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Selected aspects of adaptations to the parasitism of hair follicle mites (Acari: Demodecidae) from hoofed mammals

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Abstract The Demodecidae are one of the most specialized parasitic arthropods of mammals, so far recorded in representatives of thirteen mammalian order, therein 16 species were described from hoofed mammals. Parasitic adaptations involve size and shape of the body which is elongated, worm-like, providing a specific adaptation to life in hair follicles or in various glands and their ducts. In addition, demodecids show an extreme reduction of a number of morphological characters. Some species show, moreover, certain other, specific adaptations to various microhabitats; those adaptations may, for instance, involve, the shape and size of tagms, the shape and localisation of supracoxal spines, setae on the palps, claws or the presence of the dorsal process on the opisthosoma. Specific modifications have enabled particular species to adapt not just to life in the skin of different mammalian species, but also to the different microhabitats they have colonised there. As a result, particular host species are parasitised by synhospitalic species specific to them, usually differing in their location in the skin.

Key words: hair follicle mites, Demodecidae, ungulates, European bison, parasitism

Introduction

The hair follicle mites (Acari, Prostigmata, Demodecidae) consists of mites inhabiting the skin of mammals. The Demodecidae are one of the most specialized parasitic arthropods, to this day found in representatives of thirteen orders (Chiroptera, Scadentia, Primates, Carnivora, Pinnipedia, Edentata, Rodentia, Perissodactyla, Cetartiodactyla, Hyracoidea, Lagomorpha and Marsupialia) (e.g., Bukva 1991, Izdebska 2006a). To survive in such an environment, these mites have developed a number of adaptations to parasitism-worm-shaped body is an unusual modification, which is along with their miniature size considered as a characteristic modification for life in hair follicles, or various types of glands and their outlet ducts. Due to the adaptation for living in the host's tissue the Demodecidae suffered an extreme reduction in a number of morphological elements (Bukva 1991, Izdebska 2002, 2006a), e.g. thy have only scarce, strongly reduced bristles, which makes species identification harder. On the other hand, hair follicle mites display considerable variety with respect to shape, tagmata proportions, dimensions,

and the position and form of many morphological structures (Fig. 1, Fig. 2). Specific modifications have enabled particular species to adapt not just to life in the skin of different mammalian species, but also to the different microhabitats they have colonised there. They have also an effect on host and topical specificity.Demodecidae indicate topographic specifity, e.g. prefer the head areas (as in the case of *D. bisonianus* in European bison) or genital, or rectal areas. In skin of Ungulates often two or more synhospital species of *Demodex* mites, for example, two synhospital species can be found in horse, domestic sheep or red deer, three species are known in cattle (Table 1).

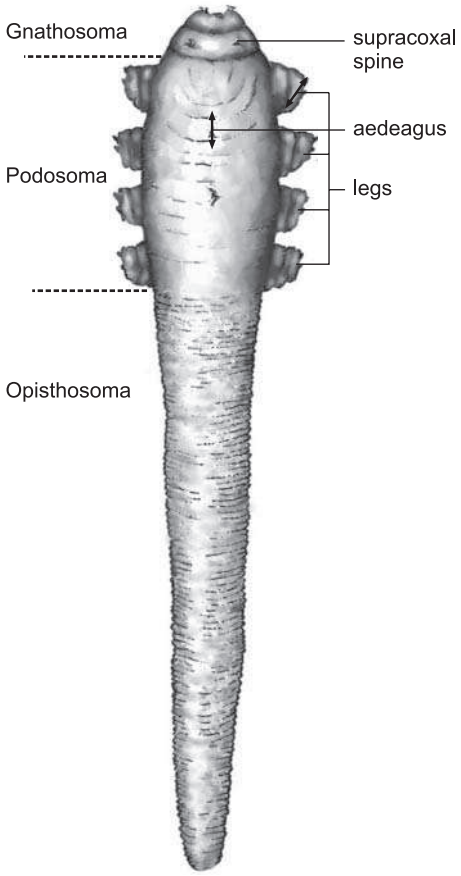

Figure 1. Morphology of *Demodex bisonianus* (male, dorsal view)

Morphological characteristics of demodecid mites at hofeed mammals

Demodecid mites are small, tinyusuallyelongated body with four pairs of short, stump-like, forward-pointing legs, displaced towards the front; stiletto-like chelicerae, three-part palpi, a massive hip element, and a number (4–5) of rod shaped bristles on the distal segment. tagmata – the gnathosoma, podosoma and opisthosoma – are clearly distinguishable in the body structure.

In view of the reduction of a number of morphological features, there are not many characters that can be used for diagnostic purposes in demodecid taxonomy. The following are usually taken into account the shape of the supracoxal spines and the distance between them, the number, position and shape of the pedipalp claws/setae, the shape and position of the pharyngeal bulb, the position and length of the aedeagus (male) and genital opening lid in the female, the presence of the opisthosomal organ (proctodeum), the shape of the posterior section of the opisthosoma, the presence of epimeral plates and their shape. Selected measurements and tagmata proportions may also be invoked as diagnostic characters: body length and breadth, length and breadth of the gnathosoma, podosoma and opisthosoma, body length-to-width ratio,

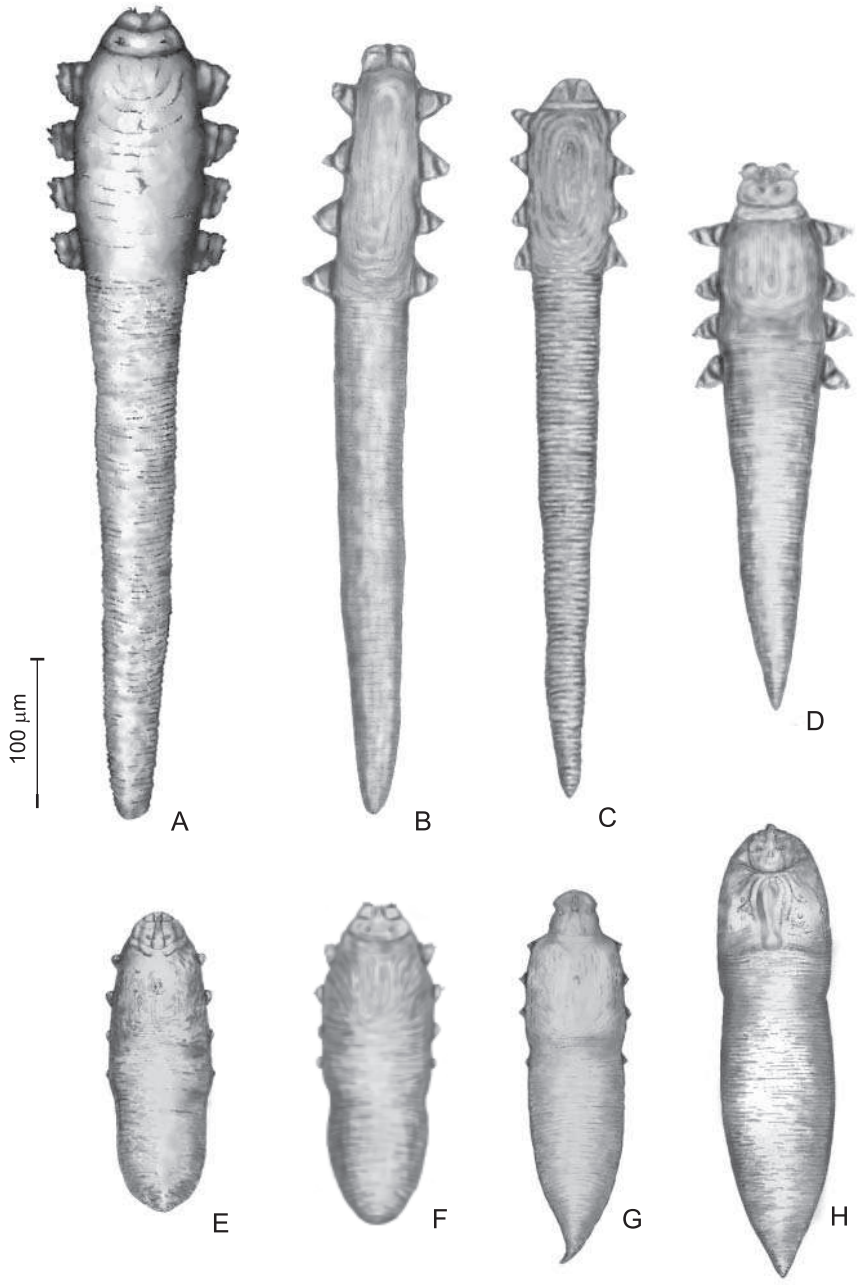

Figure 2. Demodetic mites from hoofed mammals (dorsal view) A – *Demodex bisonianus*, B – *D. ghanensis*, C – *D. caballi*, D – *D. tauri*, E – *D. equi*, F – *D. acutipes*, G – *D. phylloides*, H – *D. bovis*

Table 1. Hair follicle mites (Demodecidae) from hoofed (Cetartiodactyla, Perissodactyla)

Species of *demodex*	Host
D. acutipes Bukva et Preisler, 1988	*Cervus elaphus* (Cervidae)
D. aries Desch, 1986	*Ovis aries* (Bovidae)
D. bantengi Firda, Nutting et Sweatman, 1989	*Bos javanicus* (Bovidae)
D. bisonianus Kadulski et Izdebska, 1996	*Bison bonasus* (Bovidae)
D. bovis Stiles, 1892	*Bos taurus* (Bovidae), *Bison bonasus* (Bovidae) (accidental)
D. caballi (Railliet, 1895) (redesc. Desch, Nutting 1978)	*Equus caballus* (Equidae)
D. cafferi Nutting, Guilfoy, 1979	*Syncerus caffer caffer* (Bovidae)
D. caprae Railliet, 1895	*Capra hircus* (Bovidae)
D. cervi Prietsch, 1886; Vanselov, 1910 (? syn. *D. kutzeri* Bukva, 1987)	*Cervus arystotelis* (= *Rusa unicolor*), *Cervus elaphus* (Cervidae)
D. equi Railliet, 1895 (sensu Bennison 1943)	*Equus caballus* (Equidae)
D. kutzeri Bukva, 1987 (= *D. cervi* sensu Kutzer et Grünberg 1972)	*Alces alces*, *Cervus elaphus*, *Capreolus capreolus*, *Cervus nippon pseudaxis* (Cervidae)
D. odocoilei Desch, Nutting, 1974	*Odocoileus virginianus* (Cervidae)
D. ovis Railliet, 1895	*Ovis aries* (Bovidae)
D. phylloides Csokor, 1879	*Sus scrofa scrofa*, *Sus scrofa domestica* (Suidae)
D. pseudaxis Schpringdts-Schmidt, 1937 (? syn. *D. kutzeri* Bukva, 1987)	*Cervus hortulorum* (= *C. pseudaxis hortulorum*, *C.nippon dybowskii*), *Cervus nippon pseudaxis* (Cervidae)
D. tauri Bukva, 1986	*Bos taurus* (Bovidae)
Demodex spp.	*Bison bison* (Vestweber et al. 1999) *Bison bonasus* (Izdebska 2006b) *Capreolus capreolus* (Prietsch 1909) *Cervus elaphus* (Bukva et Preisler 1988) *Odocoileus hemionus hemionus* (Gentes et al. 2007) *Ovis aries* (Bukva 1990) *Taurotragus oryx* (Bukva et. al.1988)

the ratio of the opisthosoma length to the total body length, the shape and size of eggs and the presence in them of an operculum, presence or absence of protonymphal stages, the length of the vulva and aedeagus (e.g. Nutting 1976, Xie Hexiu *et al.* 1982). Adaptations for parasitism are in this case applicable both the size and the shape of the body. These are one of the smallest mites – average dimensions of adulti amount to 250 μm in length, the biggest representatives (*Demodex longissimus*) can reach up to 800 μm, but the smallest ones (*D. criceti, D. gatoi*) achieve no more than 80 μm in this stage (Izdebska

Table 2. Topic specificity of selected demodecid species from hoofed mammals

Host	Microhabitat	Mite
Bos taurus Linnaeus, 1758	sebaceous glands	*Demodex bovis* Stiles, 1892
	Meibomian glands (Oppong *et al*. 1975)	*Demodex ghanensis* Oppong, Lee, Yasin, 1975
	hair follicles (above or at the level of the sebaceous duct) (Bukva 1986)	*Demodex tauri* Bukva, 1986
Bison bonasus (Linnaeus, 1758)	Meibomian glands (Izdebska 2006b)	*Demodex bisonianus* Kadulski et Izdebska, 1996
	sebaceous glands	*Demodex bovis* Stiles, 1892 (accidental)
Capra aegagrus hircus (Linnaeus, 1758)	unit	*Demodex caprae* Railliet, 1895
Ovis aries Linnaeus, 1758	sebaceous glands (Desch 1986, Bukva 1990)	*Demodex aries* Desch, 1986
	hair follicles; skin of head (eyelids, head)	*Demodex ovis* Hirst, 1919 Railliet, 1895
Cervus elaphus Linnaeus, 1758	sebaceous glands	*Demodex acutipes* Bukva et Preisler, 1988
	hair follicles	*Demodex kutzeri* Bukva, 1987
Sus scrofa Linnaeus, 1758	sebaceous glands (Fryderyk and Izdebska 2001)	*Demodex phylloides* Csokor, 1879
Equus caballus Linnaeus, 1758	Meibomian glands	*Demodex caballi* (Railliet, 1895)
	general body hair follicles, hair follicles	*Demodex equi* Railliet, 1895

2006a); the biggest hair mite from Ungulates can about 580 μm (*D. bisonianus*) and the smallest – about 190–200 μm (male of *D. equi*, *D. acutipes*, *D. phylloides*). Body shape widely varies in many species, from slim and long forms (*D. bisonianus*, *D. caballi*, *D. ghanensis*), to shorter, oval ones (*D. acutipes*, *D. equi*) (fig. 2). The body can be evenly slim, or even oval (e.g. *D. acutipes*), but in some the body is distinctly narrowing towards the end (e.g. *D. bovis*, *D. phylloides*, *D. tauri*) (Hirst 1919, *et al*. 1975, Desch and Nutting 1978, Bukva 1987, Bukva and Preisler 1988, Izdebska 2000, 2006c, Izdebska and Fryderyk 2002).

Due to the adaptation for living in the host's tissue the Demodecidae suffered an extreme reduction in a number of morphological elements (Bukva 1991), e.g. thy have only scarce, strongly reduced bristles, which makes species identification harder. The body is separated into three distinct tagmas. small gnathosoma has a trapezoidal or rectangular shapeon the dorsal side there are supracoxal spines of various shapes, and on the ventral side the horseshoe-

shaped outline of the pharynx can be seen, at the level of which are the subgnathosomal setae. The podosoma supports the much-reduced legs with a pair offorked claws, which usually protrude only slightly beyond the line of the podosoma. On the ventral side of most adult mites the epimeral plates are readily discernible. The vulva of the female is situated ventrally, behind or partially between the epimeral plates of the fourth pair of legs. The aedeagus of the male is situated dorsally, in the midline of the podosoma. The opisthosoma is usuallyelongated with cuticular striations and may comprise over 80% of the body length (Hirst 1919, Nutting 1976, Xie *et al.* 1982, Bukva 1991, Izdebska 2006a) (fig. 1). Sexual dimorphism is usually weakly emphasized, by the means of slight differences in the size and proportions of the body (e.g. *D. phylloides* living in the pig and the boar) (Izdebska 2000, Fryderyk and Izdebska 2001).

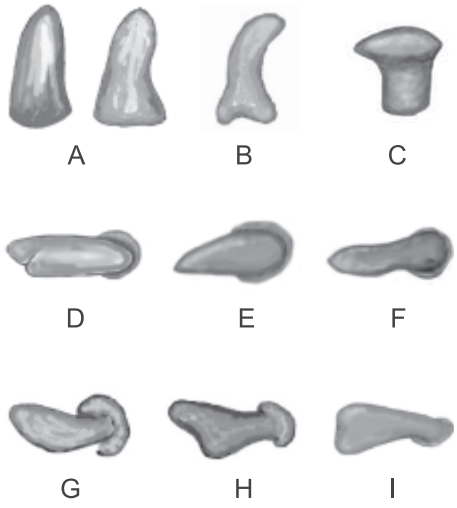

Figure 3. Shapes of supracoxal spines of demodectic mites A – *Demodex bisonianus*, B – *D. ghanensis*, C – *D. caballi*, D – *D. bovis*, E – *D. phylloides*, F – *D. equi*, G – *D. acutipes*, H – *D. tauri*, I – *D. kutzeri*

Morphological differentiation in demodecid mites as an adaptation to the microenvironments occupied in skin of hoofed mammals

Hair follicle mites have high specifity of species; in reality, only four species were observed in multiple hosts(Bukva 1991, Izdebska 2002). There is also a near universal tendency for the development of synhospitalic species – often comes across two or more synhospitalic hair follicle mites a single host species (Table 1, 2). Synhospitalic species may have diverged as a result of synhospitalic speciation, or following some modification to life cycles brought about by mutation or by microgeographic isolation. In this way variants specific to the same host could have come into existence, exhibiting considerable similarity of many morphological features; such variants have been described in a group of rodent host species (Nutting 1974).

Nonetheless, a series of unusual structural features in the Demodecidae, without doubt adaptations to parasitism, should be considered as the effect of the development not only of host specificity, but also of topical specificity. This is because hair follicle mites usually display a distinct topographic specificity, moreover, they are usually strictly associated with particular

tissues or structural features of the host's skin. Different species demodectic mites of hofeed mammals locate in the hair follicles, sebaceous glands, in modified glands (e.g. Meibomian glands) and their ducts (e.g., Oppong *et al*. 1975, Bukva 1991, 2006a), however the synhospitalic species of a given host are usually to be found in different locations.

On the basis of both original material and literature data (e.g., Izdebska 2000, 2001a, 2001b, 2002, 2005, 2006b, 2006c), the characters of synhospitalic Demodecidae species found on particular hosts have been compared with those of hair follicle mites from different mammalian species (with different degrees of relatedness) in the context of their location. Species from different hosts but colonizing roughly the same microhabitat frequently display more similarities than those living on the same host but in different microhabitats. Although these similarities appear principally in the dimensions, shape and proportions of the tagmata, marked resemblances have sometimes also been observed in other morphological characters, regarded as diagnostic in taxonomy of Demodecidae. For example, *D. bisonianus* living in the Meibomian glands of European bison, is very similar to *D. ghanensis* (Meibomian glands of cattle) or *D. caballi* (Meibomian glands of horse), in terms of size, body shape and proportions or shape of supracoxal spines and claws. Living in sebaceous glands of cattle *D. bovis* is similar to *D. phylloides* (sebaceous glands of wild boar), *D. aries* (sebaceous glands of sheep) and *D. acutipes* (sebaceous glands of red deer); *D. tauri* (hair follicles of cattle) is similar to *D. ovis* (hair follicles of sheep) or *D. kutzeri* (hair follicles of red deer) (Table 2; Fig. 2, 3). These observations suggest that *Demodex* species could have evolved along a pathway other than the one propounded earlier in the synhospitalic speciation concept. Some demodecid species, having developed the necessary adaptations for life in a particular microhabitat in mammalian skin, were able under favourable circumstances to colonise similar habitats in a closely related host species. It is also possible that the colonisation by hair follicle mites of a given microhabitat in a common ancestor preceded the divergence of the host species. The mites of this host ancestor remained occupants of their microhabitat and speciated in parallel with their host.

The Cetartiodactyla and Perissodactyla have or more synhospital species of demodectic mites, in the hair follicles, sebaceous glands and Meibomian glands. In skin of European bison was found only *D. bisonianus*. (Kadulski and Izdebska 1996, Izdebska 2000, 2006b). The extant natural populations of *B. bonasus* are products of the restitution procedures based on the limited number of individuals surviving in different zoos and the natural parasitic fauna of the European bison (e.g. another specific species of *Demodex*), probably, almost perished along with the demise of the natural host populations. Perharps vacant habitats in skin to be occupied by demodectic mites of another species from hoofed mammals.

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Wybrane aspekty przystosowania nużeńcowatych do pasożytnictwa

Streszczenie Nużeńcowate (Demodecidae) to jedne z najbardziej wyspecjalizowanych stawonogów pasożytniczych ssaków, odnotowane u przedstawicieli 13 rzędów, w tym 16 gatunków opisano u kopytnych. Wykształciło się u nich szereg niezwykłych przystosowań do pasożytnictwa (np. robakowaty kształt ciała z silnie zredukowanymi odnóżami, miniaturyzacja, redukcja szczecin i innych elementów morfologicznych), które stanowią adaptacje do bytowania w mieszkach włosowych, różnych rodzajach gruczołów skóry i ich przewodach wyprowadzających. Jednocześnie nużeńcowate wykazują znaczną zmienność pod względem kształtów, proporcji tagm, rozmiarów, lokalizacji i formy wielu cech morfologicznych, co ma związek z przystosowaniem do zasiedlania skóry różnych gatunków ssaków, rekrutujących się z różnych rzędów, ale też wykształceniem specyficzności topicznej, związanej z zasiedlaniem w obrębie żywiciela odrębnych mikrohabitatów.Zatem obok specyficzności żywicielskiej, występuje tendencja do kształtowania się w obrębie poszczególnych gatunków żywicielskich form synhospitalnych; często u jednego gatunku żywiciela spotyka się dwa lub więcej gatunków synhospitalnych nużencowatych, które mogły się różnicować (wg Nutting 1974) na drodze tzw. specjacji synhospitalnej. Jednak analiza szeregu cech morfologicznych synhospitalnych nużeńcowatych ssaków kopytnych wskazuje, że gatunki z różnych żywicieli, zasiedlające u nich zbliżony mikrohabitat, wykazują szereg podobieństw, które dotyczą rozmiarów, kształtu ciała, proporcji tagm, kształtu kolców suprakoksalnych, czy innych elementów morfologicznych, uznawanych za istotne w taksonomii Demodecidae. Może to sugerować inny wariant specjacji, w którym nużeńcowate przystosowane do bytowania w określonym mikrohabitacie skóry żywiciela, zasiedlały analogiczne, wolne habitaty pokrewnych gatunków żywicieli.