

Loriscola mjobergi* (Stobbe, 1913) sensu lato (Insecta, Psocodea, Phthiraptera, Ischnocera, Trichodectidae) from two *Nycticebus* species (Mammalia, Primates) from Vietnam, with notes on the genus *Loriscola* Bedford

Eberhard Mey

Martin-Luther-Universität Halle-Wittenberg, Zentralmagazin Naturwissenschaftlicher Sammlungen, Domplatz 4, D-06108 Halle (Saale), Germany. <mey-rudolstadt@t-online.de>

Key words: Phthiraptera, Ischnocera, Trichodectidae, Felicolini, *Lyalicola* subgen. nov., Loridae, *Nycticebus pygmaeus*, *Nycticebus bengalensis*

Summary

From the Cuc Phuong National Park in North Vietnam, the occurrence of *Loriscola mjobergi* s. l. on two new host species is presented for the first time: *Nycticebus bengalensis* Lacépède and *N. pygmaeus* Bonhote (Loridae, Lorinae). The material from both host origins cannot be sufficiently distinguished from that of *L. mjobergi* (Stobbe, 1913) ex "*Nycticebus borneanus* [?] from North Borneo" at present. Also the (poorly preserved) male of "*Trichodectes brachycephalus* Ewing" from Malaysia seems to be as conspecific with the still monotypic *Loriscola mjobergi* s. l. as a pair collected on "*Nycticebus buku*" (= *N. coucang*) on the west coast of Sumatra. Thus, *Loriscola* Bedford, 1936 has so far only been found on five of the 11 Asian Loris and *Nycticebus* species, while no finding of this unusual trichodectid has yet become known from the five African Angwatibos and Pottos (Loridae, Perodicticinae).

Loriscola mjobergi s. l. is described in detail according to literature and Vietnamese material, with special attention to head morphology including chaetotaxy. At the same time, a first attempt is made to develop a setae terminology based on homology for avian and mammalian chewing lice. It can be made clear that *Loriscola* is morphostructurally so unique within the trichodectids that it must seem absurd to place it together with *Felicola* Ewing, *Suricatoecus* Bedford and/or *Paradoxuroecus* Conci in the Tribus Felicolini Kéler, 1938, as was done after a cladistic analysis and classification presented in 1985 and remained unchallenged ever since. Several derived characters (a. o. in head shape and chaetotaxy, absence of gular plate, modified cervical sclerites, several head sutures, very large ommatidia, dorsal and ventral projection of abdominal pleurum IV, abdominal segment VII with complete tergite in ♂ and ♀, peculiar subgenital plate, simple gonapophyses lobe with 6-7 mesochaetes on the inner side, prominent male genital) clearly speak for a relative independence of *Loriscola* (at least in a separate tribus - Loriscolini - within the Trichodectinae Kellogg).

This new situation made it necessary to transfer all *Felicola* species (incl. "*Trichodectes malaysianus* Werneck"), which had previously been placed in *Loriscola*, into a subgenus of their own.

Lyalicola subgen. nov. with the subgenerotype "*Felicola hercynianus* v. Kéler, 1957" is proposed for this purpose. All 11 species belonging to the new subgenus (in comb. nov.) are listed with their type hosts. The morphological similarities between *Loriscola* and *Cebidicola* Bedford (Trichodectinae, Cebicolini), which seem to have been insufficiently considered so far, are explicitly pointed out.

* Dedicated to Tilo Nadler on his 80th birthday.

***Lorisicola mjobergi* (Stobbe, 1913) sensu lato (Insecta, Psocodea, Phthiraptera, Ischnocera, Trichodectidae) từ hai loài *Nycticebus* (Mammalia, Linh trưởng) từ Việt Nam, có ghi chú thuộc chi *Lorisicola* Bedford**

Tóm tắt

Tại Vườn Quốc gia Cúc Phương, miền Bắc Việt Nam, lần đầu tiên có sự xuất hiện của *Lorisicola mjobergi* trên hai loài ký chủ mới: *Nycticebus bengalensis* Lacépède và *N. pygmaeus* Bonhote (Loridae, Lorinae). Mẫu vật được thu thập trên hai loài ký chủ trên không thể được phân biệt với *L. mjobergi* (Stobbe, 1913) được tìm thấy trên "*Nycticebus borneanus* [?] từ Bắc Borneo". *Lorisicola mjobergi* được mô tả chi tiết theo tài liệu và tư liệu Việt Nam, đặc biệt chú ý đến hình thái của phân đầu.

Introduction

In the case of the *Lorisicola*, which lives on primitive primates and is still only known in one species, it can no longer be a matter of discretion to grant it unrestricted generic status. It might well offend the taxonomic tact of any ardent mallophagologist to deny it that. Lyal (1985), however, went a step too far in his cladistic analysis of the Trichodectidae by placing *Lorisicola mjobergi* together with 11 species once placed in *Felicola* and mostly originating from cats (Felidae) in one and the same genus and subgenus, *Lorisicola* (*Lorisicola*). This may not sound particularly exciting at first, but it does come as a surprise. Because one can easily be inclined to assume that in this case at least a secondary infestation from a cat to a monkey took place at some point in evolution. But the reverse case, i.e. a switch from monkey to cat, is hardly likely according to previous findings. This strange contrast would not change in principle if *Lorisicola* were to be degraded to a subgenus of *Felicola*, as has already happened.

In the following it will have to be shown, argued and justified why *Lorisicola mjobergi* is such a peculiar chewing louse living on loris, whose closer and more distant relationship is still unclear. And it is necessary to propose some nomenclatural changes in the Tribus Felicolini, into which *Lorisicola* has been wrongly drawn.

Material and methods

Lorisicola mjobergi s. l. has so far been reported from five Asian loris species in this order:

1. "*Nycticebus borneanus*" (= *Nycticebus* sp.?, type host) from northern Borneo (Stobbe 1913).
2. *Nycticebus coucang* (Boddaert, 1785) from Johor Lama, Malay Peninsula (Ewing 1930).
3. "*Nycticebus buku*" (= *Nycticebus coucang*) from West Coast Sumatra (Bedford 1936, Werneck 1950)
4. *Nycticebus bengalensis* (Lacépède, 1800) from North Vietnam (presented here).
5. *Nycticebus pygmaeus* Bonhote, 1907 from North Vietnam (presented here).

A deeper α -morpho-taxonomic investigation of the new *Lorisicola* material could not be done here, because the indispensable type material from the genotype (*L. mjobergi*) was not available in time. To base the description of a possibly new form only on (often incomplete) literature sources seemed to me to be an avoidable risk, especially with *Lorisicola mjobergi*. This deficit will be made up for in a later contribution.

The fact that Lyal (1985) limited his information on the hospitale distribution of trichodectids mainly to families and possibly orders and left out type host data to a large extent is not one of the strengths of his paper. Thus, a hint would have been welcome from which host(s) the approx. 100 ♂ and 100 ♀ of *Lorisicola mjobergi* he examined originated.

The results of the body measurements on *Lorisicola* are summarised in Table 1. The self-measurements were made in the established manner. Anterior head width was measured at the maximum extent of the clypeal carina, head length mediad from the lower edge of the central cibarial

sclerite (i.e. craniad of the central rhombic sclerite of the pronotum) to the tip of the head. The width of the occiput has been measured in each case with and without the protrusion of the ommatidium.

Except for the reproductions, all line drawings were made by the author. The microphotographs were made with a Keyence VHX-5000 digital microscope at the Dresden University of Applied Science, Faculty of Agriculture/Environment/Chemistry-Biodiversity/Nature Conservation in Pillnitz, Germany.

Table 1. Terminology of head setae comparing avian Ischnocera as reference (see Gustafsson & Bush 2014, Mey 1994) and some mammalian Ischnocera. Abbreviations see p. 183.

Avian Ischnocera	Mammalian Ischnocera			
	<i>Trichodectes</i> spp.	<i>Felicola subrostatus</i> (Burmeister) subgenus <i>Felicola</i>	<i>Felicola hercynianus</i> v. Kéler subgenus <i>Lyalicola</i> gen. nov.	<i>Loricicola mjobergi</i> s. l.
character	Figure 19	Figures 22-23	Figure 21	Figures 8-11
ads (each side 1)	present (1) but almost at median	present (2) but on each side at the same height one ads (as mesochaete) more	present (2) but on each side at the same height one ads (as mesochaete) more	present (2) but one ads more on each side, both microchaetae insert at the same height at a distance of twice their length
as 1-3 (each side 3)	present (3)	present (2) but as 2 absent	present (3) but as 1 submarginal at the lower edge	present (3)
avs 1-3 (each side 3)	present (3)	present (3-4)	present (3-4) but one avs more between avs 2 and 3, all standing in line	present (4) but one avs more, not standing in line
dos (0-1 or more)	present (1-2) in the ♂ 2 standing close together, in the ♀ 0-1	present (1)	absent	present (1) as Microchaete
dsms (each side 1)	present (1)	present (1) as Macrochaete	present (1) as Mesochaete	present (1) as submarginal Microchaete
mnds (each side 1)	present (1)	present (1)	present (1)	present (1)
mts (on each side mostly 5, more rarely 4, also up to 10 in Gonioididae)	present (7)	present (7)	present (7-8)	present (mostly 8, also 7 or 9)
os (each side 1-2)	present (1) marginal	present (1) marginal	present (1) submarginal	present (2) on each side marginally 2 microchaetae, anterior (os 1) dorsal, posterior (os 2) ventral
pas (each side 1)	present (2)	present (2)	present (2)	both absent
pcs (each side 1)	present	present	present	present
pns (each side 1)	present (1)	present (1)	present (1-2)	present (1)
pos (each side 1)	present	present	present	present
pts (0-1 or more)	absent	absent	absent	absent
vsms 1-2 (each side 2)	present (2)	present (2)	present (1) vsms 1 as macrochaete, but vsms 2 absent	present (2)

Type material

The whereabouts of the complete type material of “*Trichodectes mjöbergi*” is not known to me. Lectotype and/or lectoparatypes of this species have not been nomenclaturally effectively designated so far (see below Göllner-Scheiding 1973). Werneck (1950: 3) was able to examine the type series, but Stobbe’s original specimens had already been prepared in Canada balsam and newly labelled by W. Eichler (Fig. 1). “Dezeseis femeas, onze machos e cinco formas imaturas, amavelmente emprestadas pelo Dr. W. Eichler, do Museu de Berlin. Material rotulado “WEC 501, *Trichodectes mjöbergi* Stobbe, Type, ab *Nycticebus*.” [Sixteen females, eleven males and five immatures, kindly lent by Dr. W. Eichler of the Berlin Museum. Material labelled “WEC 501, *Trichodectes mjöbergi* Stobbe, Type, ab *Nycticebus*.”]. The material returned to Berlin after the war, but did not remain complete in the current holdings there after 1973. Göllner-Scheiding (1973: 39) recorded the existence of the Stobbe series of “*Trichodectes mjöbergi*”: “type (♂), allotype (♀), paratypes (1 ♂, 1 ♀)”, “10 microscope slides with several specimens each and 5 microscope slides with 1 specimen each”, on microscope slides no. 1288/11, 1 to 19, but with the irritating remark: “No information on number of animals.” The above designations “type”, “allotype” and “paratypes” have been used by Göllner-Scheiding (1973: 39), and they have no nomenclatural relevance, since they have never been published in connection with a revision of *Loricicola mjöbergi*.

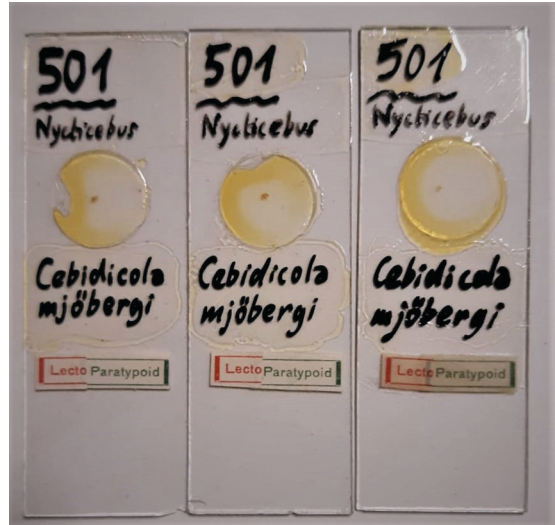


Fig.1. Microscope slides of the type material of *Loricicola mjöbergi* (Stobbe, 1916) in the Berlin Museum of Natural History (cf. Eichler 1941: 393). Original labels as well as the locality card “WEC Nr. 501” are no longer available. Nowhere is there any mention of “*Cebidicola mjöbergi*” in any publication. The slides labelled in this way were available to Werneck (1950) without him commenting on them (see p. 185). He obviously tacitly replaced “*Cebidicola*” with “*Trichodectes*”. Example of problematic handling of type material. Photo: W. Mey, October 2021.

In the Berlin Museum of Natural History, where the type series of Stobbe (1913: 380) was deposited, “*T. mjöbergi*” is not listed in a type list of the “Eichler Collection” from the beginning of the 2000s. However, the species I was looking for was found under “*Cebidicola mjöbergi*”, with three individuals on three microscope slides (Fig. 1). It is probable that no further specimens of the once 16 ♂, 11 ♀ and 5 larvae type series of “*Trichodectes mjöbergi* Stobbe, 1913” exist in the Berlin Museum of Natural History. Only after the examination of the currently unavailable preserved type material can its correct designation be thought of.

With the rigorous clearing of Prof. Eichler’s workrooms in the Berlin Museum of Natural History, where he had worked since 1969, a not inconsiderable part of his scientific estate was lost after his death in February 1994. This also included numerous microscope slides of phthiraptera, as I unfortunately had to learn from my own experience, and it does not require much imagination that the loss of type material was (unconsciously) accepted in the process. From this point of view, a revision of the mallophagan type catalogue by Göllner-Scheiding (1973) is urgently needed.

“***mjöbergi, mjoebergi or mjobergi***”? According to the “International Rules of Zoological Nomenclature”, before 1985 German umlauts ü, ö and ü in dedication names had to be transcribed into ue, oe and oe. This special rule has since been dropped. In the case of the Swede Eric Mjöberg (1882 - 1938), it was and is against the rules to use the spelling *mjöbergi* or *mjoebergi* (instead of the correct *mjobergi*) or *Mjoeberginirmus* (instead of *Mjoberginirmus*) (Eichler 1989 a, b), as did Price et al. (2003) after Lyal (1986). This also applies to the same extent to the *mjobergi* epitheta of the animal louse genera *Boopia*, *Chapinia*, *Clayia*, *Laemobothrion*, *Columbicola* and *Pediculus*.

Chaetotaxy as a taxonomic-systematic character complex in the trichodectids

In the redescription of *Damalinia (Tricholipeurus) zaganseeri* Lux et al., 1997, the authors attempted to develop a terminology for head setae (of this species). In doing so, they used the head setae terminology that is already in relatively widespread use in avian ischnoceran lice (Mey 1994). This was a courageous step in this connection, because Kéler (1938) had already drafted the outlines of a special nomenclature of the chaetotaxy of the Trichodectidae, which, however, has not been taken up or even further developed since then. Kéler (1938: 418 f.) states:

“I have long noticed that the Mallophaga in general and the chewing lice of mammals in particular show great regularity in chaetotaxy. In contrast to the stigmas, the setae are characteristic of higher groups, superior to the species, and as a very constant feature they are of great taxonomic value. [...] The setae of the head and partly of the thorax are particularly constant. Those of the abdomen are partly fluctuating in number, but the setae groups are constant.” [Translation from German into English by the author.]

The setae patterns of both mammalian and avian ischnocera are similar in some details. However, the extent to which these similarities are sufficient to demonstrate homologous formations in both groups (which are to be expected per se according to their systematic position) has not yet been investigated enough to develop a common terminology for both groups. In the case of the extraordinary *Loricicola*, it is worthwhile to attempt to compare its head chaetotaxy with that of *Trichodectes* spp. and *Felicola* s. l. on the one hand, and with the terminology used today for the avian ischnocera on the other. Here, too, Kéler (1940: 35-38)¹ had already done pioneering work.

However, it will not be so easy to establish homology in chaetotaxy in avian and mammalian ischnocera, especially according to the criterion of position (Remane 1956). Even with these minute characteristics, we are dealing with a diversity and variability that is still difficult to grasp. The preliminary result compiled in Table 1, however, makes it clear enough that we should progress along this path of inferring relationships between the taxa.²

Abbreviations used

ads: anterior dorsal seta

as 1-3: anterior (marginal) setae am Clypeus

ATP: anterior tentorial pit

avs 1-3: basal clypeal setae

CC: clypeal carina

dos: dorsal occipital setae, dos 1-2 or more

dsms: dorsal submarginal seta auf Clypeus

GP: gular plate

LCS: lateral cervical sclerite

mids: mandibular seta

mts: marginal temporal setae

OCC: occipital carina

os: ocularis (1) or ocular setae 1-2

PAN: preantennal nodus

pas: preantennal seta

pcs: preconal seta

pns: postnodal seta

pos: preocularis or preocular seta

ppss: pronotal post-spiracular seta

PON: postocular nodus

PRN: preocular nodus

PST: Prostigma

PTP: posterior tentorial pit

pts: first posttemporal seta

RS: rhombic sclerite

TC: temporal carina

TMC: temporal marginal carina

VC: ventral carina

vsms 1-2: ventral submarginal seta, **1** chomaris, **2** oscularis (clypeal setae)

¹ This fundamental paper is still circulating with an incorrect year of publication (“1939”). Most recently, Mey (2009: 185-187) clarified that it was actually published in January 1940.

² On the back of the head of some avian ischnoceras (e.g. *Brueelia* complex) there are often tiny unpigmented dimples called sensilla, which are sometimes difficult to detect on prepared material (Gustafsson & Bush 2017). In other groups (e.g. *Lipeurus* s. l. and *Oxylipeurus* s. str. or *Anatoecus*) one will find fully developed setae instead of sensilla. This suggests that, figuratively speaking, we may be dealing with “sleeping setae” that have rudimentarily regained or preserved their original shape in evolution. This phenomenon should not go unnoticed in an attempt to homologate the setae dress of all ischnoceran groups.

More questionable type host of “*Trichodectes mjobergi*” and the status of “*T. brachycephalus*”

According to Stobbe (1913: 380), *Lorisicola mjobergi* is supposed to originate from “*Nycticebus borneanus*” from North Borneo, where, however, it does not occur, but only these two sympatric species live: *N. menagensis* Lydekker, 1893 and *N. kayan* Munds, Nekaris & Ford, 2013 (Nekaris 2013, 2020). Eichler (1941: 357) gives “*Nycticebus tardigradus borneanus* Lyon” as the type host of *L. mjobergi* without explanation. However, *Nycticebus tardigradus* (Linnaeus, 1758) is endemic to Sri Lanka (Ceylon) (Nekaris 2013, 2020), so it is indeed not a possible host of *L. mjobergi*. It remains to be stated that it is still unclear from which of these host species *Lorisicola mjobergi* actually originates. Thus, *Nycticebus coucang* can no longer be considered the characteristic host of *L. mjobergi*, as it is still reported in the literature (Hopkins & Clay 1952, Lyal 1987, Price et al. 2003). The species status of *Lorisicola brachycephalus* (Ewing) also needs to be re-examined.

Ewing (1930) describes “*Trichodectes brachycephalus*” after a male collected from the fur of a *Nycticebus coucang* (elsewhere it is said of the same host: “flying lemur” [sic!]) originating from Johor Lama, Malay Peninsula. Werneck (1950: 7) examined the specimen and comes to this conclusion:

“O macho holótipo de *T. brachycephalus* é um péssimo exemplar, descolorado e deformado, cujo estudo jamais poderá proporcionar senão juízo imperfeito sobre o parasito. Não permite, por exemplo, a devida observação da vesícula-penis, tão característica em *L. mjobergi*, mas deixa perceber uma linha mediana que nos parece indicar o sulco longitudinal, bordado de escamas, que este órgão possui, e duas faixas laterais, provavelmente correspondentes aos ramos da placa quitinosa da vesícula. É possível, portanto, que existam caracteres subespecíficos distinguindo os parasitos descritos por Ewing e Stobbe, embora isto não nos pareça verossímil. Mas quanto à identidade das espécies, cremos não haver a menor dúvida.”

[“The male holotype of *T. brachycephalus* is a very poor specimen, discoloured and deformed, whose study can only give an imperfect judgement on the parasite. It does not allow, for example, the proper observation of the vesicula-penis, so characteristic in *L. mjobergi*, but it allows us to perceive a median line which seems to indicate the longitudinal groove, embroidered with scales, which this organ possesses, and two lateral bands, probably corresponding to the branches of the chitinous plate of the vesicle. It is possible, therefore, that there are subspecific characters distinguishing the parasites described by Ewing and Stobbe, although this does not seem likely. But as to the identity of the species, we believe that there is not the slightest doubt.”]

According to Nekaris (2013, 2020), the ranges of *Nycticebus bengalensis* (from the north) and *N. coucang* (from the south) overlap approximately in the middle of the Malay Peninsula. The characteristic host specimen of *Lorisicola brachycephalus* clearly comes from the southern range, where both loris species do not occur together. Therefore, it can be assumed that the present Vietnamese material is of previously unstudied host origin.

Doubts about the generic assignment of “*Trichodectes mjobergi*”

After Bedford’s (1936) well-argued erection of *Lorisicola* per “*Trichodectes mjobergi*”, Hopkins (1949) seemingly unreservedly, but Werneck (1950) with “bellyache” argued for its independence. Hopkins & Clay (1952: 201) did not deviate from this insofar as they listed *Lorisicola* as a valid genus, but declared it “doubtfully distinct from *Felicola*” almost in the same breath, thus accommodating the widely presented doubts of Werneck (1950) in their own way. From a parasitophyletic point of view, Hopkins (1949: 540) had stated:

„... for the very interesting fact that *Lorisicola*, which occurs on an Asiatic lemur, and *Cebidicola*, which is found on several American members of the family Cebidae, are obviously closely related. It seems highly significant both that the Lemuroidea and Ceboidea are the two most primitive groups of the Primates after the Tupaiidae, and that those Cebidae on which *Cebidicola* occurs are precisely those which appear not to be normally infested with Anoplura. I am convinced that *Lorisicola* and *Cebidicola* are the remnants of a once very wide-spread primary infestation of the Primates with Trichodectidae, but the supposed occurrence of *Procavicola colobi* [3] on a monkey is not evidence in this connection because it is almost certainly erroneous and if correct is obviously secondary.”

Werneck (1950), who emphasised more morphological aspects in his discussion and also placed

them against the background of hospital distribution, located *L. mjobergi* in terms of relationship on the one hand close between *Cebidicola* (with three species) and "*Felicola jucci*" [= *Paradoxuroecus jucci* Conci, 1942 ex *Paguma l. larvata* (C. H. Smith, 1827)⁴ and on the other hand further between *Felicola* and *Trichodectes*. On the systematic position of *Lorisicola*, Werneck (1950: 1) details these thoughts:

"A diagnose acima representa mera tentativa e de definição do gênero *Lorisicola*, que até hoje comporta apenas uma espécie, na qual é difícil distinguir entre caracteres genéricos e específicos.

O genótipo em questão possui, em igual dose, caracteres dos gêneros *Trichodectes* e *Felicola*. Do primeiro apresenta a predominância da largura sobre o comprimento da cabeça, o acentuado dimorfismo sexual das antenas, o número de estigmas abdominais e a ausência de saliência posterior no abdômen do macho; do segundo, a forma subtriangular da região preantenal, o diminuto comprimento das cerdas e, até certo ponto, a pigmentação do abdômen. Nestas condições, talvez fosse mais acertado confundir-lo com as formas atípicas de posição genérica duvidosa que, arbitrariamente, incluímos no gênero *Felicola*.

Situa-se também entre o gênero *Felicola* ou, mais precisamente, entre *Felicola jucci* e o gênero *Cebidicola* (fig. 1). De fato, a semelhança entre esta última espécie e *L. mjobergi* é tão flagrante que nos repugna separá-los em gêneros distintos. Mas, como dissemos ao tratar da divisão genérica dos trichodectídeos, na primeira parte deste trabalho, é impossível os dividir sem incidir em absurdos semelhantes.

No entanto, e apesar do acima exposto, cumpre reconhecer que *L. mjobergi* se afasta um pouco mais das espécies características do gênero *Felicola* que *F. jucci*, não só pelo número de estigmas respiratórios abdominais, como pela pigmentação do abdômen da fêmea, pela forma das gonapófises e da região cefálica posterior às antenas. Nesta, as margens laterais convergem fortemente de diante para trás e de fora para dentro, a partir dos tubérculos oculares, tal como sucede nas espécies do gênero *Cebidicola*. Deste último gênero, *L. mjobergi* se aproxima ainda pela pigmentação abdominal da fêmea, que ocupa todo o tergito do anel correspondente ao último par de estigmas.

No momento, não podemos avaliar, com o necessário rigor, das afinidades de *L. mjobergi* para com os gêneros *Felicola* e *Cebidicola*, embora nos pareça não haver espécie mais relacionada a *mjobergi* que *F. jucci*. E este é o principal motivo que nos faz adotar o gênero *Lorisicola*, a título precário, como unidade sistemática, não convindo incluir sua única espécie num dos referidos gêneros sem perfeito conhecimento de causa. No momento, não podemos avaliar, com o necessário rigor, das afinidades de *L. mjobergi* para com os gêneros *Felicola* e *Cebidicola*, embora nos pareça não haver espécie mais relacionada a *mjobergi* que *F. jucci*. E este é o principal motivo que nos faz adotar o gênero *Lorisicola*, a título precário, como unidade sistemática, não convindo incluir sua única espécie num dos referidos gêneros sem perfeito conhecimento de causa. Tão estranho fato, de um maléfago de lemures mais se parecer a maléfagos de felinos* que aos dos macacos sulamericanos, nos impõe todas as medidas de prudência."

No momento, não podemos avaliar, com o necessário rigor, das afinidades de *L. mjobergi* para com os gêneros *Felicola* e *Cebidicola*, embora nos pareça não haver espécie mais relacionada a *mjobergi* que *F. jucci*. E este é o principal motivo que nos faz adotar o gênero *Lorisicola*, a título precário, como unidade sistemática, não convindo incluir sua única espécie num dos referidos gêneros sem perfeito conhecimento de causa. No momento, não podemos avaliar, com o necessário rigor, das afinidades de *L. mjobergi* para com os gêneros *Felicola* e *Cebidicola*, embora nos pareça não haver espécie mais relacionada a *mjobergi* que *F. jucci*. E este é o principal motivo que nos faz adotar o gênero *Lorisicola*, a título precário, como unidade sistemática, não convindo incluir sua única espécie num dos referidos gêneros sem perfeito conhecimento de causa. Tão estranho fato, de um maléfago de lemures mais se parecer a maléfagos de felinos* que aos dos macacos sulamericanos, nos impõe todas as medidas de prudência."

[The above diagnosis is only an attempt to define the genus *Lorisicola*, which up to now comprises only one species, and it is difficult to distinguish between general and specific characters.

This genotype possesses, in equal doses, characters of the genera *Trichodectes* and *Felicola*. From the former, it presents the predominance of the width over the length of the head, the accentuated

^[3] The current status of this species is: *Procaviphilus (Meganarionoides) colobi* (Kellogg, 1910) ex *Colobus guereza caudatus* O. Thomes, 1885 (Cercopithecidae). See Lyal (1985: 278 f.). In his cladistic system of the Trichodectidae (p. 286), *Lorisicola* and *Cebidicola* are relatively far apart in different subfamilies (the latter in the Dasyonyginae Kéler, 1938). Does this really clarify that there are no kinship ties between the two genera, which, after Kéler (1938), were first suggested for discussion by Eichler (1940)? Without substantiating his statements with concrete characters, Eichler (1940: 160) states: "*Meganarionoides* and *Cebidicola* are obviously closely related, while the position of *Lorisicola* to *Cebidicola* is still quite unclear." A little later Eichler (1941: 381) places *Cebidicola* and *Lorisicola* with *Meganarionoides* in the Cebidicolinae Eichler within the Trichodectidae. Lyal (1985) breaks up this "association". In my opinion, there are morphological similarities between the latter two genera (e.g. similar head structures, exceptionally large ommatidia, ventral projection of pleurum IV and very similar male genitalia), which are worth closer examination (Emerson & Price 1975, Werneck 1950). According to Hopkins (1949), a closer relationship between *Lorisicola* and *Cebidicola* could be considered. *Cebidicola* lives with three species on South American Atelidae (type hosts: Southern Muriquê, Columbian Red Howler and Ursine Red Howler).

⁴ Werneck (1948: 221), however, synonymises *Paradoxuroecus* with *Felicola*. - Conci (1942, 1947) gives as type host "*Paguma larvata grayi* Bennett", which is explicitly said to come from Burma, where, however, only the nominate form of the Masked Palm Civet occurs (Burgin et al. 2020). In Conci's publication of 1942, printed in the "Bollettino della Società Entomologica Italiana", Volume 74, N. 10, the date of publication is given: "31 Dicembre 1942". According to Poggi (2008), there is no indication to doubt the date given (as one could initially assume according to the circumstances of the time).

sexual dimorphism of the antennae, the number of abdominal stigmata and the absence of posterior prominence in the abdomen of the male; from the latter, the subtriangular shape of the preantennal region, the diminutive length of the bristles and, to a certain extent, the pigmentation of the abdomen. Under these conditions, it might be better to confuse it with the atypical forms of doubtful general position which we have arbitrarily included in the genus *Felicola*.

It is also situated between the genus *Felicola*, or, more precisely, between *Felicola juccii* and the genus *Cebidicola* [...]. In fact, the similarity between this last species and *L. mjobergi* is so flagrant that it repels us to separate them into different genera. But, as we have said in dealing with the general division of the trichodectids, in the first part of this paper, it is impossible to divide them without falling into similar absurdities.

However, and in spite of the above, we must recognize that *L. mjobergi* is a little more distant from the characteristic species of the genus *Felicola* than *F. juccii*, not only by the number of abdominal respiratory stigmata, but also by the pigmentation of the abdomen of the female, the shape of the gonapophyses and the cephalic region posterior to the antennae. In the latter, the lateralis margins converge strongly from front to back and from outside to inside, from the ocular tubercles, as occurs in the species of the genus *Cebidicola*. *L. mjobergi* is similar to the latter genus in the abdominal pigmentation of the female, which occupies the entire tergite of the ring corresponding to the last pair of stigmata.

At the moment, we cannot evaluate, with the necessary rigour, the affinities of *L. mjobergi* with the genera *Felicola* and *Cebidicola*, although we are able to evaluate, with the necessary rigour, the affinities of *L. mjobergi* with the genera *Felicola* and *Cebidicola*, although it seems to us that there is no species more related to *mjobergi* than *F. juccii*. This is the main reason that makes us adopt the genus *Loricicola*, on a precarious title, as a systematic unit, not being convenient to include its only species in one of the referred genera without perfect knowledge of cause. Such a strange fact, that a lemur malophagus looks more like feline malophagus* than to those of South American monkeys, imposes all precautionary measures on us.]

Apart from personal qualification and basic attitude in systematic questions, different currents and schools of thought in animal louse taxonomy of the 20th century meet here, such as reservations towards monotypic genera, insufficiently studied and/or underestimated traits, overcritical or glorified views on host specificity and co-evolution, and prevailing conservative zeitgeist in animal louse taxonomy.

***Loricicola* Bedford, 1936** gen. rev.

Figs. 1-5, 7-17, Tables 1-2

Generotype: "*Trichodectes mjobergi* Stobbe, 1913".

Loricicola Bedford, 1936, Onderstepoort J. vet. Sci. 7, 51 f. Generotype: "*Trichodectes mjobergi* Stobbe".

Meganarion Kéler, 1938 (generotype: "*Trichodectes armatus* Neumann, 1913"). Eichler 1940: 160, absolute synonym of *Cebidicola* Bedford, 1936. Pro parte.

Loricicola Bedford: Werneck (1950: 1)

Loricicola Bedford: Hopkins & Clay (1952: 201).

Loricicola (*Loricicola*) Bedford: Lyal (1985: 312). Pro parte.

Loricicola (*Paradoxuroecus*) Bedford: Lyal (1985: 318). Pro parte.

Felicola (*Loricicola*) Ewing, 1929: Timm & Price (1994: 114).

Felicola (*Loricicola*) Ewing, 1929: Price et al. (2003: 258, 268).

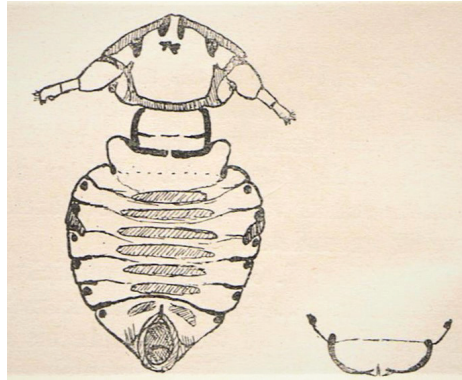


Fig.2. The two line drawings of *Loricicola mjobergi* from the original description by Stobbe (1913: Figs. 8a, b). Left: male, dorsal; right: ventral abdominal end of female.

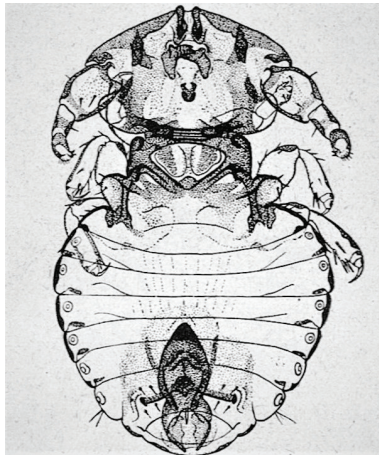


Fig.3. *Loricicola mjobergi*, male. Line drawing by Hilda Sikora after Stobbe's type material. From Eichler (1941: Fig. 19).

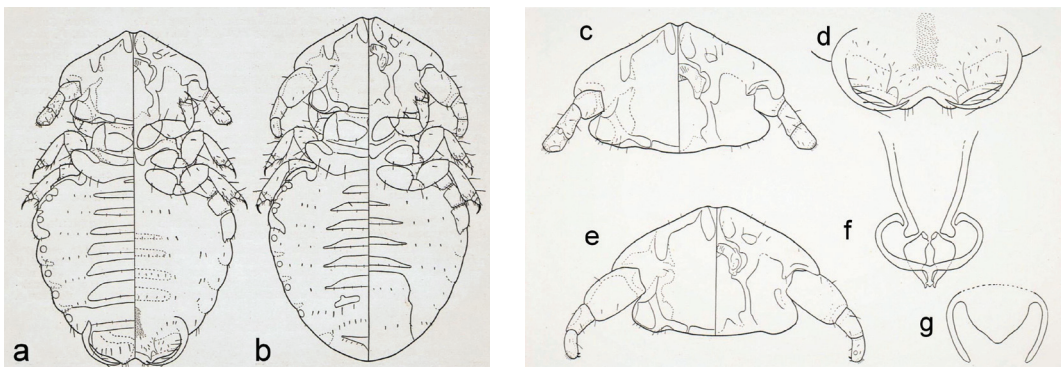


Fig.4. *Loricicola mjobergi*. **a:** female. **b:** male. **c:** Head, female. **d:** Terminalia, ventral, female. **e:** Head, male. **f:** Genitalia, male. **g:** Genital sclerite, male. From Werneck (1950: 4-5), after Stobbe's type material.

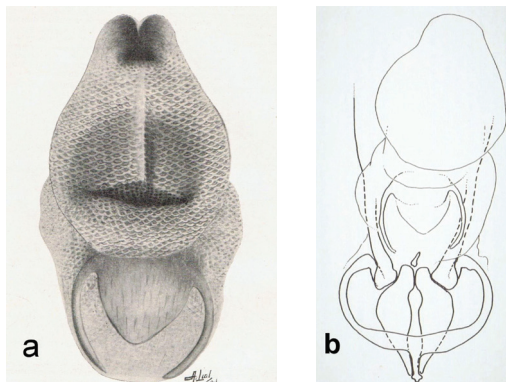


Fig.5. *Lorisicola mjobergi*, male. **a:** Endosclerite and preputial sac. From Werneck (1950: 6), after Stobbe's type material **b:** Genital apparatus. From Lyal (1985: 319).

Diagnosis

Long broad clypeal carina ending above the scapus without having formed a cone. Clypeal nodus in middle of clypeal carina. Two preantennal setae (*pcs 1-2*) absent. Ommatidium very large, with one anterior-dorsal and one posterior-ventral ocularis. Arched cervical sclerite just above temple leading to occipital carina and forming a “shoulder joint” with prothorax. Ventral and dorsal projection both on pleurum IV. Abdominal tergite VII almost completely covering segment. Mesomerall arch of male ending in a lumened trident. Subgenitalplate of female with two pointed and slightly curved chitinous teeth on each side, margin between the two inner chitinous teeth provided with numerous minute brush-like spines.

Description

Males and females about the same size, average body length 1.12 mm (Table 2).⁵ Philopteroid habitus with broad almost rectangular compressed head (Fig. 7). The entire head of *Lorisicola* has undergone considerable changes in pre- and postantennals due to compression, which are not so conspicuous in any other trichodectid.

⁵ However, it remains to be seen whether a statistical analysis of the measured individuals can reveal significant differences in certain body measurements of the different clans.

Table 2. Body measurements (mm) and head index (occiput width [with eyes] divided by head length) of *Loricicola mjobergi* sensu lato (Ischnocera, Trichodectidae s.l.) ex Bengal Slow Loris *Nycticebus bengalensis* and Pygmy Slow Loris *Nycticebus pygmaeus* both from Cuc Phuong National Park, Vietnam. In addition, the sparse measurements of the type material according to Stobbe (1913), Ewing (1930) and Werneck (1950) are given.

Louse species	<i>Loricicola mjobergi</i> s. l.									
Hosts	<i>Nycticebus bengalensis</i> Lacépède		<i>Nycticebus pygmaeus</i> Bonhote		<i>Nycticebus</i> sp. from North Borneo		<i>Nycticebus coucang</i> (Boddaert)			
					Stobbe (1913: 379)	Werneck (1950: 4, 6)			Ewing (1930: 121)	
Sex	♂ (n = 1)	♀♀ (n = 6)	♂♂ (n = 14)	♀♀ (n = 36)	♂	♀	♂	♀	♂	
slide(s)	4011.a	4011.a-b	4052. a-e, 4318.a-c	4052. a-f, 4318.a-d	type material					
Total length	1.12*	1.11-1.20 (x = 1.15)	1.05 - 1.13 (x = 1.065)	0.93 - 1.20 (x = 1.11)	1:20 AM	1:28 AM	1:19 AM	1:17 AM	1:15 AM	
Head length	0.34	0.33 - 0.36 (x = 0.348)	0.33 - 0.35 (x = 0.331)	0.30 - 0.36 (x = 0.336)	0.33	0.34				
Forhead width	0.50	0.51 - 0.55 (x = 0.525)	0.47 - 0.50 (x = 0.487)	0.50 - 0.55 (x = 0.521)						
Occiput width (with eyes)	0.47	0.47 - 0.50 (x = 0.48)	0.42 - 0.43 (x = 0.427)**	0.46 - 0.50 (x = 0.476)*	0.53	0.55				
Occiput width (without eyes)	0.43	0.44 - 0.47 (x = 0.453)	0.40 - 0.42 (x = 0.413)*	0.43 - 0.47 (x = 0.445)						
Head index	0.72	0.69 - 0.73 (x = 0.723)	0.72 - 0.81 (x = 0.784)**	0.64 - 0.77 (x = 0.708)*						
Prothoracic width	0.30	0.32 - 0.35 (x = 0.335)	0.29 - 0.32 (x = 0.307)	0.30 - 0.34 (x = 0.328)						
Mesometathoracic width	0.47	0.48 - 0.51 (x = 0.495)	0.44 - 0.46 (x = 0.441)	0.44 - 0.50 (x = 0.481)	0.46	0.50				
Abdominal width	0.68	0.68 - 0.75 (x = 0.705)	0.64 - 0.70 (x = 0.663)	0.60 - 0.74 (x = 0.686)	0.70	0.70				
			* n = 13	* n = 35						
			** n = 9							

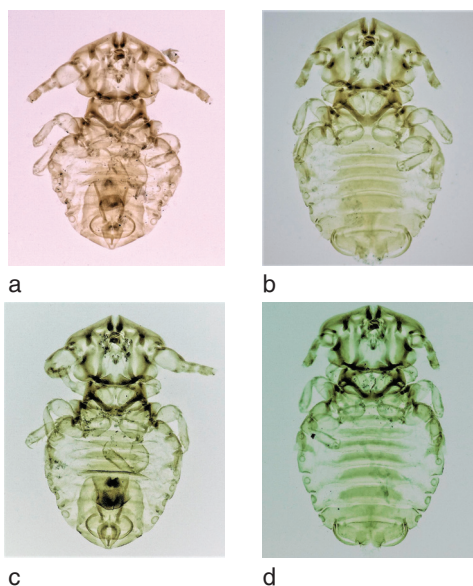


Fig.7. *Loricicola mjobergi* s. l. ex *Nycticebus* spp. **a:** male (M. 4011. a), total length 1.12 mm, ex *N. bengalensis*. **b:** female (M. 4011. a), total length 1.2 mm, ex *N. bengalensis*. **c:** male (M. 4052. a, left), total length 1.11 mm, ex *N. pygmaeus*. **d:** female (M. 4052. b, top left), total length 1.17 mm, ex *N. pygmaeus*.

Male with powerful scapus, which is apically armed on a pronotum with a pair of thick blunt spines (Fig. 12). Females without such (Fig. 8).

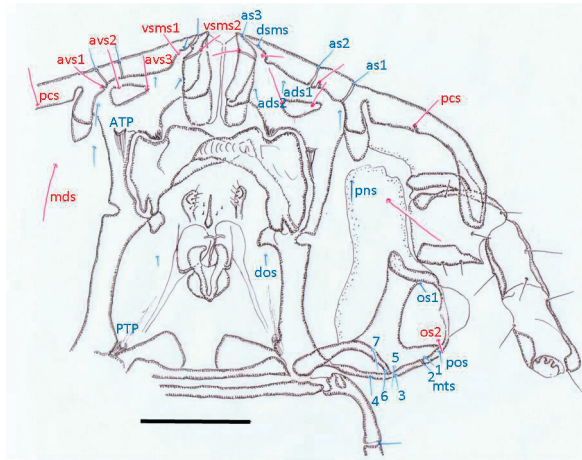


Fig.8. Pro parte head and prothorax with dorsal and ventral structures of *Loriscola mjobergi* s. l., female (M. 4052. d) ex *Nycticebus pygmaeus*. Dorsal setae blue, ventral red, also abbreviations of other structures. Abbreviations see p. 183. Scale 0.1 mm.

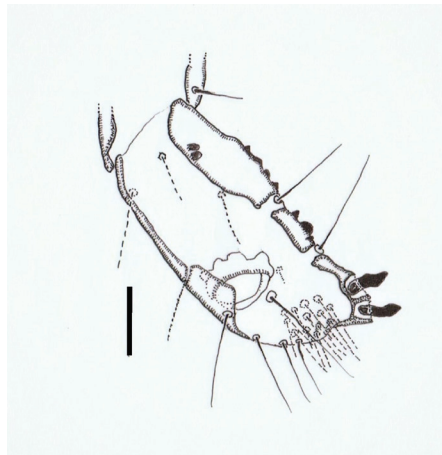


Fig.12. Flagellum of *Loriscola mjobergi* s. l., male (M. 4318. b), ex *Nycticebus pygmaeus*. Ventral setae dotted. Scale 0.02 mm.

The clypeal carina encloses the anterior head between the antennal pits as a broad band, interrupted only by the relatively narrow osculum. The clypeo-frontal nodus divides the clypeal carina into two equal sections on each side. It rises obliquely caudad above the plane of the front of the head and serves as an abutment during movement in the host pelage. On top of head several sutures. Unpigmented cheek pit enclosing space between ventral and clypeal carina minute. Ventral carina broad but very short. Cibarial sclerite (Fig. 13) deviates from that typical of trichodectids (Haub 1972, 1973).

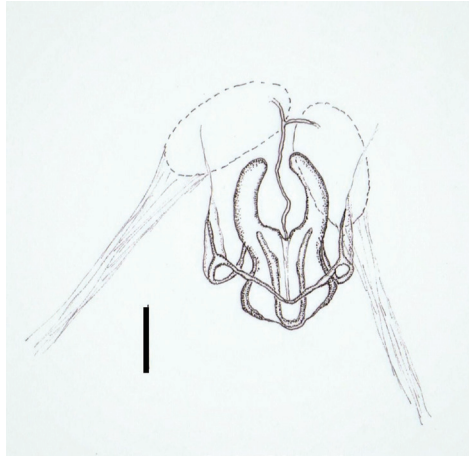


Fig.13. Cibarial sclerite of *Loricicola mjobergi* s. l., larva (M. 4052. g), ex *Nycticebus pygmaeus*. Scale 0.02 mm.

There is no cone set off in front of the antennal pits. The free, rigid, slightly curved end piece of the clypeal carina, which protrudes slightly above the scapus, cannot be interpreted as a cone. However, it probably fulfils the same function as the cone. This unique formation, already present in the larval stage, lacks the setae common in trichodectids. In these, three constantly occurring setae (according to Kéler 1938) insert between conus and clypeo-frontal nodus: dorsally lower (*pas 2*) and upper (*pas 1*) bar pit seta and ventrally the peg seta (*pcs*). In *Loricicola*, only the *pcs* located between the nodus and the posterior end of the clypeal carina remains (Figs. 8-9). Unusually, there are two anterior dorsal setae (*ads*) on each side of the anterior head as microchaetae (in Fig. 8 *ads 1-2*, see Table 1).

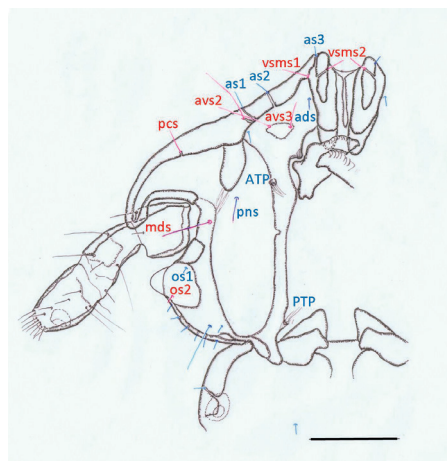


Fig.9. Head half, dorsal, of *Loricicola mjobergi* s. l., larva (L III) (M. 4052. f) ex *Nycticebus pygmaeus*. Dorsal bristles blue, ventral red, also abbreviations of other structures. Abbreviations see p. 183. Scale 0.1 mm.

Further peculiarities of *Loricicola* associated with chaetotaxic details are found on their temples. First of all, an unusually large ommatidium, which takes up about one third of the length of the occipital carina, is noticeable on each side of the relatively small occiput, which has a thimble-like shape in the imagines and a more pointed shape in the larvae. It is very reminiscent of the very similarly shaped eyes of the three *Cebidicola* species. On the *Loricicola* ommatidium two oculari (Figs. 8-9) are situated marginally on the temple (not on the ommatidium itself), anteriorly a dorsal, posteriorly a ventral ocular seta. The former is new in this allocation and position and has apparently remained

unnoticed until now. The latter is the only one in the row of temporal setae (*os*, *pos* and *mts*) that sits ventrally. Both eye microchaetae are of approximately the same size. They are followed by marginal preocularis and 7-9 temporal setae (Figs. 8-9). The constancy in the number (8) of temporal setae in trichodectids emphasised by Kéler (1938) also seems to apply to *Loricicola*. In 21 individuals (4 ♂, 17 ♀), 22 times eight, 3 times nine and 7 times seven setae were found on each side of the head.

Broad short temporal carina strongly sclerotised, not crossing with occipital carina. A visible gular plate covering the occipital hole is completely absent (Figs. 7-9, 11). Prominent arched cervical sclerite extending over the tempora to the occipital carina and fused with it (Figs. 8-10). Between this cervical arch and the occipital carina fits an articular head on the anterior corner of the prothorax (“shoulder joint”), the (lateral) mobility of the head and thorax. This organelle, apparently unique among trichodectids, is provided with a group of 4-5 setae of different lengths, three of which (*mts* 5-7) insert submarginal to the marginal carina but on the cervical sclerite.

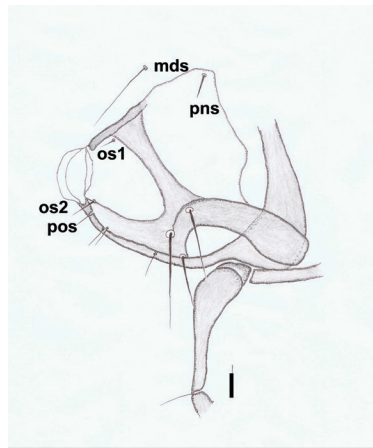


Fig.10. Tempora and prothoracic margin (half-sided, dorsal) of *Loricicola mjobergi* s. l., male (M. 4052. b) ex *Nycticebus pygmaeus*. Abbreviations see p. 183. Scale 0.02 mm.

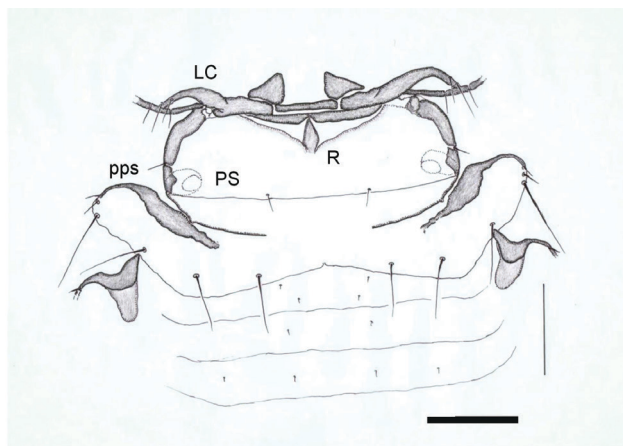


Fig.11. Occipital margin, pro- and mesometanotum and pro parte first two abdominal segments (with pleurum I) of *Loricicola mjobergi* s. l., female (M. 4052. c), ex *Nycticebus pygmaeus*. Abbreviations see p. 183. Scale 0.1 mm.

Head setae as in Figs. 8-11 (see also Table 1). One setae on each side proximal to the clypeal nodus (marked with ?) remains unclear in its assignment.

As in *F. (Felicola) subrostratus*, the anterior corner setae of the prothorax is missing in *Loricicola*

mjobergi. However, it is present in *F. (Lyalicola) hercynianus* as well as in most species of this subgenus (as can be inferred from their descriptions). Dorsal thoracic setae sparse (Fig. 11). Prostigma of larva about a quarter larger than its six abdominal stigmata. Femura II and III distally ventrally each with a relatively long strong spine.

Abdomen of male and female similar in basic shape, widest at segment IV and with six pairs of stigmata (III-VIII). Abdominal setae almost exclusively with microchaetae. Sternites and tergites only central. Tergite VIII almost completely covering segment between stigmata, reduced on anterior part in female. Pleurites III-IV with antero- and postero-lateral short spines. Pleurium IV with ventral and dorsal projection, ventral more sclerotised and with short spine in male and female.

Gonapophyses simple slender sabre-like processes reaching almost to median, each with 6-7 non-tuberculate mesochaetes internally. Terminalia (ventral) with hypogynium as in Fig. 17. Distinctive male genitalia with massive preputial sac and (barely visible) genital sclerite (Figs. 4-5, 15). Mesomeres apparently neither fused to the apical basal apodemes nor to the basiparamerous sclerites (which seems to be the case in *L. mjobergi* s. str. ?). Mesomer arch terminating in a cruciform apex (with lumen) (Fig. 15). Hypandrium forming a large rectangular plate with rounded tip posteriorly. Genital opening posterior-dorsal. On its posterior margin on each side five (sometimes on one side six) weakly sclerotised setal tubercles (Fig. 16). These apparently absent in *L. mjobergi* s. str.

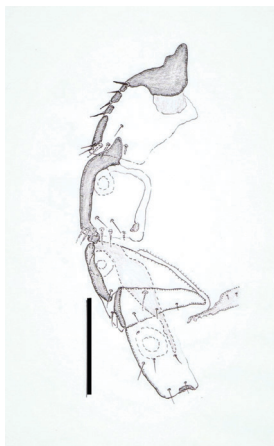


Fig.14. Abdominal pleurae II-V of *Loricicola mjobergi* s. l., female (M. 4052. g), ex *Nycticebus pygmaeus*. Ventral setae dotted. Scale 0.1 mm.

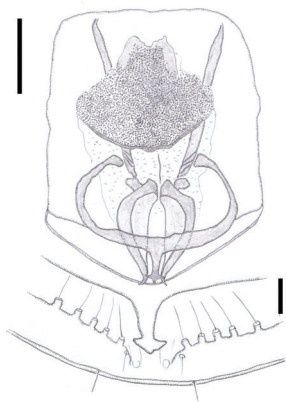


Fig.15-16. *Loricicola mjobergi* s. l., males, ex *Nycticebus pygmaeus*. **15:** Hypandrium (on VII-IX/X segments) and genital (M. 4052. d). Scale 0.1 mm. **16:** Genital opening (dorsal) with setal tubercles. Paramers indicated (M. 4318. b). Scale 0.02 mm.

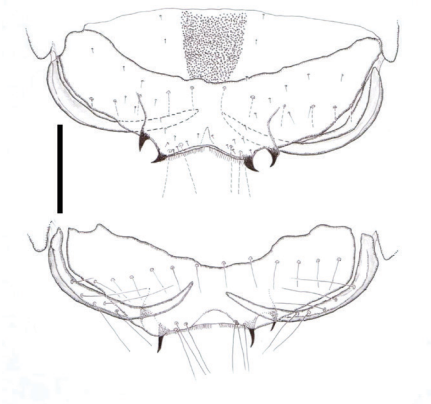


Fig.17. Terminal segment with gonapophyses and subgenital midlobe of *Lorisicola mjobergi* s. l., female (M. 4052. g, two different individuals), ex *Nycticebus pygmaeus*. Ventral setae dotted. Scale 0.1 mm.

Hospitale and zoogeographical distribution

Parasitic monotypically on Lorisinae, Primates; previously known from five *Nycticebus* spp. from Orientalis.

Presumed relationships

That there should be a habitual similarity between *Lorisicola* and *Felicola* s. l., as Werneck (1950) thinks, is in my opinion hardly comprehensible today. Not only the overall impression, but also some individual features speak against it. The more one delves into their morphology, the clearer it becomes that the two do not have much in common. Whether, on the other hand, a closer relationship between *Cebidicola* and *Lorisicola* actually exists, which Werneck (1950) also considers not to be excluded, has yet to be established by autopsy on authentic material. According to Lyal (1985), however, this seems to be excluded from the point of view of morphology (see footnote 3).

Lyal (1987: 19 f.) returns to his "*Lorisicola* group" and comments on its hospital distribution, among other things, as follows: „Species of this genus are associated with Viverridae, Felidae, Hesperpestidae and Primates [...]. The distribution of host associations on the cladogram suggests clearly that the last two groups named [*L. mjobergi*] ex "*Nycticebus coucang*" (Lorisidae) und *L. malaysianus* ex *Cynogale bennetti* (Viverridae)] are associated with *Lorisicola* following secondary infestations. The association with a primate probably took place in Southeast Asia, as both the louse concerned and its sister-species are distributed there, and that with Herpestidae in Africa as, again, both the clade concerned and sister-group are sympatric in that continent." This hypothesis, as far as *Lorisicola* is concerned, is in stark contradiction with the morphological findings and conclusions presented here.

Lorisicola mjobergi (Stobbe, 1913) sensu lato

Figs. 1-5, 7-17, Tables 1-2

Type host: "*Nycticebus borneanus* Lyon, 1906." Bornean Slow Loris. Host association in need of revision from today's perspective (see p. XX).

Trichodectes mjobergi Stobbe, 1913: 379, fig. 8 a-b, from a skin of "*Nycticebus borneanus*, Nord-Borneo" in the Berlin Museum of Natural History.

Trichodectes mjobergi Stobbe: Kellogg 1914, Amer. Nat. 48: 276.

Trichodectes mjobergi Stobbe: Harrison 1916, Parasitol. 9: 71.

Trichodectes brachycephalus Ewing, 1930: 120 f. ex "*Nycticebus coucang*, from Johor Lama, Malay Peninsula".

Lorisicola mjobergi (Stobbe): Bedford 1936, Onderstepoort J. Vet. Sci. & Animal. Ind. 7, 52.

Trichodectes brachycephalus Ewing, 1930: Bedford (1936: 52), synonym of *Lorisicola mjobergi* (Stobbe).

Meganarion mjobergi (Stobbe): Kéler 1938: Nova Acta Leopoldina N.S. 5: 465. Pro parte.

Meganarion brachycephalus Ewing, 1930: Kéler (1938: 465). Pro parte.

Loricicola mjobergi (Stobbe): Bedford (1931: 51).

Loricicola mjobergi (Stobbe): Eichler 1941: Arch. Naturgesch. N.F. 10, Abb. 19, p. 393.

Loricicola "brachycephala" [Ewing, 1930]: Hopkins (1949: 445), synonym of *Loricicola mjobergi*.

Loricicola mjobergi (Stobbe, 1913): Hopkins (1949: 540).

Loricicola mjobergi (Stobbe, 1913): Werneck (1950: 3 ff., figs. 1-8). "ex *Nycticebus borneanus* Lyon, do norte de Borneo."

Trichodectes brachycephalus Ewing, 1930: Werneck (1950: 3), synonym of *Loricicola mjobergi*.

Loricicola mjobergi (Stobbe, 1913): Hopkins & Clay (1952: 202) ex "*Nycticebus [coucang] borneanus* Lyon".

"Doubtfully distinct from *Felicola*."

Loricicola (Loricicola) mjobergi (Stobbe, 1913): Lyal 1985, Bull. Br. Mus. nat. Hist. (Entomol.) 51 (3), p. 312 ff., fig. 207, 214, 219.

Felicola (Loricicola) mjobergi (Stobbe, 1913): Timm & Price 1994, Proc. Biol. Soc. Wash. 107, 114 ff.

Felicola (Loricicola) mjobergi (Stobbe, 1913): Price et al. (2003: 258) "ex *Nycticebus coucang borneanus* Lyon".

Material examined from two host species (Fig. 6)

I. 1 ♂, 6 ♀, 6 larvae (M. 4011. a-c) from a living adult Bengal Slow Loris *Nycticebus bengalensis* (Lacépède, 1800) (Fig. 6 a), adultus, 21.6.1994 Cuc Phuong National Park, Vietnam, leg. Tilo Nadler (collected from the dorsal fur of the host).

New host-parasite association record.

II. 14 ♂, 36 ♀, 16 larvae from two living pygmy slow lorises *Nycticebus pygmaeus* Bonhote, 1907 (Fig. 6 b), namely 1. 9 ♂, 30 ♀, 13 larvae (M. 4052. a-f) ex *N. pygmaeus* adultus, 20.7.1995 Cuc Phuong National Park, Vietnam, leg. M. Klöden. - 2. 5 ♂, 8 ♀, 3 larvae (M. 4318. a-d) ex *N. pygmaeus* adultus, 2.12.1998 Cuc Phuong National Park, Vietnam, leg. Tilo Nadler.

New host-parasite association record.



Fig.6. left: Pygmy slow loris *Nycticebus pygmaeus*, right: Bengal slow loris *Nycticebus bengalensis*, Cuc Phuong National Park, Vietnam. Photos: Tilo Nadler.

The description of the species largely coincides with that of the genus (see above).

The genital sclerite in the endophallus of *Loricicola* is barely visible in all the males I examined, and without having looked closely at the illustrations by Werneck (1950) and Lyal (1985), I would probably have missed its existence. On the other hand, a taxonomic difference could be hidden behind the clouded perception, because a compact sclerite, as depicted by these authors and reproduced here in Figure 5, is indeed not present in my material. Be that as it may. The entire genital apparatus of *Loricicola mjobergi* appears as a uniquely complicated formation, which cannot be compared to any other within the trichodectids. This also underlines the special taxonomic position of *Loricicola*. It is very unlikely that the occurrence of *Loricicola* on lorises is due to secondary infestation.

Does *Loricicola* belong to the Felicolini?

Those who study the morphology of the Felicolini more closely and try to get to the bottom of their systematic-taxonomic structures will become aware of some rough edges that are obvious in Lyal's (1986) cladistic analysis of trichodectids. However, apart from Timm & Price (1994), they have not been recognised and clearly addressed in detail by anyone else to my knowledge. These authors assume that the following classification of the Felicolini by Lyal (1985) is in need of revision at the generic level:

Subfamily Trichodectinae Kellogg, 1896

Tribe Felicolini Kéler, 1938

Genus *Felicola* Ewing, 1929

Subgenus *Felicola* Ewing, 1929 (hosts: Felidae, Herpestidae and Viverridae)

Subgenus *Suricatoecus* Bedford, 1932 (hosts: Canidae and Herpestidae)

Genus *Loriscicola* Bedford, 1936

Subgenus *Loriscicola* Bedford, 1936 (hosts: Lorisidae, Felidae and Viverridae)

Subgenus *Paradoxuroecus* Conci, 1942 (hosts: Herpestidae and Viverridae)

Timm & Price (1994: 117) propose a different classification by assigning the four subgenera *Felicola*, *Suricatoecus*, *Loriscicola* and *Paradoxuroecus* to the genus *Felicola* and justify it as follows:⁶

"We accept Lyal's placement of 18, 11, 12 (+ our new species), and 13 louse species, respectively, in these four subgenera. However, we believe it more appropriate that all four be recognized as subgenera of *Felicola*. We come to this conclusion because of the difficulties encountered in the key by Lyal (1985: 335-338) to genera and subgenera. The longest and most complex couplets are used for *Felicola* sensu lato, character states are nondiscrete and overlapping, and separations are ambiguous. There is simply no clear break between these groups that warrants generic level distinction. This action on our part is not a severe departure from Lyal's classification, and is one that we feel is justified."

Timm & Price (1994) also rightly point out that *Felicola subrostratus* is the only felid chewing louse species placed in *Felicola (Felicola)* by Lyal (1985), while all the others (11 spp.) are said to belong to *Loriscicola (Loriscicola)*. In addition, it is particularly striking that the two cat's chewing lice "*Trichodectes subrostratus* Burmeister" (genotype of *Felicola* Bedford !) and "*Felicola hercynianus*" are placed in different genera (the latter in *Loriscicola*), especially as the hosts of both species were still considered conspecific or very closely related to each other at that time. In the meantime there is increasing evidence that *Felis lybica* and *F. silvestris* are two distinct wildcat species according to genetic and morphological evidence and that the domestic cat *Felis catus* arose from the domestication of *F. lybica* in W Asia (probably Mesopotamian region) c. 9500 years ago (Burgin et al. 2020: 406). Against this background stands the question, basically also posed by Timm & Price (1994), whether there are facts that speak more for or more against a generic separation between *Felicola subrostratus* and *Loriscicola hercynianus*.⁷ From a comparative-morphological point of view, there is no doubt about the affinity of the subgenera *Felicola* and *Suricatoecus*. With *Paradoxoecus*⁸ however, one cannot be so sure. And with *Loriscicola* alone, this constellation sensu Lyal (1985) can no longer be maintained, in my opinion.

The conflict is defused with the re-evaluation of the taxonomic status of *Loriscicola mjobergi*. It leads in consequence beyond the proposal of Timm & Price (1994), in that *Loriscicola* is to be separated from the Felicolini. This does much more justice to its independence than leaving it in a seemingly forced alliance with *Felicola* s. l. The presence of several autapomorphic features of *mjobergi* (see p. XX), some of which have so far remained unnoticed, leaves no doubt that we are

⁶ In the checklist of Price et al. (2003) this suggestion has been followed.

⁷ In this context, I will let follow a text that appeared in the wildcat monograph by Piechocki (1990: 212 f.) and was translated by me from the German: "So far, we have not encountered any heavily loused wildcats, but only found 33 mallophages on an escaped kuder from Rübeland [18.1.1985 Harz Mountains, GDR]. According to E. Mey's grateful determination, these were 5 ♂, 27 ♀ and one larva of *Felicola hercynianus*. Mey points out in this context that the morphological differences between *subrostratus* and *hercynianus* speak against a closer relationship of the two chewing louse species, so that obviously the opinion that our domestic cat descends from *Felis silvestris* is not supported from a parasitological point of view. It should also be mentioned that, according to the current state of knowledge, the wild cat chewing louse has been placed in a different genus and, according to Mey (1988) [sensu Lyal 1985], now bears the following name: *Loriscicola (Loriscicola) hercynianus* (v. Kéler, 1957)."

⁸ Further research is pending here.

dealing here with an exceptional trichodectid, which should not only be (re)granted full generic status, but for which it should also be considered whether it belongs in its own tribus (Loricicolini). But what happens to the other species that were previously classified in *Loricicola* (nevertheless as genus or subgenus)? Without *Loricicola mjobergi* (and with reservations also without “*Trichodectes malaysianus*”) they form an undoubtedly natural grouping, for which a new name, *Lyalicola* subgen. nov. is now necessary.



Fig.18. The European Wildcat *Felis s. silvestris* is the type host of the subgenero type *Felicola (Lyalicola) hercynianus* v. Kéler. This specimen lives in an enclosure near Hütsheroda in the Hainich National Park, Thuringia, Germany. Photo: E. Mey, 10.10.2019.

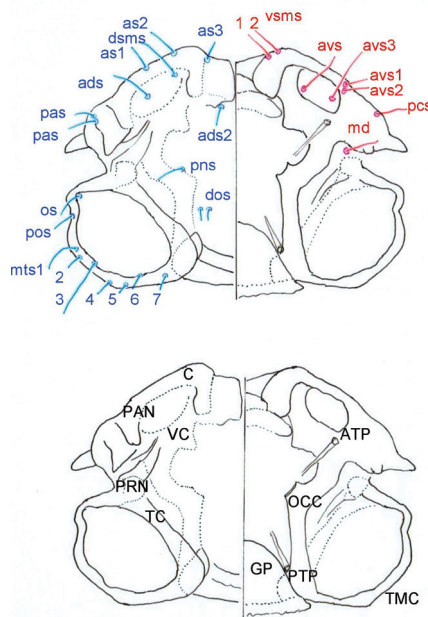


Fig.19. Chaetotaxy and some other head structures of *Trichodectes melis* (J. C. Fabricius, 1805) ex *Meles meles* (Linnaeus, 1758). Dorsal setae blue, ventral red, also abbreviations of other structures. Abbreviations see p. 183. After Kéler 1938, modified, and Symmons (1952).

***Felicola (Lyalicola* subgen. nov.)**

Figs. 20-21, Table 1.

Subgenerotype: *Felicola hercynianus* v. Kéler, 1957 ex *Felis s. silvestris* Schreber, 1777. European Wildcat.

Material: 5 ♂, 27 ♀, 1 larva (M. 3077. a-gg) from a 6.5-year-old European Wildcat *Felis s. silvestris* Schreber, ♂, 18.1.1985 Rübeland, Harz Mountain, Germany, leg. leg. R. Piechocki.

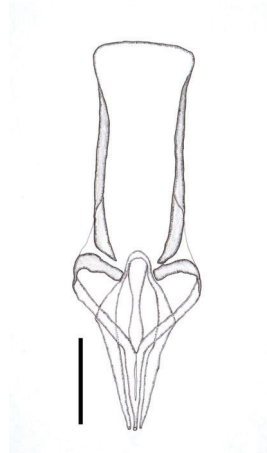


Fig.20. Male genital of *Felicola (Lyalicola* gen. nov.) *hercynianus* v. Kéler, 1957, (M. 3077. ff) ex *Felis s. silvestris*. Scale 0.05 mm.

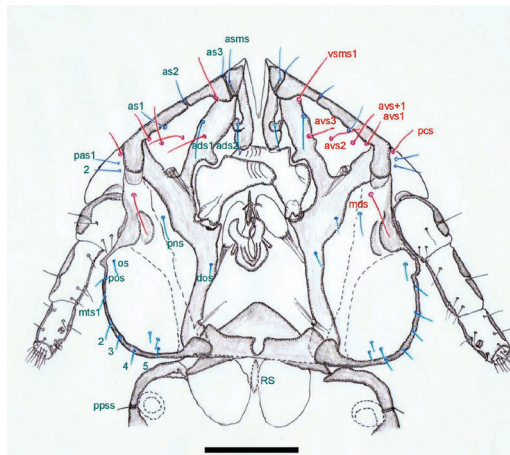


Fig.21. Head (ventral) with dorsal setae of *Felicola (Lyalicola* gen. nov.) *hercynianus*, male (M. 3077. bb) ex *Felis s. silvestris*. Dorsal setae blue, ventral red. Abbreviations see p. 183. Scale 0.1 mm.

The erection of *Lyalicola* subgen. nov. refers to the description of *Loricicola (Loricicola)* by Lyal (1985: 302 ff.) to the sole exclusion of *Loricicola mjobergi*. Incidentally, reference should be made to Emerson & Price (1983), who alone describe seven species in detail and assemble them in the *Felicola felis* complex, which has now been merged into *Lyalicola*.

The idea that their *felis* complex should have something to do with *Loricicola*, as Lyal (1985) put it a little later, was probably not only alien to them until then.

Finally, attention should be drawn to the following differences in head chaetotaxy. In *F. (Felicola)* and *Loricicola*, *vsms 1-2* are present, while in *F. (Lyalicola)* *vsms 2* is absent. Only *F. (Felicola)* lacks *as 2*, while it is present in *F. (Lyalicola)* and *Loricicola* (Table 1).

Derivatio nominis: *Lyalicola* is a neologism in honour of C. H. C. Lyal (British Museum, London), who made a name for himself with several pioneering works on Phthiraptera. An -i- is inserted between his name and the suffix *cola* for better pronunciation. The grammatical gender of the new name is male.

List of species belonging to *Felicola* (*Lyalicola* subgen. nov.)

The names of the type hosts differ in part from those given in Price et. al. (2003) are updated here according to Burgin et al. (2020). Since *Lorisicola mjobergi* (Lorisidae, Primates) is here taken out of the deceptively appearing relationship of *Felicola* s. l. and the generic affiliation of "*Trichodectes malaysianus* Werneck, 1948" (see below) seems to be in question, the type hosts of the Felicolini named below are without exception carnivores (Felidae).

***Felicola* (*Lyalicola* subgen. nov.)**

1. *Lyalicola americanus* (Emerson & Price, 1983) comb. nov. ex *Lynx r. rufus* (Schreber, 1777). Felidae. Texas.
2. *Lyalicola braziliensis* (Emerson & Price, 1983) comb. nov. ex *Leopardus baccatus* (Cope, 1782). Felidae. Brazil.
3. *Lyalicola caffra* (Bedford, 1919) comb. nov. ex *Felis lybica caffra* Desmarest, 1822. Felidae. S Africa.
4. *Lyalicola felis* (Werneck, 1934) comb. nov. ex *Leopardus p. pardalis* (Linnaeus, 1758). Felidae. Guatemala.
5. *Lyalicola hercynianus* (v. Kéler, 1957) comb. nov. ex *Felis s. silvestris* Schreber, 1777. Felidae. Europe. Germany.
6. *Lyalicola isidoroi* (Perez & Palma, 2001) comb. nov. ex *Lynx pardinus* (Temminck, 1827). Felidae. Europe, Spain.
7. *Lyalicola neofelis* (Emerson & Price, 1983) comb. nov. ex *Leopardus geoffroyi* d'Orbigny & Gervais, 1844. Felidae. Brazil.
8. *Lyalicola oncae* (Timm & Price, 1994) comb. nov. ex *Panthera onca* (Linnaeus, 1758). Felidae. Costa Rica.
9. *Lyalicola siamensis* (Emerson, 1964) comb. nov. ex *Prionailurus b. bengalensis* Kerr, 1792. Felidae. Malaya.
10. *Lyalicola similis* (Emerson & Price, 1983) comb. nov. ex *Herpailurus yagouarundi* É. Geoffroy Saint-Hilaire, 1803. Felidae. Paraguay.
11. *Lyalicola spenceri* (Hopkins, 1960) comb. nov. ex *Lynx canadensis* (Kerr, 1792). Felidae. Canada.
12. *Lyalicola sudamericanus* (Emerson & Price, 1983) comb. nov. ex *Leopardus t. trigrinus* (Schreber, 1777). Felidae. Colombia.

It is not without some constraint that "*Trichodectes malaysianus* Werneck, 1948" ex *Cynogale bennettii* J. E. Gray, 1837, (Viverridae. Sumatra) can be placed with *Felicola* (*Lyalicola*).

***Felicola* (*Felicola*) Ewing, 1929**

Genotype: "*Trichodectes subrostratus* Nitzsch" = "*Trichodectes subrostratus* Burmeister, 1838".

***Felicola* (*Felicola*) *subrostratus* (Burmeister, 1838)**

Figs. 22-23, Table 1.

Type host: *Felis catus* Linnaeus, 1758

Material: 3 ♂, 10 ♀, 1 larva (M. 3137. a-n) from a Domestic Cat *Felis catus*, 16.8.1980 Herbsleben near Bad Langensalza, Thuringia, Germany, leg. R. Bellstedt.

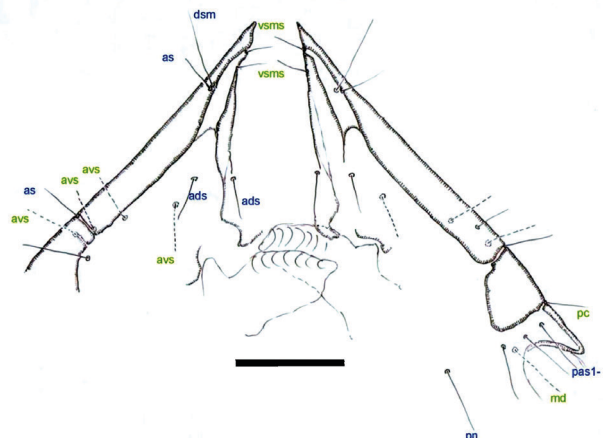


Fig.22. Preantennale with setae of *Felicola* (*Felicola*) *subrostratus* (Burmeister, 1838), male (M. 3137. a). Dorsal setae blue, ventral red. Abbreviations see p. 183. Scale 0.05 mm.

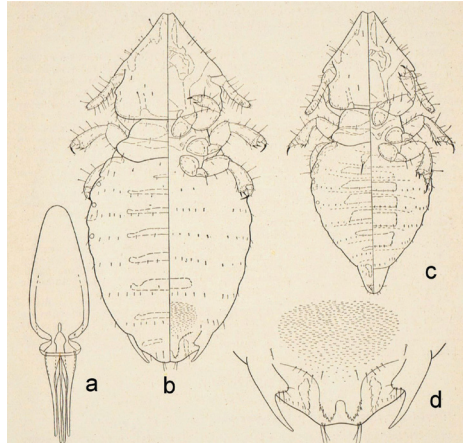


Fig.23. *Felicola (Felicola) subrostratus* (Burmeister). **a:** Male genitalia. **b:** Female. **c:** Male. **d:** Terminalia, female (ventral). From Werneck (1948: 195).

There are a number of detailed descriptions of *Felicola (Felicola) subrostratus* of which the one by Werneck (1948) stands out (Fig. 23). The subgenero types of *Felicola (F. subrostratus)* and of *Lyalicola* subgen. nov. (*L. hercynianicus*) are so different (e.g. Figs. 21 and 22) that no one would think of placing them even closer together than their respective subgenus status already indicates.

It is remarkable that *F. subrostratus* is the only species in the subgenus *Felicola* that lives on a felid. All other species (at least 17) placed in *Felicola (Felicola)* are known from Mongooses (Herpestidae) and Civets, Genets and Oryzomys (Viverridae) (Lyal 1985). In contrast, all other felids are known so far to harbour only *Felicola (Lyalicola)* species, which easily proves to be a morphologically very cohesive kinship group. The evolutionary background of this strange exception in the hospital distribution of *Felicola* (with the subgenera *Felicola* and *Lyalicola*) has not yet been clarified.

In agreement with Lyal (1987), there currently seems to be much to suggest that *Felicola (Felicola) subrostratus* settled secondarily on *Felis catus* and spread cosmopolitically with this host.

Acknowledgements

I owe the *Lorisicola* material to the kindness of Tilo Nadler and Manuela Klöden (both Cuc Phuong National Park, Vietnam). Dr. Wolfram Mey and Dipl.-Biol. Birgit Jaehnicke (both Natural History Museum Berlin) made efforts to locate type material of "*Trichodectes mjobergi* Stobbe". I thank them very much for finding the microscope slides that were thought to be lost. Microphotographic images were taken by the author thanks to the kind support of Dipl.-Ing. (FH) Georg Sprößig (Dresden-Pillnitz). I thank M. Sc. Gaetano Fichera (Jena) and Dr. Fabrizio Turrisi for their literature research.

References

- Bedford GAH** (1936): Notes on Species of Trichodectidae with Description of New Genera and Species. Onderstepoort J. vet. Sci. 7(1), 33-58.
- Burgin CJ, Wilson DE, Mittermeier RA, Rylands AB, Lacher TE & Sechrest W** (eds.) (2020): Illustrated Checklist of the Mammals of the World. Volume 2. Eulipotyphla to Carnivora. Lynx Edicions, Barcelona.
- Conci C** (1942): Diagnosi preliminare di tre nuovi generi e di una nuova specie di Trichodectinae (Mallophaga). Boll. Soc. entomol. Italiana 74(10), 140-142.
- Conci C** (1946): Il Genere "*Paradoxuroecus*" ed il suo generotipo (Mallophaga). Rev. Brasil. Biol. 7(2), 247-249.
- Göllner-Scheiding U** (1973): Katalog der im Zoologischen Museum Berlin vorhandenen Mallophagentypen. Lounais-Hämeen Luonto (Forssa) 46, 29-46.
- Eichler W** (1940): Notulae Mallophagologicae. I. Neue Gattungen und Subfamilien von Haarlingen. Zool. Anz. 129(5/6), 158-162.
- Eichler W** (1941): Zur Klassifikation der Lauskerfe (Phthiraptera Haeckel: Rhynchophthirina, Mallophaga und Anoplura). Arch. Naturgesch., N.F. 10(3), 345-398.
- Eichler W** (1989 a): Konsequenzen der Third Edition der Zoologischen Nomenklaturregeln für die Parasitologie. Angew. Parasitol. 30(1), 51-55.

- Eichler W** (1989 b): Wichtiges von den neuen Nomenklaturregeln / Die Third Edition des Code. Dtsch. entomol. Z., N.F. 36(1-3), 45-55.
- Emerson KC & Price RD** (1975): Mallophaga of Venezuelan Mammals. Brigh. Young Univ. Sc. Bull., Biol. Ser. 20(3), 1-77.
- Ewing HE** (1930): Six new species of Mallophaga. Proc. Entomol. Soc. Washington 32(7), 117-121.
- Gustafsson DR & Bush SE** (2017): Morphological revision of the hyperdiverse *Brueelia*-complex (Insecta: Phthiraptera: Ischnocera: Philopteridae) with new taxa, checklists and generic key. Zootaxa 4313(1), 1-443.
- Harrison L** (1916): The genera and species of Mallophaga. Parasitology 9(1), 1-156.
- Haupt F** (1972): Das Cibarialsklerit der Mallophaga-Amblycera und der Mallophaga-Ischnocera (Insecta). Z. Morphol. Tiere 73, 249-261.
- Haupt L** (1973): Das Cibarium der Mallophagen Untersuchungen zur morphologischen Differenzierung. Zool. Jb. Anat. 90, 483-525.
- Hopkins GHE** (1949): The host-associations of the lice of mammals. Proc. Zool. Soc. London 119, 387-604.
- Hopkins GHE & Clay T** (1952): A check list of the genera & species of Mallophaga. Trustees of the British Museum, London.
- Kéler S** (1938): Baustoffe zu einer Monographie der Mallophagen. I. Teil: Überfamilie der Trichodectoidea. Nov. Acta Leopold., Abh. Kaiserl. Leopold.-carol. Deut. Aka. Naturf. N. F. 5(32), 395-467.
- Kéler S** (1940) [„1939“]: Baustoffe zu einer Monographie der Mallophagen. II. Teil: Überfamilie Nirmoidea (1). Nov. Acta Leopold., Abh. Kaiserl. Leopold.-carol. Deut. Aka. Naturf. N.F. 8(51), 3-254 + Taf. 1-4.
- Kéler Sv** (1957): Der Haarling der Wildkatze (*Felicola hercynianus* n. sp.) (Mallophaga, Trichodectidae). Dtsch. entomol. Z., N.F. 4(3/4), 172-178.
- Lux E, Mix HM & Zedev B** (1997): *Damalinia (Tricholipeurus) zaganseeri*, n. sp. (Phthiraptera: Trichodectidae), a Parasite from *Procavia gutturosa* (Artiodactyla, Bovidae) in Mongolia. J. Med. Entomol. 34(6), 599-604.
- Lyal CHC** (1985): A cladistics analysis and classification of trichodectid mammal lice (Phthiraptera: Ischnocera). Bull. Br. Mus. Nat. Hist. (Entomol.) 51(3), 187-346.
- Lyal CHC** (1987): Co-evolution of trichodectid lice (Insecta: Phthiraptera) and their mammalian hosts. J. Nat. Hist. 21, 1-28.
- Mey E** (1988): Übersicht über die Säugetier-Mallophagen Europas. Angew. Parasitol. 29, 113-126.
- Mey E** (1994): Beziehungen zwischen Larvenmorphologie und Systematik der Adulti bei den Vogel-Ischnozeren (Insecta, Phthiraptera, Ischnocera). Mitt. Zool. Mus. Berlin 70, 3-84.
- Mey E** (2009): Die Mallophagen (Insecta, Phthiraptera: Amblycera & Ischnocera) der Galloanseres (Aves) – ein Überblick. Beitr. Jagd- u. Wildforsch. 34, 151-188.
- Nekaris KAI** (2013): Family Loricidae (Angwantibos, Pottos and Lorises). In: Mittermeier RA, Rylands AB & Wilson DE (eds.): Handbook of the Mammals of the World. Vol. 3. Primates; pp. 210-235. Lynx Edicions, Barcelona.
- Nekaris KAI** (2020): Family Loricidae. In: Burgin CJ, Wilson DE, Mittermeier RA, Rylands AB, Lacher TE & Sechrest W (eds.): Illustrated Checklist of the Mammals of the World. Vol. 1. Monotremata to Rodentia; pp. 166-170. Lynx Edicions, Barcelona.
- Piechocki R** (1990): Die Wildkatze *Felis silvestris*. Die Neue Brehm-Bücherei No. 189. Wittenberg Lutherstadt, A. Ziemsen Verlag.
- Poggi R** (2008): Le date di stampa dei periodici editi dalla Società Entomologica Italiana dal 1869 al 2007. Memorie Soc. entomol. ital. 87, 157-188.
- Price RD, Hellenthal RA & Palma RL** (2003): World checklist of chewing lice with host associations and keys to families and genera. In: Price RD, Hellenthal RA, Palma RL, Johnson KP & Clayton DH (eds): The chewing lice: world checklist and biological overview. Special Publication 24, pp. 1-447. Illinois Natural History Survey.
- Remane A** (1956): Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik / Theoretische Morphologie und Systematik I. Second Edition. Akademische Verlagsgesellschaft Geest & Portig K.-G., Leipzig.
- Stobbe R** (1913): Mallophagen. 3. Beitrag: Die Trichodectiden des Berliner Museums für Naturkunde. Sitzungsber. Gesellsch. naturforsch. Freunde, Berlin 1913, 365-383.
- Symmons S** (1952): Comparative anatomy of the Mallophagan head. Trans. Zool. Soc. London 27(4), 349-436.
- Timm RM & Price RD** (1994): A new species of *Felicola* (Phthiraptera: Trichodectidae) from a Costa Rican Jaguar, *Panthera onca* (Carnivora: Felidae). Proc. Biol. Soc. Wash. 107(1), 114-118.
- Werneck FL** (1948): Os Malófagos de Mamíferos. Parte 1: Amblycera e Ischnocera (Philopteridae e parte de Trichodectidae). Instituto Oswaldo Cruz, Rio de Janeiro.
- Werneck FL** (1950): Os Malófagos de Mamíferos. Parte II: Ischnocera (continuação de Trichodectidae) e Rhyncophthirina [sic]. Instituto Oswaldo Cruz, Rio de Janeiro.