females, were also employed. This material was stored in 70% ethanol since the end of the 19th century and was probably originally preserved in alcohol. The same specimens were used in the previous morphological analysis of the adhesive discs, and the material was subjected to routine procedures for histological examination (for details see SCHLIEMANN 1970).

Results

External anatomy of the adhesive organs

The adhesive organs are skin accessories, which form plate-like structures with their greatest extension in the transversal direction, becoming thinner from their centres towards the periphery (Fig. 2). The disc of the front limb is situated ventral to the proximal phalange of the thumb and measures 6 mm or slightly more in breadth (transversally) and about 4 mm in length (longitudinally).

The disc of the hindlimb lies ventral to the metatarsalia, its breadth being about 5 mm and the length about 3 mm. 28 adult males of *Myzopoda aurita* captured by RISKIN & RACEY (2010) weighed 9.18 ± 0,82 g (mean ± SD mass), the area of the forelimb pads averaged 21.8 ± 2,3 mm^2 and that of the hindlimb averaged 12,5 ± 1,3 mm^2.

The rims of both organs are distally and laterally rounded in an arch-like manner, while being slightly turned over towards the ventral surface, which is in contact with the substratum during adhesion. This surface is almost entirely even and smooth, not convex as described by THEWISSEN & ETNIER (1995). The slight surface folds in the older specimens are probably associated with preservation shrinkage. This surface shows less pigmentation than other dermal portions of the specimens, and in the recently collected material, the whole surface is translucent. In the older material, the ventral surface shows a multitude of skin gland openings, which are evenly distributed in transverse lines, the latter being slightly concave in proximal direction (SCHLIEMANN 1970, SCHLIEMANN & MAAS 1978).

Scanning electron micrographs of the corneocytes at higher magnification show quite a different and unusual surface view of the adhesive epithelium (see below).

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Internal anatomy of the adhesive organs

Besides the covering epithelia, the adhesive organs are composed of corium tissue, mainly connective and adipose tissue in which glands, blood vessels, nerves and sense organs are embedded. The adipose tissue is structured throughout the discs in cylindrical compartments lying in transverse and slightly concave lines. Each compartment is inclined from a distal/dorsal towards proximal/ventral position and contains a gland in its dorsal part, which opens by a long duct to the ventral surface. The longest compartments occur in the middle portion of the adhesive organ, whereas towards the periphery the compartments are smaller (Fig. 3).

In the dorsal portions of these compartments, the adipose tissue is encased by rather delicate collagenous septa, the fibres of which run in a parallel direction to the length of the compartment, being associated with elastic material. In the ventral parts of the compartments, however, the encasement is reinforced by coarse, tendinous fibre bundles, which are associated with the M. palmaris longus and the M. flexor tibialis of fore- and hindlimb organs, respectively. The long tendon of the palmaris longus is in continuation with a tendinous membrane situated ventral to the metacarpus and the short thumb-musculature. This palmar aponeurosis is the origin of the tendinous fibre bundles that pass through the adhesive organ. In the disc of the hindlimb, an

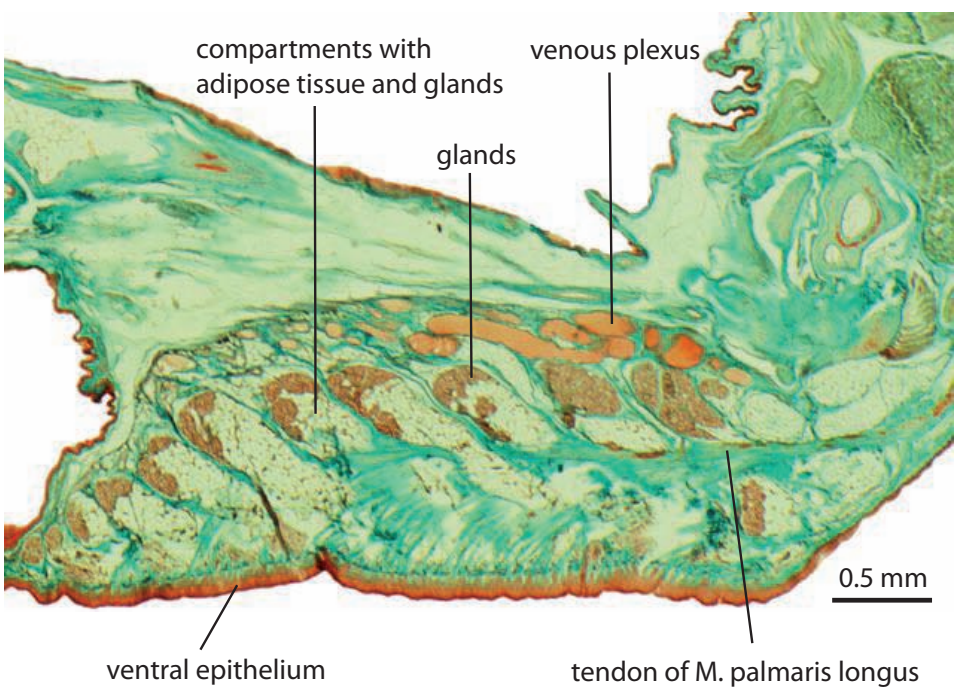

Fig. 3 Longitudinal section of the adhesive organ of the forelimb of *Myzopoda aurita*. Note the ventral thickened epithelium, the compartments filled with adipose tissue and glands, the venous plexus, the tendon material and fibre bundles running to the ventral epithelium.

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aponeurosis near the proximal rim of the organ is the origin of collagenous fibre strands passing through the organ. This aponeurosis is connected with a strong tendon belonging to the flexor tibialis.

The architecture of the tendinous fibre bundles is complicated and identical in both the fore- and hindlimb organs. In longitudinal and horizontal sections, the strong tendon-like fibre bundles enter the disc in the middle of the organ and from a proximal direction. The fibre bundles encase the adipose tissue compartments in a wavelike manner (Fig. 4). Further, these fibre bundles give rise to a series of smaller bundles, which run in an arcuate manner towards the ventral epithelium where they terminate.

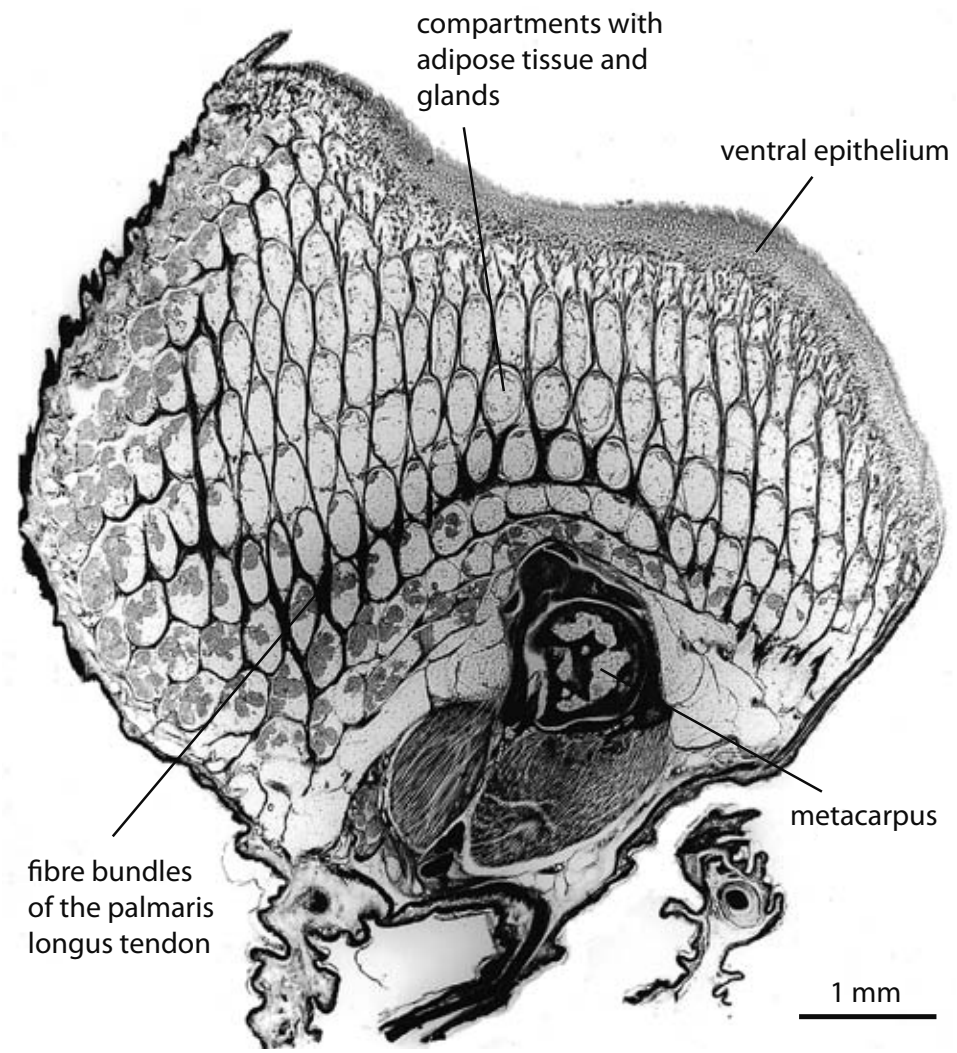

Fig. 4 Horizontal section of the adhesive organ of the forelimb of *Myzopoda aurita*. The level of the section is slightly declined from dorsal (left side of the figure) towards ventral (right side). Note the strong fibre bundles encasing the adipose tissue compartments.

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The ventral epithelium

Under the stereomicroscope, the epithelium of the ventral side of the adhesive discs does not show any surface structure, except for the openings of the glands; these openings are only visible in the older material. When compared to the normal body epidermis, the thickness of the epithelium and its complex structure towards the corium shows some important differences. Whereas the epithelium of the dorsal side of the adhesive disc and elsewhere in the body measures about 12 µm, the ventral epidermis of the adhesive disc is at least 70 µm thick. The inner side of the epidermis bordering the corium shows a very peculiar morphology: cone-shaped protrusions of the epithelium projected into the corium, lying closely together and encasing between them small portions of the papillary layer of the corium (Fig. 5A). The inner surface of each of the epidermal cones is densely covered by these fibre bundles, which, as previously mentioned, are orientated in an arcuate manner towards the epithelium. These fibre bundles terminate in the cleft-like distal parts of the papillary layer between the epidermal cones (Fig. 5B).

Dorsal to the epidermis is a dense net of elastic fibres, which are in contact with the tips of the epidermal cones just extending into the fibre net (Fig. 5A).

Histologically, the ventral epidermis of the disc forms a multilayered, cornified squamous epithelium generally characteristic of parts of the skin under mechanical strain. In the epithelial cones, there are up to 15 cell-layers from the stratum basale to the rather thin stratum corneum, whereas in the thinner portions of the epithelium, between the cone-shaped protrusions, less than 10 cell-layers are found. Irregularly shaped keratohyalin granula are visible outside the stratum spinosum in a layer of two cell lines. A stratum lucidum does not appear to be present. The pigmentation of the ventral epithelium is very faint.

In transmission electron micrographs, the basal cell layer shows numerous half-desmosomes, and basal lamina and bundles of collagen fibrils in the dermal papillae are clearly visible. The spinous layer is typically characterized by numerous mitochondria, many desmosomes, wide intercellular spaces with many microvilli, and filamentous material. The intercellular spaces are significantly reduced under the granular layer, but some nuclei towards the stratum corneum are still present. Keratohyalin granula and filaments are abundant. The stratum corneum is clearly demarcated with respect to the granular layer and may be composed of 4–5 cell lines; at higher magnification, narrow remnants of the intercellular spaces are identifiable. The surface shows tiny bumps and ridges (Fig. 6A).

These surface structures of the stratum corneum are clearly observable at higher magnification in the scanning electron micrographs (Fig. 6B). The whole surface of the adhesive epithelium is unusually characterized by pegs, ridges, pits and troughs

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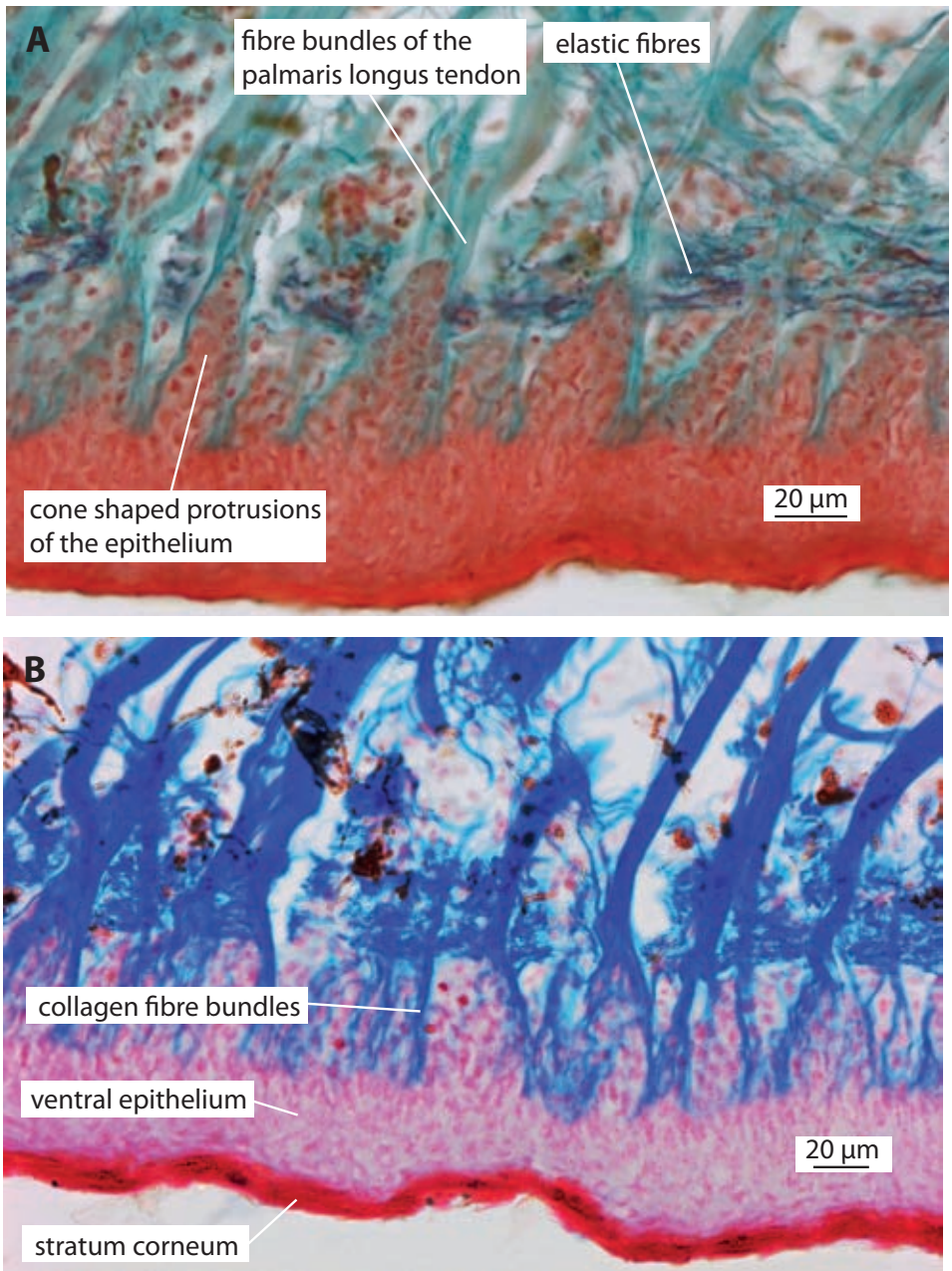

Fig. 5 Longitudinal section of the ventral epithelium and adjacent corium of the adhesive organ (forelimb) of *Myzopoda aurita*. **A.** Goldner-orcein stain. Note the particular interface between epithelium and corium, the elastic fibre net, and the fibre bundles ending in the stratum papillare. **B.** Pasini stain. Note the well-confined stratum corneum and the collagen fibre bundles, surrounding the epidermal cones and ending directly underneath the epithelium.

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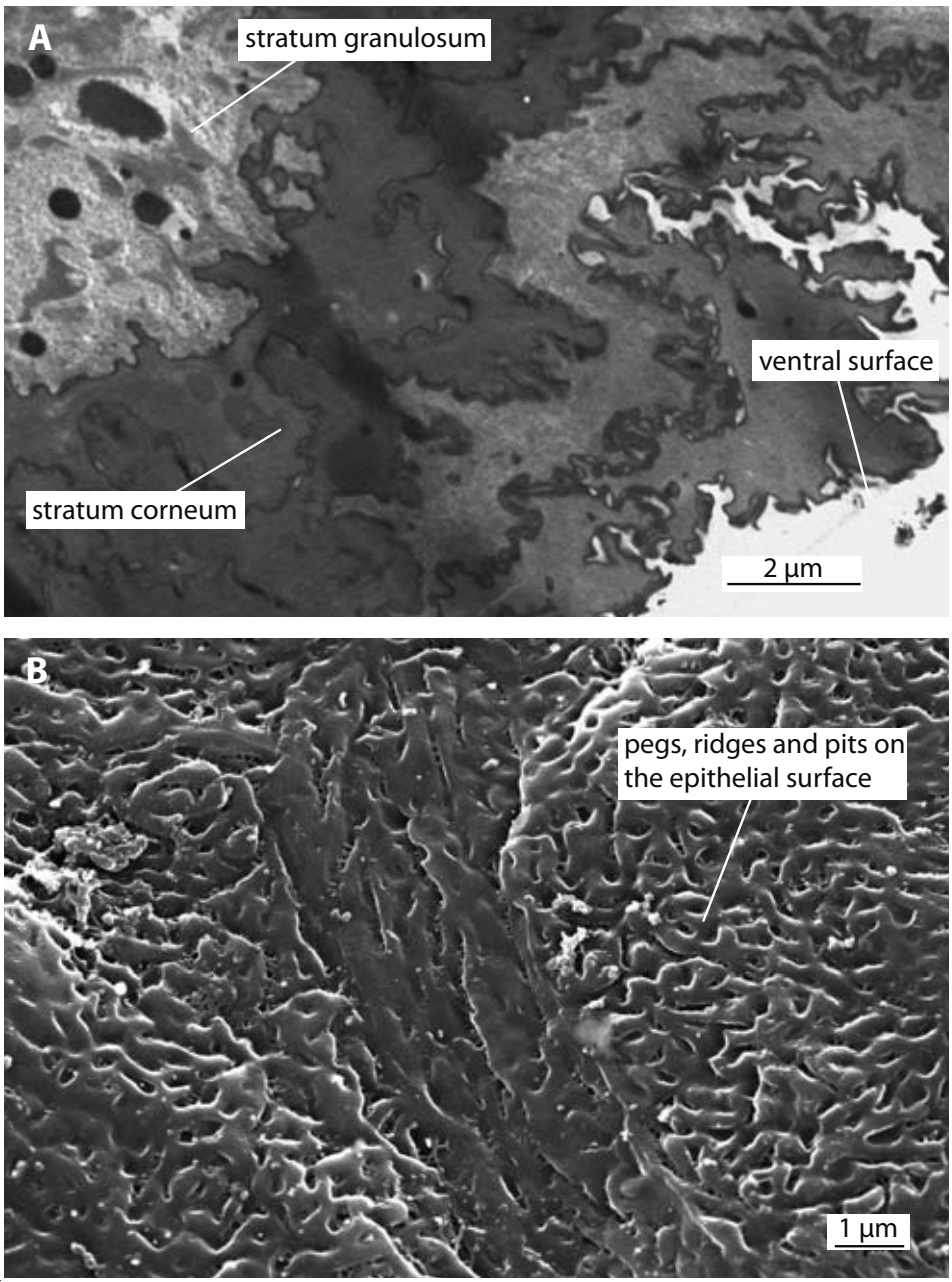

Fig. 6 **A** Electron micrograph of the stratum granulosum and stratum corneum of the ventral epithelium of the adhesive organ of *Myzopoda schliemanni.* Note the unusual protrusions and ridges on the surface. **B.** Scanning electron micrograph of the surface of the ventral epithelium of the adhesive Organ of *Myzopoda schliemanni.* Note the many pegs, ridges, pits, and troughs on the surface of the epithelium.

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between them, all these structures measure notably less than 1 µm, a topography notably different from the surface of the stratum corneum elsewhere on the organ.

Glands of the adhesive organs

Each of the cylindrical compartments contains a gland, the secretory portions of which are mainly situated in a dorsal position within these compartments, whereas in the periphery of the organs, the compartments are nearly filled by the glands. A long and relatively thin main excretory duct shows a straight alignment from the dorsal part of the compartment towards a ventral direction and opens on the ventral surface of the epithelium. Proximally, this duct divides into some smaller ducts surrounded by the secretory cells, which in the microscopic section show a cluster-like grouping of rounded acini (Fig. 7A, Fig. 7B).

The straight excretory duct is lined by a low columnar epithelium with large central or slightly apical nuclei. In some sections of the distal portions of the duct, underneath the lining cells, a second layer is visible composed of basal cells. Further, distally, in close proximity to where the glands open, underneath the ventral epithelium, the duct attenuates, and one or two additional layers of rather flat cells are present. The duct near the ventral epithelium shows inner keratinisation. The major portion of the ex-

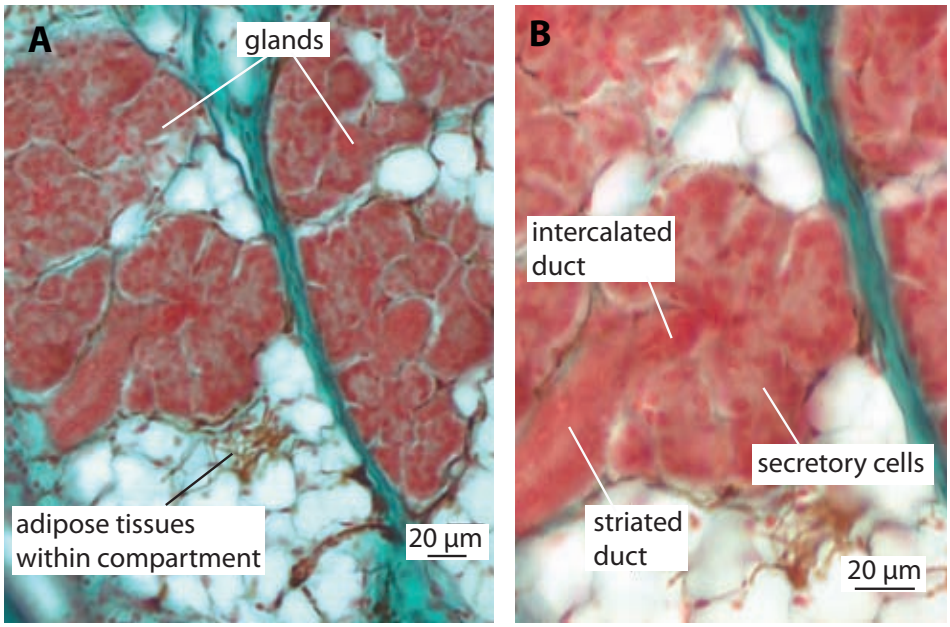

Fig. 7 **A** Longitudinal section of the adhesive organ of *Myzopoda aurita*, showing two adipose tissue compartments, each with a gland in the dorsal part. Goldner-orcein stain. **B.** Longitudinal section of a gland of the adhesive organ of *Myzopoda aurita* (enlarged detail of Fig. 7A). Note the cluster-like grouping of the secretory cells around an intercalated duct and the striated duct. Goldner-orcein stain.

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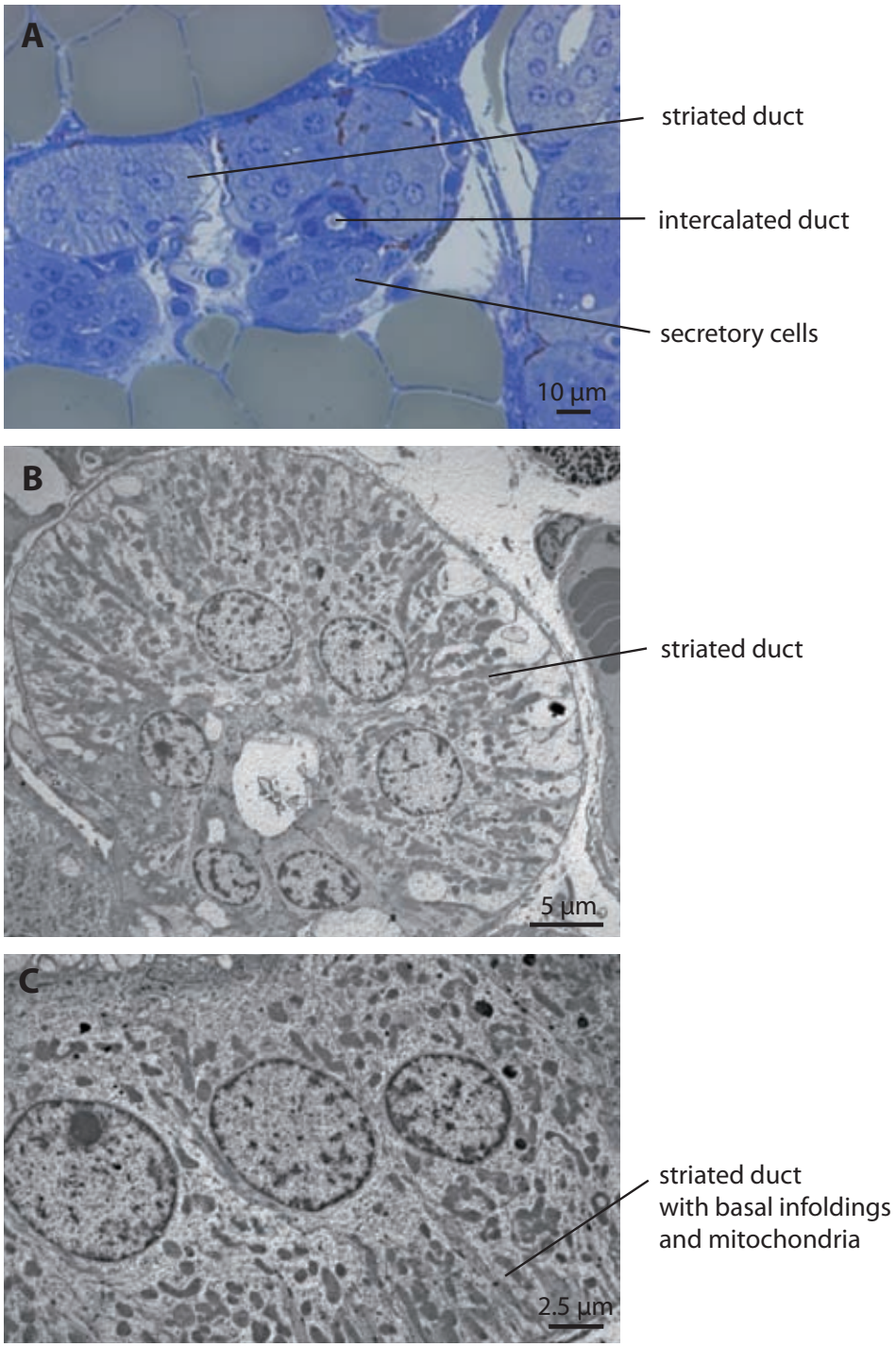

Fig. 8 **A** Semi-thin section of a gland of the adhesive organ of *Myzopoda schliemanni*. Note secretory cells around an intercalated duct, striated duct. Toluidin-blue stain. **B.** Electron micrograph of a gland of the adhesive organ of *Myzopoda schliemanni*, showing a cross section of the striated duct. **C.** Electron micrograph of a gland of the adhesive organ of *Myzopoda schliemanni*, showing the wall of a striated duct with infolding of the basal cell membrane and parallel orientation of numerous mitochondria.

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cretory duct resembles striated salivary gland ducts, characterized by parallel striation caused by numerous infolding of the basal cell membrane and the orientation of large mitochondria. Apically, the lining cells are equipped with some low microvilli (Fig. 8B, Fig. 8C).

Proximally, within the secretory part, the ducts have a notably small diameter with rather flat cells that are largely filled with elongated nuclei with very dense chromatin, notably similar in structure to intercalated ducts of oral cavity glands (Fig. 8A, Fig. 7A, 7B). The terminal portions are arranged in acini, which surround the intercalated duct. Cleft-like lumina are visible in micrsoscopic slides but they can hardly be seen in the electron micrographs. The secretory cells are cone-shaped, with their nuclei in a basal position, often with a central nucleolus. Using electron-microscopic and semi-thin preparations, the apical portions of these cells are filled with numerous secretory granules, Golgi complexes and granular endoplasmatic reticula are visible.

Venous tissue of the adhesive organs

The glands containing compartments are dorsally bordered by loose connective tissue containing fat cells and a considerable number of heavily filled veins lying closely together (Fig. 3, Fig 9); this is particularly the case in central and proximal parts of the adhesive organs. In transverse section of the pads, numerous vessel bundles and

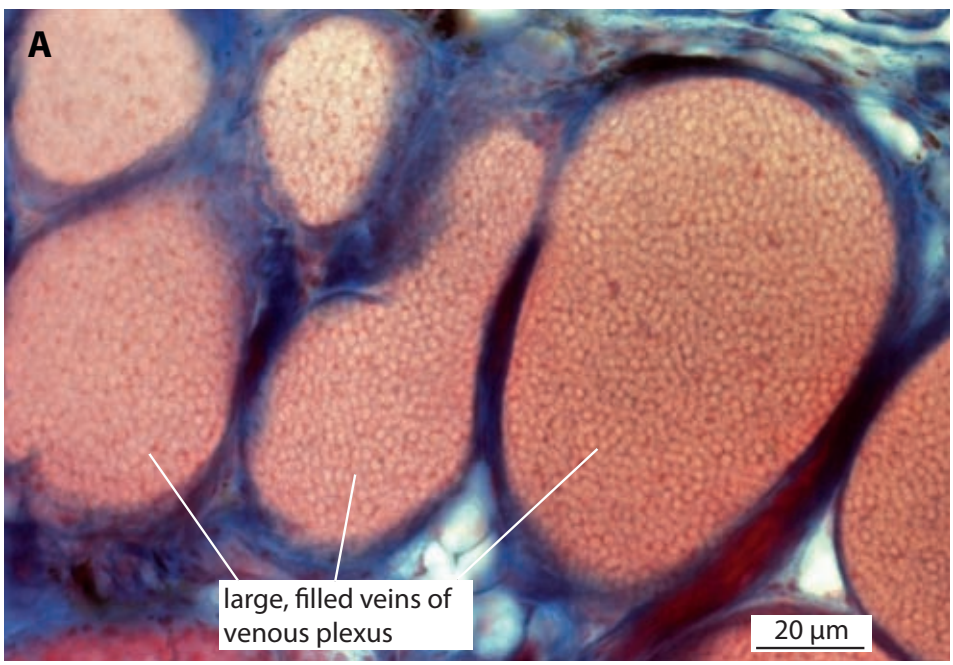

Fig. 9 Cross-section of the venous plexus of the adhesive organ of *Myzopoda aurita* with heavily filled veins. Pasini stain.

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nerves are visible, which contain small arteria (Aa. digitales colares comm.), often in the neighbourhood of Vater-Pacini corpuscles. The manner of how blood flows in these veins and associated regulation has been previously discussed (Schliemann 1970). Altogether, it seems plausible that these numerous veins act as cavernous tissue complexes.

Discussion

Numerous types of animals are able to cling and walk on vertical surfaces or even upside-down on ceilings; these include different taxa of arthropods, amphibians and reptiles, but this capacity is notably rare in mammals (Nachtigal 1974, Hanna & Barnes 1991, Autumn et al. 2000, Autumn 2007, Autumn & Gravish 2008, Beutel & Gorb 2001, Persson 2007, Riskin & Racey 2010). Research conducted on the adhesive organs of different arthropods and geckos attracted interest and contributed considerably to the understanding of the function of these organs (e.g. Autumn et al. 2000, Peattie 2009).

Among the few mammals possessing adhesive organs and having the capability to stick to vertical surfaces are members of two Chiroptera families, namely the Thyropteridae of South and Central America and the Myzopodidae of Madagascar. There is a substantial and in several cases recent literature on the morphology and operating modes of the adhesive organs of these bats. However, with exception of the external morphology, the anatomy of the adhesive organs in both families has been given only modest attention (Schliemann 1970, Wimsatt & Villa-R. 1970). The functional modes of these discs have been investigated by a few authors (Schliemann 1970, Wimsatt & Villa-R. 1970, Thewissen & Etnier 1995, Riskin & Racey 2010). On the basis of the material studied herein, no notable differences were found in the anatomy of the two different *Myzopoda* spp.

The complex morphology of the adhesive organs of *Myzopoda* deserves closer attention. From a comparative point of view, the ventral epithelium with its connections to the tendons of the palmaris longus muscle (adhesive organ of the thumb) and the flexor tibialis muscle (adhesive organ of the planta pedis) is apparently unique within the animal world. The interface between epidermis and corium characterized by epithelial cones, which are immersed into a net of elastic fibres, is, as far as we can determine, not known in another organism. Furthermore, the glands of the adhesive organs with their striated and intercalated ducts and the secretory cells resemble glands of the oral cavity. These structures do not show any resemblance with the common palma or planta pedis skin glands of mammals, which are of the eccrine type (Montagna 1956, Rosenberg & Rose 1999). The glands of the adhesive organs of the bat genus *Thyrop-*

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tera are also of the eccrine type (SCHLIEMANN 1970, WIMSATT & VILLA-R. 1970), highlighting convergence in these structures between these two genera.

The central question on how these organs work in a functional sense has only been recently answered. Whereas it has never been questioned that the adhesive organs of *Thyroptera* work by suction (SCHLIEMANN 1970, WIMSATT & VILLA-R. 1970, FINDLEY & WILSON 1974, WILSON 1978, THEWISSEN & ETNIER 1995, RISKIN & FENTON 2001), in the case of *Myzopoda* several ideas have been advanced, which include suction and adhesion (SCHLIEMANN 1970), and even gluing (THEWISSEN & ETNIER 1995).

Very comprehensive experiments performed with 28 living specimens of *M. aurita* by RISKIN & RACEY (2010) proved beyond doubt that the attachment of the adhesive organs is by wet adhesion, with no evidence of suction or gluing. RISKIN & RACEY (2010) demonstrated that the adhesive force on an acrylic surface, was nine-fold stronger when pulled in a shear direction, which corresponds to a downward movement of the animal in a head-up position (35.6 ± 9,6 mN mm^{-2}, forelimb pad), compared to a perpendicular lift to the surface (3,7 ± 1,9mN mm^{-2}, forelimb pad). These authors also detected a fluid film between the ventral surface of the adhesive organ and the substratum necessary for this mode of function. They clearly observed that the ventral surface of the pads was covered with a fluid and once dry it subsequently became wet.

An interesting aspect is that the adhesive pad morphology and associated operational mode is different between *Thyroptera* and *Myzopoda*, which are not phylogenetically immediately related (TEELING et al. 2005). Also remarkable is the similarity in roosting ecology of members of these two genera. For their day-roost sites, *Thyroptera* uses funnel-shaped leaves of *Heliconia* spp. (Heliconiaceae) and *Calathea* spp. (Marantaceae), in which these bats stick to the surfaces in an unusual head-up position (CARVALHO 1939). In a convergent manner, the day-roost sites of *Myzopoda aurita* are in coiled leaves of *Ravenala madagascariensis* (Strelitziaceae) (RALISATA et al. 2010) and those of *M. schliemanni* in folded palm fronds of *Bismarckia nobilis* (Arecaceae) (GOODMAN 2011). However, *M. schliemanni* has also been found roosting on cave walls in the same head up position (KOFOKY et al. 2006). As suggested by RISKIN & RACEY (2010) that an earlier evolutionary stage in the functional mode of the pads of *Thyroptera* was via wet adhesion is doubtful. Considering the shape of the pads of *Thyroptera* and the specialized central insertion of the M. flexor pollicis within the pad, it seems more likely that these pads have been functioning by suction from an early stage in their differentiation.

The known morphological findings to date and new aspects presented herein strongly support wet adhesion in *Myzopoda*. Observations on how *Myzopoda* employ the adhesive pads on leaf surfaces (GÖPFERT & WASSERTHAL 1995, RISKIN AND RACEY 2010), namely the agility and speed individuals bring these organs into contact with the substratum, release, and then reattach, are contrary to the assumption of a gluing effect.

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Different morphological aspects of the adhesive organs in *Myzopoda* correspond to their functional utilization. These aspects ca be summarized as follows:

The thickened ventral epithelium is an adaptation to the *increased mechanical strain* of the ventral side of the adhesive organs. In contrast to the situation in *Thyroptera, Myzopoda* lacks a central skeleton substrate within its adhesive pads. The *morphological stability* of the whole organ in *Myzopoda*, as well as a certain degree of *elasticity*, is achieved by connective and adipose tissue in combination with a complex venous plexus; the complicated arrangement of the adipose tissue, and the formation of glands in numerous cylindrical compartments and neighbouring veins play a role in this function. Important in this context are the strong tendons of palmaris longus and flexor tibialis, which surround the ventral portions of the cylindrical compartments. When the muscles contract, these tendons exert tension on the contents of the compartments. The tissue within these compartments, fat cells and glands, would be moved in a dorsal direction, evading this tension, in the case of venous plexus bordering the dorsal side of the compartments did not counteract this movement. It is presumed that this construction is essential for maintaining shape and form stability of the pads, particularly that of the forelimb. It seems that this form of support is especially important for the adhesive organ of the forelimb, which along its longitudinal axis is only supported by the proximal phalanx of the thumb. In contrast, the adhesive organ of the hindlimb broadly rests underneath the metatarsals and the proximal phalanges.

Given the observations of Riskin & Racey (2010), the complicated course of the tendons of the M. palamaris longus (forelimb) and of the M. flexor tibialis (hindlimb), which all end at the ventral epithelium, have an additional functional significance. These authors describe that the *detachment* of the adhesive organ of the forelimb from the acrylic surfaces they used in their experiments commences with a central furrow on the ventral surface of the adhesive organs, specifically at the distal margin of the organ and tapers in a proximal direction, followed by a deformation of the pad. They assumed that contractions of the aforementioned muscles are responsible to generate this furrow. According to Schliemann (1970), taking into account the course of the tendons of both muscles, it is plausible that contraction first lifts off central parts of the ventral epithelium and only afterwards detaches the whole organ from the substratum. In accordance with this consideration, Riskin & Racey (2010) found that the adhesive forces during a fore- and hindlimb push, i.e. in an upward direction, are much weaker than in downward direction.

Vater-Pacini corpuscles have been associated with the function of sense organs measuring acceleration (Halata 1993). The obvious and large Vater-Pacini corpuscles found in the pads might be involved in *controlling adhesion* and detachment procedures.

The glands and their secretion in *Myzopoda* are of special significance and *wet ad-*

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hesion is the functional mode. An evenly moistened ventral side of the adhesive organ is necessary to generate the liquid film between the adhesive organ and the substratum observed during the experiments of RISKIN & RACEY (2010). The glands of the adhesive discs with the narrow lumina of the secretory endpieces, and intercalated and striated duct parts, very much resemble oral cavity glands. Such structures are apparently not previously described from skin glands. According to the morphology of these glands, it seems likely that the secretion is a thin watery fluid, an assumption supported by the long excretory and striated duct. The latter is presumed to function for the exchange of ions and water between the gland lumina and the tissue surrounding the duct; it certainly modifies the primary secretion, probably into a hypotonic fluid, and altogether, these morphological aspects indicate that the secretion is not mucus. The regularly patterned arrangement of the gland openings on the ventral epithelium is an indication that the functional purpose of this arrangement is to provide a uniform liquid film on the ventral surface of the adhesive disc.

In this connection, it is notable that the corneocytes of the ventral epidermis of the pads, forming a keratinized stratified squamous epithelium, exhibit very unusual surface structures. The whole surface is laced with closely packed pegs, ridges and clefts between them, all under 1 µm in size, so that the uniform liquid film is maintained in the fashion of a blotter paper. In adhesive organs of other animal species using wet adhesion, the ventral epithelium is also equipped with similar structures, which produce a liquid film on the epithelium. ROSENBERG & ROSE (1999) found in the marsupial *Acrobates*, which less effectively than *Myzopoda* can also cling on smooth and vertical surfaces, the ventral epithelium of the pads moistened by eccrine sweat glands secretions. However, in this marsupial, the stratum corneum of the epithelium has no surface structures in the range of a micrometer. In contrast, in frogs, which independently have evolved adhesive toe pads in several families, these organs show intricate surface structures (WELSCH et al. 1973, EMERSON & DIEHL 1980, HANNA & BARNES 1991, OHLER 1995, FEDERLE et al. 2010). Despite the independent acquisition of this structure across several taxa, all show enlarged toe pad surfaces with similar peg-studded hexagonal cells separated by deep channels into which mucus glands open. These pegs are much smaller (0,1–0,4 µm) than the surfaces structures of *Myzopoda* pads. Besides their function to maintain a fluid film on the pad surface necessary for clinging by wet adhesion, there is good evidence (FEDERLE et al. 2010) that during adhesion the pegs are in very close contact to the substratum and the capillary and viscous forces of wet adhesion are enhanced by boundary friction.

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References

AUTUMN, K. (2007): Gecko adhesion: Structure, function, and applications. Material Research Bulletin 32 (6): 473–478.

AUTUMN, K., LIANG, Y. A., HSIEH, S. T., ZESCH, W., CHAN, W. P., KENNY, T. W., FEARING, R. & FULL, R. J. (2000): Adhesive force of a single gecko foothair. Nature 405: 681–685.

AUTUMN, K. & GRAVISH, N. (2008): Gecko adhesion: Evolutionary nanotechnology. Philosophical Transactions of the Royal Society A 366 (1870): 1575 -1590.

BEUTEL, R. G. & GORB, S. (2001): Ultrastructure of attachment specialisations of hexapods (Arthropoda): Evolutionary patterns inferred from a revised ordinal phylogeny. Journal of Zoological Systematics and Evolutionary Research 39: 177–207.

CARVALHO, A. L. DE (1939): Zur Biologie einer Fledermaus (*Thyroptera tricolor* Spix) des Amazonas. Sitzungsberichte Gesellschaft Naturforschender Freunde zu Berlin (1939): 249–253.

DOBSON, G. E. (1878): Notes on *Myxopoda aurita*, Miln.-Edw. Proceedings of the Zoological Society of London (1878): 871–873.

EMERSON, S. & DIEHL, D. (1980): Toe pad morphology and mechanisms of sticking in frogs. Biological Journal of the Linnean Society 13: 199–216.

FEDERLE, W., BARNES, W. J. P., BAUMGARTNER, W., DRECHSLER, P., & SMITH, J. M. (2006): Wet but not slippery: Boundary friction in tree frog adhesive toe pads. Journal of the Royal Society Interface 3: 689–697

FINDLEY, J. S. & WILSON, D. E. (1974): Observations on the Neotropical disk-winged bat, *Thyroptera tricolor* Spix. Journal of Mammalogy 55: 562–571.

GÖPFERT, M. C. & WASSERTHAL, L. T. (1995): Notes on echolocation calls, food and roosting behaviour of the Old World sucker-footed bat *Myzopoda aurita* (Chiroptera, Myzopodidae): Zeitschrift für Säugetierkunde 60: 1–8.

GOODMAN, S. M. (2011): Les chauves-souris de Madagascar. 129 pp. Association Vahatra, Antananarivo.

GOODMAN, S. M., RAKOTONDRAPARANY, F. & KOFOKY, A. F. (2007): The description of a new species of *Myzopoda* (Myzopodidae: Chiroptera) from western Madagascar. Mammalian Biology – Zeitschrift für Säugetierkunde 72 (2): 65–81.

HALATA, Z. (1993): Die Sinnesorgane der Haut und der Tiefensensibilität. In: Handbuch der Zoologie ed. by J. NIETHAMMER, H. SCHLIEMANN, D. STARCK, 8, 57, 80 pp. Walter de Gruyter, Berlin, New York.

HANNA, G. & BARNES, W. J. P. (1991): Adhesion and detachment of the toe pads of tree frogs. Journal of Experimental Biology 155: 103–125.

KOFOKY, A. F., ANDRIAFIDISON, D., RAZAFIMANAHAKA, H. J., RAMPILAMANANA, R. L. & JENKINS, R. K. B. (2006): The first observation of *Myzopoda* sp. (Myzopodidae) roosting in western Madagascar. African Bat Conservation News 9: 5–6.

KOOPMAN, K. (1994): Chiroptera: Systematics. In: Handbuch der Zoologie ed. by J. NIETHAMMER, H. SCHLIEMANN, D. STARCK, 8, 60, 217 pp. Walter de Gruyter, Berlin, New York.

KULZER, E. (2005): Chiroptera: Biologie. In: Handbuch der Zoologie ed. by M. S. FISCHER, H. SCHLIEMANN, 8, 62, 250 pp. Walter de Gruyter, Berlin, New York.

MILNE-EDWARDS, A. & GRANDIDIER, A. (1878): Note sur un nouveau genre de Chiroptère. Bulletin Société Philomathique de Paris 2 (7): 220–221.

MILLER, G. S. (1907): The families and genera of bats. United States National Museum Bulletin 57: 1–282.

MONTAGNA, W. (1956): The structure and function of the skin. 356 pp. Academic Press. Inc., New York.

NACHTIGALL, W. (1974): Biological mechanisms of attachment. The comparative morphology and bioengineering of organs for linkage, suction, and adhesion. 194 pp. Springer-Verlag Berlin, Heidelberg, New York.

OHLER, A. (1995): Digital pad morphology in torrent-living ranid frogs. Asiatic Herpetological Research 6: 85–96.

PEATTIE, A. M. (2009): Functional demands of dynamic biological adhesion: An integrative approach. Journal of Comparative Physiology B 179: 231–239.

PERSSON, B. N. J. (2011): Wet adhesion with application to tree frog adhesive toe pads and tires. Journal of Physics: Condensed Matter 23: doi: 10.1088/0953–8984/23/1/0115003.

RALISATA, M., ANDRIAMBOAVONJY, F. R., RAKOTONDRAVONY, D., RAVOAHANGIMALALA, O. R., RANDRIANANDRIANINA, F. H. & RACEY, P. A. (2010): Monastic *Myzopoda*: the foraging and roosting ecology

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of a sexually segregated Malagasy endemic bat. Journal of Zoology 282 (2): 130–139.

Riskin, D. K. & Fenton, M. B. (2001): Sticking ability in Spix's disk-winged bat, *Thyroptera tricolor* (Microchiroptera: Thyropteridae). Canadian Journal of Zoology 79: 2261–2267.

Riskin, D. K. & Racey, P. A. (2010): How do sucker-footed bats hold on, and why do they roost head-up? Biological Journal of the Linnean Society 99: 233–240.

Rosenberg, H. I. & Rose, R. (1999): Volar adhesive pads of the feathertail glider, *Acrobates pygmaeus* (Marsupialia; Acrobatidae). Canadian Journal of Zoology 77: 233–248.

Schliemann, H. (1970): Bau und Funktion der Haftorgane von *Thyroptera* und *Myzopoda* (Vespertilionoidea, Microchiroptera, Mammalia). Zeitschrift für wissenschaftliche Zoologie 181(3/4): 353–400.

Schliemann, H. (1971): Die Haftorgane von *Thyroptera* und *Myzopoda* (Microchiroptera, Mammalia) – Gedanken zu ihrer Entstehung als Parallelbildung. Zeitschrift für zoologische Systematik und Evolutionsforschung 9(1): 61–80.

Schliemann, H. & Maas, B. (1978): *Myzopoda aurita.* Mammalian Species 116: 1–2.

Schliemann, H. & Goodman, S. M. (2003): *Myzopoda aurita,* Old World Sucker-footed Bat. In: The natural history of Madagascar ed. by S. M. Goodman, J. P. Benstead. 1303–1306.The University of Chicago Press, Chicago.

Starck, D. (1995): Säugetiere. In: Lehrbuch der Speziellen Zoologie ed. by D. Starck, II 5/1, 5/2, 1241 pp. Gustav Fischer Verlag, Jena, Stuttgart.

Teeling, E. C., Springer, M. S., Madsen, O., Bates, P., O'Brien, S. J., & Murphy, W. J. (2005): A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307: 580–584.

Thewissen, J. G. M. & Etnier, S. A. (1995): Adhesive devices on the thumb of vespertilionoid bats (Chiroptera). Journal of Mammalogy 76(3): 925–936.

Welsch, U., Storch, V. & Fuchs, W. (1973): The fine structure of the digital pads of rhacophorid tree frogs. Cell and Tissue Research 148(3): 407–416.

Wilson, D. E. (1978): *Thyroptera discifera.* Mammalian Species 104: 1–3.

Wimsatt, W. A. & Villa-R., B. (1970): Locomotor adaptations in the Discwinged bat *Thyroptera tricolor.* 1. Functional organization of the adhesive discs. American Journal of Anatomy 129: 89–119.