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## The *Corvonirmus* group (Insecta, Psocodea, Phthiraptera, Ischnocera) of corvids (Aves, Corvidae). I. *Stubbenirmus* gen. nov.<sup>1</sup>

E. Mey

### Abstract

1. The genera *Corvonirmus* Eichler, 1944 (with 11 spp.), *Hecatrishula* Gustafsson & Bush, 2017 (with 8 spp.) and *Lycocoranirmus* Mey, 2017 (with 5 spp.), which belong to the *Brueelia* complex (Phloptoridae s. l.), are morpho-structurally characterized mainly by head structures and chaetotaxy. They are defined as a group of related taxa that should be placed in the rank of a subfamily (Corvonirminae subfam. nov.) if the former Brueeliinae sensu EICHLER (1963:177) would get the status of a separate family (Brueeliidae).
2. Within the *Corvonirmus* group, the former *Hecatrishula biguttata* species group is assumed to be classified as new genus. *Stubbenirmus* gen. nov. with *S. stubbeae* spec. nov. (generotype) ex *Podoces hendersoni* Hume and *S. koslovae* (Clay, 1936) ex *Podoces biddulphi* Hume most likely represent the phylogenetically oldest branch within the *Corvonirmus* group. This pair (*koslovae* group) is closely related to *S. docilis* (Ansari, 1957) ex *Pyrrhocorax pyrrhocorax barbarus* Vaurie, but for the time being it represents a separate species group as well as *Stubbenirmus biguttatus* (Kellogg & Paine, 1914) ex *Pyrrhocorax graculus forsythi* Stoliczka. *Stubbenirmus biguttatus* mediates to *Hecatrishula*, from which *Corvonirmus* and *Lycocoranirmus* can be derived. So far it has not been investigated in detail how *Olivinirmus* Złotorzycka, 1964 is related to the *Corvonirmus* group and whether it is correct to include the Australian *Brueelia* of the Cracticidae (supposedly "*Nirmus semiannulatus* Piaget, 1883" on at least four host species) in the group or not.
3. The taxonomic-systematic block (1. and 2.) is preceded by a scientific-historical discourse on the prehistory of the *Stubbenirmus* species, in which reasonable doubts about the identity of *Hecatrishula multipunctata* (Clay, 1936) are presented.
4. The hypothesis that *Stubbenirmus biguttatus* and *S. docilis* synhospital would live on both *Pyrrhocorax* species is rejected.
5. Attention is drawn to the fact that of the four genera of the *Corvonirmus* group, only species of *Corvonirmus* and *Hecatrishula* synhospital (both on host species and on host individual) are regularly found. In a case still to be studied in more detail, *Lycocoranirmus* and *Corvonirmus* also appear to live on one host species (*Corvus orru*), but according to current knowledge they belong to different host subspecies (*orru* in New Guinea and Moluccas and *ceciliae* in Australia).
6. Parasitophyletic considerations on the *Corvonirmus* group indicate that the genera *Podoces* and *Pyrrhocorax* are probably at the root of the corvids.

**Keywords:** *Brueelia* complex, *Corvonirmus* group, *Stubbenirmus stubbeae* gen. & spec. nov., taxonomy, Corvidae.

### 1. Introduction

In the following, the term "*Corvonirmus* group" is used to refer to the probably very closely related genera *Corvonirmus* Eichler, 1944, *Hecatrishula* Gustafsson & Bush, 2017, *Lycocoranirmus* Mey, 2017 and *Stubbenirmus* gen. nov. So far, they are restricted to a host range that includes the

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<sup>1</sup> Results of the Mongolian-German Biological Expeditions since 1962, No. 362.

genera *Pyrrhocorax*, *Podoces*, *Pica* and *Corvus*, in total about 45 % of the species of the Corvidae (questionable exception *Nucifraga*, see page 403). The author owns extensive material (covering the globe with exception of South America) of a large part of the species of these genera, which forms the basis for further reworking of the *Corvonirmus* group (cf. tab. 1). Only part of this material is used here, insofar as it is necessary for the first generic structuring of the *Corvonirmus* group presented here. For this purpose, it seems useful to concentrate  $\alpha$ -taxonomically on the new genus *Stubbenirmus* and to start from a historical perspective.

## 2. Material and Method

In the species chapters, feather lice species and other ectoparasites collected together with the Brueelian are additionally listed under "Material". This is to draw attention to the individual, not infrequently occurring mixed infections in corvids. If a mixed infection could not be proven (in the material collected by E. MEY = EM), this does not mean per se that it did not actually exist. Thus, no reliable statements about the intensity of infestations can be derived from the quantitative data on mixed infections.

The material evaluated here, as far as it does not concern loan material, was obtained by me by "tapping" museum skins, prepared and embedded in Canada balsam on microscope slides. The whereabouts of the specimens are given in the species chapters. In addition, some microscope slides from the Zoological Research Museum "Alexander Koenig" in Bonn have recently become available. Dr. Heinrich F. Klockenhoff (1937-1984) had already sent me extensive "*Brueelia*" material from Afghanistan collected by himself in the 1960s.

The microphotographs were made with a Keyence VHX-5000 digital microscope at the Dresden University of Applied Sciences, Faculty of Agriculture/Environment/Chemistry- Biodiversity/Nature Conservation in Pillnitz. The line drawings were made by EM.

Body measurements [mm] were determined according to the methodology described by MEY (1997: 4). For the body measurements presented in the running text (from-to ranges in mm) these abbreviations are used:

- TL = Total length
- HL = Head length,
- FW = Forehead width
- OW = Occiput width
- HI = Head index (OW divided by HL)
- PW = Prothoracic width
- MW = Mesometathoracic width
- AW = Abdominal width.

The statistical tests and presentation of the data were carried out by Reinhard Mey.

To test for differences in body measurements between the individual *Stubbenirmus* species, pairwise Mann-Whitney U-tests (with Bonferroni correction for multiple testing) were performed. Males and females were considered separately. Statistical tests were applied at the 5 % significance level.

Due to preparation-related changes, not all *Stubbenirmus n. gen.* individuals recorded under "Material" were considered in statistical evaluation and recording of morphological data (especially chaetotaxy).

It must be explicitly stated that in this paper the formation of species groups has not been done as in *Stubbenirmus n. gen.* also in the other three genera of the *Corvonirmus* group, but is to be regarded as a preliminary conception for a differentiation on a morphological basis to be substantiated more precisely later.

The abdominal "sutural seta (ss)" of GUSTAFSSON & BUSH (2017: 17, 31) does not insert on a (actually non-existent) suture, but always submarginal on the membranous border of the tergopleurites. However, it makes sense to conceptually preserve the former "ss" and replace it with *mtps* (mediad tergoposterior seta). Therefore, we include the "ss" (now *mtps*) in the series of tergal posterior setae (*tps*), in which it is closest to the body median (in divided tergopleurites) in each case. In the *Corvonirmus* group, the *mtps* is usually less than half as long in males as in females (*i.e.*: ♂ with mesochaete, ♀ with macrochaete).

The incorrect distinction of the clypeal setae (*as* 1-3) in GUSTAFSSON & BUSH (2017) has been pointed out by MEY (2020 a: 99). In the *Corvonirmus* genus group, anterior seta *as* 2 is absent in *Corvonirmus* and *Lycocoranirmus*, while it is present in *Stubbenirmus g. nov.* and *Hecatrishula* (see Figs. 1-3). Where the *as* 2 is normally absent, it may be present in single individuals at least on one side of the body. On the other hand, there are also individuals in *Hecatrishula* in which one looks in vain for the *as* 2 on at least one side of the body. The clypeal setae *as* 1 and *as* 3 are always present in the *Corvonirmus* group.

*Brueelia sensu stricto* is strongly derived from some *Brueelia*, such as the *Corvonirmus* group, in many, if not most characters and this must be taken into account in phylogenetic considerations including appropriate terminology. Especially in the chaetotaxy it becomes clear that an apomorphic group like *Brueelia s. str.* cannot be used as a standard or starting point for relationships in the *Brueelia* complex.

In the "chaetotaxic ground plan" of the *Brueelia* complex, GUSTAFSSON & BUSH (2017: 17) assume a sternal seta (*sts*) on each side of the abdominal segment II-VI. Other bristles are described as accessory sternal setae on pp. 87 or 208, each inserted between the sternite and pleurite and/or on the posterior margin of the sternite and distal to it. In contrast, of all 38 genera of the *Brueelia* complexes examined by GUSTAFSSON & BUSH (2017: table 2), only two, namely *Aratricerca* Gustafsson & Bush and *Turdinirmoides* Gustafsson & Bush, are reported to possess a *sts* on the segment VII on each side, and only in their males! It should be noted that in both cases this probably has something to do with the fact that the VII abdominal sternite has remained independent and has not fused with the following ones to form the subgenital plate. It is somewhat surprising that apart from these two special cases, according to GUSTAFSSON & BUSH (2017: table 2), there should be no other examples of the presence of accessory *sts* anterior-distal next to the hypogynium, although these authors document it for the two species of *Nemuus* p. 209 and p. 213. That this feature also occurs in the *Corvonirmus* group has been overlooked by the authors, but this does not explicitly imply that there is a closer relationship between *Nemuus* and *Corvonirmus*. It is remarkable that *sts* as macrochaetes only occur in the females of the genera or groups mentioned. It can be expected that this probably phylogenetically valuable detail will also be found in other species.

The high systematic importance of some anterior head structures and the seemingly original abdominal tergopleurite pattern (of *Stubbenirmus g. nov.*) may be misjudged by GUSTAFSSON & BUSH (2017). Whether a tergopleurite is "medianly continuous" or only "connected by narrow bridge" does not matter more than that they are connected medianly. This is a unique feature in the *Brueelia* complex. That the tergopleurite pair IX/X of the males of the former "*Hecatrishula biguttata* species-group" forms a continuous plate, we cannot confirm in any case.

#### **Acronyms:**

- MTD – Museum für Tierkunde Dresden, Naturhistorische Sammlungen  
Senckenberg Dresden, Germany
- SMF – Senckenberg Museum Frankfurt/M., Germany
- FMK – Zoologisches Forschungsmuseum „Alexander Koenig“ Bonn, Germany
- ZSM – Zoologische Staatssammlung München, Germany
- ZMB – Zoologisches Museum, Naturkundemuseum Berlin, Germany
- ZNSH – Zentralmagazin Naturwissenschaftlicher Sammlungen Halle/Saale,  
Martin-Luther-Universität Halle-Wittenberg, Germany

### 3. About the previous history of the *Stubbenirmus* species

The taxonomic previous history of all four species placed here in *Stubbenirmus g. nov.* shows how errors and conservative views, once committed, can stubbornly persist as long as no better, fact-based arguments are presented. The pivotal point is the authenticity of host-parasite relationships, which is essential for taxonomic research. The history of the species currently classified as *Stubbenirmus g. nov.* began with KELLOGG & PAINE (1914), was continued by CLAY (1936) and ANSARI (1956), and came to a tentative end in GUSTAFSSON & BUSH (2017).

KELLOGG & PAINE (1914) prefaced their species descriptions, including that of "*Nirmus biguttatus*", with the following remarkable lines:

"At the suggestion of Mr. C. W. Beebe, Curator of Birds in the New York Zoological Park, who visited the Indian Museum of Calcutta in 1910, Superintendent N. Anundale of this Museum sent to us a collection of Mallophaga taken from bird skins of the Museum. These Mallophaga were taken from the skins of crows, jays and pheasant, most of which had been collected in India. [...] The collecting of dead parasites from dry bird skins in Museums would, at first sight, seem to be a proceeding attended with a dangerous lack of certainty concerning the relation of parasite and host. A good deal of straggling might be expected. As a matter of fact, this danger is not a serious one. The comparison of host records based on collections made from dried skins with records based on collecting from freshly obtained hosts in the field, show that on the whole the records from the dried skins are not misleading. Indeed a great majority of the records in Piaget's "Les Pediculines", which is the monumental basis for all of our knowledge of the Mallophaga and their host relations, were made on a basis of examination of skins in European museums. The lack of danger from straggling comes about from the sedentary habits of the parasites themselves and their early death after the host's death." (KELLOGG & PAINE 1914: 217).

This is admittedly a far too optimistic view of guaranteeing the authentic value of a host-parasite relationship (very close, as in the case of animal lice) detected by this collection method. When certain mallophagan mummies have been recovered from dry bird skins kept in scientific collections, it can never be completely ruled out that one can thereby be taken in by a host-parasite relationship that has ultimately been falsified by human hands.<sup>2</sup> The relevant animal lice literature is unfortunately full of such tendentious false findings. Not only Eduard Piaget, but also Vernon Kellogg and co-workers themselves have produced numerous such cases, certainly unintentionally but probably due to insufficient caution. However, this timeless chalice will not spare even the most industrious animal louse taxonomist. But we would consider it foolish to avoid it altogether by refraining from collecting museum brats. With the beginning of the Nitzschian era in animal lice research in the first half of the 19<sup>th</sup> century, a very high proportion of feather lice described since then is due to this collecting technique. Especially in case of doubt, it must be critically questioned and verified for authenticity at any time. Once the type host has been established, it is not a sacred cow that may not be slaughtered. In the Code (ICZN), recommendation 76.A. Type localities [incl. type host], states: "A statement of a type locality that is found to be erroneous should be corrected."

The description of "*Nirmus biguttatus*" is based on: "Males and females from *Graculus graculus* (Gilgit, Sarhad and Little Pamir, N.W. frontier of India; Khambajong, Tibet), also from *Nucifraga*

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<sup>2</sup> Any other non-anthropogenic secondary infestation that has become permanent over generations does not have the high evolutionary significance that is sometimes attributed to for example the phenomenon of phoresy in Phthiraptera. In any case, there is no empirically based study that can convincingly demonstrate that rather ephemeral host change could seriously challenge the host specificity that has naturally evolved over long periods of time in animal lice. Even EICHLER (1944: 315 f.) does not attribute any essential dispersal strategy to this "Raumparasitismus" ["spatial parasitism"]. The picture of the geographic-hospital distribution of the animal louse taxa, drawn by coevolutionary processes and appearing structured to us, appears like a rock in the surf. All bird groups of the most diverse taxonomic rank harbour a characteristic ensemble of chewing lice species and genus groups unique to them. This picture has been further consolidated in recent years, and it is also confirmed by the results of this study. In this context, we consider it a foolish contradiction in terms to speak of a "Fahrenheitian" phase of louse taxonomy that is coming to an end (GUSTAFSSON & BUSH 2017: 6).

*multipunctata* (Gilgit)" (KELLOGG & PAINE 1914: 234). The fact that the Large-spotted Nutcracker is also named as a host of "*Nirmus biguttatus*" has not been taken up by anyone after CLAY (1936: 908) except GUSTAFSSON & BUSH (2017) and MEY (2017).<sup>3</sup> CLAY (1936) states:

"Kellogg & Paine [...] described *Degeeriella biguttata*, giving as hosts *Pyrrhocorax g. graculus* and *Nucifraga caryocatactes multipunctata*. An examining of thirteen specimens of *Degeeriella* from the former host and nine from the latter discloses two distinct species. On comparing these with Kellogg and Paine's description and figures it was found that *D. biguttata* referred to the species found on *Pyrrhocorax g. graculus*, that from *Nucifraga c. multipunctata* being new."

CLAY (1936: 908) describes "*Degeeriella biguttata koslovae*" after 11 ♂ and 13 ♀ ex *Podoces biddulphi* and 6 ♂ and 8 ♀ ex *P. hendersoni*. The type (slide no. 2994, coll. Meinertzhagen) of *koslovae* is from *Podoces biddulphi* from Kashgaria, Turkestan, China. Thus, *Podoces biddulphi* is determined to be the type host of "*D. b. koslovae*". However, when HOPKINS & CLAY (1952: 57) do not mention *Podoces hendersoni* as host of *koslovae*, this is inexplicably contrary to their practice, and that of others, of naming all host taxa from which an animal louse species was originally described. Moreover, it was a purely formal act of HOPKINS & CLAY (1952) to elevate "*D. b. koslovae*" to the rank of a species, since they upgraded in their checklist all forms originally described as subspecies (i.e. there is no subspecies in their checklist). PRICE et al. (2003) proceeded in a similar but inconsistent manner when they listed subspecies for some genera (such as *Quadriceps*, *Luniceps* or *Saemundssonina*), but not at all for the vast majority (as also for "*Brueelia*").

#### 4. Is *Hecatrishula multipunctata* (Clay, 1936) a synonym of *Hecatrishula biocellata* (Piaget, 1880) ?

Although the genus *Hecatrishula* will be treated in more detail in another manuscript, it seems reasonable in connection with the above remarks to draw attention to a possible problem of identity of "*Degeeriella multipunctata* Clay". When KELLOGG & PAINE (1914: 234 ff.) described "*Nirmus biguttata*" ex *Pyrrhocorax graculus*, they also assigned to this species collection material (details are unknown) from "*Nucifraga multipunctata*" from Gilgit. (Gilgit is a town in the part of Kashmir now administered by Pakistan). CLAY (1936: 906) states: "An examination of thirteen specimens of *Degeeriella* from the former host [*graculus*] and nine from the latter [*multipunctata*] discloses two distinct species." She christened the latter "*Degeeriella multipunctata*". Without the material examined by KELLOGG & PAINE *l. c.*, CLAY could not (in my opinion) coming to this statement. In any case, their description lacks an explicit reference to the use or non-use of that material from the Himalayan Jay. We consider the latter. Their redescription is based on 3 ♂, 6 ♀ "from skins [...] collected in Kashmir". The "type" (according to IRZN Art. 73.1.1. = holotype) of "*Degeeriella multipunctata*" (♂ or ♀ ?, "slide no. 978" according to CLAY 1936: 908; but according to ANSARI 1956: 400 "male, slide no. 778") originates from a skin of the "Meinertzhagen collection". According to the documentation of the Meinertzhagen material of *Hecatrishula multipunctata* examined by GUSTAFSSON & BUSH (2017: 429), the following somewhat different data situation presents itself compared to that reported by CLAY (1936):

1. There is one paratype (1 ♂) more than indicated (incl. holotype, i.e. 4 instead of 3 ♂).
2. The type series of *H. multipunctata* originates from two skins with the finding dates "Kashmir, Mar. [ch] 1925" and the slide numbers "978" for the holotype and "974, 976" for the paratypes.
3. Not taken into account by CLAY *l. c.* as well as by ANSARI (1956: 400) was the collection of 7 ♂, 26 ♀ with the dates "Kashmir, India, Mar. 1935, R. Meinertzhagen, 974", which was

<sup>3</sup> ŠUMILO & LUNKAŠU (1972: 50) incomprehensibly list "*Brüelia multipunctata* (Clay, 1936)" for the Soviet Union and Ukraine, respectively, and they think that this species originates from England. They refer to KISTIAKOWSKY (1926), who notes on page 135: "*N. [irmus] olivaceus* N. [itzsch]. Several ex. [emplare] of *Nucifraga caryocatactes macrorhynchus* Br[e]hm. Kiev district." This feather louse is *Olivinirmus olivaceus* (Burmeister, 1838).

available to GUSTAFSSON & BUSH (2017: 429, "non-types"). What is particularly irritating about this is that the slide number "974" was already assigned to the type series of *H. multipunctata*. And why was this series not considered by CLAY (1936) on the one hand, and especially by ANSARI (1956) on the other?

It should be investigated whether *H. multipunctata* (Clay, 1936) is a synonym of *Hecatrishula biocellata* (Piaget, 1880). Some circumstantial evidence seems to give reason for this assumption. The original description of Theresa Clay<sup>4</sup>, who was at that time very young and inexperienced in systematic questions, raises the question of whether she was dealing with contaminated collection material which, for example, had spilled over from Magpie *Pica pica* to Himalayan Jay *Nucifraga multipunctata* in the "hunting bag". In our opinion, Clay's description seems to point to *H. biocellata* in all the diagnostic characters listed. The male genitalia are similar, abdominal plates and bristles are pronounced as in *H. biocellata*. (The abdominal equation with "*Degeeriella biguttata*" stated by Clay is, however, completely absurd). Ansari's re-description of "*Brüelia multipunctata*" does not give any new clues either (ANSARI 1956: 399). How could he, since no material other than Meinertzhagen's type series was available to him. It is difficult to accept the similarity of "*Brüelia multipunctata*" (= *Hecatrishula multipunctata*) with "*Brüelia olivacea*" (= *Olivinirmus olivaceus*) emphasised by ANSARI (1956: 398), which CLAY (1936: 906) had still excluded according to head shape and male genitalia. In this context it should also be considered that a comparison with the lectotype of "*Nirmus biocellatus* Piaget, 1880" ex "*Pica leucoptera*" (= *Pica pica bactriana* Bonaparte, 1850) seems to be necessary (see THOMPSON 1939).

Since ANSARI (1956: 392, 394) and GUSTAFSSON & BUSH (2017: 89, 95) already dealt uncritically with the findings of CLAY (1936) in the case of "*Degeeriella b. biguttata*" and "*Degeeriella biguttata koslovae*", the question arises whether this was also the case with "*Degeeriella multipunctata*". In sum, all these facts in need of clarification find themselves involuntarily, if not necessarily, placed against the background of the "Meinertzhagen-Clay tag frauds", hitherto little known among phthirapterologists or covered with the cloak of silence. The topic should be taken up in a discourse on the history of science (DALGLEISH & MEINERS 2006, GARFIELD 2007: xi; RASMUSSEN & PRŶS-JONES 2003; see also BIRKHEAD 2015: 170).

## 5. The *Corvonirmus* group

Within the *Brueelia* complex sensu GUSTAFSSON & BUSH (2017), the genera *Stubbenirmus g. nov.*, *Corvonirmus* Eichler, 1944, *Hecatrishula* Gustafsson & Bush, 2017 and *Lycocoranirmus* Mey, 2017 according to their morphology form a group of related taxa that could be placed in the rank of a subfamily (*Corvonirminae subfam. nov.*). However, this would only appear to be well founded if the former Brueeliinae sensu EICHLER (1963: 177) were redefined and elevated to the rank of a family of their own (Brueeliidae) and consequently considered to be of equal rank to the Philopteridae Burmeister, 1838, which were also to be redefined.

Hospital, the *Corvonirmus* group is restricted to the Corvidae, whereby, according to previous knowledge (see Table 1), it is only represented on these host genera: on *Corvus* with *Corvonirmus*, *Hecatrishula* and *Lycocoranirmus*, on *Pica* with *Hecatrishula*, on *Podoces* and *Pyrrhocorax* with *Stubbenirmus g. nov.*

GUSTAFSSON & BUSH (2017) assign the species of the *Corvonirmus* group to two genera: *Corvonirmus* and *Hecatrishula*. In doing so, they treat all previously known forms as species (24 spp. in total); no new ones were added. *Hecatrishula* with 14 species is divided into two groups

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<sup>4</sup> Clay's article "New Species of Mallophaga recorded from Asiatic Birds", submitted on 26.6.1935 and published on 10. January 1936, is at the beginning of her career as a "Mallophagan Pontiff". It is her second article on Mallophaga taxonomy, "communicated by Col. R. Meinertzhagen, F. Z. S.", and it admittedly lacks the high professional maturity of her later contributions, with which she decisively shaped and dominated the development of systematic phthirapterology in the 20th century through her (today, however, very conservative and outdated) systematic-taxonomic view.

("atherae- and *biguttata*-groups").<sup>5</sup> *Corvonirmus* with 14 species is not grouped. The generotype of *Hecatrishula* and *H. biguttata* are treated in detail, and only the generotype of *Corvonirmus*. All other species of both genera are listed by name, some with annotations. The authors assured (p. 15) that they have studied all these species. In the paper by MEY (2017), published only about three weeks later, 25 species of *Corvonirmus* (incl. 2 ssp.) are listed, five of which were introduced as *nova species*. *Lycocoranirmus* is mistaken for a Bird of Paradise feather louse. However, it originates from a Long-billed Crow (see page 429). The existence of *Hecatrishula* still eluded MEY (2017). The *Corvonirmus* group with *Stubbenirmus stubbeae* sp. nov. currently includes 33 described species.

**Description – Habitus:** body colouration blackish brown, brown to strongly lightened, partly with plate reductions and decorative pattern on the sexually dimorphic short to long oval abdomen. Body size of the ♂ (1.3-2.1 mm) in all species always smaller than that of the associated ♀ (1.5-2.5 mm). *Hecatrishula* includes the largest, *Stubbenirmus* and *Corvonirmus* the smallest species in the *Corvonirmus* group. In between are the *Lycocoranirmus* species. Mostly with dome-shaped heads, more rarely (only *Lycocoranirmus*) with pentagonal to trapezoidal head shape. Habitually, the species can usually be assigned to one of these four genera at first glance. They are among the most abdominally bristly groups within the *Brueelia* complex, surpassed only by *Sturnidoecus* Eichler, 1944, *Schizosairhynchus* Gustafsson & Bush, 2017 and *Meropoecus* Eichler, 1940.

**Head:** from circumfasciate (with even pigmentation of the clypeal carina in *Stubbenirmus* except *biguttatus*) to semi-circumfasciate (with uneven pigmentation). The latter means that the clypeal carina has taken on a different stability and functionality in the area of the osculum, when it is clearly weaker to no longer pigmented there and even loses its rounded shape, as it is ± depressed at the frontal above the osculum area. This could result in a larger clypeal hyaline, which is the only morpho-structural expression in *Lycocoranirmus* (fig. 3) within the *Corvonirmus* group. Undivided, apparently only in *Stubbenirmus* (figs. 1-2) and *Hecatrishula nawabi* very narrow clypeal carina with indicated (figs. 1 A & B, 9) to distinct clypeal hyaline (figs. 1, 8 G & H). Dorsal and ventral clypeal signature completely absent in *Corvonirmus* group only in *Stubbenirmus* (except *biguttatus*), as is the case in other few genera, such as *Anarchonirmus* Gustafsson & Bush, 2017, *Sychraella* Gustafsson & Bush, 2017 and *Saepocephalum* Gustafsson & Bush, 2017. In *Stubbenirmus biguttatus*, *Hecatrishula* and *Corvonirmus*, there are some obvious formation approaches to dorsal and ventral clypeal signatures between and below the two *vsm*s 2 (oscularis) and the dorsal clypeal area thereof, respectively (Figs. 8 G & H). Ventral carina branches ending blindly in the middle of the anterior head (only in *Stubbenirmus*, Figs. 1-2, except *biguttatus* [and possibly also in *Hecatrishula nawabi* and *H. variegata* ?]) or leading to the clypeal carina below as 3, to which they are connected by a deep brown pigmented, nodus-like chitinous field. Ventral carinae usually distinctly broader than clypeal carina, but both of the same pigmentation (in *Stubbenirmus biguttatus*, *Hecatrishula* and *Corvonirmus*). Clypeal carina in *Lycocoranirmus* distinctly broader and more pigmented than narrower and much more weakly coloured ventral carina branches. Posterior-median of the inverted dorsal clypeal carina, except in *Stubbenirmus* (without *biguttatus*), there is a crescent-shaped suture (dorsal clypeal suture), which is probably identical to the one mentioned by ANSARI (1956, 1957), but disregarded or not recognised by GUSTAFSSON & BUSH (2017).

Tiny conus with tip barely protruding above head margin (♂ and ♀ in *Stubbenirmus*). Conus in the other three genera sexually dimorphic (in ♂ > ♀), usually smaller than scapus. Only in *Lycocoranirmus* females is the conus as long as the scapus (with *hamatofasciatus* even longer). In their males, it is slightly more than half the length of the scapus, despite the latter's large size. Antennae in all species weakly to markedly sexual dimorphic, especially the scapus of ♂ in contrast to that of ♀ ±, sometimes extremely enlarged.

All frontal clypeal setae (anterior setae as 1 - 3) present (*Stubbenirmus*, *Hecatrishula*) or as 1 and 3 present, but as 2 absent (*Corvonirmus*, *Lycocoranirmus*).

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<sup>5</sup> From the apparently uncorrected remark of GUSTAFSSON & BUSH (2017: p. 93, 2<sup>nd</sup> line) one could read that initially it was intended to separate *Hecatrishula* into subgenera.



Table 1: Occurrence of genera representatives of the *Brueelia* complex on Corvidae  
 (● = according to ANSARI 1956, 1957, GUSTAFSSON & BUSH 2017 and/or MEY 2017  
 and \* = according to unpublished evidence of E. Mey and ? = see note 5)

Corvonirmus group: *Stubbenirmus* gen. nov., *Hecatrishula* Gustafsson & Bush 2017, *Corvonirmus* Eichler, 1944 and *Lycocoranirmus* Mey, 2017. With unclear affiliation: *Olivinirmus* Zlotoryzcka, 1964, *Thescelovora* Gustafsson & Bush, 2017 nov. comb. and *Brueelia sensu stricto* Kéler, 1937. Order of corvid species according to Del HOYO (2020) and Del HOYO & COLLAR (2016). Of all corvid species not mentioned in the overview (in total approx. 60), no representatives from the *Brueelia* complex are known so far. The taxonomic status of "*Nirmus semiannulatus* Piaget, 1883" ex *Gymnorhina tibicen* is unclear. In my opinion, contrary to GUSTAFSSON & BUSH (2017), this species does not belong to *Olivinirmus*.

genus  host species	Corvonirmus group				other genera			notes
	<i>Stubbenirmus</i>	<i>Hecatrishula</i>	<i>Corvonirmus</i>	<i>Lycocoranirmus</i>	<i>Olivinirmus</i>	<i>Thescelovora</i>	<i>Brueelia</i> s. str.	
<i>Platylophus galericulatus</i> (Cuvier, 1816)						●		1.
<i>Platysmurus leucopterus</i> (Temminck, 1824)								
<i>Platysmurus aterrimus</i> (Temminck, 1829)								
<i>Crypsirina temia</i> (Daudin, 1800)					●			
<i>Dendrocitta vagabunda</i> (Latham, 1790)					●			
<i>Dendrocitta formosae</i> Swinhoe, 1863					*			
<i>Dendrocitta occipitalis</i> (S. Müller, 1846)					*			
<i>Dendrocitta cinerascens</i> Sharpe, 1879					●			
<i>Pyrrhocorax pyrrhocorax</i> (Linnaeus, 1758)	●							
<i>Pyrrhocorax graculus</i> (Linnaeus, 1766)	●							
<i>Urocissa caerulea</i> Gould, 1863					●			
<i>Urocissa flavirostris</i> (Blyth, 1846)					●			
<i>Urocissa erythroryncha</i> (Boddaert, 1783)					●			
<i>Perisoreus canadensis</i> (Linnaeus, 1766)					●			
<i>Perisoreus infaustus</i> (Linnaeus, 1758)					●			
<i>Cyanopica cooki</i> Bonaparte, 1850							●	
<i>Cyanopica cyanus</i> (Pallas, 1776)					*		*	2.
<i>Garrulus glandarius</i> (Linnaeus, 1758)					●			
<i>Garrulus lanceolatus</i> Vigors, 1830					*			
<i>Garrulus lidthi</i> Bonaparte, 1850					●			
<i>Zavattariornis stresemanni</i> Moltoni, 1938							●	3.
<i>Ptilostomus afer</i> (Linnaeus, 1766)							●	4.
<i>Podoces hendersoni</i> Hume, 1871	●							
<i>Podoces biddulphi</i> Hume, 1874	●							
<i>Pica pica</i> (Linnaeus, 1758)		●			●			
<i>Pica hudsonia</i> (Sabine, 1823)		●						
<i>Pica nutalli</i> (Audubon, 1837)		●						
<i>Nucifraga caryocatactes</i> (Linnaeus, 1758)					●			
<i>Nucifraga multipunctata</i> Gould, 1849		?						5.
<i>Corvus dauuricus</i> Pallas, 1776		●						
<i>Corvus monedula</i> Linnaeus, 1758		●						
<i>Corvus nasicus</i> Temminck, 1826			●					
<i>Corvus capensis</i> M.H.C. Lichtenstein, 1823		●	●					

**Table 1 continuing**

<i>Corvus ossifragus</i> A. Wilson, 1812			•				
<i>Corvus frugilegus</i> Linnaeus, 1758			•				
<i>Corvus crassirostris</i> Rüppell, 1836			*				
<i>Corvus albicollis</i> Latham, 1790		*	•				
<i>Corvus corax</i> Linnaeus, 1758		•	•				
<i>Corvus cryptoleucus</i> Couch, 1854		•	•				
<i>Corvus ruficollis</i> Lesson, 1831		*	*				
<i>Corvus albus</i> Statius Müller, 1776		•	•				
<i>Corvus rhipidurus</i> E. Hartert, 1918			•				
<i>Corvus brachyrhynchos</i> C.L. Brehm, 1822			•				
<i>Corvus caurinus</i> S.F. Baird, 1858			•				
<i>Corvus corone</i> Linnaeus, 1758			•				
<i>Corvus cornix</i> Linnaeus, 1758		*	•				
<i>Corvus typicus</i> (Bonaparte, 1853)			*				
<i>Corvus enca</i> (Horsfield, 1821)				•			
<i>Corvus compiler</i> Richmond, 1903				*			
<i>Corvus validus</i> Bonaparte, 1850				•			
<i>Corvus moneduloides</i> Lesson, 1831			*				
<i>Corvus woodfordi</i> (Ogilvie-Grant, 1887)				*			
<i>Corvus fuscicapillus</i> G.R. Gray, 1859				*			
<i>Corvus tristis</i> Lesson & Garnot, 1827				*			
<i>Corvus insularis</i> Heinroth, 1903			?	*			6.
<i>Corvus orru</i> Bonaparte, 1855			•	*			
<i>Corvus bennetti</i> North, 1901			•				
<i>Corvus mellori</i> Mathews, 1912			•				
<i>Corvus coronoides</i> Vigors & Horsfield, 1827			•				
<i>Corvus splendens</i> Vieillot, 1817				•			
<i>Corvus macrorhynchos</i> Wagler, 1827				•			
<i>Corvus leuallantii</i> Lesson, 1831				*			
<i>Corvus culminatus</i> Sykes, 1832				*			
<i>Corvus philippinus</i> (Bonaparte, 1853)				•			
<i>Cyanocitta cristata</i> (Linnaeus, 1758)					•		
<i>Cyanocitta stelleri</i> (J.F. Gmelin, 1788)					•		
<i>Cyanocorax violaceus</i> du Bus de Gisignies, 1847					•		
<i>Cyanocorax cyanomelas</i> (Vieillot, 1818)					•		
<i>Cyanocorax morio</i> (Wagler, 1829)					•		
<i>Cyanocorax yncas</i> (Boddaert, 1783)					•		
<i>Cyanocorax affinis</i> von Pelzeln, 1856					•		
<i>Cyanocorax chrysops</i> (Vieillot, 1818)					•		
<i>Cyanocorax cayanus</i> (Linnaeus, 1766)					•		

**Table 1, Note 1:** "*Priceiella* (*Thescelovora*) *aliocephala* Gustafsson & Bush, 2017" is monotypic, and its morphology is so different from the three other, much more closely related groups "*Priceiella* (*Priceiella*) Gustafsson & Bush, 2017", "*Priceiella* (*Camurnirmus*) Gustafsson & Bush, 2017" and "*Priceiella* (*Torosinirmus*) Gustafsson & Bush, 2017" that it seems justified to grant generic status to *Thescelovora*. However, it undoubtedly does not belong to the *Corvonirmus* group either. GUSTAFSSON & BUSH (2017) and "Zootaxa" have apparently not yet made clear the nomenclatural faux pas that the two subgenera of *Priceiella* (grammatically feminine), "*Torsonirmus*" and "*Camurnirmus*" (both masculine), are placed in the "wrong sex" contrary to the rules. According

to the Code, the genus determines the sex of the subgenus(es) assigned to it, since both categories have coordinated nomenclatural status (IRZN Art. 30).

**Note 2:** We have a female of an undescribed *Olivinirmus* and a *Brueelia* species from this host species. The latter does not seem to be conspecific with *B. deficiens*.

**Note 3:** A *Brueelia* s. str.-species (*B. zavattariornis* Ansari, 1956) on such an exquisite and rare corvid with a very small area needs further investigation.

**Note 4:** *Ptilostomus afer* is said to harbour two *Brueelia* s. str.-species: *B. zohrae* Ansari, 1956 and *B. moreli* Ansari, 1957, which we believe needs confirmation. Two *Brueelia* s. str.-species in one species of Corvids is extremely unusual in two respects.

**Note 5.** The status of *Hecatrishula multipunctata* (Clay), which we question, is discussed on page 403.

**Note 6.** If our unpublished finding of one male each of *Corvonirmus* sp. and *Lycocoranirmus* sp. is confirmed, it would be the first case of synhospitality of both genera.

The pair of ocellar setae (*osms* 2) is located submarginal to the posterior margin of the clypeal carina in *Stubbenirmus* and *Hecatrishula* (figs. 1-2), in *Corvonirmus* and *Lycocoranirmus* it inserts "under the roof" of the frontal clypeal carina (fig. 3). The position and size of the clypeal setae, which vary slightly from genus to genus, allow us to trace certain functional-morphological changes in the anterior head (preantennals) in the *Corvonirmus* group (figs. 1-3).

Ocellar setae (*os*) and preocular setae (*pos*) both insert on either the ommatidium or the latter close to or on the posterior margin of the latter. It is highly probable that the preocular seta (which in many genera of the *Brueelia* complex is inserted on the occipital carina at a distance from the ommatidium) was originally derived from an ocular seta. Ocellar setae and preocular setae unequal in length only in *Stubbenirmus* (except *S. biguttata*): *os* as fine spine, *pos* as mesochaete (fig. 1).

**Thorax:** prostigma ventral in posterior outer corner of prothorax. Above it the pronotal postspiracular seta, which clearly extends beyond the posterior margin of the mesometanotum.<sup>6</sup> On mesometanotum posterior-marginal on each side a row of 5-10 macrochaetae. Rarely equal number of setae on both sides, usually 1-3 setae less on one side. On outer corner (ventral) of mesometathorax on each side one trichobothrium (as mesochaete) and one spine or rarely (only in *Hecatrishula* sp.) trichobothrium and one mesochaete.

Tarsi with two unequal claws. The apical half of the non-impacted claw is hyaline and usually barely visible. In fact, this reaches about three quarters of the length of the larger strongly brown-pigmented movable claw.

**Abdomen:** *Corvonirmus uncinosus* (Burmeister) (generotype) has seven (!) abdominal stigmata, of which only the first (on the segment II) is scarred and usually hardly visible, but to each of which a tracheal cord leads. This is also the case with a *Lycocoranirmus* sp. ♀ (M. 6106. a). Functional respiratory openings on the abdominal segment II may also be found in other species of the *Corvonirmus* group on closer examination.

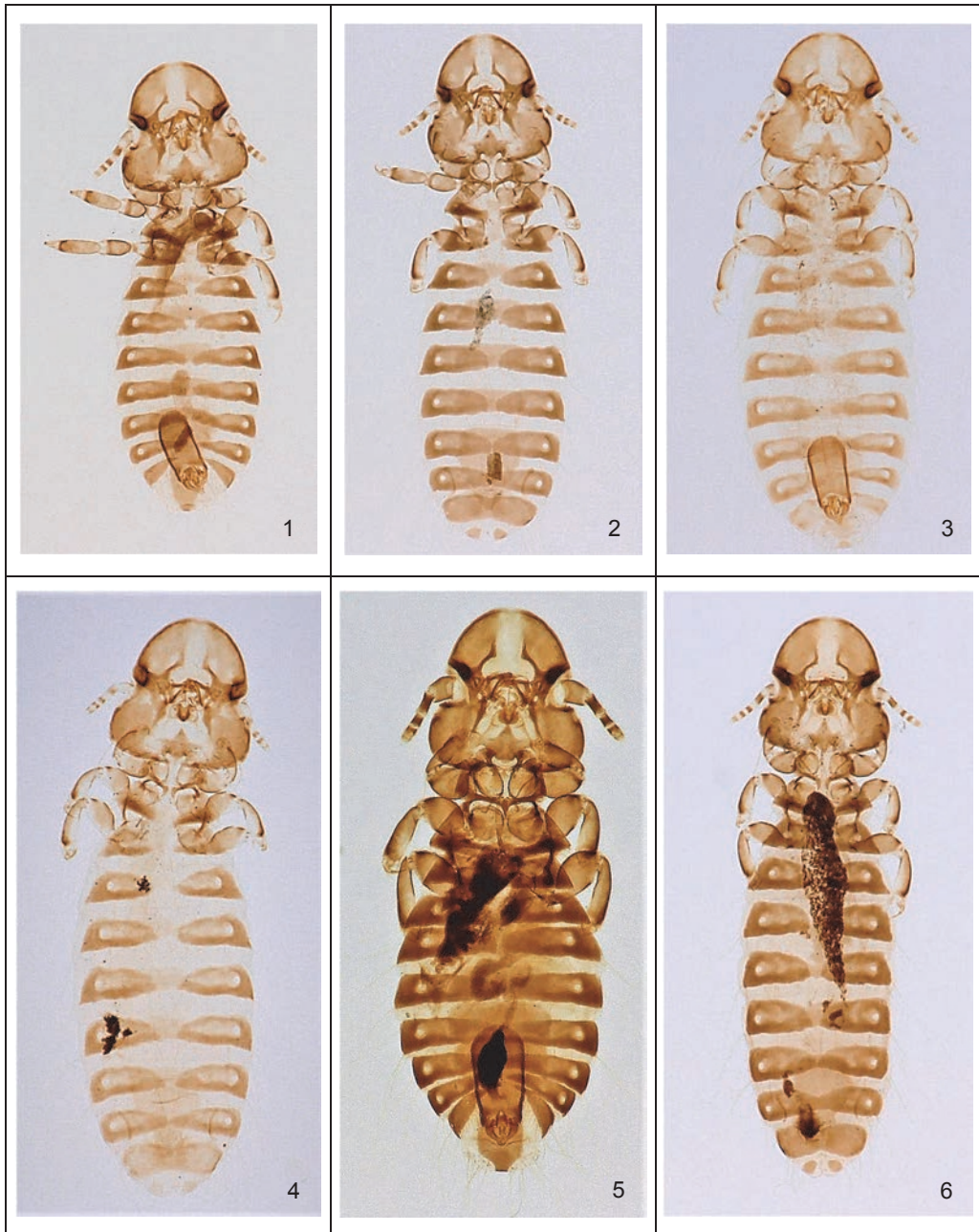
Pleural abdominal incassations and re-entrant heads absent (in *Stubbenirmus* except *S. biguttatus* on segments II-III, *Hecatrishula* and *Corvonirmus*) or present on segments II-VIII (*Lycocoranirmus*).

Tergopleurites II-VIII (in ♂ also IX/X) median not fused together, only Tergopleurite IX/X of ♀ forming a closed plate (*Hecatrishula*, *Corvonirmus* and *Lycocoranirmus*). But tergopleurites VIII-IX/X of ♀ of *Stubbenirmus* (all four species) each forming a plate, others (V-VII) variable, divided or undivided (Table 2). All tergopleurites of the ♂ of *Stubbenirmus koslovae* - and *S. biguttatus* group divided, in *S. docilis* group variable (V-VII undivided or divided).

Abdominal sternites central on segments II-VI (II smallest, crescent-shaped or often hardly pigmented, III-VII ± rectangular in ♀, narrower and pointed on both sides in ♂).

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<sup>6</sup> I cannot follow the divergent accounts of prostigma and pronotal post-spiracular setae in *Hecatrishula* and *Corvonirmus* in GUSTAFFSON & BUSH (2017: 130-131, 319-320).



**Plate I** (figs. 1-6): **1:** *Stubbenirmus stubbeae* sp. nov., ♂, paratype (ZFMB 1975-112), TL 1.53 mm, ex *Podoces hendersoni* from E Turkestan, China. **2:** *Stubbenirmus stubbeae* sp. nov., ♀, paratype (ZFMB 1975-111), TL 1.91 mm, ex ditto. **3:** *Stubbenirmus koslovae* (Clay), ♂ (M. 5542. c), TL 1.84 mm, ex *Podoces biddulphi* from Turkestan, China. **4:** *Stubbenirmus koslovae* (Clay), ♀ (M. 5542. b), TL 2.02 mm, ex ditto. **5:** *Stubbenirmus docilis* (Ansari), ♂ (M. 6046. d), TL 1.44 mm, ex *Pyrrhocorax pyrrhocorax himalayensis* from Nepal. **6:** *Stubbenirmus docilis*, ♀ (M. 6179. b), TL 1.85 mm, ex *P. pyrrhocorax centralis* from Mongolia.



**Plate II** (figs. 1-6): 1: *Stubbenirmus biguttatus* (Kellogg & Paine), ♂ (M. 6308. a), TL 1.72 mm, ex *Pyrhocorax graculus digitatus* from Taurus, Turkey. 2: *Stubbenirmus biguttatus*, ♀ (M. 6308. a), TL 1.81 mm, ex ditto. 3: *Hecatrishula atherae* (Ansari) ♂ (ZFMB 1979-889), TL 1.97 mm, ex *Corvus corax laurencei* from Afghanistan. 4: *H. atherae* ♀ (ZFMB 1975-889), TL 2.26 mm, ex ditto. 5: *Corvonirmus argulus* (Burmeister), ♂ (M. 6133. e), TL 1.3 mm, ex *Corvus c. corax* from Bavaria, Germany. 6: *Corvonirmus argulus*, ♀ (M. 6133. e), TL 1.7 mm, ex ditto.

**Chaetotaxy:** paratergal setae (of ♂ and ♀) in *Stubbenirmus*, *Hecatrishula* and *Corvonirmus* from segment III or only from segments IV to VIII, in *Lycocoranirmus* always from segments IV to VIII with at least one seta.

Post-spiracularis (= principal post-spiracular seta) in *Stubbenirmus* (♂ and ♀) on segments II-VIII, in *Hecatrishula* (♂ and ♀) on III-VIII, in *Corvonirmus* and *Lycocoranirmus* ♂ on II-VIII, ♀ on segments IV-VIII.

Abdominal sternites II-VI posterior-lateral on each side with one seta (in males and females of *Lycocoranirmus* and the *Corvonirmus orruaticus* group), in the other three genera in variable number with usually more than two setae on each side.

In females of *Stubbenirmus* (except *S. koslovae*) and *Corvonirmus* sternal on abdominal segment VII (lateral to hypogynium) one macrochaete each (mostly one on each side = 1/1 or 0/1) or completely absent, as in all males of *Corvonirmus* group and in females of *Hecatrishula* and *Lycocoranirmus*. In the *Brueelia* complex there otherwise only in *Nemuus* Gustafsson & Bush, 2017 2-4 setae on each side (see material and method).

**Genitalia:** hypogynium (female subgenital plate) complete crosspiece, middle part sometimes absent or barely pigmented (*Corvonirmus*, *Lycocoranirmus*), or with lateral submarginal bulge (*Hecatrishula*) or this only indicated (*Stubbenirmus biguttatus*) or drop-shaped (*Stubbenirmus*) (fig. 13). Male genitalia large in relation to abdomen (0.29-0.5 mm long), basal plate anteriorly often widest, parameres ± strongly curved and appearing short (*Hecatrishula*, *Stubbenirmus*, fig. 7, plate I, II) or wedge-shaped elongated and appearing long (*Corvonirmus*, *Lycocoranirmus*, fig. 14, plate II). Hypandrium large (fig. 14).

**Food:** on one male and female of *Stubbenirmus koslovae* (M. 6217. d) there are remains of body plates and antennae of analgescids in the proventriculus. The same can also be reported from one male and three females of *Lycocoranirmus mollii* (M. 6207.b, 6127.b). In other, but still undescribed *Lycocoranirmus* species, remains of analgescids have been found in the intestinal tract. Feather mites as a food source may be of greater importance for many Ischnocera than previously thought (according to unpublished data from EM).

### 5.1. *Stubbenirmus* gen. nov.

Tables 1-2, figs. 1, 2, 5-7, 9, 10, 13, plates I-II.

*Nirmus* Nitzsch, 1818: KELLOGG & PAINE (1914: 234). *Pro parte*.

*Degeeriella* Neumann, 1906: CLAY (1936 [1935]: 908). *Pro parte*.

*Brüelia* Kéler, 1936: HOPKINS & CLAY (1952: 52). *Pro parte*.

*Brueelia* Kéler, 1936: PRICE et al. (2003: 152). *Pro parte*.

*Hecatrishula* Gustafsson & Bush, 2017: 87. *Pro parte*.

Generotype: *Stubbenirmus stubbeae* spec. nov.

**Description:** mostly delicate habit (table 1-2). Body size ♂ 1.3 - 1.5, ♀ 1.6 - 2.1 mm.

**Head:** completely circumfasciate (figs. 1 & 2 above, 9 A-F) or semi-circumfasciate (figs. 1, below, 9 G-H). Clypeal carina very narrow (broadest in *S. biguttatus*). Median frontal with narrow hyaline fringe, broader and sunken only in *S. biguttatus*. Thin ventral carinae branches end blindly in the middle of the forehead, without connection to the clypeal carina (*koslovae* and *docilis* group) or much broader ventral carinal branches come in connection with the clypeal carina (*biguttatus* group). The position of the clypeal setae (anterior setae, as 1-3, dorsal submarginal seta, *dsms*, and ventral submarginal setae, *vsms* 1-2) is group-specific. *Koslovae* group: as 1 is far from the *dsms* (forming an equidistant group of three with as 2 and 3); *docilis* group: as 1 is close to the *dsms* (both in an equidistant group of four with as 2 and 3); *biguttatus* group: forming an equidistant setae group as in the *docilis* group. However, in *biguttatus* the *vsms* 1 inserts close to the seta canal of as 2, while in *docilis* group the *vsms* 1 sits close below the *dsms* and in *koslovae* group the *vsms* 1 is clearly distant from the *dsms* (see fig. 1-2).

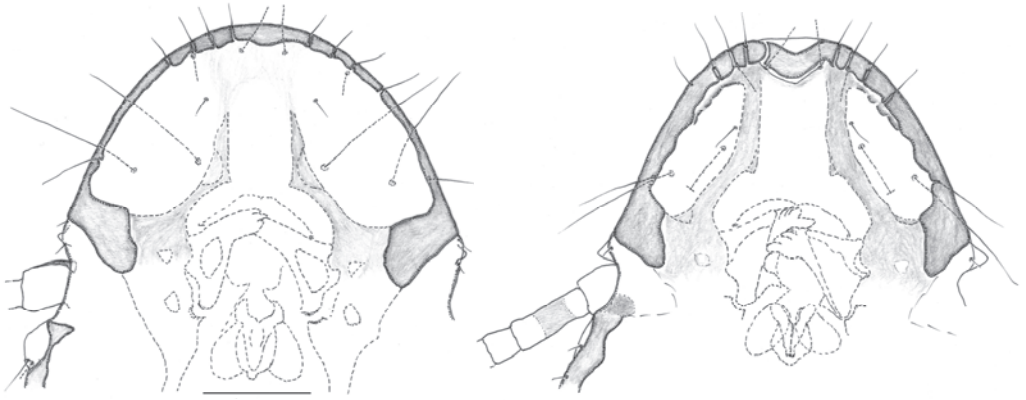


Fig. 1: Left - dorsal anterior head structures (ventral setae dashed) of *Stubbenirmus docilis* (Ansari) ♀, ex *Pyrrhocorax pyrrhocorax himalayanus*, Nepal (M. 6260. a, bottom right); right - *Stubbenirmus biguttatus* (Kellogg & Paine) ♀, ex *Pyrrhocorax g. graculus*, Switzerland (M. 6229. d, bottom right). Scale 0.1 mm.

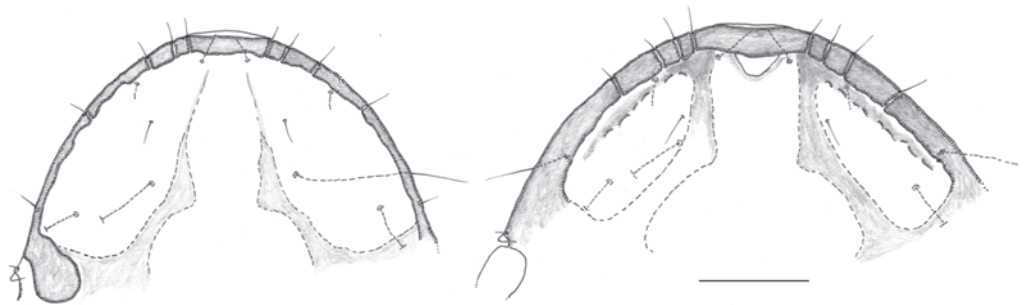


Fig. 2: Left - dorsal anterior head structures (ventral setae dashed) of *Stubbenirmus stubbeae* sp. n. ♂, ex *Podoces hendersoni*, Turkestan, China (ZFMK 1975-112); right - ditto of *Hecatri-shula atherae* (Ansari) s. lat. ♂, ex *Corvus corax kamtschaticus*, Mongolia (M. 493. bb). Scale 0.1 mm.

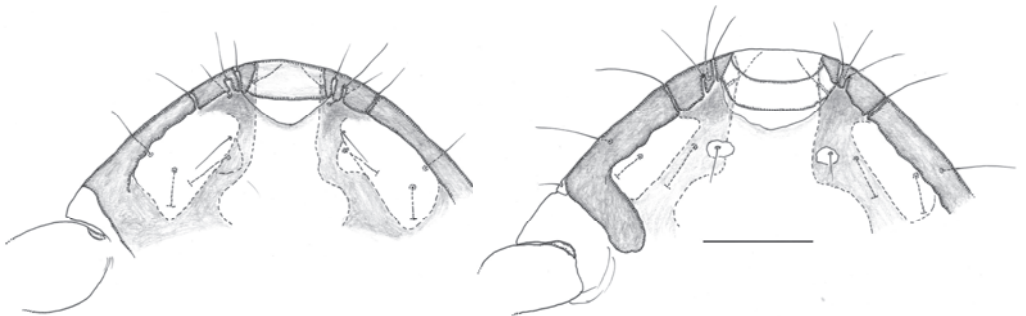


Fig. 3: Left - dorsal anterior head structures (ventral setae dashed) of *Corvonirmus quadrangularis* (Rudow) ♂, ex *Corvus albus*, Tanzania (M. 6424. b); right - *Lycocoranirmus giloloensis* Mey ♂, ex *Corvus validus*, Halmahera, Indonesia (M. 6159. d). Scale 0.1 mm.

Table 2: Tergopleurites of abdominal segments II - IX/X of some species of *Corvonirmus* group

Basic shape and distribution of tergopleurites (a median divided or abdominal segment spanning chitinous plate) are constant only in *Hecatrishula*, *Corvonirmus* and *Lycocoranirmus*. Characters: ● = median divided (paired), — = median not divided (unpaired)

abdominal segment / species	number of investigated specimen	II	III	IV	V	VI	VII	VIII	IX/X
<i>Stubbenirmus stubbeae</i>	♂♂ N=3	n = 1	●	●	●	●	●	●	●
		n = 1	●	●	●	—	—	●	●
		n = 1	●	●	—	—	—	●	●
	♀♀ N=7	n = 3	●	●	●	●	●	●	—
		n = 4	●	●	●	●	●	—	—
<i>Stubbenirmus koslovae</i>	♂♂ N = 12		●	●	●	●	●	●	●
	N = 12	n = 1	●	●	●	●	●	●	—
		n = 11	●	●	●	●	●	●	●
<i>Stubbenirmus docilis</i>	♂♂ N = 23	n = 8	●	●	●	—	—	—	●
		n = 2	●	●	●	●	—	●	●
		n = 3	●	●	●	●	—	—	●
		n = 1	●	●	●	—	—	●	●
		n = 2	●	●	●	●	●	—	●
		n = 4	●	●	●	●	—	—	●
		n = 3	●	●	●	—	—	●	
	♀♀ N = 24	n = 18	●	●	●	●	●	—	—
		n = 6	●	●	●	●	—	—	—
<i>Stubbenirmus biguttatus</i>	♂♂ N = 8		●	●	●	●	●	●	
	♀♀ N = 15		●	●	●	●	●	—	
<i>Hecatrishula spp.</i>	♂♂		●	●	●	●	●	●	
	♀♀		●	●	●	●	●	—	
<i>Corvonirmus spp.</i>	♂♂		●	●	●	●	●	●	
	♀♀		●	●	●	●	●	—	
<i>Lycocoranirmus spp.</i>	♂♂		●	●	●	●	●	●	
	♀♀		●	●	●	●	●	—	

Hyaline conus barely or not at all protruding above the edge of the sclerotised anterior corners of the head. In *S. biguttatus* ♂ it is most strongly developed. Ommatidium with two laterally offset posterior setae at the same level. The dorsal one is a thin mesochaete about 0.05 mm long (broken off in many individuals). It is about half as long as the pediculus, the ventral one is a fine spine only 0.01 mm long. Apparently males and females have the same ommatidia seta. Only in *S. biguttatus* are ocularis and preocularis fine spines of the same size.

**Abdomen:** Chaetotaxy dominant with macrochetae (fig. 6). Pleural abdominal incrassations and re-entrant heads completely absent (except in *S. biguttatus* on segments II and III, see fig. 10). The least variation in the division of the tergopleurites is seen in *S. biguttatus* (see table 2 for details).



**Chaetotaxy:** unusual in the *Corvonirmus* group is the occurrence of an accessory postspiracular seta (*aps*) only on one side of the body of some females of *Stubbenirmus stubbeae* ( $n = 2$ , on abdominal segment VI) and *S. koslovae* ( $n = 3$ , on abdominal segment V twice and VI once). The *aps* are normally possessed only by the males of *Corvonirmus* and *Lycocoranirmus*, and probably not at all (since we have not examined them more closely so far) by both sexes of *Hecatrishula*.

All four species of *Stubbenirmus* (82 individuals in total, ♂ and ♀), have no paratergal seta (*ps*) on the abdominal segment II. On the segment II, however, the paratergal seta is different between *S. koslovae* and *S. stubbeae* of both sexes, at least in tendency. Indeed, one male of *S. koslovae* has a paratergal seta only on one side, while all the others ( $n = 16$ ) are without seta there on both sides; they are also absent in the three males of *S. stubbeae*. On the other hand, the females of *S. koslovae* and *S. stubbeae* differ clearly in this character, the latter being the one with more setae. Of 12 females of *S. koslovae*, 10 have none, two each only on one side a paratergal seta on the segment III. Of the *S. stubbeae* -♀ ( $n = 7$ ), two have none, two have one on one side only, but one individual each has one or even two on each side and finally one individual has one paratergal setae on one side and two on the other. Of males and females (46 individuals in total) of *S. docilis* and *S. biguttatus* together, only one male of *S. docilis* has no paratergal setae on the III abdominal segment. All other individuals ( $n = 45$ ) have setae there. Postspiracular setae in ♂ and ♀ on segments II to VIII (Fig. 6). Accessory postspiracular seta (*aps*) absent. Tergal posterior seta (*tps*) including mediad tergo posterior seta (*mtps*) on segments II-VIII on each side in females mostly three, in males on segments II-VII four, on VIII even four to five *tps*. Sternal on segments II-VI (only on ♀) each 2-10 setae (*sts*). On segment VII 0-2 *sts*, distributed as follows: in *koslovae* ( $n = 11$ ) *sts* absent, in *stubbeae* twice two and five times 0, *docilis* six times two (fig. 13 F), four times one, once 0, *biguttatus* nine times two, seven times one, twice 0. This means that out of 45 females of all four species examined, 1-2 sternal setae were found on segment VII on 26 of them.

**Diagnosis:** within the *Brueelia* complex (with currently about 40 genera), *Stubbenirmus gen. nov.* is the only known genus in which the females, besides the fused tergo pleurite on the abdominal segments IX/X (as in all other Brueelians), also have the abdominal segment VIII undivided (table 2). Equally unique to *Stubbenirmus* (*koslovae* and *docilis* groups only) is that further abdominal tergites (VI-VII in ♂ and ♀) are still connected to each other by a ± narrow bar (which can be interpreted as a rudimentation of the abdominal tergo pleurites originally consisting of one plate). Postspiracular setae as in *Hecatrishula* (segment II to VIII), but different from *Corvonirmus* (only ♀ segments III to VIII) and *Lycocoranirmus* (only ♀ segments IV to VIII). Hypogynium pear-shaped (*koslovae* and *docilis* group) or similar to *Hecatrishula* (*biguttatus* group), but never taking the shape as in *Corvonirmus* and *Lycocoranirmus* (fig. 13).

According to the absence or presence of clypeal hyalines and clypeal sutures, all three species groups differ clearly from each other (figs. 1-2, 9 A-H). Morphologically (head, genitalia), *S. biguttatus* is intermediate between *Stubbenirmus koslovae* and *-docilis* group on the one hand and *Hecatrishula* on the other. The decision to assign *biguttatus* to *Stubbenirmus* was based on the unique characteristic of this genus in the *Brueelia* complex: all females of *Stubbenirmus* have a tergo pleurite consisting of a whole plate on abdominal segment VIII.

**Hospital distribution:** *Pyrrhocorax* Tunstall, 1771 and *Podoces* J.G. Fischer von Waldheim, 1821.

**Zoogeographical distribution:** deserts and high mountains of the Palearctic.

### **Species (4) and groups (3):**

*koslovae* group (2 spp.):

1. *Stubbenirmus stubbeae spec. nov.* ex *Podoces hendersoni*. Holotype (♂) from Somon Mjanganag, Mongolia.
2. *Stubbenirmus koslovae* (Clay) ex *Podoces biddulphi*. Holotype (♂) from Kashgar, East Turkestan [Xinjiang Province, China].

*docilis* group (1 sp.):

3. *Stubbenirmus docilis* (Ansari) ex *Pyrrhocorax pyrrhocorax barbatus*. Holotype (♂) from Morocco.

*biguttatus* group (1 sp.):

4. *Stubbenirmus biguttatus* (Kellogg & Paine) ex *Pyrrhocorax graculus forsythi*. Lectotype (♂) from Indian Museum, Calcutta.

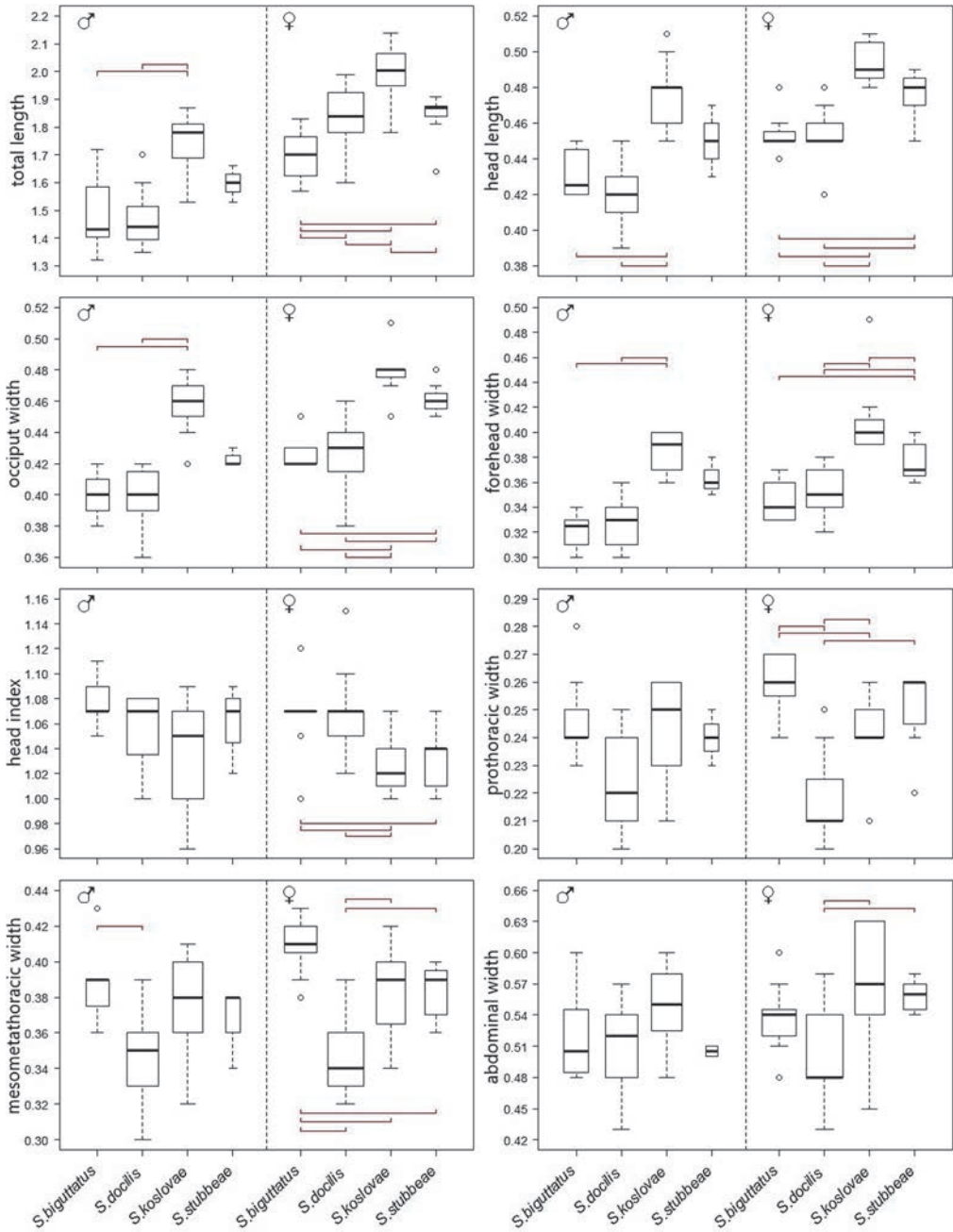


Fig. 5: Expression of different morphological characters (body measurements) for males and females of four *Stubbenirmus* species (n: 8 ♂, 15 ♀ *biguttatus*; 15 ♂, 19 ♀ *docilis*; 14 ♂, 11 ♀ *koslovae*; 3 ♂, 7 ♀ *stubbeae* sp. nov.). Significant differences ( $p < 0.05$ ) between the individual species are marked with red.

### 5.1.1. *Stubbenirmus stubbeae* spec. nov.

Table 2, figs. 1, 2, 5-7, 9, 13; plate I - figs.1-2.

*Degeeriella biguttata koslovae* Clay, 1936 [1935]: 908. Pro parte.

*Brüelia koslovae* (Clay, 1936): HOPKINS & CLAY (1952: 57). Pro parte.

*Brüelia koslovae* (Clay, 1936): ANSARI (1956: 394). Pro parte.

*Brueelia koslovae* (Clay, 1936): PRICE et al. (2003: 156). Pro parte.

*Hecatrishula koslovae* (Clay, 1936): GUSTAFSSON & BUSH (2017: 89). Pro parte.



**Type host:** *Podoces hendersoni* A. O. Hume, 1871 - Mongolian Ground Jay, Mongolenhäher (fig. 4).

**Material:** 3 ♂, 7 ♀ from 3 skins, namely 1. 2 ♀ (M. 6175.) ex *P. hendersoni* ad. ♂, 14.2.1980 15 km N Somon Mjangag, Mongolia, coll. M. Stubbe; ex skin 1849 ZNSH, leg. E. Mey 12.3.2019. - 2. 2 ♂ (M. 6234.) ex *P. hendersoni* juv., 25.6.1908 Uital, Kashgaria, Turkestan [China], coll. M. Menzbier; ex skin F VII.II.a ζ ZFMK, leg. E. Mey 12.6.2019. - 3. 1 ♂, 5 ♀ (ZFMK 1975, 111-113) ex *P. hendersoni*, Kashgar, East Turkestan [China]; ex skin (without number) ZFMK, [leg. H. Klockenhoff ?] (Note: no finding dates other than those noted on the slides were available).

Fig. 4: Mongolian Ground Jay *Podoces hendersoni*, 29.9.2017, oasis Zun mod (43°57'N/99°13' E), Mongolia (photo: A. STUBBE).

Holotype ♂ (M. 6234. right) and three paratypes in ZNSH as well as six paratypes in ZFMK.

**Description:** habitus (♂, ♀) see Table I, Figs. 1-2. Body colour light brown. Measurements [mm]: ♂ (Holotype + n = 2) TL 1.66 + 1.53-1.6, HL 0.45 + 0.43-0.47, FW 0.35 + 0.36-0.38, OW 0.42 + 0.42-0.43, HI 1.07 + 1.02-1.9, PW 0.24 + 0.23-0.25, MW 0.38 + 0.34-0.38, AW 0.51 + 0.5 (once). ♀ (n = 7) TL 1.64-1.91, HL 0.45-0.48, FW 0.36-0.4, OW 0.45-0.48, HI 1-1.07, PW 0.22-0.26, MW 0.36-0.4, AW 0.54-0.58.

**Head:** dorsal anterior head structures see fig. 2. Frontal section of clypeal carina with *dsms* and as 2 und as 3 see Fig. 9 A-B.

**Thorax** (♂ n = 3, ♀ n = 7): macrochaetae row posterior-marginal on mesometanotum (each side n/n setae): ♂ 6/6 and twice 6/7; ♀ twice each 5/5, 6/7 and 7/7 (3 variants; Σ from 10-14, range of variation). See Fig. 6.

**Abdomen** (♂ n = 2, ♀ n = 7; fig. 6): abdomen (♀) with chitinous plates and setae as in Fig. 6. Segment II of ♂ without **paratergal seta**. Number of paratergal setae segments III-VIII (each n/n; meso- and macrosetae): **III**, 0-2 (♀, twice each 0/0 and 0/1, once each 1/1, 1/2 and 2/2) (= 5 variants). **IV**, 1-2 (♂, 1/1 and 1/2) and 2-3 (♀, five times 2/2, once each 2/3 and 3/3) (= 3 variants). **V**, 2-2 (♂ 2/2) and 1-4 (♀, four times 2/2, 2x 3/3, once 1/2) (= 3 variants). **VI**, 1-2 (♂, once each 2/2 and 1/1) and 2-4 (♀, once 2/2, thrice 2/3, 2x 3/3 and 3/4) (= 4 variants). **VII**, 2-2 (♂, twice 2/2) and 2-5 (♀, thrice 2/3, 2x 3/3, once each 2/2 and 4/5) (= 4 variants). **VIII**, 2/2 (♂, twice 2/2) and 2-3 (♀, five times 2/2 and twice 3/3) (= 2 variants). **Postspiracular** (macro)setae (incl. trichobothrium [= trichoid seta] on segment VIII) on ♂ and ♀ on segments II-VIII. ♂ without, but two females each with one **accessory postspiracular seta** only on one side of segment VI. **Tergal posterior setae** (including *mtps* with one pair of setae) on segments II-VII: **II**, 2-3 (♂, 2/3 and 2/2 and ♀, four times 2/2, once each 2/3 and 3/3) (= 3 variants). **III**, 1-3 (♂, once each 3/3, 2/2 and 1/2 and

♀, thrice 3/3, twice 2/3, once each 4/4 and 2/2) (= 4 variants). **IV**, 1-3 (♂, once each 3/3, 2/2 and 1/1 (= 3 variants) and ♀, thrice 3/3, twice 2/3, once each 2/2 and 1/2, = 4 variants). **V**, 1-3 (♂, once each 2/3, 2/2 and 1/1 = 3 variants) and 1-4 (♀, twice each 2/3 and 2/2, once each 1/2, 3/3 and 3/4, = 5 variants). **VI**, 2-3 (♂, once each 3/3, 2/3 and 2/2 (= 3 variants) and 1-4 (♀, twice 3/3, four times 2/2 and once 1/2, = 3 variants). **VII**, 0-3 (♂, once each 3/3 and 1/2, = 2 variants) and 0-3 (♀, thrice 1/1, twice each 1/0, 1x 3/3 and 2/3, = 4 variants). **Sternal setae** posterior-lateral and central of ventral plates (sternites) II-VII: **II**, 3-4 (♂) or 4-6 (♀, five times 4, once 6) (= 2 variants), **III**, 4-6 (♂) or 5-8 (♀, thrice 5, twice 6, once each 7 and 8) (= 4 variants). **IV**, 4 (♂) or 6-10 (♀, four times 6, twice 7, once 10) (= 3 variants). **V**, 4 (♂) or 4-10 (♀, thrice 7, once each 4.5, 6 and 10, = 5 variants). **VI**, 4-5 (♂) or 5-9 (♀, thrice 6, twice 5, once 9) (= 3 variants), **VII**, 0 (♂) and 0-2 (♀, five times 0, twice 1/1) (= 2 variants).

Male genitalia see fig. 7. Length 0.29-0.33 (n = 2), width of basal plate cranial and at paramere insertion 0.11 mm each. Hypogynium 0.3 mm long, 0.19 mm wide, variable in shape (figs. 13 A, B).

**Diagnosis:** in all morphological characters (body measurements) of the four *Stubbenirmus* species, the females differ more than the males (fig. 5), which may partly be explained by the smaller sample sizes of the males. Significant are the differences in the forehead width between the females of *S. koslovae* and *S. stubbeae* sp. n. Also the total length of the females of *S. koslovae* is significantly larger than the total length of *S. stubbeae*. Significant differences exist between the females of *S. docilis* and *S. biguttatus* in prothorax width, and between the males and the females of both species in mesometathoracic width. These biometric findings (fig. 5) underline the separate classification of four species in the genus *Stubbenirmus*. All four *Stubbenirmus* species can be differentiated according to the shape of the abdominal tergopleurites (table 2).

**Derivatio nominis:** *Stubbenirmus* gen. nov. is dedicated to Prof. Dr. sc. Michael Stubbe, who has rendered lasting services to the study of the biological resources of Mongolia. To have his name permanently associated with the mallophagan name "Nirmus" used by Prof. Dr. Christian Ludwig Nitzsch allows us to draw a historical bow between two scholars active at the Alma mater halensis for animal lice research: C. L. Nitzsch, who founded this discipline and developed it from 1810 to 1836; M. Stubbe, in deep awareness of this tradition, an impulse giver who has known how to promote it in many ways since about 1979. *Stubbenirmus* is grammatically masculine.

It is an obvious expression of this dedication to dedicate the new Mongolian featherlouse species *Stubbenirmus stubbeae* spec. nov., whose identity has so far been misunderstood, to Dr. Dr. h. c. Annegret Stubbe. Together with her husband, M. Stubbe, she played a major role in the success of zoological field research in Mongolia over the past 40 years, both from a professional and logistical sense.

### 5.1.2. *Stubbenirmus koslovae* (Clay, 1936) nov. comb.

Tab. 1, 2; fig. 5, 9, 13; plate I - figs. 3-4.

*Degeeriella biguttata koslovae* Clay, 1936 [1935]: 908, fig. 3, pl. I, fig. 3. (ex "*Podoces biddulphi*" and "*Podoces hendersoni*").

*Brüelia koslovae* (Clay, 1936): HOPKINS & CLAY (1952: 57). (ex "*Podoces biddulphi*"). Status after formal, unjustified upgrading to species.

*Brüelia koslovae* (Clay, 1936): ANSARI (1956: 394), (ex "*Podoces biddulphi*" and "*Podoces hendersoni*").

*Brueelia koslovae* (Clay, 1936): PRICE et al. (2003: 156), (ex "*Podoces biddulphi*" and "*Podoces hendersoni*").

*Hecatrishula koslovae* (Clay, 1936): GUSTAFSSON & BUSH (August 2017: 89), (ex "*Podoces biddulphi*" and "*Podoces hendersoni*").

*Corvonirmus koslovae* (Clay, 1936): MEY (September 2017: 115), (ex "*Podoces biddulphi*").

**Type host:** *Podoces biddulphi* A. O. Hume, 1874 – Xinjiang Ground-jay, Weißschwanzhäher.

**Material:** 14 ♂, 12 ♀, 3 larvae of four skins, namely 1. 4 ♂, 2 ♀, 2 larvae (M. 5542. a-d) ex *P. biddulphi* ♀, October 1890 Jarbut tarja, Turkestan [China], coll. A. Laubmann 291 (R. Tancré); ex

skin 17.613 ZSM, leg. E. Mey 5.10.2016. Numerous *Stubbenirmus* nits on flanks. - 2. 3 ♂, 4 ♀, 1 larva (M. 6217. a-d) ex *P. biddulphi*, 28.8.1888 Chadirkul, E Turkestan [China], coll. Rev. Henry Lansdell D.D. in coll. Hans von Berlepsch without number; ex skin SMF, leg. E. Mey 23.5.2019. - 3. 2 ♂ (1 immature), 1 ♀ (M. 6236.) ex *P. biddulphi* ad. ♂, April [year ?] Lob-Nor, E Turkestan, purchased from R. Tancre IV; ex skin F VII.II.b.y ZFMKB, leg. E. Mey 12.6.2019. From the same skin 4 ♂, 3 ♀, 1 larva (ZFMK 1975-107-110), [leg. H. Klockenhoff ?] - 4. 1 ♂, 2 ♀ (ZFMK 1986-526-528) ex *P. biddulphi*, Chadirkul, Turkestan [China], ex skin (no details) ZFMK, [leg. H. Klockenhoff ?].

**Description:** habitus (♂, ♀) see Table I, Figs. 3-4. Body colour light brown. Measurements [mm]: ♂♂ (n = 14) TL 1.53-1.87, HL 0.44-0.5, FW 0.36-0.4, OW 0.42-0.48, HI 0.96-1.06, PW (n = 13) 0.22-0.26, MW (n = 13) 0.33-0.41, AW (n = 12) 0.49-0.6. ♀♀ (n = 12) TL 1.78-2.14, HL 0.48-0.51, FW 0.39-0.42, OW 0.45-0.51, HI 1-1.07, PW 0.23-0.26, MW 0.35-0.42, AW 0.49-0.63.

**Thorax** (♂ n = 13, ♀ n = 12): macrochaetae row posterior-marginal on mesometanotum (sum from/to and each side n/n setae): 10-14 (♂, twice each 6/8 and 7/7, six times 6/7, once each 6/6, 4/6 and 5/5, = 6 variants) and 10-13 (♀, once 6/7, thrice 6/6, four times 5/6, once 5/7, twice 5/5 and once 4/6, = 6 variants).

**Abdomen** (♂ n = 13, ♀ n = 12): segment II of the ♂ and ♀ without **paratergal setae**. Number of paratergal setae III-VIII (each n/n; meso- and macrosetae): **III**, 0-1 (♂, twelve times 0/0 and once 0/1, = 2 variants) and 0-1 (♀, eleven times 0/0 and twice 0/1, = 2 variants). **IV**, 0-2 (♂, thrice each 2/2 and 1/2, six times 1/1 and once 0/0, = 4 variants) and 1-2 (♀, seven times 2/2, thrice 1/2 and twice 1/1, = 3 variants). **V**, 1-2 (♂, four times 2/2, thrice 1/2, six times 1/1, = 3 variants) and 1-2 (♀, ten times 2/2 and twice 1/2, = 2 variants). **VI**, 1-3 (♂, four times each 3/3 and 2/3, thrice 2/2 and once 1/1, = 4 variants) and 1-3 (♀, four times 2/3, twice 3/3, thrice 2/2, once each 1/2 and 1/1, = 5 variants). **VII**, 1-3 (♂, four times 2/3, seven times 2/2, once 1/2, = 3 variants) and 1-3 (♀, five times 3/3, thrice 2/3, once each 2/2 and 1/2, twice 1/1, = 5 variants). **VIII**, 1-3 (♂, once 2/3, seven times 2/2, twice each 1/2 and 1/1, = 4 variants) and 1-3 (♀, four times 2/3, once each 2/2 and 1/2, = 3 variants). **Postspiracular (macro)setae** on ♂ and ♀ on segments II-VIII. Without **accessory postspiracular seta**. **Tergal posterior setae** (including *mtps* with one pair of setae) on segments II-VIII: **II**, 2 (♂, thirteen times 2/2, = 1 variant) and 1-3 (♀, nine times 2/2, once each 3/3 and 2/3, = 3 variants). **III**, 2-3 (♂, six times 2/3, seven times 2/2, = 2 variants) and 1-3 (♀, once 3/3, four times 2/3, six times 2/2, once 1/2, = 4 variants). **IV**, 1-3 (♂, once 3/3, four times 2/3, seven times 2/2 and once 1/2, = 4 variants) and 2-3 (♀, thrice 3/3, four times 2/3, five times 2/2, = 3 variants). **V**, 2-3 (♂, once 3/3, four times 2/3 and eight times 2/2, = 3 variants) and 1-3 (♀, twice 2/3, nine times 2/2 and once 1/2, = 3 variants). **VI**, 2-3 (♂, once each 3/4 and 3/3, four times 2/3 and six times 2/2, = 4 variants) and 1-2 (♀, eleven times 2/2 and once 1/2, = 2 variants). **VII**, 1-3 (♂, six times 3/3, twice 2/3, once each 2/2 and 1/3, twice 1/1, = 5 variants) and 1-3 (♀, once 2/3, thrice 1/2, eight times 1/1, = 3 variants). **VIII**, 1-4 (♂, once 3/4, four times 3/3, twice 2/3, thrice 2/2, twice 1/1 (5 variants) and 0-2 (♀, once each 2/2 and 0/1, ten times 1/1, = 3 variants). **Sternal setae** posterior-lateral and central of ventral plates (sternites) II-VII: **II**, 2-5 (♂, once each 5 and 2, elfen times 4, = 3 variants) and 4-6 (♀, once 6, thrice 5 and six times 4, = 3 variants). **III**, 4-5 (♂, six times each 5 and 4, = 2 variants) and 4-7 (♀, once each 7 and 4, six times 6 and four times 5, = 4 variants). **IV**, 4-6 (♂, twice each 6 and 5, eight times 4 and once 3, = 4 variants) and 3-7 (♀, once 7, thrice 6, seven times 5, once 3, = 4 variants). **V**, 1-4 (♂, nine times 4, thrice 3 and once 1, = 3 variants) and 4-6 (♀, four times 6, four times 5, thrice 4, = 3 variants). **VI**, 4-6 (♂, four times each 6, 5 and 4, = 3 variants) and 5-6 (♀, eight times 6 and four times 5, = 2 variants). **VII**, without sternal seta.

Male genitalia [mm] (n = 11): Length 0.3-0.34, width of basal plate craniad 0.11-0.16 and at paramere insertion 0.10-0.13 mm. Hypogynium (n = 6) 0.29-0.32 mm long, 0.19-0.26 mm wide, variable in shape (figs. 13 A, B).

Male genitalia see fig. 7. Length 0.29-0.33 (n = 2), width of basal plate craniad and at paramere insertion 0.11 mm each. Hypogynium 0.3 mm long, 0.19 mm wide, variable in shape (fig. 13 C).

**Diagnosis:** see table 2 and fig. 5.

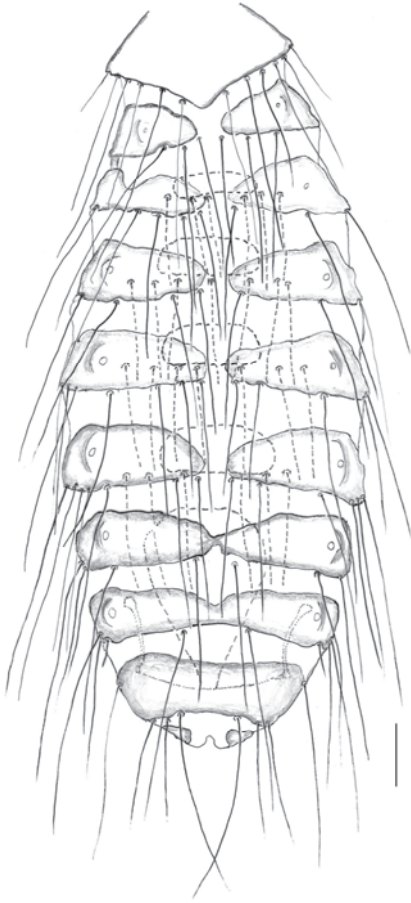


Fig. 6: Mesometanotum (partly) and abdomen (ventral structures and setae dashed) of *Stubbenirmus stubbeae* spec. nov. ♀, ex *Podoces hendersoni*, Turkestan, China (ZFMK 1975-112). Note plate disturbance on left side of abdominal segment III. Scale 0.1 mm.



Fig. 7: *Stubbenirmus stubbeae* spec. nov., ♂. Top: Genitalia (paratype). Scale 0.1 mm. Bottom: Endomeron (mesosome) from holotype. Scale 0.05 mm.

### 5.1.3. *Stubbenirmus docilis* (Ansari, 1956) nov. comb.

Tab. 2; fig. 1, 5, 9-10, 13; plate I – Fig. 8figs. 5-6.

*Brüelia biguttata docilis* Ansari, 1956: 393, figs. 76-83. (ex "*Pyrrhocorax p[yrhocorax] docilis* (Gmelin)").

*Corvonirmus biguttatus docilis* (Ansari, 1956): ZŁOTORZYCKA 1997: 190. (ex "*Pyrrhocorax pyrrhocorax docilis* (Gmelin)").

*Brueelia docilis* (Ansari, 1956): PRICE *et al.* (2003: 154), (ex "*Pyrrhocorax pyrrhocorax docilis* (Gmelin)"). Status after formal, taxonomically not justified upgrading to species.

*Hecatrishula docilis* (Ansari, 1956): GUSTAFSSON & BUSH (2017: 88 f., 429), (ex "*Pyrrhocorax pyrrhocorax barbarus*") (= revised type host)

*Corvonirmus docilis* (Ansari, 1957): MEY 2017: 115), (ex "*Pyrrhocorax pyrrhocorax barbarus* Vaurie, 1954") (= revised type host).

**Type host:** *Pyrrhocorax pyrrhocorax barbarus* (Vaurie, 1954)<sup>7</sup> - Red-billed Chough, Alpenkrähe (fig. 8).



Fig. 8: Red-billed Chough *Pyrrhocorax pyrrhocorax*, 28.8.2011 Sichuan, Tibet, China (Photo: A. GEBAUER).

**Material:** 29 ♂, 23 ♀, 12 larvae of 10 skins resp. individuals, namely 1. 7 ♂, 7 ♀, 3 larvae (M. 6046. b-f) ex *Pyrrhocorax pyrrhocorax himalayanus* (Gould, 1862) ♂, 21.6.1962 Khumbu, Khumjung, 3950 m a.s.l., Nepal; coll. Research Company Nepal Himalaya 661; ex skin 62.513 ZSM, leg. E. MEY 29.8.2018. Mixed infection with *Philoaterus thryptocephalus* (Kellogg & Paine, 1914) (2 ♂, 1 ♀ legit). - 2. 4 ♂, 4 ♀, 3 larvae (6260. a-c) ex *P. p. himalayanus*, 12.11.1969 Thakkhola, Nabrikot, 2750 m a.s.l., Nepal, coll. J. Martens 25; ex skin 71.799 ZFMK, leg. E. Mey 14.6.2019. - 3. 4 ♂ (2 immat.), 1 ♀, 2 larvae (M. 6173. a-b) ex *P. p. centralis* Stresemann, 1928 ad. ♂, 30.5.1962 Arc-bogd-ul, Somon Bogd, Mongolia, coll. Mongolian-German Biological Expedition 1962, no. 304; ex skin (without catalogue number) ZNSH, leg. E. Mey 12.3.2019. Mixed infection with *Philoaterus thryptocephalus* (Kellogg & Paine, 1914) (1 ♂, 4 ♀ legit). - 4. 1 ♂, 3 ♀ (M. 6179. a-b) *P. p. centralis* ad. ♀, 15.2.1980 Somon Chovd, 2 km SE, Mongolia, coll. M. Stubbe, Mongolian-German Biological Expedition 1980, no. 80/26; ex skin 1779 ZNSH, leg. E. Mey 11.3.2019. *Stubbenirmus* nits sparse on flanks. - 5. 2 ♂, 2 ♀ (1 torso), 4 larvae (M. 6193. a-d) ex *P. p. erythroramphos* (Vieillot, 1817) ad. ♂, 11.11.1935 Linares de Riofrio Salamanca, Spain, leg. H. Grün in coll. J. Riemer 48750; ex skin C 46682 MTD, leg. E. Mey 25.3.2019. Mixed infection with *Myrsidea* sp. (1 larva legit) and *Olivinirmus* sp. (1 ♂, straggler?). - 6. 1 ♀ (M. 6197. c) ex *P. p. erythroramphos* ♂, 25.9.1895 Graubünden, Switzerland, coll. C. Schneider; ex skin C 59090 MTD, leg. E. Mey 25.3.2019. Mixed infestation with *Myrsidea* sp. (1 ♂, 1 larva legit) and *Philoaterus* sp. (only nits on head). - 7. 3 ♂, 1 ♀ (ZFMK 1972-336, 344, 996, 997) ex *P. p. docilis*, ♀, 3.10.1963 Bamian, 2700 m a.s.l., Central Afghanistan, leg. H. Klockenhoff 193/196. - 8. 7 ♂, 1 ♀ (ZFMK 1979-317, 1001, 1003, 1009, 1012, 1020-1022) ex *P. p. docilis*, ♂ & ♀, 25.1.1968 Kandahar-Kalat, Afghanistan, leg. H. Klockenhoff 683/684. - 9. 2 ♀ (ZFMK 1979-991, 993) ex *P. p. docilis*, 29.1.1968 Kandahar-Kalat, Afghanistan, leg. H. Klockenhoff 692. - 10. 1 ♂, 2 ♀ (Vasjukova E 188) ex *P. p. docilis*, 5.2.1992 N Ossetia, Caucasus (slide also contains 1 *Philoaterus* larva).

New for Mongolia (see MEY 1985).

**Description:** habitus (♂, ♀) see plate I, figs. 5-6. Dark brown. Body measurements [mm]: ♂ (n = 15) TL 0.35-0.7, HL 0.39-0.45, FW 0.3-0.36, OW 0.36-0.42, HI 1-1.08, PW 0.2-0.25, MW 0.3-0.39, AW 0.39-0.57 (ex host subspecies: *himalayanus* ten times; *centralis* thrice; *erythroramphos* twice). ♀ (n = 19) TL 1.6-1.99, HL 0.42-0.48, FW 0.32-0.38, OW 0.38-0.46, HI 1.02-1.15, PW 0.2-0.25, MW 0.32-0.39, AW (n = 17) 0.43-0.58 (ex host subspecies: *himalayanus* 14 times; four times each *centralis* and *erythroramphos*). Without clypeal hyaline and clypeal suture Figs. 2 and 9 D-F.

<sup>7</sup> The type host named by ANSARI (1956: 394) is *Pyrrhocorax pyrrhocorax docilis* (S. G. Gmelin, 1774). This information is based on Meinertzhagen material, where "Morocco" is indicated as the place of origin on the slides. The correct host has already been pointed out by MEY (2017: 115) as well as by GUSTAFSSON & BUSH (2017: 89, but instead of "barbarous" correctly *barbarus*).

**Thorax** ( $\sigma$  n = 10,  $\text{♀}$  n = 12): macrochaetae row posterior-marginal on mesometanotum (sum from/to and each side n/n setae): 13-14 ( $\sigma$ , seven times 7/7 and thrice 6/7 = 2 variants) and 12-17 ( $\text{♀}$ , once 9/8, thrice 7/7, seven times 6/7 and once 6/6, = 4 variants).

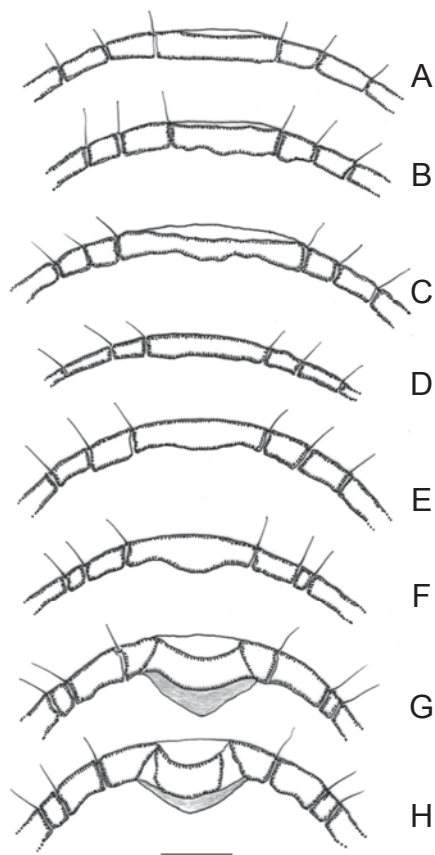


Fig. 9: *Stubbenirmus* spp. frontal section of clypeal carina with clypeal hyaline and only in G and H clypeal suture (shaded) as well as three setae, each from the very outside: dorsal submarginal seta (*dsms*), then marginal setae as 2 and as 3. **A:** *S. stubbeae* n. sp.  $\text{♀}$  (paratype), Mongolia (M. 6175., right). **B:** *ditto*, Turkestan, China (M. 6175., left). **C:** *S. koslovae* (Clay)  $\text{♀}$ , Turkestan, China (M. 5542. b). **D:** *S. docilis* (Ansari)  $\sigma$ , Mongolia (M. 6179. a). **E:** *S. docilis*  $\text{♀}$ , Nepal (M. 6046. a, lower left). **F:** *ditto*, lower left. **G:** *S. biguttatus* (Kellogg & Paine)  $\text{♀}$ , Switzerland (M. 6225. b). **H:** *S. biguttatus*  $\text{♀}$ , Turkey (M. 6308. a). Scale 0.1 mm.

**Abdomen** ( $\sigma$  n = 10,  $\text{♀}$  n = 13): segment II of the  $\sigma$  and  $\text{♀}$  without **paratergal setae**. Number of paratergal setae III-VIII (each n/n; meso- and macrosetae): **III**, 0-2 ( $\sigma$ , once 2/2, thrice each 1/2 and 1/1, twice 0/1 and once 0/0, = 5 variants) and 1-2 ( $\text{♀}$ , twice 2/2, four times 1/2, seven times 1/1, = 3 variants). **IV**, 0-2 ( $\sigma$ , once 2/3, six times 2/2, once each 1/2 and 0/2, = 4 variants) and 1-4 ( $\text{♀}$ , once 3/4, six times 2/3, twice 1/3 and thrice 2/2, = 4 variants). **V**, 2-3 ( $\sigma$ , once 3/3, thrice 2/3 and four times 2/2, = 3 variants) and 1-4 ( $\text{♀}$ , once each 3/4 and 3/3, twice 2/3, seven times 2/2 and once 1/3, = 5 variants). **VI**, 2-3 ( $\sigma$ , five times 3/3 and twice 2/3, = 2 variants) and 2-4 ( $\text{♀}$ , once 3/4, six times 3/3, four times 2/3, once 2/2, = 4 variants). **VII**, 2-3 ( $\sigma$ , five times 3/3 and twice 2/3, = 2 variants) and 3-4 ( $\text{♀}$ , once 3/4 and ten times 3/3, = 2 variants). **VIII**, 2-3 ( $\sigma$ , four times 3/3, twice 2/3 and once 2/2, = 3 variants) and 2-3 ( $\text{♀}$ , nine times 3/3, thrice 2/3 and once 2/2, = 3 variants). **Postspiracular (macro)setae** on  $\sigma$  and  $\text{♀}$  on segment II-VIII. Without **accessory postspiracular seta**. **Tergal posterior setae** (including *mtps* with one pair of setae) on segment II-VIII: **II**, 1-3 ( $\sigma$ , six times 3/3, once each 2/3, 2/2 and 1/2, = 4 variants) and 2-3 ( $\text{♀}$ , ten times 3/3 and thrice 2/3, = 2 variants). **III**, 2-4 ( $\sigma$ , once each 3/4 and 2/3, seven times 3/3, = 3 variants) and 2-3 ( $\text{♀}$ , eleven times 3/3 and twice 2/3, = 2 variants). **IV**, 1-4 ( $\sigma$ , twice each 4/4 and 3/4, four times 3/3 and once 1/3, = 4 variants) and 2-3 ( $\text{♀}$ , seven times 3/3 and five times 2/3, = 2 variants). **V**, 2-5 ( $\sigma$ , once 5/5, thrice 4/4, twice 3/4, once each 2/4, 3/3 and 2/3, = 6 variants) and 2-3 ( $\text{♀}$ , eight times 3/3, thrice each 2/3 and 2/2, = 3 variants). **VI**, 3-5 ( $\sigma$ , once 4/5, thrice 4/4, four times 3/4,



once 3/3, = 4 variants) and 2-3 (♀, twice each 3/3 and 2/3, ten times 2/2, = 3 variants). **VII**, 3-5 (♂, once 5/5, twice each 4/4 and 3/4, thrice 3/3, = 4 variants) and 1-2 (♀, twelve times 2/2 and twice 1/2, = 2 variants). **VIII**, 2-6 (♂, once each 6/6 and 5/6, thrice 5/5, once each 3/3, 3/4 and 2/2, = 6 variants) and 1-3 (♀, twice 3/3, once 2/3; twice 2/2, four times 1/2, five times 1/1, = 5 variants). **Sternal setae** posterior-lateral and central of ventral plates (sternites) II-VII: II, 3-4 (♂, thrice 4, once 3, = 2 variants) and 3-6 (♀, once each 6 and 5, thrice 4 and twice 3, = 4 variants). **III**, 3-4 (♂, twice 4, once 3, = 2 variants) and 3-6 (♀, once each 6 and 5, thrice 4, twice 3, = 3 variants). **IV**, 5-8 (♂, once each 8 and 7, twice 6 and once 5, = 4 variants) and 6-8 (♀, thrice 8, five times 7 and twice 6, = 3 variants). **V**, 6-9 (♂, once each 9 and 8, twice 7 and once 6, = 4 variants) and 7-8 (♀, four times 8 and six times 7, = 2 variants). **VI**, 6-7 (♂, twice each 7 and 6, = 2 variants) and 6-9 (♀, once 9, twice 8, four times 7, twice 6, = 4 variants). **VII**, 0-2 (♀, five times 1/1, twice each 0/1 and 0/0, = 3 variants) and 0/0 (♂).

**Genitalia:** male genitalia [mm]: length 0.29-0.33 (n = 11), width of basal plate cranial 0.11-0.15 and at paramere insertion 0.1-0.13 (both n = 13). Hypogynium (see Figs. 9 D-F) 0.25-0.28 mm long and 0.19-0.24 mm wide (n = 3).

**Diagnosis:** See table 2 and fig. 5.

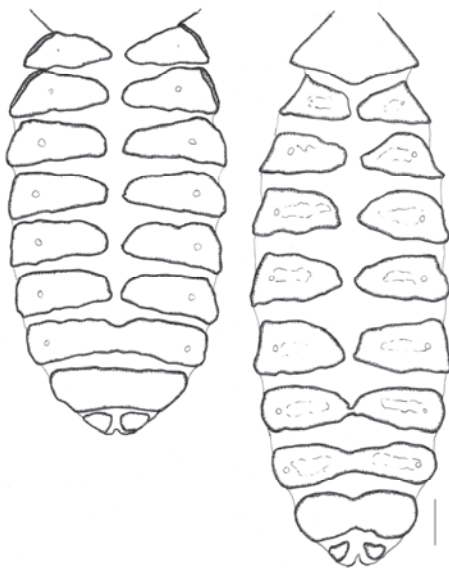


Fig. 10: Left - Abdomen (schematic) of *Stubbenirmus biguttatus*, ♀ (dorsal). Note tergopleurites, especially VIII (last one with stigmata) and IX/X as well as pleural incrasation on segments II and III; right - Abdomen (schematic) of *Stubbenirmus docilis*, ♀ (dorsal, only tergopleurites). Scale 0.1 mm.

#### 5.1.4. *Stubbenirmus biguttatus* (Kellogg & Paine, 1914) nov. comb.

Table 2, fig. 1, 5, 9-10, 13, plate II - figs. 1-2.

*Nirmus biguttatus* Kellogg & Paine, 1914: 234, pl. 14, fig. 2, (ex "*Graculus graculus*" and "*Nucifraga multipunctata*").

*Degeeriella biguttata* (Kellogg & Paine, 1914): HARRISON (1916: 109), (ex "*Graculus graculus*").

*Degeeriella biguttata biguttata* (Kellogg & Paine, 1914): CLAY (1936 [1935]: 908), (ex "*Pyrrhocorax graculus*" and "*Pyrrhocorax pyrrhocorax*").

*Brüelia biguttata* (Kellogg & Paine, 1914): HOPKINS & CLAY (1952: 53), (ex "*Pyrrhocorax g. graculus* (Linn.)").

*Brüelia biguttata biguttata* (Kellogg & Paine, 1914): ANSARI (1956: 390), (ex "*Pyrrhocorax g. graculus* (Linn.)" and "*Pyrrhocorax p. pyrrhocorax*, *P. p. himalayanus*, *P. p. pontifex*").

*Corvonirmus biguttatus* (Kellogg & Paine, 1914): ZŁOTORZYCKA (1964: 244), (ex "*Pyrrhocorax g. graculus* (L.)" and "*Nucifraga caryocatactes multipunctata* Gould").

*Corvonirmus biguttatus* (Kellogg & Paine, 1914): ZŁOTORZYCKA (1977: 59, figs. 224-226), (ex “*Pyrrhocorax graculus* (L.)” and “*Pyrrhocorax pyrrhocorax* (L.)”).

*Brueelia biguttata* (Kellogg & Paine, 1914): LAKSHMINARAYANA (1982 [1979]: 64), (ex “*Pyrrhocorax g. graculus* (Linne)”).

*Brueelia biguttata* (Kellogg & Paine, 1914): MARTÍN MATEO & BLASCO-ZUMETA (1996: 84), (ex “*Pyrrhocorax pyrrhocorax* (L.)”) (= host ?).

*Corvonirmus b. biguttatus* (Kellogg & Paine, 1914): ZŁOTORZYCKA (1997: 190, fig. 148 a-g), (ex “*Pyrrhocorax g. graculus* (Linn.)”).

*Brueelia biguttata* (Kellogg & Paine, 1914): PRICE et al. (2003: 153), (ex “*Pyrrhocorax g. graculus* (L.)”).

*Brueelia biguttata* (Kellogg & Paine, 1914): MARTÍN MATEO (2009: 187, fig. 39 A-C), (ex “*Pyrrhocorax pyrrhocorax* [*erythroramphus* (Vieillot, 1817)]”) (= host ?).

*Hecatrishula biguttata* (Kellogg & Paine, 1914): GUSTAFSSON & BUSH (2017: 92, figs. 138-145), (ex type host: *Pyrrhocorax graculus digitatus* Ehrenberg, 1833; other hosts: *Pyrrhocorax g. graculus* (Linnaeus, 1758), *P. pyrrhocorax erythroramphos* (Vieillot, 1817), *P. pyrrhocorax himalayanus* (Gould, 1862), *P. pyrrhocorax docilis* (S. G. Gmelin, 1774).

*Corvonirmus biguttatus* (Kellogg & Paine, 1914): MEY (2017: 115) ex *Pyrrhocorax graculus forsythi* Stoliczka, 1874 (= revised type host).

**Type host.** *Pyrrhocorax graculus forsythi* Stoliczka, 1874<sup>8</sup> - Yellow-billed Chough, Alpendohle (figs. 11-12).



Fig. 11: Yellow-billed Chough *Pyrrhocorax g. graculus* at "apple harvest". A group of about 400 birds had dispersed on the outskirts of Grindelwald (ca. 1200 m a.s.l.) on 27.9.2020 before flying off together. Canton Berne, Switzerland (photo: E. MEY).



Fig. 12: Yellow-billed Chough *Pyrrhocorax g. graculus*. Eggishorn summit station (2869 m a.s.l.), 13.8.2021 Canton Wallis, Switzerland (photo: E. MEY).

<sup>8</sup> According to the localities mentioned by KELLOGG & PAINE (1914: 234), type host is probably not the nominate form, but *Pyrrhocorax graculus forsythi* (MEY 2017: 115). GUSTAFSSON & BUSH (2017: 95) are mistaken when they suggest *Pyrrhocorax graculus digitatus* (cf. DICKINSON & CHRISTIDIS 2014: 230; DEL HOYO & COLLAR 2016: 346).

**Material:** 12 ♂, 11 ♀, 8 larvae from three skins, namely 1. 1 ♀ (M. 6225. b) ex *P. g. graculus* (Linnaeus, 1766) ♀, 23.4.1898 Näfels, Canton Glarus, Switzerland, leg. F. HAUSER, coll. O. Kleinschmidt 6093; ex skin ZFMK (olim Reichsmuseum A. Koenig), leg. E. Mey 12.6.2019. Mixed infection with *Philoaterus dumani* Price & Hellenthal, 1998 (1 ♂ legit) and *Menacanthus* sp. (1 ♂ legit). - 2. 9 ♂, 7 ♀, 7 larvae (M. 6229. a-c) ex *P. g. graculus* ♂, 5.7.1898 Kärf, Canton Glarus, Switzerland, leg. F. HAUSER, coll. O. Kleinschmidt 6092; ex Balg ZFMK (olim Reichsmuseum A. Koenig), leg. E. Mey 12.6.2019. - 3. 3 ♂, 3 ♀, 1 larva (M. 6308. a-c) ex *P. graculus digitatus* Ehrenberg, 1833 ♂, 18.5.1907 Taurus, Turkey, coll. P. Niedieck; ex skin 2000/31319 ZMB, leg. E. Mey 13.9.2019. Mixed infection with *Allocolpocephalum* sp. (4 ♀ legit).

**Description:** habitus (♂, ♀) see plate II, figs. 1-2. Dark brown. Body measurements [mm]: ♂ (n = 8) TL 1.32-1.72, HL 0.42-0.45, FW 0.3-0.34, OW 0.38-0.42, HI 1.05-1.11, PW 0.23-0.28, MW 0.36-0.43, AW 0.48-0.6 (ex host subspecies: *graculus* five times, *digitatus* thrice).

♀ (n = 15) TL 1.57-1.83, HL 0.44-0.48, FW 0.33-0.37, OW 0.42-0.45, HI 1-1.12, PW 0.24-0.27, MW 0.38-0.43, AW 0.48-0.6 (ex host subspecies: *graculus* 12 times, *digitatus* thrice).

**Head:** clypeal carina frontal-median recessed with posterior clypeal suture barely visible. Ausgeprägte Clypealhyaline (fig. 9 G-H).

**Thorax** (♂ n = 8, ♀ n = 14): Macrochaetae row posterior-marginal on mesometanotum (sum from/to and on each side n/n setae): 10-15 (♂, once 7/8, six times 7/7, once 5/5, = 3 variants) and 11-14 (♀, four times 7/7, six times 6/7, twice each 5/7 and 5/6, = 4 variants). **Abdomen** (♂ n = 8, ♀ n = 15): segment II of the ♂ and ♀ without paratergal setae. Number of paratergal setae III-VIII (each n/n; meso- and macrosetae): **III**, 0-2 (♂, once 2/2, thrice 1/1 and four times 0/1, = 3 variants) and 1-2 (♀, twice 2/2, once 1/2 and 12 times 1/1, = 3 variants). **IV**, 0-2 (♂, six times 2/2 and twice 0/2, = 2 variants) and 2-3 (♀, 14 times 2/2 and once 2/3, = 2 variants). **V**, 1-3 (♂, once 2/3, five times 2/2 and twice 1/2, = 3 variants) and 2-3 (♀, once 3/3, five times 2/3 and nine times 2/2, = 3 variants). **VI**, 0-3 (♂, twice each 3/3 and 2/3, twice 2/2, once each 3/0 and 1/2, = 5 variants) and 2-4 (♀, once 3/4, eight times 3/3 and six times 2/3, = 3 variants). **VII**, 2-3 (♂, four times 3/3, twice 2/3 and once 2/2, = 3 variants) and 0-4 (♀, once 3/4, 11 times 3/3, twice 2/3 and once 0/3, = 4 variants). **VIII**, 2-3 (♂, four times 3/3, thrice 2/3 and once 2/2, = 3 variants) and 1-3 (♀, 11 times 3/3, thrice 2/3 and once 1/2, = 3 variants). **Postspiracular (macro)setae** on ♂ and ♀ on segments II-VIII. Without **accessory postspiracular seta**. **Tergal posterior setae** (including *mtps* with one pair of setae) on segments II-VIII: **II**, 2-3 (♂, once 3/3, thrice 2/3 and four times 2/2, = 3 variants) and 2-3 (♀, thrice 3/3, six times each 2/3 and 2/2, = 3 variants). **III**, 1-3 (♂, thrice each 3/3 and 2/3, once each 1/3 and 2/2, = 4 variants) and 2-3 (♀, eight times 2/3 and seven times 2/2, = 2 variants). **IV**, 2-4 (♂, twice each 3/4, 3/3 and 2/3, once each 2/4 and 2/2, = 5 variants) and 2-3 (♀, twice 3/3, six times 2/3 and seven times 2/2, = 3 variants). **V**, 3-4 (♂, twice 4/4 and six times 3/3, = 2 variants) and 2-3 (♀, twice 2/3 and 13 times 2/2, = 2 variants). **VI**, 3-4 (♂, five times 3/4 and thrice 3/3, = 2 variants) and 2-3 (♀, once 3/3, twice 2/3 and 12 times 2/2, = 3 variants). **VII**, 3-6 (♂, once each 5/6, 4/6, 4/5 and 4/4, thrice 3/4 and once 2/3, = 6 variants) and 2-4 (♀, once 2/4 and 14 times 2/2, = 2 variants). **VIII**, 3-7 (♂, once 7/7, four times 5/6, once 4/5 and twice 3/4, = 4 variants) and 1-3 (♀, thrice 2/3, 11 times 2/2 and once 1/2, = 3 variants). **Sternal setae** posterior-lateral and central of ventral plates (sternites) II-VII: **II**, 3-5 (♂, once 5, five times 4 and twice 3, = 3 variants) and 4-6 (♀, four times each 6 and 5, six times 4, = 3 variants). **III**, 6-7 (♂, twice 7 and six times 6, = 2 variants) and 6-10 (♀, once 10, four times 9, seven times 8, twice 7 and once 6, = 5 variants). **IV**, 4-7 (♂, twice 7, four times 6 and once 4, = 3 variants) and 6-10 (♀, four times each 10 and 9, thrice each 8 and 7, once 6, = 5 variants). **V**, 4-8 (♂, once each 8 and 5, thrice 6 and twice 4, = 4 variants) and 6-9 (♂, thrice 9, five times 8, six times 7 and once 6, = 4 variants). **VI**, 3-5 (♂, once each 5 and 3, five times 4, = 3 variants) and 5-8 (♀, four times each 8 and 7, six times 6 and once 5, = 4 variants). **VII**, 0-1 (♀, nine times 1/1 and six times 0/1, = 2 variants). Only one male has a mesochaete with bristle court anterior-laterally on the subgenital plate!

**Genitalia:** Male genitalia (n = 8): Length 0.27-0.43, width of basal plate cranial 0.11-0.15 and at paramere insertion 0.1-0.13 mm (both n = 13).

**Diagnosis:** see table 2 and fig. 5.

### 5.1.5. Do live *Stuppenirmus biguttatus* and *S. docilis* synhospital on *Pyrrhocorax graculus* and *Pyrrhocorax pyrrhocorax* ?

ANSARI (1956: 392) soberly states that "material collected from *Pyrrhocorax p. pyrrhocorax* from Pyrenees and Crete, *Pyrrhocorax p.[pyrrhocorax] himalayanus* from Afganistan and *Pyrrhocorax p. [pyrrhocorax] pontifex* from East Persia in Meinertzhagen collection is indistinguishable from *Brüelia biguttata* (Kellogg & Paine)." Apparently ANSARI (1956) got so confused by this that he finally put *docilis* only as a subspecies of "*Brüelia biguttata*", which may surprise us today. GUSTAFSSON & BUSH (2017: 95) come to this conclusion on the basis of the same Meinertzhagen material: "Whether these two morphologically very distinct forms are actually two morphs of the same species [*S. biguttatus*], or two different species [*S. biguttatus* and *S. docilis*] is not known, and should be established genetically. One possibility is that these taxa are in the early stages of morphological differentiation into different ecomorphs." Much more obvious than this absurd speculative construction of purpose is to first give room to the thought of whether the individual finds of *S. docilis* on skins of *Pyrrhocorax graculus* are not in fact man-made contamination ("stragglers"), which have taken place, for example, during collection work from skin to skin. Uncritically compiled material and host-parasite lists (see GUSTAFSSON & BUSH 2017: 378)<sup>9</sup> may have reinforced the completely erroneous impression that *S. biguttata* and *S. docilis* live side by side on both *Pyrrhocorax pyrrhocorax* and *Pyrrhocorax graculus*.

There is no credible authentic finding of natural permanent synhospital cohabitation of *S. biguttatus* and *S. docilis* on *Pyrrhocorax pyrrhocorax* (as well as on *Pyrrhocorax graculus*)! The report by MARTÍN MATEO & BLASCO-ZUMETA (1996: 84) about findings of "*Brueelia biguttata*" on four individuals of *Pyrrhocorax pyrrhocorax* in the region of Aragon in NE Spain, which seems to fit into the above picture, also raises doubts about the identification of these birds (see also MARTÍN MATEO 2009: 187). The doubts are not weakened by the fact that these authors report the (credible) finding of a male of *Philopterus thryptocephalus* (Kellogg & Paine, 1914) on *Pyrrhocorax pyrrhocorax* from the same area. MARTÍN MATEO & BLASCO-ZUMETA (1996) were not yet aware of the *Philopterus* revision by PRICE & HELLENTHAL (1998: 787 f.), in which, contrary to KELLOGG & PAINE (1914), the Yellow-billed Chough turned out to be the actual type host of *P. thryptocephalus* and *P. dumani* was described for the first time by the Red-billed Chough (see also MARTÍN MATEO 2009: 153).

### 5.2. *Hecatrishula* Gustafsson & Bush, 2017

Tab. 1-3, fig. 2, 13, plate II - figs. 3-4.

*Philopterus (Nirmus)* Nitzsch, 1818: BURMEISTER (1839: 427). Pro parte.

*Philopterus (Nirmus)* Nitzsch, 1818: DENNY (1842: 112). Pro parte.

*Nirmus* Nitzsch, 1818: GIEBEL (1874: 121). Pro parte.

*Nirmus* Nitzsch, 1818: PIAGET (1880: 7). Pro parte.

*Nirmus* Nitzsch, 1818: KELLOGG (1908: 20). Pro parte.

*Degeeriella* Neumann, 1906: HARRISON (1916: 107). Pro parte.

*Brüelia* Kéler, 1936: HOPKINS & CLAY (1952: 52). Pro parte.

<sup>9</sup> "The feather lice collected by Snodgrass in 1898-1899 on the Galapagos Islands were processed by Kellogg & Kurwana. As far as the hospital distribution of the 45 (of which 28 were new) described mallophagan species is concerned, it can be assumed that the realisation of these collections was accompanied by a methodological disaster. The aspect of host specificity has obviously been ignored, even if the authors claim the opposite. Thus, the particularly emphasised report seems very implausible that 20 (!) feather lice species alone have been found on *Geospiza fuliginosa*, the occurrence of which is supposed to be associated with a natural change of host in most cases. In our opinion, all host information reported by KELLOGG & KUWANA (1902) should be treated with great caution, at least until the results have been verified. *Brueelia chelydensis* Hopkins, 1951 (*nomen novum* for *Nirmus vulgatus galapagensis* Kellogg & Kurwana, 1902 ex *Geospiza fuliginosa* and another 17 host species!) must also be seen in this light" (MEY & BARKER 2014: 92 f. in German, translated here). The fact that GUSTAFSSON & BUSH (2017: 406, 423) simply replicate such windy data page by page does not make them any more useful.

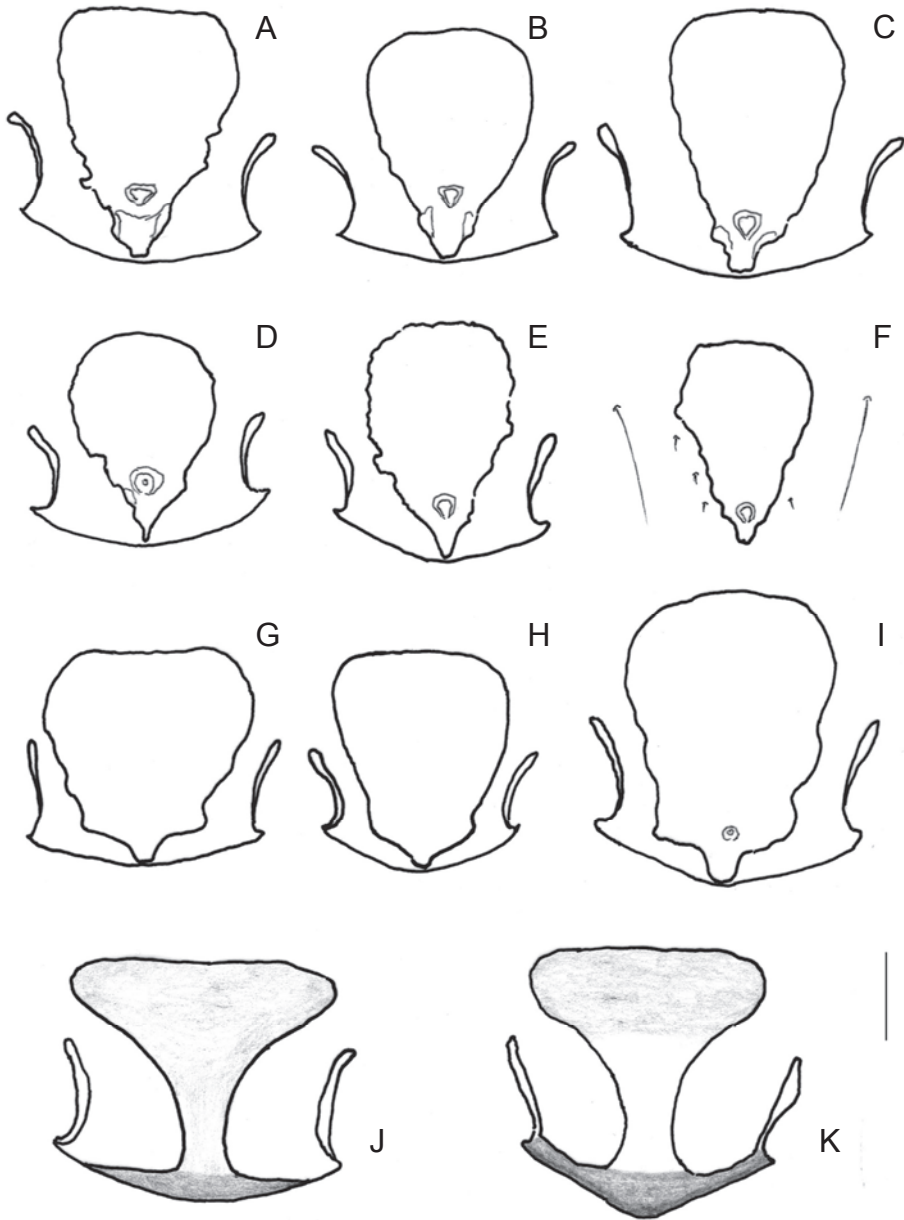


Fig. 13: Hypogynium (subgenital plate ♀) without vulval setae. **A:** *Stubbenirmus stubbeae* sp. n., paratype, ex *Podoces hendersoni*, Turkestan, China (ZFMK 1975-112). **B:** ditto, ZFMK 1975-111. **C:** *S. koslovae* (Clay), ex *Podoces biddulphi*, Turkestan, China (M. 5542. a). **D:** *S. docilis* (Ansari), ex *P. pyrrhocorax centralis*, Mongolia (M. 6173. a). **E:** *S. docilis* (Ansari), ex *P. pyrrhocorax himalayanus*, Nepal (M. 6260. a). **F:** ditto, M. 6260. b, right. **G:** *S. biguttatus* (Kellogg & Paine), ex *Pyrrhocorax g. graculus*, Taurus, Turkey (M. 6308. c). **H:** ditto, Switzerland (M. 6229. b, above). **I:** *Hecatrishula perforata* (Złotorzycka), ex *Corvus f. frugilegus*, Afghanistan (ZFMK 1979-921, right). **J:** *Corvonirmus uncinus* (Burmeister), ex *Corvus cornix cornix*, Amrum, Germany (M. 5669. e). **K:** *Lycocoranirmus giloensis* Mey, ex *Corvus validus*, Halmahera, Indonesia (M. 6159. d). Scale 0.1 mm.

*Corvonirmus* Eichler, 1944: ZŁOTORZYCKA (1964: 242). Pro parte.

*Bruelia* Kéler, 1936: LEDGER (1980: 141). Pro parte.

*Bruelia* Kéler, 1936: LAKSHMINARAYANA (1982 [1979]: 63). Pro parte.

*Corvonirmus* Eichler, 1944: ZŁOTORZYCKA (1997: 184). Pro parte.

*Bruelia* Kéler, 1936: PRICE et al. (2003: 152). Pro parte.

*Corvonirmus* Eichler, 1944: MEY (2017: 113). Pro parte.

Generotype: "*Brüelia atherae* Ansari, 1957" ex *Corvus corax laurencei* Hume, 1873.

GUSTAFSSON & BUSH (2017) divide eight species of *Hecatrishula* into *atherae* and *biguttata* group. These groupings are not followed for formal reasons, firstly because the latter has been transferred to a new genus (*Stubbenirmus*) and secondly because the oldest valid species name is usually used for (non-nomenclatural) group names (neutral prerogative of the oldest name).<sup>10</sup>

There is no doubt about the morphological independence of both *Hecatrishula* and *Corvonirmus* (GUSTAFSSON & BUSH 2017: 87 ff. and 195 ff.).

Two inconsistencies occur in the *Corvonirmus* species list of GUSTAFSSON & BUSH (2017: 195). Firstly, "*Nirmus bipunctatus* Rudow, 1870" is listed as a synonym of *Corvonirmus quadrangularis* (Rudow, 1869), which is, however, already p. 88 correctly listed by the authors as *Hecatrishula bipunctata* (Rudow, 1870). On the other hand, "*Brüelia variegata* Ansari, 1957" does not belong to *Corvonirmus* according to the original description, but is clearly *Hecatrishula variegata* (Ansari, 1957). This, however, creates the seemingly "skewed picture" of two *Hecatrishula* species living on *Corvus capensis* (but on two geographically isolated subspecies).

The status of "*Hecatrishula multipunctata* (Clay, 1936)" ex *Nucifraga multipunctata* remains unclear for the time being according to the arguments presented at page 403.

**Diagnose:** see page 404. For the rest, please refer to the detailed description by GUSTAFSSON & BUSH (2017: 87 ff.).

**Hospital distribution:** *Corvus* Linnaeus, 1758. *Pica* Brisson, 1760.

**Zoogeographical distribution:** Nearctis. Palaearctis. Aethiopsis. Orientalis.

### **Species (8) and groups (3):**

*varia* group (2 spp.):

1. *Hecatrishula varia* (Burmeister, 1838) ex *Corvus monedula spermolegus* Vieillot, 1817. Type material from Central Germany no longer available.
2. *Hecatrishula perforata* (Złotorzycka, 1964) ex *Corvus f. frugilegus* Linnaeus, 1758. Holotype (♂) from Opatowice near Wrocław, Poland.

*bipunctata* group (4 spp.):

3. *Hecatrishula bipunctata* (Rudow, 1870) ex *Corvus albicollis* Latham, 1790. Type material from [Tanzania] no longer available.
4. *Hecatrishula biocellata* (Piaget, 1880) ex *Pica pica bactriana* Bonaparte, 1850). Lectotype (♂) from skin of Leiden museum (without dates).
5. *Hecatrishula atherae* (Ansari, 1957) ex *Corvus corax laurencei* A.H. Hume, 1873. Holotype (♂) from Shibar pass, Afghanistan.
6. *Hecatrishula cryptoleuca* (Ansari, 1957) ex *Corvus cryptoleucus* Couch, 1854. Unclear host affiliation, see GUSTAFSSON & BUSH (2017: 89). Holotype (♂) from Texas, U.S.A.

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<sup>10</sup> The same is to be noted here in addition in two cases for the *Olivinirmus* species groups formed by GUSTAFSSON & BUSH (2017: 201). *Olivinirmus olivaceus* (Burmeister, 1838) must replace *O. glandarii* (Denny, 1848) and *O. nitzschi* (Kéler, 1938) must replace *O. morionus* (Carriker, 1956).

*variegata* group (2 spp.):

7. *Hecatrishula variegata* (Ansari, 1957) nov. comb. ex *Corvus capensis kordofanensis* Laubmann, 1919. Holotype (♂) from Somalialand [Somalia].
8. *Hecatrishula nawabi* (Ansari, 1957) ex *Corvus c. capensis* M. H. C. Lichtenstein, 1823. Holotype (♂) from Damaraland, SW Africa [Namibia].

### 5.3. *Corvonirmus* Eichler, 1944

Table 1-2, figs. 3, 13 J, plate II - figs. 5-6.

*Philopterus (Nirmus)* Nitzsch, 1818: BURMEISTER (1839: 427). Pro parte.

*Philopterus (Nirmus)* Nitzsch, 1818: DENNY (1840: 112). Pro parte.

*Nirmus* Nitzsch, 1818: GIEBEL (1874: 121). Pro parte.

*Nirmus* Nitzsch, 1818: PIAGET (1880: 7). Pro parte.

*Nirmus* Nitzsch, 1818: KELLOGG (1908: 20). Pro parte.

*Degeeriella* Neumann, 1906: HARRISON (1916: 107). Pro parte.

*Brüelia* Kéler, 1936: HOPKINS & CLAY (1952: 52). Pro parte.

*Corvonirmus* Eichler, 1944: ZŁOTORZYCKA (1964: 242). Pro parte.

*Brueelia* Kéler, 1936: LEDGER (1980: 141). Pro parte.

*Brueelia* Kéler, 1936: LAKSHMINARAYANA (1982 [1979]: 63). Pro parte.

*Corvonirmus* Eichler, 1944: ZŁOTORZYCKA (1997: 184). Pro parte.

*Brueelia* Kéler, 1936: PRICE et al. (2003: 152). Pro parte.

*Corvonirmus* Eichler, 1944: GUSTAFSSON & BUSH (2017: 193). Pro parte.

*Corvonirmus* Eichler, 1944: MEY (2017: 113).

Generotype: "*Nirmus uncinus* Burmeister, 1838" ex *Corvus cornix cornix* Linnaeus, 1758

**Diagnosis:** see page 404 ff. For the rest, see the detailed description by GUSTAFSSON & BUSH (2017: 193 ff.). The *orruaticus* group seems to be very closest to *Lycocoranirmus*.

**Hospitale Verbreitung:** *Corvus* Linnaeus, 1758.

**Zoogeographische Verbreitung:** Holarktis, Neotropis, Aethiopsis, Orientalis, Australis.

#### **Species (15 spp., 1 ssp.) and groups (6):**

*uncinus* group (3 spp.):

1. *Corvonirmus u. uncinus* (Burmeister, 1838) ex *Corvus c. cornix* Linnaeus, 1758.<sup>11</sup> Neotype from South Uist, Scotland, GB.
2. *Corvonirmus uncinus plenus* (Ansari, 1957) ex *Corvus c. corone* Linnaeus, 1757. Holotype from Devon, England, GB.
3. *Corvonirmus orientalis* Mey, 2017 ex *Corvus corone orientalis* Eversmann, 1841. Holotype (♂) from Mandshuria, China.
4. *Corvonirmus tasniemae* (Ansari, 1957) ex *Corvus f. frugilegus* Linnaeus, 1758. Holotype (♂) from Kabul, Afghanistan.

*argulus* group (3 spp.):

5. *Corvonirmus argulus* (Burmeister, 1838) ex *Corax c. corax* Linnaeus, 1758. Neotype (♂) from Northern Uist, Outer Hebrides, Scotland, GB.
6. *Corvonirmus leucocephalus* (Nitzsch in Giebel, 1866) ex *Corvus albicollis* Latham, 1790. Neotype (♂) from Basutoland (Lesotho), South Africa.
7. *Corvonirmus quadrangularis* (Rudow, 1869) ex *Corvus albus* Statius Müller, 1778. Neotypus (♂) from SW Africa [Namibia].

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<sup>11</sup> Here SHIRIHAI & SVENSSON (2018) have been followed, considering Carrion Crow and Hooded Crow as different species.

**theresae** group (1 sp.):

8. *Corvonirmus theresae* (Ansari, 1957) ex *Corvus r. rhipidurus* E. Hartert, 1918. Holotype (♂) from Aden, Jemen.

**rotundatus** group (1 sp.):

9. *Corvonirmus rotundatus* (Osborn, 1876) ex *Corvus b. brachyrhynchos* C.L. Brehm, 1822. Neotype (♂) from Stillwater, Oklahoma, U.S.A.

**afzali** group (2 spp.):

10. *Corvonirmus afzali* (Ansari, 1957) ex *Corvus cryptoleucus* Couch, 1874. Holotype (♂) from Illinois, Texas, U.S.A.

11. *Corvonirmus perwienae* (Ansari, 1957) ex *Corvus nasicus* Temminck, 1826. Holotype (♂) from Cuba.

**orruaticus** group (4 spp.):

12. *Corvonirmus orruaticus* Mey, 2017 ex *Corvus orru ceciliae* Mathews, 1912. Holotype (♂) from Marandoo, Western Australia.

13. *Corvonirmus barkeri* Mey, 2017 ex *Corvus coronoides perplexus* Mathews, 1912. Holotype (♂) from Chudalup State Forest, Western Australia.

14. *Corvonirmus wakuaiacus* Mey, 2017 ex *Corvus bennetti* North, 1901. Holotype (M. 5324. a, ♂) from McHugh Bore, Edgar Ranges, Western Australia (= correction of the statement by MEY 2017: 120).

15. *Corvonirmus pleuropelios* Mey, 2017 ex *Corvus mellori* Mathews, 1912. Holotype (♂) from Toganmain bei Groongal, New South Wales, Australia.

#### 5.4. *Lycocoranirmus* Mey, 2017

Tables 1-2; figs. 3, 13 K, 14; plate III -figs. 1, 2.

*Nirmus* Nitzsch, 1818: PIAGET (1880: 7). Pro parte.

*Nirmus* Nitzsch, 1818: KELLOGG (1908: 20). Pro parte.

*Degeeriella* Neumann, 1906: HARRISON (1916: 107). Pro parte.

*Brüelia* Kéler, 1936: HOPKINS & CLAY (1952: 52). Pro parte.

*Brueelia* Kéler, 1936: LAKSHMINARAYANA (1982 [1979]: 63). Pro parte.

*Brueelia* Kéler, 1936: PRICE et al. (2003: 152). Pro parte.

*Corvonirmus* Eichler, 1944: GUSTAFSSON et al. (2019: 264).

Generotype: *Lycocoranirmus giloloensis* MEY, 2017.

*Lycocoranirmus* was described as a new genus after a female found with several larvae on the skin of a Halmahera Paradise-crow *Lycocorax p. pyrrhopterus*. This host individual, which also had some *Philoaterus* larvae, is a false host. The actual host (= type host) of *Lycocoranirmus giloloensis* is undoubtedly *Corvus validus* (cf. below in "material" 1.-3.). In the original description attention is drawn to similarities, but also to differences to *Corvonirmus*. To synonymise *Lycocoranirmus* with *Corvonirmus* under doubt, as GUSTAFSSON et al. (2019) believed they had to do only on the basis of the original description, cannot be approved. If the necessary type material is not available (for whatever reason), a green table decision on the status of a taxon cannot be a good alternative.<sup>12</sup>

<sup>12</sup> A few words about GUSTAFSSON et al. (2019) should be noted here. These authors, led by D. GUSTAFSSON, have taken it upon themselves to "validate" the taxonomic findings of MEY (September 2017), after GUSTAFSSON & BUSH (August 2017) have presented a much more comprehensive and profound revision of the *Brueelia* complex on the same topic. Many new genus and species descriptions by MEY (2017) had to be moved to the synonymy for reasons of priority. Many other taxa, however, were declared genera or species inquirendae (incl. taxa *incertae sedis*) and in many cases assigned a new status. Since the investigations of E. MEY on the *Brueelia* complex should (and will) be continued, a loan of the published material was not considered for the time being. Upon request in 2018, I had informed D. GUSTAFSSON. That he nevertheless "initiated a revision" without having been able to consult the authentic material was both surprising and disconcerting for me.



**Description:** coloured imagines (with the exception of *L. saliemii*) usually strongly pigmented deep brown to sometimes blackish brown.

**Head:** with distinct hyaline section (= clypeal hyaline) on osculum. Frontal median anterior margin never round, but straight or slightly concave. Dorsally above the broad osculum a broad barely pigmented band spans, connecting the two clypeal carina branches and appearing to represent the modified frontal section of the clypeal carina. Blackish brown clypeal carina slightly wider or equal in width to barely pigmented ventral carina. Antennae strongly sexually dimorphic (scapus of ♂ more than twice as large as that of ♀). Hyaline conus of ♀ almost as long or slightly longer than scapus, but almost as large as that of ♂. Scapus and pedicellus of ♂ and ♀ colourless except for margins, flagellum pigmented entirely light to dark brown.

**Abdomen:** tergopleurites III-VIII around the stigmata only with a relatively small fenestra, the mediade is usually only indicated. Only in *L. saliemii* are the tergopleurites lightened and the mediad "in the process of dissolution". Pleural abdominal incassations and re-entrant heads on segments III-VII or VIII. Segments II and III without paratergal setae (only sometimes a seta on one side on tergopleurite III). Except for *mtps* on segments II-VIII (on ♂ mesochaete, on ♀ macrochaete) no other tergal posterior seta (*tps*). Sternal setae (*sts*, ♂, ♀): on each side one macrochaete on segment II posterior-central and on segments III-VI posterior-lateral of sternites. Sternite II mostly absent.

**Diagnosis:** see page 404 ff. Close to *Corvonirmus* according to clypeus setae, genitalia and subgenital plates, but clearly different from *Corvonirmus* in the structures of the anterior head (fig. 3). The *Corvonirmus orruaticus* group seems to be closest to *Lycocoranirmus*.

**Hospital distribution:** *Corvus* Linnaeus, 1758.

**Zoogeographical distribution:** [Palaeartic] Orientalis, Australis.

### **Species (5 spp.) and groups (2):**

*latifasciatus* group (4 spp.):

1. *Lycocoranirmus latifasciatus* (Piaget, 1880) nov. comb. ex *Corvus enca mangoli* Vaurie, 1958 [= revised type host]. Lectotype (♀) from Sulu Islands, Sulawesi.
2. *Lycocoranirmus hamatofasciatus* (Piaget, 1890) nov. comb. ex *Corvus philippinus* (Bonaparte, 1853) [revised type host]. Lectotype (♀) from N Philippines.
3. *Lycocoranirmus mollii* (Ansari, 1957) nov. comb. ex *Corvus m. macrorhynchos* Wagler, 1827. Holotype (♂) from Malay Peninsula, Malaysia.
4. *Lycocoranirmus giloloensis* Mey, 2017 ex *Corvus validus* Bonaparte, 1850 [= revised type host]. Holotype (♀) from Halmahera, North Maluku, Indonesia.

*saliemii* group (1 sp.):

6. *Lycocoranirmus saliemii* (Ansari, 1957) nov. comb. ex *Corvus s. splendens* Vieillot, 1817. Holotype (♂) from Nepal.

#### **5.4.1. *Lycocoranirmus giloloensis* Mey, 2017**

Table 1-2, Figs. 3, 13 K, 14.

*Corvonirmus giloloensis* (Mey, 2017): GUSTAFSSON et al. 2019: 264 (*species inquirenda*).

**Type host** (revised): *Corvus validus* Bonaparte, 1850 - Long-billed Crow, Molukkenkrähe. Halmahera, North Maluku [erroneous host: *Lycocorax p. pyrrhopterus*, see MEY 2017: 138].

**Material:** 2 ♂, 17 ♀, 4 larvae from three skins, namely 1. 1 ♀ (holotype; M. 5487. a) ex *Lycocorax p. pyrrhopterus* (Bonaparte, 1850) [= erroneous host] juv. ♂, 5.4.1931 Jailolo, Halmahera, North Maluku, [Indonesia], coll. Gerd Heinrich-Expedition 1931 No. 4182; ex skin 55/273 ZMB. Stragglers from *Corvus validus* from the following one or two host individuals. - 2. 1 ♂, 14 ♀, 1 larva (M. 6159. a-f) ex *C. validus* ad. ♀, 22.4.1931 Gamkonora, Halmahera, North Maluku, [Indonesia], coll. Gerd Heinrich Expedition No. 4448; ex skin 55.286 ZMB. Mixed infection with *Allocolpocephalum* sp. (2 ♂, 6 ♀ legit) and *Myrsidea* sp. (9 ♂, 8 ♀, 4 larvae legit). - 3. 1 ♂, 2 ♀ (M. 6166. a) ex

*C. validus* ad. ♂, 5.4.1931 Jailolo, Halmahera, coll. Gerd Heinrich Expedition 1931 No. 4170; ex skin 55.287 ZMB. Mixed infection with *Allocolpocephalum* sp. (6 ♂, 3 ♀ legit) and *Myrsidea* (sp. 1: 4 ♂ and sp. 2: 3 ♂, 4 ♀ legit). All leg. E. Mey 17.1.2019.



**Plate III** (figs. 1-2): 1: *Lycocoranirmus giloloensis* Mey, ♂ (M. 6166.a), TL 1.66 mm, ex *Corvus validus* Bonaparte from Halmahera, Moluccas, Indonesia. 2: ditto, ♀ (M. 6166.a), TL 2.00 mm.

**Description:** habitus (♂, ♀) see plate III and fig. 14. Body colour dark brown. Body dimensions (mm). Males (n = 2): TL 1.66, HL 0.46-0.47, FW 0.4-0.43, OW 0.5-0.51, HI 0.92, PW 0.34-0.35, MW 0.56-0.57, AW 0.65-0.66. - Females (n = 15): TL 2 (1.81-2.29), HL 0.54 (0.51-0.56), FW 0.46 (0.42-0.48), OW 0.56 (0.53-0.59), HI 0.95 (0.91-1.02), PW 0.35 (0.33-0.36), MW 0.59 (0.56-0.62), AW 0.72 (0.65-0.79).

**Head:** anterior head structures with clypeus setae see Fig. 3. Anterior dorsal seta (ads) inset in circular sutures. Area enclosed by clypeal and ventral carina, in which only basal clypeal seta (avs 2) inserts, relatively small. Clypeal and ventral carinae about equal in thickness or the latter distinctly broader. Clypeal carina, however, strongly pigmented blackish brown, whereas ventral carina posterior to avs 3 appears almost colourless. Ventral submarginal setae (vsms 1 and 2) sit at about the same height. To vsms 2 (ocularis), which inserts there on the inner edge of the dorsal/ventral stiffened ventral carina, leads a mostly well visible seta canal (fig. 3). Two ocular spines (os and pos) of equal size on each side (on ommatidium).

**Thoracic chaetotaxy:** (♂ n = 2, ♀ n = 14): posterior-lateral each one macrochaete (pronotum seta), extending to abdominal segment III. Posterior-marginal in ventral outer corner of mesometathorax on each side one short spine + trichobothrium (mesochaeta). Macrochaetae row posterior-marginal on mesometanotum (n/n setae on each side): ♂ 7/9 and 8/9. ♀ five times 6/7, thrice 6/6, once each 5/6, 2/6, 6/8, 7/7, 7/8 and 8/10 (= 8 variants;  $\Sigma$  from 8-18, range of variation).

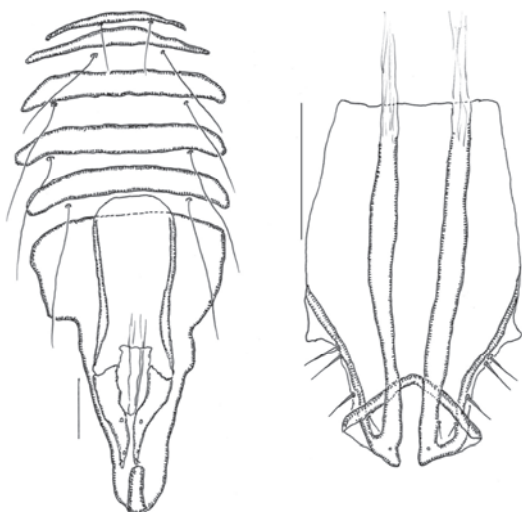


Fig. 14: *Lycocoranirmus giloloensis* Mey, ♂. Left: abdominal sternal plates with setae and genitalia, scale 0.1 mm; right: endomeron (mesosome), scale 0.05 mm.

**Abdominal chaetotaxy** (♂ n = 2, ♀ n = 14): segments II-III of ♂ and ♀ without paratergal setae. Number of **paratergal setae** on segments IV-VIII (each n/n; meso- and macrosetae): ♂ - **IV**, once each 1/1 and 1/2. **V**, once each 2/2 and 2/3. **VI**, twice 3/3, **VII**, once each 2/3 and 3/3. **VIII**, twice 3/3. ♀ - **IV**, five times 2/2, fourth times 3/2, thrice 3/3, twice 1/2 (= 4 variants). **V**, seven times 3/2, five times 3/3, twice 2/2 (= 3 variants). **VI**, five times each 4/3 and 3/3 (= 2 variants). **VII**, ten times 3/3, thrice 2/3, once 2/2 (= 3 variants). **VIII**, 13 times 3/3, once 3/2 (= 2 variants). **Postspiracular (macro)setae** (incl. trichobothrium [= trichoid seta] on segment VIII) in ♂ on segments III-VIII, in ♀ on segments IV-VIII. **Accessory postspiracular seta** only on the males on segments IV-VII. **Tergal posterior setae (tps)** ♂, segments II-VII on each side a fine mesoseta (= *mtps*, mediad tergo posterior seta); one ♂ only in one male additionally on segments VI-VII each 0/1 macrochaetes = *tps*, segment VIII once each 4/4 and 5/5 setae. ♀, segments II-VIII one macroseta (= *mtps*) on each side. **Sternal setae** (Fig. 15): ♂ and ♀ posterior-lateral to sternites on each side one seta on segments II-VI.

**Genitalia**: male genitalia (n = 2; see fig. 14 incl. mesosome): length 0.467 mm, width of basal plate cranial 0.16-0.17 mm and at paramere insertion 0.15 mm. Female subgenital plate see fig. 13 K. The narrowing middle part of the hypogynium is often barely pigmented and thus seems to be barely visible (see MEY 2017: figs. 66/67).

**Larvae**: the initially complete and evenly sclerotised circumfasciate clypeal carina in ontogeny (across all larval stages) has finally changed to a new, "semifasciate" form in the area of the osculum of the imago.

**Diagnosis**: uniformly brown hypogynium of *L. latifasciatus* and *L. hamatofasciatus* narrower than in *S. giloloensis*, in which the narrow middle part up to the vulva is hardly pigmented (see too *L. latifasciatus* and *L. hamatofasciatus*).

#### 5.4.2. *Lycocoranirmus latifasciatus* (Piaget, 1880) nov. comb.

*Nirmus latifasciatus* Piaget, 1880. Les Pédiculines: 143, plate 11, fig. 11.

*Nirmus latifasciatus* Piaget, 1880: KELLOGG (1908: 26).

*Degeeriella latifasciata* Piaget, 1880: HARRISON (1916: 116).

*Brüelia latifasciata* (Piaget, 1880): HOPKINS & CLAY (1952: 57).

*Brüelia latifasciata* (Piaget, 1880): ANSARI (1957: 175), Figs. 24, 56-57.

*Brueelia latifasciata* (Piaget, 1880): PRICE et al. (2003: 156).

*Corvonirmus latifasciatus* (Piaget, 1880): GUSTAFSSON & BUSH (2017: 194).

*Corvonirmus latifasciatus* (Piaget, 1880): MEY (2017: 115).

**Type host** (revised): *Corvus enca mangoli* Vaurie, 1958 - Slender-billed Crow, Sundakrähe. Sula Islands ("Sula Mangola"), Sulawesi, Indonesia [in PIAGET 1880 without host name, only erroneous host-label "Xulla Mangola", repeated without comment by KELLOGG 1908 and HARRISON 1916].

**Material:** 6 ♀, 1 larva of 2 skins, namely 1. 5 ♀, 1 larva (M. 6219. b-d) ex *Corvus enca celebensis* Stresemann, 1936, ♀, 27.5.1930 Makassar, South Sulawesi, coll. Gerd Heinrich Expedition 1930 No. 229; ex skin 33/1088 ZMB, leg. E. Mey 6.5.2019. Mixed infection with *Philoptyerus* sp. (2 ♀, 1 larva legit), *Myrsidea* sp. (4 ♂ legit) and *Allocolpocephalum* sp. (1 ♂, 1 ♀ legit). All *Philoptyerus* and *Lycocoranirmus* specimens collected from feathers of beak base. - 2. 1 ♀ (M. 6281. a) ex *C. e. celebensis* ♀, 14.2.1931 Ruruku, North Sulawesi, coll. Gerd Heinrich Expedition 1930/31 No. 3719; ex skin 33.1084 ZMB, leg. E. Mey 6.5.2019. Mixed infection with *Myrsidea* (sp. I: 8 ♂, 3 ♀; sp. II: 4 ♂, 2 ♀ legit) and *Allocolpocephalum* (2 ♂, 2 ♀ legit).

1 ♂, 1 ♀ of 2 skins, namely 1. 1 ♂ (M. 6214. a) ex *Corvus enca pusillus* Tweeddale, 1878, 2.9.1887/8 Palawan, Philippines, Steere Expedition to the Philippines, Puerto Pinasa, Palawan, coll. E. L. Moseley No. 141; ex skin 73301 SMF, leg. E. Mey 23.5.2019. - 2. 2 ♀ (M. 6275. a) ex *C. e. pusillus*, ♂, [no date] Balabac, Philippines, leg. A. Everett, don. E. Gerrard jr. in London, coll. H. von Berlepsch; ex skin 73307 SMF, leg. E. Mey 23.5.2019. Mixed infection with *Philoptyerus* (1 ♂, 1 ♀, 2 larvae legit), *Myrsidea* (sp. I: 2 ♂; sp. II: 6 ♂, 1 ♀, 2 larvae legit) and *Allocolpocephalum* (2 ♀ legit).

Of "*Nirmus latifasciatus* Piaget, 1880" only the lectotype (♀) is known so far, which has been re-described by ANSARI (1957: 175). CLAY (1940: 432) is credited with the clarification that this individual is very probably from *Corvus enca celebensis*. Why HOPKINS & CLAY (1952: 57)<sup>13</sup> and ANSARI (1957) and PRICE et al. (2003: 156) following them, state that its type host is the nominate form of *Corvus enca* is unclear. GUSTAFSSON & BUSH (2017: 418) cause even more confusion when they even assign *Corvus enca pusillus* as type host to the lectotype of *latifasciatus* without any explanation. In the Sula Islands E Sulawesi, the subspecies *mangoli* of *Corvus enca*, which only became known in the late 1950s, but not *pusillus* from the Philippines, lives (Del HOYO & COLLAR 2016, DICKINSON & CHRISTIDIS 2014; and currently online.versions of these checklists).

It is provisionally assumed that the *Lycocoranirmus* material available from *Corvus enca celebensis* belongs to one and the same species with the still unknown one from *Corvus enca mangoli*. The latter apparently also lives on *Corvus enca pusillus*.

**Diagnosis:** males with 1.29-1.38 mm (n = 2) and females (n = 3) with 1.7-1.81 mm body size clearly smaller than *L. giloensis*. About the same size as *L. hamatofasciatus*, but the conia are clearly smaller than in *L. latifasciatus*.

#### 5.4.3. *Lycocoranirmus hamatofasciatus* (Piaget, 1890) nov. comb.

*Docophorus hamatofasciatus* Piaget, 1890. Tijdschr. Entomol. **33**, 225, plate 8, fig. 3.

*Docophorus hamatofasciatus* Piaget, 1880: KELLOGG (1908: 15).

*Philoptyerus hamatofasciatus* (Piaget, 1880): HARRISON (1916: 96).

*Brüelia hamatofasciata* (Piaget, 1890): HOPKINS & CLAY (1952: 56).

*Brüelia hamatofasciata* (Piaget, 1890): ANSARI (1956: 402), figs. 104-107.

*Brueelia hamatofasciata* (Piaget, 1890): PRICE et al. (2003: 155).

*Corvonirmus hamatofasciatus* (Piaget, 1890). GUSTAFSSON & BUSH (2017: 194).

*Docophorus hamatofasciatus* Piaget, 1890. MEY (2017: 116), *species inquirenda*.

**Type host** (revised): *Corvus philippinus* (Bonaparte, 1853) – Philippine Jungle Crow, Philippinen-Dschungelkrähe.

**Material:** 1 ♂, 5 ♀ (M. 6198. a-d) ex *Corvus philippinus* ad. ♂, July 1893 Sibutu Island, Philippines, coll. A. Everett; ex skin C 12796 MTD, leg. E. Mey 25.3.2019. Mixed infection with *Myrsidea* 2 spp. (I: 2 ♂, 1 ♀, 4 larvae legit; II: 1 ♂, 1 ♀ legit) and *Allocolpocephalum* (3 ♂, 1 ♀ legit).

<sup>13</sup> According to these authors alone, the erroneously adopted host statement in MEY (2017: 115) was made.

"*Docophorus hamatofasciatus*" has been described after a female found on the Philippine bucerotid *Penelopides manillae* (Boddaert) (= false host). ANSARI (1956) redescribes this specimen and, following HOPKINS & CLAY (1952: 56), considers it to be a corvid relative ("Corvinae"), which in his opinion would be most likely to be seen in the magpie "*Pica p. nuttali*" [= *Pica nuttali* (Audubon)]. MEY (2017: 116) is of the opinion that *hamatofasciatus*, according to PIAGET's and ANSARI's descriptions, cannot be either a *Corvonirmus* or an *Olivinirmus* form and therefore considers it to be a "*species inquirenda*". GUSTAFSSON & BUSH (2017) have examined the lectotype (♀) of *hamatofasciatus*, but in our opinion have not solved the problem of its generic affiliation. Without describing *hamatofasciatus* again, they place it initially (p. 88) into *Hecatrishula*, but otherwise always into *Corvonirmus*. The verbal description by ANSARI (1956: 404) largely fits *Corvonirmus* (except for the tergopleurites outlined by him in fig. 106). After re-examining this case, we come to the conclusion that, according to Piaget's description of "*Docophorus hamatofasciatus*", it is clearly a *Lycocoranirmus* species, whose type host is very probably *Corvus philippinus* (Bonaparte, 1853). The other corvid species, *Corvus enca*, which is native to the Philippines in three subspecies, is very probably not the type host of *Lycocoranirmus hamatofasciatus*.

**Diagnosis:** like *L. latifasciatus* clearly smaller than *L. giloloensis*. Large hyaline conus of the female clearly protrudes over the length of the scapus. In the male it extends over the middle of the slightly swollen scapus.

## 6. Synhospital occurrence within the *Corvonirmus* group

Of the four genera of the *Corvonirmus* group, only *Corvonirmus* and *Hecatrishula*, are known to be synhospital to host species and/or host individuals. Table 3 summarises the four cases known so far. However, after comparison with table 1, which presents much more extensive but still unprocessed material, it becomes clear that the number of cases of synhospital occurrences of *Corvonirmus* and *Hecatrishula* in *Corvus spp.* has doubled in the meantime. In contrast, there seems to be no example (yet) of *Stubbenirmus* and/or *Lycocoranirmus* living together with *Corvonirmus* and/or *Hecatrishula* on corvids. At least there is a suspicion for this, because on *Corvus o. orru* (from New Guinea and Moluccas) lives an undescribed *Lycocoranirmus* species, but on *Corvus orru ceciliae* (from Australia) *Corvonirmus orruaticus* Mey.

Table 3: Synhospital occurrence of *Corvonirmus* and *Hecatrishula* on *Corvus spp.* according to the findings of ANSARI (1957) and GUSTAFSSON & BUSH (2017)

Host species	<i>Corvonirmus</i>	<i>Hecatrishula</i>	Continent
<i>Corvus corax corax</i>	<i>argulus</i>	<i>atherae</i>	Europe
<i>Corvus corax laurencei</i>	<i>argulus</i>	<i>atherae</i>	Asia
<i>Corvus corax tibetanus</i>	<i>argulus</i>	<i>atherae</i>	Asia
<i>Corvus f. frugilegus</i>	<i>tasniemae</i>	<i>varia</i>	Europe
<i>Corvus albus</i>	<i>quadrangularis</i>	<i>bipunctata</i>	Africa
<i>Corvus cryptoleucus</i>	<i>afzali</i>	<i>cryptoleuca</i>	North America

## 7. Parasitophyletic notes

From a parasitophyletic point of view, there is a remarkable, hardly coincidental correspondence between the genetic findings obtained in Red-billed Chough and Yellow-billed Chough reported by JØNSSON et al. (2020) and the result of the morphological study presented here on two chewing lice living in both bird species. On the one hand, CIBOIS & PASQUET (1999), ERICSON et al. (2005) and BONARCCORSO & PETERSON (2007) have elaborated, "that the most basal

clade within the Corvidae is the genus *Pyrrhocorax*" (JØNSSON et al. 2020: 168). On the other hand, it now appears that the *Stubbenirmus* species living host-specifically on *Pyrrhocorax* represent a rather original group in the *Brueelia* complex of the Passeres, which will foreseeably become more and more finely branched as research progresses rapidly. Within the representatives of the *Corvonirmus* genus group, so far known only from corvids, *Stubbenirmus* undoubtedly has a basal place. This is based on several synapomorphies, of which the constant character "abdominal segments VIII and IX/X of females each covered by an undivided tergopleurite" is the most important of *Stubbenirmus*. But what does it mean in this genus that morphologically *koslovae* and *docilis* groups are much closer than either of these two to the *biguttatus* group? The former is known from the desert birds *Podoces hendersoni* and *P. biddulphi*, the latter from the high mountain bird *Pyrrhocorax pyrrhocorax*. All three harbour closely related *Stubbenirmus* species of their own, whereas *S. biguttatus* shows intermediate characters to *Hecatrishula*, as expressed in the head morphology (figs. 1-2). This would suggest a closer relationship between *Podoces* and *Pyrrhocorax*, which would be somewhat expanded with *Stubbenirmus biguttatus*. However, according to JØNSSON et al. (2020: 167), there is no reason to place *Podoces* closer to *Pyrrhocorax* in the phylogenetic tree. Instead, the African *Ptilostomus afer* forms the sister group of *Podoces*. The *Brueelia* s. str. species known so far from the Piapiac (strangely enough two) are hardly suitable to make a well-founded statement on this from a parasitophyletic point of view (see table 1).

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## Zusammenfassung

### Die *Corvonirmus*-Gruppe (Insecta, Psocodea, Phthiraptera, Ischnocera) der Rabenvögel (Aves, Corvidae). I. *Stubbenirmus* gen. nov.

1. Die zum *Brueelia*-Komplex (Phloptera s. l.) gehörigen Gattungen *Corvonirmus* Eichler, 1944 (mit 11 spp.), *Hecatrishula* Gustafsson & Bush, 2017 (mit 8 spp.) und *Lycocoranirmus* Mey, 2017 (mit 5 spp.) werden morpho-strukturell vor allem nach Kopfstrukturen und Beborstung umrissen und als eine Verwandtschaftsgruppe definiert, die man in den Rang einer Unterfamilie (*Corvonirminae* subfam. nov.) stellen sollte, wenn die früheren *Brueeliinae* sensu EICHLER (1963: 177) den Status einer eigenen Familie (*Brueeliidae*) erhalten würden.
2. Innerhalb der *Corvonirmus*-Gruppe wird der früheren *Hecatrishula biguttata*-Artengruppe Gattungstatus zuerkannt. *Stubbenirmus* gen. nov. mit *S. stubbeae* spec. nov. (generotype) ex *Podoces hendersoni* Hume und *S. koslovae* (Clay, 1936) ex *Podoces biddulphi* Hume vertreten sehr wahrscheinlich den phylogenetisch ältesten Zweig innerhalb der *Corvonirmus*-Gruppe. Diesem Paar (*koslovae* group) steht *S. docilis* (Ansari, 1957) ex *Pyrrhocorax pyrrhocorax barbarus* Vaurie nahe, doch vertritt er vorläufig ebenso eine eigene Artengruppe wie *Stubbenirmus biguttatus* (Kellogg & Paine, 1914) ex *Pyrrhocorax graculus forsythi* Stoliczka. *Stubbenirmus biguttatus* vermittelt zu *Hecatrishula*, von der sich *Corvonirmus* und *Lycocoranirmus* ableiten lassen. Wie nahe *Olivinirmus* Złotorzycka, 1964 der *Corvonirmus*-Gruppe steht und ob es richtig ist, zu jener auch die australischen *Brueelien* der *Cracticidae* („*Nirmus semiannulatus* Piaget, 1883“ angeblich auf mindestens 4 Wirtsarten) zu ziehen, ist noch nicht näher untersucht worden.

3. Dem taxonomisch-systematischen Block (1. und 2.) ist ein wissenschaftshistorischer Diskurs über die Vorgeschichte der *Stubbenirmus*-Arten vorangestellt, worin begründete Zweifel an der Identität von *Hecatrishula multipunctata* (Clay, 1936) vorgetragen werden.
4. Es wird die vage Aussage und davon abgeleitete Spekulation zurückgewiesen, wonach *Stubbenirmus biguttatus* und *S. docilis* synhospital auf beiden *Pyrrhocorax*-Arten leben würden.
5. Es wird darauf aufmerksam gemacht, dass von den vier Genera der *Corvonirmus*-Gruppe regelmäßig nur Arten von *Corvonirmus* und *Hecatrishula* synhospital (sowohl auf Wirtsart als auch auf Wirtsindividuum) vorkommen. In einem noch genauer zu untersuchenden Fall (*Corvus orru* spp.) scheinen auch *Lycocoranirmus* und *Corvonirmus* synhospital auf einer Wirtsart (*Corvus orru*) zu leben, die aber nach bisherigen Kenntnisstand verschiedenen Wirtssubspezies (*orru* in Neuguinea und Molukken und *ceciliae* in Australien) angehören.
6. Parasitophyletische Überlegungen anhand der *Corvonirmus*-Gruppe weisen darauf hin, dass die Genera *Podoces* und *Pyrrhocorax* an der Wurzel der Corviden stehen.

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