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Putting the cart before the horse: taxonomy of the species of *Philopterus* (Phthiraptera: Ischnocera: Philopteridae) of the goldcrest, *Regulus regulus* (Linnaeus, 1758) (Aves: Passeriformes: Regulidae)

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Abstract. The concept of "type host" denotes the host with which the holotype (or equivalent) of a parasitic species was associated at the time of collection. This concept is often erroneously conflated with the concept of a "natural host(s)", which refers to the host(s) with which the parasite species is naturally and normally associated in the wild. In cases where these two concepts are not kept apart, and when parasites like lice (Phthiraptera) are believed to be strictly host specific, a culture of identification by host association may develop. Here, I look at the consequences of such a case, the recent rejection of *Philopterus reguli* Denny, 1842 as the valid name of the louse species that normally parasitizes *Regulus regulus* (Linnaeus, 1758), and the erection of a new name for this taxon, which was subsequently synonymized with the new name based on a proposed neotype for *Ph. reguli*. I discuss the history of *Philopterus reguli*, the known specimens of this species, and the present controversy, as well as the validity of the neotype designation. In conclusion, the neotype designation of *Ph. reguli* is rejected, as it has not been shown that the syntype is unidentifiable, suspicious, or otherwise invalid, and a change in nomenclature has not been shown to be a problem for the stability of taxonomy. Moreover, the neotype designation is invalidated by at least three separate violations of the International Code of Zoological Nomenclature. I call for more care in both specimen identification and louse taxonomy and open up for a discussion about how the louse research community can move forward together on the issue of poorly described species.

Key words. Type host, natural host, Phthiraptera, *Philopterus*, neotype designation.

CHEWING LICE

Chewing lice (Phthiraptera) are small, wingless parasites of birds and mammals. In general, chewing lice do not easily spread between hosts except when two hosts come into physical contact, but many exceptions are known (e.g., Gustafsson & Najer 2022). Moreover, lice lack free-living life stages, and the host's feathers or fur serve as both habitat, egg-laying surface, and food for lice. As a result, lice have evolved to be exceptionally dependent on their hosts, making them excellent model systems for, for example, research into co-evolution (Clayton et al. 2016).

However, research on lice is often hampered by difficulties in identifying lice, sometimes even to genus level. This is partially due to the relatively little attention lice have received in the last century, compared to larger and more easily collected insect groups. For instance, there were no general checklists with illustrations of all different genera until Price et al. (2003), there are almost no national or regional checklists of lice (but see, e.g., Ilieva 2009; Palma 2017; Oslejskova et al. 2021), and no general genus-level key to the largest group of lice, the Ischnocera, has ever been published. In addition to this lack of resources, the most significant obstacle to louse identification is the generally poor descriptions and illustrations provided for a large proportion of the known lice. At least partially, this is due to an overreliance on host associations over louse morphology by many of the most prolific louse taxonomists throughout the 20th century. Here, I examine a recent case in louse taxonomy that highlights the shortcomings of this approach.

THE REVERSE OF HELPFUL

The concept of the "type host" of chewing lice has accrued an undeserved and irrational importance in chewing louse taxonomy over the last century. If a host species has been designated the type host of a louse species, then any congeneric louse specimens on the same host species have sometimes been assumed to be conspecific with the known louse species. Conversely, if a louse specimen is found on a host that has not previously been designated

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the type host of any louse of that genus, this has been seen as sufficient evidence that this specimen must be novel.

Examples of this are numerous throughout the published louse literature, although some are more egregious than others: Eichler (1950) described two new subspecies of *Auricotes* Kéler, 1940, based on specimens he himself had not studied, but which were discussed by Kéler (1940). In both cases, Kéler (1940) mentioned that specimens from some non-type hosts deviated slightly from specimens from type hosts, but no details were given, and Kéler considered the specimens he had examined to be too few to draw any conclusions. No morphological argument for their division was thus ever published by Kéler (1940), nor did Eichler (1950) add any morphological detail. It seems reasonable to consider these names to be in violation of Article 13.1.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999; hereafter: the Code), and thus unavailable. Hopkins & Clay (1953: 443) chided Eichler for exactly this behaviour, and memorably called it "the reverse of helpful".

Similarly, Złotorzycka (1964a, b) made a habit of separating species she had not examined based on the family-level classification of their hosts. She also in many cases restricted or fixed type hosts of species she had not examined, but which were described as occurring on more than one host species, then declared that lice living on the other listed host were "most probably some other not yet described species". Typically, she then removed the non-type hosts from the lists of host associations of the lice, thus asserting that the observations of other researchers are invalid, without ever having seen any of the specimens in question. Gustafsson & Najer (2022) recently discussed many other similar examples.

More generally, checklists and revisions typically explicitly separate type hosts from other hosts or denote which host species in a list of known species is the type host (e.g., Price et al. 2003; Gustafsson & Bush 2017). However, from a broadly biological point of view, type host information is irrelevant. The type host is nothing more than the identity of the host individual the louse specimen designated as the holotype (or equivalent) was associated with at the time of collection (cf. the 'Glossary" of the Code). That is, the information conveyed by stating the type host of a louse species is that at least once, this louse species was associated with this host species. It does not, strictly speaking, imply that there will be any future records of associations between these two taxa.

In contrast, the biologically relevant term is the "natural host" (cf. Palma 2015), which may be defined generally as the host species (or set of host species) on which there is reason (based on some criteria) to believe that the vast majority of the world population of a louse species can be found under non-artificial circumstances. This concept conveys a very different kind of information, as a "natural host" designation is the assertion that this louse species could in theory be found on other specimens of this host in the future.

The type host and the natural host may be the same but may also be different. The louse literature is replete with taxa described from hosts later considered to be non-natural (e.g., Palma 1994, 2005; Adams et al. 2005; Gustafsson et al. 2019a). Recently, a new family of amblyceran lice was even proposed based on specimens from an unknown host that could not be determined even to class level [bird or mammal; Mey (2019)]. The only way to ascertain whether the type host is also the natural host is to examine more conspecific hosts and establish (to some satisfactory level of regularity) that lice from this host species are habitually conspecific with a given louse holotype.

Moreover, in my opinion, knowledge of the type host of is largely irrelevant even from a taxonomic point of view. Classification of organisms should be based on data derived from intrinsic characters of the organisms examined, not from extrinsic circumstances of their collection. From a strictly taxonomic point of view, there is no clear difference between stating "these two lice were both collected from the same host species, therefore they are conspecific" and saying, "these two lice were both collected on June 26th, therefore they are conspecific". In both cases, only intrinsic characters (e.g., morphology, genetics) of the specimens can determine if the statements are correct. "Type host", in contrast, is an extrinsic character that is irrelevant to the classification of the louse taxon.

Similarly, species identity and species limits cannot be ascertained by type host data alone; they require intrinsic data from the species in question. Arguments of identification that center on host identity are by definition spurious, and relevant only if the holotype (or equivalent) is known to be lost or ambiguous, and there is reason to clarify the identity of a taxon name by designating a neotype. In those cases, the type host serves much the same purpose as a type locality for free-living organisms, and neotypes from the same host should be ideally selected to increase the likelihood that the old types and the new types are conspecific (cf. Recommendation 75A of the Code). Crucially, these neotypes should then also be selected from a geographically similar location to the old types, given that there may be geographical variation in the lice as well as their hosts (e.g., Escalante et al.2016).

Although no overview of this development has been published, it seems reasonable to assume that at least part of this obsession with type hosts stems from the widespread belief of many earlier authors that louse data could assist in establishing relationships between hosts in cases where the data from the hosts were inconclusive (e.g., Clay 1950). This was assumed because 1) lice were believed to evolve slower than their hosts and thus could retain phylogenetic information that had been lost

in their hosts through, for example, convergence, and 2) host switching was believed to be rare. Type hosts could then be used as the hooks on which to hang hypotheses of host associations, but that required the assumption that type hosts and natural hosts are the same. If they are, and the two assumptions mentioned above are valid, then two closely related louse species implicitly must have type hosts that are closely related. Seen in this light, the focus on the type host at the expense of the natural host becomes more understandable, but it does not make this shift in focus correct.

In fact, combined with the "Eichlerian methodology" (sensu Gustafsson & Najer 2022), according to which lice are considered strictly host specific and invariably following Fahrenholz's rule (Eichler 1940), the focus on type hosts rather than natural hosts may blind researchers to more interesting questions in evolutionary biology and biogeography. For instance, Eichler insisted that it is "methodologically more appropriate to say that 'we cannot yet tell two parasites from different hosts apart' than 'this parasite occurs on both these different hosts'" (Eichler 1940: 256), and that "a future review may nevertheless prove that there are morphological differences" (Eichler 1980: 412) as responses to assertions of multi-host parasites. This line of argument is intentionally blinding oneself to the possibility that lice vary in their level of host specialization, and that important general principles of louse biology may be behind this variation.

Recent research into phoresy of lice on hippoboscid flies resulting in the erosion of genetic variation among lice (DiBlasi et al. 2018) and the establishment of vast networks of host-louse associations that may span different families of hosts on different continents (e.g., Bush et al. 2016; Lee et al. 2022) has revealed a more accurate picture of louse biology. Similarly, host generalists have repeatedly been shown to exist through genetic analyses, and often be closely related to host specialists (e.g., Martinů et al. 2015; Bush et al. 2016). In other cases, host associations and species-level evolution of lice appear to be influenced by biogeography (e.g., Escalante et al. 2016) or macroevolutionary events in the history of their hosts (e.g., Boyd et al. 2022). These lines of research are possible because the bias of strict host-specificity has been removed, and collectively they reveal a much more interesting louse biology. This research has also established a more appealing worldview in which lice are not the flotsam of host evolution, but active agents to some extent responsible for their own evolutionary fate. Somewhat belatedly, lice are entering the set of organisms that may be suspected of having behaviours more sophisticated than eating, reproducing, and dying.

Nevertheless, type host designations, and discussions of type hosts, are prevalent in the chewing louse literature, and the roots may be too deep to do away with the concept altogether. Moreover, as the type host concept has some use under more strictly taxonomic circumstances, there is a need to retain the concept. However, it is important to keep in mind that the host associations – or lack thereof – of the name-bearing type specimen(s) have no bearing on the validity of the name, nor do they restrict the natural hosts of the species denoted by the name. The sooner the chewing louse community can extract itself from the obsession with type hosts, the sooner we can collectively progress to a state where louse biology and classification can be established based on data derived from the lice themselves, rather than from preconceived scenarios that may not fit the data.

To exemplify the problems that arise when type hosts and natural hosts are conflated, we will look at the species *Philopterus reguli* Denny, 1842. This will hopefully show that it is necessary to establish identity and species limits in lice based on characters of the lice themselves, and not circumstances of their collection. We will then assess the validity of recent nomenclatorial decisions made for this taxon, and finally make some general recommendations on how to approach louse identification in the future.

THE CASE OF *PHILOPTERUS REGULI* (DENNY, 1842)

Two publications during 2020 discussed the identity of *Philopterus reguli* Denny, 1842 (Najer et al. 2020; Mey 2020), a rarely reported species of head louse. Its type host is *Regulus regulus* (Linnaeus, 1758). These two publications reached complete opposite conclusions based largely on the same data. The history of the name *Philopterus reguli* can briefly be summarized as follows:

Denny (1842: 45, 91) described *Philopterus* (*Docophorus*) *reguli* based on an unknown amount of specimens from at least two collection events. At least one specimen was collected by another person, L. Jenyns, but the collection localities or methods of Jenyns' specimen and Denny's other specimens were omitted from the original description. Denny stated that the species showed "great variation" in the "colour and extent of the abdominal fasciae" [= tergal plates]. The host of this species was given as "Golden-crested Regulus (*Regulus aurocapillus*)" [= *R. regulus*]. At least some of Denny's specimens of this species were obtained by the British Museum [= Natural History Museum, London; hereafter NHML] (Gray 1852). Other specimens may or may not have been lost (cf. Thompson 1937; Clay 1947; Hopkins & Clay 1952; Mey 2020; see below).

Najer et al. (2020) reported that only a single specimen of *Ph. reguli* from Denny's collection remained at the NHML. They referred to this specimen as the "holotype", which is erroneous, as Denny did not designate any holotype. This specimen is here referred to as the "London syntype", for simplicity (see below). Subsequent reports of this species are few (see Najer et al. 2020 and below),

and the only attempts at redescribing or illustrating the species prior to 2020 were published by Złotorzycka (1964b, 1977) and Złotorzycka & Lucińska (1976), as well as possibly by Fedorenko (1987; not seen). Notably, these redescriptions were done without reference to the London syntype, evidently based on the assumption that any *Philopterus* specimen found on *R. regulus* must be *Ph. reguli*.

There can be no argument about that both the illustrations and descriptions of *Ph. reguli* by Denny (1842), Złotorzycka (1964b, 1977), and Złotorzycka & Lucińska (1976) are subpar, and largely useless for identifying the species. The first useful illustrations of a species of *Philopterus* from this host are thus those published by Najer et al. (2020) and Mey (2020); there is no doubt that the species described and illustrated in these two publications represent the same species. Nor is it disputed that the species illustrated by Najer et al. (2020) and Mey (2020) is the one whose natural host is *R. regulus*. This louse species was reported by Najer et al. (2020) from numerous subspecies of *R. regulus* from across much of its range, as well as from *Regulus ignicapilla* (Temminck, 1820), and is here referred to as the "Brno species" for brevity, as the specimens illustrated by Najer et al. (2020) are deposited at the Moravian Museum in Brno, Czech Republic.

Najer et al. (2020) reported that the Brno species is not conspecific with the London syntype, with differences "e.g., in shape of head, shape of dorsal preantennal head plate [= dorsal anterior plate], thoracic and abdominal chaetotaxy, shape of subgenital plate". The London syntype was neither illustrated, nor photographed, nor described in text by Najer et al. (2020), and no detailed comparison between the London syntype and the Brno species was published, for which they were rightly criticized by Mey (2020). The London syntype is a female, meaning that details of the male genitalia that are believed to be crucial to species identity in *Philopterus* (see Gustafsson et al. 2022) cannot be examined. The statement that the London syntype specimen is not conspecific with the Brno species was not disputed by Mey (2020).

There is also no dispute that the redescription of Złotorzycka (1964b, 1977) and Złotorzycka & Lucińska (1976) are not based on specimens conspecific with the London syntype, but with the Brno species. Najer et al. (2020) examined at least part of the specimens examined by Złotorzycka to confirm this. They also examined some other specimens reported by other authors and found these to be conspecific with the Brno species. Thus, the species illustrated and described by Złotorzycka (1964b, 1977), Złotorzycka & Lucińska (1976), Najer et al. (2020), and Mey (2020), and the specimens on which these descriptions are based, are all conspecific, and constitute the Brno species.

To date, no other specimens conspecific with the London syntype are known. Najer et al. (2020) stated that the London syntype is different from all other *Philopterus* material they examined from any host in Regulidae. Beyond *Regulus regulus* and *Regulus ignicapilla*, Najer et al. (2020) did not state which other regulid species, if any, they examined material from. They also did not state whether any systematic effort was made to go through the Denny collection at the NHML to find other specimens that may be conspecific with the London syntype, but this is in any case not necessary. Moreover, no other species of *Philopterus* Nitzsch, 1818, have been described from any other host in the family Regulidae (Price et al. 2003). The closest relatives of the Brno species appear to parasitize tits and chickadees (Paridae; Najer et al. 2020; Mey 2020).

Thus far, there is no disagreement between Najer et al. (2020) and Mey (2020). However, Najer et al. (2020) declared that the London syntype is a straggler (specimen accidentally associated with a host) and suggested that most published records of *Ph. reguli* may not be this species. Instead, they gave a new name to the Brno species, *Philopterus gustafssoni* Najer et al., 2020. Moreover, they incorrectly refer to *Ph. reguli* as an "invalid name"[1] (Najer et al. 2020). If accepted, this treatment would mean that the London syntype retains the name *Philopterus reguli* Denny, 1842, and retains the type host *R. regulus*, but has an unknown natural host. Moreover, this would mean that *Ph. gustafssoni* is the valid name for the Brno species, whose type host and natural host is *R. regulus*. This would also be the only species of *Philopterus* known to parasitize *R. regulus* on a regular basis.

In contrast, Mey (2020) rejected the taxonomic decisions of Najer et al. (2020). As will be discussed below, Mey (2020) argued that the London syntype "is of dubious type status and cannot be used taxonomically". Instead, he rejected the London syntype, and designated a neotype and four "neoparatypes" (not recognized by the Code) for *Ph. reguli* Denny, 1842, from collections deposited at the Martin Luther University Halle-Wittenberg, in Halle (Saale), Germany. This neotype is here referred to as the "Halle neotype", for simplicity. If accepted, this would mean that the Brno species retains the name *Philopterus reguli* Denny, 1842 through this transfer of name-bearing type status. *Philopterus reguli* would retain the type host *R. regulus* and gain the natural host *R. reguli*. *Philopterus gustafssoni* would become a subjective junior synonym of *Ph. reguli*. Simultaneously, the London syntype would become nameless and have no known natural host but retain the "ghost type host" *R. regulus*, as that is the host upon which the specimen purportedly was found.

[1] Confusingly, Najer et al. (2020) do not appear to mean that the name *Ph. reguli* is invalid in the sense of the Code, but invalid in the sense of "incorrect". No argument that the name is invalid in the sense of the Code was presented by Najer et al. (2020).

Due to the fundamental differences between these two taxonomic conclusions, overviews of the known history and identity of the London syntype and the name *Philopterus reguli* are necessary.

THE KNOWN HISTORY OF THE LONDON SYNTYPE

The history of Denny's collection following the publication of his monograph is only partially known. Already in 1838, he advertised for specimens from around Great Britain (Denny 1838), and many of the species he described in his monograph are based on specimens received by various correspondents. In some cases, he appears to have sent specimens back to their original collector. For instance, under *Nirmus stramineus*. Denny (1842: 139) stated that he was allowed "to retain [L. Jenyns' collection of lice] during the entire process of this work [i.e., the monograph]". The L. Jenyns in question is Leonard Jenyns, who later donated most or all of his collection of biological specimens to the Museum of Zoology in Cambridge, UK (Suarez Ferreira 2021). I have been unable to establish whether any Phthiraptera were included in this donation, which would be especially relevant, given that the "first specimen" of *Ph. reguli* was sent to Denny by L. Jenyns.

Part of Denny's collection was obtained by the NHML before 1852, when Gray (1852) listed all the specimens in the museum's possession. Gray stated that the museum "possesses the type specimens described and figured by [Henry Denny]" without qualification, implying that any and all specimens Denny considered types were obtained by the NHML. However, not all species described by Denny are noted as being in the NHML's possession, meaning that some types may have been deposited elsewhere. In Table 1, the species of "*Philopterus*" described by Denny are listed, along with information on which of these species were said to be in the NHML's possession by Gray (1852). Note that many of the species listed in Table 1 have since been moved to other genera or are considered synonyms of other species. Notably, types of *Ph. reguli* are listed as being in the possession of the NHML by Gray (1852). However, it should be noted that Article 72.4.7 of the Code states that a subsequent work stating that a specimen is a "type" does not necessarily mean this specimen is fixed as a type specimen in that work.

Denny's specimens were mounted on cards when they arrived at the NHML (Thompson 1937), but at some point between 1852 and 1937, at least part of the collection was cleared in KOH and slide-mounted by an unknown person. Thompson (1937) suggested that either Bruce F. Cummings or James Waterston may have been responsible for the slide-mounting but could not determine who. Cummings died in 1919, Waterston in 1930, suggesting that the transfer of specimens from cards to slides were done between 1852 and 1930.

The Denny slides have a certain style to them, not shared by most other slides at the NHML. Whoever mounted these slides used slide labels with a red outline for types, sealed the mounts with black rubber circles, and positioned the lice "horizontally" on the slide; the labels are also written in a neat cursive hand. This style of mounting, and the handwriting, are the same as that of type slides of species described by Cummings in the same collection. In contrast, the handwriting and overall mounting style of slides in the Waterston collection differs from this. Most likely, Denny's specimens were thus mounted by Cummings, or someone he employed to mount specimens for him. On the online photo database of slides at the NHML, all specimens from the Denny collection appear to be mounted in this way, indicating that they were all transferred from cards to slides by the same person(s) at the same time. Moreover, apart from Cummings type slides, no other slides in this collection appear to be mounted in the same style; however, no exhaustive search for other slides mounted in this style was conducted.

Thompson (1937) listed the specimens from the Denny collection present in the NHML at the time but did not note whether the specimens constituted types. Among the "*Philopterus*" species described by Denny (1842), Thompson (1937) listed specimens from only 24 species (Table 1); *Philopterus semisignatus* Denny, 1842, is not included in Thompson's list at all. Based on Thompson's list, specimens of nine species of "*Philopterus*" described by Denny (1842) are thus implied to have been lost between 1852–1937; as neither Denny (1842) nor Gray (1852) list any numbers of specimens, the loss may have been larger. A single female *Ph. reguli* is listed as being in the collection of the NHML by Thompson (1937).

However, Clay (1947) noted that Thompson (1937) had made several omissions, and that a total of 20 species not included in Thompson's list were actually present at the NHML. No details are given as to how these could have been overlooked, nor which these 20 species are (with two exceptions that are irrelevant to the present discussion). Hopkins & Clay (1952) marked all the species for which types were present in the NHML with an asterisk. Among the "*Philopterus*" species described by Denny (1842), this includes 32 species, omitting only two species that were noted as present by Gray (1852) (Table 1). Notably, *Ph. reguli* is noted by an asterisk. Again, as neither Gray (1852) or Hopkins & Clay (1952) include any information on the number of specimens from Denny's collection that were present, it is impossible to tell how many specimens may have been lost in the 100 years between these publications.

No further details are known about the London syntype until Najer et al. (2020) examined it. Under the current system at the NHML, the syntype has accession number

Table 1 (continued next page). History of the species of "*Philopterus*" described by Denny, listed in alphabetical order based on the name used by Denny (1842). Note that many of these species are today either moved to other genera or considered synonyms of other species (see Price et al. 2003). For each species, the number of collections or specimens mentioned, and the way they were mentioned, are summarized in the second column. Species are marked with "BM" in the third column if they are listed as being in the NHNL collection by Gray (1852); dashes ("–") indicate species not marked "BM" by Gray (1852). Species listed by Gray (1852) that were not described by Denny (1842) are not included. In the fourth column, we indicate the number of specimens of each species listed by Thompson (1937), with dashes where Thompson (1937) used dashes. For species that are absent in Thompson's list altogether, "NL" is given. Hopkins & Clay (1952) indicated with an asterisk species for which type material was present at the NHML, and these are here indicated with an asterisk as well. A more thorough, in-person examination of the collection at the NHML is needed to establish which specimens are still present there.

Species	Denny (1842)	Gray (1852)	Thompson (1937)	Hopkins & Clay (1952)
Philopterus alcedinis	single specimen, sent by L. Jenyns	–	–	–
Philopterus aquilinus	"tolerably common"; sent by W. Little, W. Jardine, Mr Calvert, G.R. Denny, Mr Thompson, as well as at least one collection by Denny himself	BM	–	*
Philopterus canuti	one specimen, sent by W.M. Tweedy	–	–	–
Philopterus ceblebrachys	specimens sent by A. Clapham, Mr Selby, and Mr Thompson	BM	3 ♀♀	*
Philopterus cephalus	Denny found it on two host species, and were sent specimens from at least five other collection events	BM	–	*
Philopterus chrysophthalmi	single specimen sent by Mr P.J. Selby	BM	–	*
Philopterus cincli	unknown number of specimens sent by A. Clapham, and Denny also collected	BM	–	*
Philopterus colymbinus	many specimens, sent by Mr Selby, Mr Tweedy, Mr Heysham, and collected by Denny himself. Additional specimens, considered a variety, from other host species, were sent by Mr Heysham and Denny's brother	BM	4 ♀♀	*
Philopterus conicus	single specimen collected by Denny	–	–	–
Philopterus cygni	multiple specimens from Mr Thompson, and from T.C. Heysham from two different host species	BM	4 ♂♂, 1 ♀	*
Philopterus fringillae	"communicated by Mr A. Clapham", no specimens mentioned	BM	2 ♀♀	*
Philopterus fusiformis	single specimen sent by Mr Thompson	–	–	–
Philopterus guttatus	unknown number sent from L. Jenyns, Denny subsequently found a single specimen	BM	3 ♂♂, 2 ♀♀	*
Philopterus humeralis	unknown number of specimens sent by Mr Thompson, and collected by Denny from three different host species	BM	4 ♀♀	*
Philopterus incompletus	unknown number of specimens collected by Denny himself	BM	2 ♀♀	*
Philopterus latifrons	Denny found it common on the host (implying he collected specimens from multiple birds?), and also received it from Mr Tweedy and Mr Doubleday, who sent him specimens from two hosts	BM	–	*
Philopterus limosae	unknown number of specimens sent by W. Thompson and G.R. Denny, from different host species	BM	1 ♀	*
Philopterus megacephalus	Denny found a single specimen	BM	–	–
Philopterus merguli	one specimen, sent by T.C. Heysham	–	–	–
Philopterus meropis	single specimen sent by W. Thompson	BM	2 ♀♀	*
Philopterus merulae	unknown number of specimens sent by W. Jardine, Mr Selby, and L. Jenyns who found it on two host species; Denny also collected a single specimen	BM	1 ♂, 7 ♀♀	*
Philopterus modularis	Multiple specimens sent by Denny's brother	BM	2 ♀♀	*
Philopterus nisi	unknown number of specimens sent by L. Jenyns and G.R. Denny	BM	1 ♂, 3 ♀♀	*
Philopterus ostralegi	"common upon the Oyster-catcher" = multiple collections?	BM	2 ♂♂, 1 ♀	*
Philopterus pallescens	unknown number of specimens sent by L. Jenyns and G.R. Denny	BM	–	–

Table 1 (continued).

Species	Denny (1842)	Gray (1852)	Thompson (1937)	Hopkins & Clay (1952)
Philopterus pari	unknown number of specimens sent by L. Jenyns, and Denny found specimens on two host species	BM	1 ♂	*
Philopterus passerinus	unknown number of specimens sent by L. Jenyns and G.R. Denny, Denny also collected a single specimen	BM	1 ♀	*
Philopterus pastoris	multiple specimens, sent by W. Thompson	BM	1 ♀	*
Philopterus picae	one specimen, from L. Jenyns	BM	1 ♀	*
Philopterus plataleae	"I found an abundance of this insect" on a single host	BM	1 ♂, 5 ♀♀	*
Philopterus platygaster	collected by Denny himself, with additional specimens from two hosts sent by his brother	BM	–	*
Philopterus ralli	unknown number of specimens sent by L. Jenyns	–	–	–
Philopterus reguli	one specimen form L. Jenyns, and Denny subsequently collected more	BM	1 ♀	*
Philopterus rubeculae	unknown number of specimens collected by Denny, and additional specimens sent by L. Jenyns from two host species	BM	1 ♂, 3 ♀♀	*
Philopterus semisignatus	unknown number of specimens sent by W. Thompson	BM	NL	*
Philopterus testudinarius	unknown number of specimens sent by Mr Thompson and Mr Heysham	BM	–	*
Philopterus thalassidromae	unknown number of specimens sent by W.M. Tweedy	BM	2 ♀♀	*
Philopterus turdi	"specimens" indicate multiple, collected by Denny himself	BM	2 ♀♀	*
Philopterus upupae	unknown number of specimens sent by W.M. Tweedy and T.C. Heysham	BM	5 ♂♂, 2 ♀♀	*
Philopterus variabilis	unknown number of specimens sent by W.M. Tweedy	BM	1 ♀	*

NHMUK010710741, and is located in the Denny collection. According to Najer et al. (2020), all other specimens labelled as *Philopterus reguli* at the NHML represent other genera from outside the *Philopterus*-complex; these specimens are not in the Denny collection and are mounted in different style.

Thus, at least one type specimen of *Ph. reguli* was listed by Gray (1852), exactly one was listed by Thompson (1937), at least one was listed by Hopkins & Clay (1952), and exactly one was found in that collection by Najer et al. (2020). If there were ever more than one type specimen of *Ph. reguli* in the NHML's possession, those specimens must have been lost before 1937, after which the number of type specimens of *Ph. reguli* in this museum appears to be constant. If specimens disappeared from the collection, it is most likely that this happened before or during the slide-mounting; if it is assumed that Cummings mounted these specimens, the time window for their loss must be between 1842–1919. This is too long a period with too much change at the NHML to establish any more detail. However, no evidence for such a loss has ever been presented, and there is no published evidence to suggest we should not take the identity of the London syntype at face value. Any contrasting opinion would need a sounder basis of argument than has hitherto been presented.

HOW MANY "SYNTYPES" DID DENNY HAVE?

Najer et al. (2020) erroneously referred to the London syntype as the "holotype", overlooking the fact that only the original author can designate a holotype, and that subsequent authors can only designate lectotypes (from a syntype series) or neotypes. It is clear from reading his monograph that Denny (1842) examined multiple specimens before publication: he stated that he first examined a single ["first"] specimen, and that he "since then have obtained others". Mey (2020: 160) pointed out the error of Najer et al. (2020) and correctly stated that "several individuals ("syntypes") were available [to Denny]". Mey (2020) at several points refer to the London syntype as the "remaining" or "surviving" syntype.

Article 72.4.1 of the Code states that the "type series of a nominal species-group taxon consists of *all the specimens included by the author* in the new nominal taxon […] except any that the author expressly excludes from the type series […] or refers to as distinct variants (e.g. by name, letter or number), or doubtfully attributes to the taxon" (my italics). Based on this Article, it is clear that at the time of printing of Denny's monograph, more than one syntype existed, as no express exclusion of any specimens from the type series was made by Denny. Denny's text implies a minimum of three syntype specimens. Assuming that the London syntype was included among

these syntypes, it is fair to say that at present only a single syntype of *Ph. reguli* is known to exist.

As a side note, the above is based on our modern concept of a syntype and may not be consistent with how Denny or people at his time saw it. The absence of more than one specimen of *Ph. reguli* at the NHML may be due to Denny only considering his first specimen a type, and the others non-types, similar to how for instance Najer et al. (2020) listed only a small number of specimens under "Holotype" and "Paratype" for the Brno species and left the vast majority as "Other material". The cases of *Nirmus* [= *Quadraceps*] *alcae* Denny, 1842, and *Nirmus* [= *Brueelia*] *stramineus* Denny, 1842, almost exactly parallel that of *Ph. reguli*. Denny first saw a single specimen and then obtained others, these are listed by Gray (1852), and only a single specimen of each is today present in the NHML, mounted in the same style as *Ph. reguli*. However, whereas Thompson (1937) lists only a single *Nirmus alcae*, he lists a total of three *Nirmus stramineus*, suggesting that there is no uniform pattern.

While the above scenario is a possibility, it can be overruled by Article 72.4.1 of the Code, which unequivocally shows that Mey (2020) is correct in his statement that more than one syntype existed at some point, whether or not they were considered as such by Denny.

IS THE LONDON SYNTYPE A SYNTYPE?

Mey (2020) asserted that "it can be shown that no name-bearing type of *Philopterus reguli* ex *Regulus regulus* any longer exists […] and the only existing "syntype" is of dubious origin". It is unclear what this is based on.

No evidence has been presented by either Najer et al. (2020), Mey (2020) or anyone else to suggest that the London syntype is not a (syn)type of *Ph. reguli*, as stated on the slide label. It is clear that syntypes were present at the time of the publication of Denny's monograph in 1842, that types described and figured in this monograph were in the possession of the NHML in 1852, that at least one specimen of *Ph. reguli* from the Denny collection was present at the NHML in 1937, and again in 1952. There is no evidence presented that any specimens of *Ph. reguli* have been lost from the NHML after 1952, nor that the specimen reported in 1952 is not among those reported in 1842, 1852, or 1937. The London syntype may not be one of Denny's original syntypes, but that has to be demonstrated rather than asserted.

Above all, if the London syntype had been conspecific with the Brno species, there would have been no question that the London syntype was a valid syntype. This is thrown in doubt only because two species are involved here, and the London syntype does not correspond to the Brno species. I find it impossible to rule out, based on our current knowledge, that the London syntype is a genuine syntype that has been handed down to us from Denny, a journey that is documented by at least four publications now (Gray 1852; Thompson 1927; Hopkins & Clay 1952; Najer et al. 2020).

I therefore find that the neotype designation of Mey (2020) is in violation of Article 75.1 and 75.3.4 of the Code, as it cannot be assumed, and has not been demonstrated, that no name-bearing types exist. Furthermore, I find the neotype designation to be in violation of Article 75.3.4 as Mey (2020) does not outline any "steps that had been taken to trace" any other syntypes, for instance those potentially sent back to L. Jenyns (see above). As the London syntype was never lost, Article 75.8 does not come into effect; however, if additional specimens are found, for instance at the Museum of Zoology, Cambridge, this Article may also become relevant.

CAN THE LONDON SYNTYPE BE IDENTIFIED?

As neither Najer et al. (2020) nor Mey (2020) included any text description, photo, or illustration of the London syntype, these publications cannot be used to ascertain whether this specimen can be identified today. However, the photo of the London syntype provided by the NHML homepage does not appear to be destroyed, distorted, or otherwise impossible to identify, given adequate study and comparison with other specimens. *Philopterus* specimens are relatively common in museums across the world; the NHML alone hosts over 3000 slides with *Philopterus*, many of which contain more than one specimen. Most of this material is undescribed, and many of the described species are presently unidentifiable.

Systematically comparing the London syntype with all other species of *Philopterus* at the NHML and other collections would be time-consuming, but there is no published evidence that suggest it would be impossible. Moreover, not all slides would need to be compared. For instance, as Najer et al. (2020) stated that the London syntype does not have the row of pronotal setae found in the Brno species, all species bearing these setae can be excluded from the comparisons. It is also evident from the digital photo of the London syntype that it is probably morphologically different from the group of *Philopterus* that is normally found on crows and allies (Corvidae; Price & Hellenthal 1998) and the group that parasitizes swallows (Hirundinidae; Gustafsson et al. 2022). As more species of *Philopterus* are described and redescribed, and the morphological variation within this genus becomes better known, other groups of *Philopterus* may also be possible to exclude from comparisons. Moreover, all *Philopterus* species that do not plausibly occur in the UKs or Europe may be excluded. No type locality of *Ph. reguli* was given by Denny (1842), but as his aim was to treat the species found in the UK, the specimens of *Ph. reguli* he examined are likely from this re-

gion, even if the host association is incorrect. That would limit the number of taxonomically relevant comparisons to a few dozen. This may have its own taxonomical consequences, especially if the London syntype is found to be conspecific with another described species.

It is worth pointing out that a substantial amount of the European species of *Philopterus* are formally described but largely unidentifiable without comparison with type specimens. This is due to the unfortunate tradition in European louse taxonomy to consider Fahrenholz's rule to be strictly applied to louse evolution, and thus every host species having its own louse species (Gustafsson & Najer 2022). This applies not least to the many species described by Jadwiga Złotorzycka, which are often only known from a short, uninformative text, some measurements, and outline drawings of some morphological characters, with no or little detail. The difficulties in identifying the London syntype may thus be more due to the poor taxonomic practices of, for example, Złotorzycka, than with the state of the London syntype itself.

In my opinion, it has not been shown that the London syntype is unidentifiable. If it is accepted that this specimen is a syntype, as I provisionally do here, this would mean that the neotype designation of Mey (2020) is in violation of Article 75.5 of the Code, which allows for neotype designation only when the name-bearing type is judged to be unidentifiable. This has, in my opinion, not been shown either by Najer et al. (2020) or Mey (2020), although a reexamination of the London syntype may very well show that this is correct.

CAN "THE FIGURE 4 SPECIMEN" BE IDENTIFIED TODAY?

Quite separate from the possibility of identification of the London syntype is the identification of the specimen illustrated in Denny (1842; plate VI, fig. 4; hereafter: "the Figure 4 specimen"). This is particularly important since Article 75.3.5 states that in order to be validly designated, a neotype must be shown to be "consistent with what is known of the former name-bearing type from the original description and from other sources". If it is assumed that the London syntype is not a syntype, but a contamination, mix-up or other error, then the neotype needs to be consistent with what is known from the only other source of data we have, Denny's original description and illustration. Notably, "other sources" correspond only to sources about the original name-bearing types, not about the species as such, or the prevailing understanding of the species.

An analysis of the Figure 4 specimen is necessary, because if it is found that the neotype designation of Mey (2020) is invalid, and it is accepted that the London syntype either is not a genuine syntype or does not correspond to the taxon *Philopterus reguli* as presently understood, it is possible to select the specimen on which Figure 4 is based as the lectotype of *Ph. reguli*, following Article 74.4. This Article also explicitly states that "the fact that the specimen no longer exists or cannot be traced does not of itself invalidate the designation". This means that it is possible to stabilize the nomenclature of *Ph. reguli* by reference to the only specimen that can unequivocally be stated to have represented this species at the time of the publication of Denny's monograph.

As stated above, Denny's original description and illustration are insufficient to identify *Philopterus reguli*. It could be argued that nothing in the description can be used to definitely identify this species even to the genus level, as louse genera are understood today. Similarly, Denny's original drawing could be virtually any species of *Philopterus*; more than that, it could show virtually any species in the *Philopterus*-complex and is not clearly different from representatives of some other genera that are more distantly related. Two characters are particularly noteworthy.

THE PRONOTAL SETAE

As noted above, the Brno species and the Halle neotype both have a row of setae on the posterior margin of the pronotum, called the *pronotal submarginal setae* or *psms sensu* Mey (1994). These setae are indicative of a small group of species within *Philopterus*, which Złotorzycka & Lucińska (1976: 286) termed the "*reguli* species group". The limits of this group have varied (Złotorzycka & Lucińska 1976; Mey 1983, 1988, 2020; Najer et al. 2020), but both Najer et al. (2020) and Mey (2020) agreed that the Brno species should belong to this group.

The chaetotaxy of *Philopterus reguli* is ignored almost completely in Denny's description, and only the setae of the pterothorax (as "metathorax") are mentioned: "posterior margin ciliated with stiff hairs" (Denny 1842: 91). In Figure 4, the pteronotal setae are illustrated, but the pronotal setae are not. The pronotal and pteronotal setae appear to be of roughly the same length and thickness in both the illustrations of Najer et al. (2020) and Mey (2020). While single, more lateral setae may have been overlooked by Denny, it seems likely that he would have been able to observe rows of setae on both segments and illustrated both sets. At the very least, no argument against this hypothesis has been published.

However, the lack of pronotal setae in the Figure 4 specimen should not automatically be interpreted as a difference between this specimen and the Brno species. Pronotal setae appear to be absent in all species illustrated by Denny. Notably, this includes not only species in which the pronotal setae are even longer and stouter than those of *Ph. reguli*, such as "*Goniocotes hologaster*" (Nitzsch, 1818) [= *Goniocotes gallinae* (De Geer, 1778)] (Denny 1842: plate XIII, fig. 4), but even another species

placed in the *reguli* species-group, *Philopterus pallecens* Denny, 1842 (ibid*.,* plate I, fig. 8). It would appear that for whatever reason Denny did not see any pronotal setae on any of his specimens. Possibly, this was due to the mounting method that may have damaged pronotal setae, or the rudimentary microscopy technology of the time. The real reason will never be known.

Thus, presence or absence of pronotal submarginal setae in the illustration of the Figure 4 specimen may not be significant for establishing its identity, nor to establish the identity of *Philopterus reguli*. However, the apparent lack of these setae in Denny's illustration remains a character that any neotype would need to consistent with in order to be validly designated.

THE TRABECULA OR CONI

All members of the *Philopterus*-complex have trabeculae, which are almost always longer than the antennal scape (e.g., Mey 2004; Gustafsson et al. 2022). This is a defining character of the complex, as trabeculae are not known from any other group of lice. In the Brno species, Najer et al. (2020) illustrated the trabeculae as almost reaching the distal end of the pedicel (ibid., fig. 6c), whereas Mey (2020) illustrated them as reaching around half the length of the pedicel in his "neoparatypes" (ibid., fig. 6). In both illustrations, these structures are clearly illustrated as trabeculae, rather than coni (sensu Clay 1946). Although there are developmental and structural differences between these two structures, the most pertinent aspect for the present discussion is that coni are almost invariably simply triangular, whereas trabeculae have a narrowed proximal base, a swollen mid-section, and a tapering distal end. Especially in older illustrations, where the term "trabecula" is used for both structures, the overall shape may be helpful to determine what structure is actually illustrated.

This difference in shape is visible in some, but not all, of Denny's other illustrations. For instance, trabeculae are illustrated in their characteristic shape for species such as *Philopterus picae* Denny, 1842 (plate I, fig. 9) and *Philopterus communis* Denny, 1842 (plate 5, fig. 10). In illustrations of species today placed in *Philopterus*, the trabeculae seem to invariably be drawn as much longer than the scape, regardless of whether the narrowed proximal section is illustrated. In contrast, species belonging to other groups in which trabeculae are not found have either long or short structures drawn; for instance, *Philopterus* [= *Penenirmus*] *pari* Denny, 1842 (plate VI, fig. 6a). This reflects the fact that in some groups the coni will be as long as the trabeculae of the *Philopterus*-complex but shaped differently and of a different developmental origin. In short, the generic identity of Denny's illustrated specimens cannot be assumed based on the trabeculae or coni when these are longer than the scape, unless they have the characteristic shape of trabeculae, but if they are at most as long as the scape, they are likely coni rather than trabeculae.

This is notable as in the detailed drawing of the antenna of the Figure 4 specimen (Denny 1842; plate VI, fig. 4a), the trabecula is entirely absent. This is not the case with any other *Philopterus* species illustrated by Denny; the illustration of *Ph. pallescens* Denny, 1842 (plate I, fig. 8a) appears to be an exception, but the illustrated specimen seems to be a nymph, and trabeculae may be significantly smaller in nymphs than in adults in *Philopterus* (Mey 1994). However, coni are not illustrated for in several illustrations of species that are not in the *Philopterus*-complex. Moreover, no trabeculae are visible in the full-body illustration of the Figure 4 specimen either (*ibid.,* plate VI, fig. 4), whereas these are clearly illustrated in all other species of *Philopterus*. In the text description, Denny (1842) stated that the trabeculae of *Ph. reguli* are "small".

The obvious conclusion to this observation is that the Figure 4 specimen is also not conspecific, or even congeneric, with the Brno species or the Halle neotype. Moreover, as Najer et al. (2020) examined the London syntype and considered it to belong to *Philopterus*, it must also have trabeculae, and thus not be congeneric with the illustrated specimen. The trabeculae are visible in the photo of the London syntype provided by the NHML homepage.

THE IDENTITY OF FIGURE 4

The variation of two morphological characters across the specimens and species discussed here is summarized in Table 2. Based on this data, it appears that the identity of the Figure 4 specimen is at least consistent with the text description, but is not consistent with either the London syntype, the Brno species, or the Halle neotype. Potentially, as many as three species are involved: a species with small trabeculae (= coni?) and possibly no *psms* (Figure 4 specimen and also the text description), a species with large trabeculae and no *psms* (London syntype), and a species with large trabeculae and *psms* (Brno species and Halle neotype). At the very least, it cannot be excluded that the Figure 4 specimen represents a different species than the Brno species, regardless of the status of the London syntype.

If the above arguments are correct, the (presumably now lost) Figure 4 specimen is also not conspecific with *Philopterus reguli* as we currently understand the taxon, and should not be designated a lectotype, if current prevailing usage is to be maintained. That would mean that if prevailing usage of *Ph. reguli* is to be maintained, a neotype is needed, as neither of the two syntypes that we have any information about are conspecific with the Brno species.

Table 2. Summary of the morphological characters relevant for identifying the various specimens discussed here, and their distribution across various illustrations and descriptions. Data for the London syntype is taken from Najer et al. (2020) and the photo of the specimen on the NHML homepage.

character	original description (Denny 1842)	Figure 4 specimen (Denny, 1842)	London syntype	Brno species (Najer et al. 2020)	Halle neotype (Mey 2020)
Pronotal submarginal setae	not mentioned	not illustrated, may be absent	absent	present	present
Trabeculae	"small"	not illustrated	large	large	large

This close analysis of the Figure 4 specimen implies that regardless of the status of the London syntype, Denny's original type series appears to have included at least one straggler, which unfortunately appears to be the one specimen he illustrated in Plate VI, fig. 4. Possibly, the Figure 4 specimen is the one Denny obtained first, from L. Jenyns, but this is presently impossible to establish, unless the Jenyns collection of lice is still extant and includes this specimen.

It is difficult to establish from Denny's illustration what the Figure 4 specimen may have been, if it is not conspecific with the Brno species. Overall, it appears smaller and slenderer than most other *Philopterus* species illustrated by Denny, and more slender than *Ph. gustafssoni* as illustrated by Najer et al. (2020). However, as the specimen is drawn from a card-mounted specimen rather than a slide-mounted specimen, these differences may be illusory. Other aspects of the illustration, such as the apparently medianly divided tergopleurite IX+X, may be erroneous; this tergopleurite is medianly continuous in all *Philopterus*-complex genera (e.g., Mey 2004; Najer et al. 2020; Gustafsson et al. 2022). In general, there are so many aberrant aspects of this illustration that any genus-level identification will require intentionally ignoring some clearly illustrated characters while accepting others. It is therefore best to consider the Figure 4 specimen unidentifiable to genus level, and possibly either fanciful or chimeric or based on an aberrant individual.

CONSERVATION OF PREVAILING USAGE

Mey (2020) does not argue for the need for a neotype, and the synonymization of *Ph. gustafssoni* with *Ph. reguli*, out of idleness or spite. Instead, his actions go to the heart of what the International Rules of Zoological Nomenclature are about: stability and predictability of usage of names for animals. Article 75.6 of the Code allows a researcher to request that the Commission set aside any name-bearing type if it is found not to be "in taxonomic accord with the prevailing usage of names and stability and universality is threatened thereby." Mey (2020: 160) explicitly established his neotypes "in the interest of the stability of this taxon" and mentioned that the Commission may "have to be called upon to take a definitive decision if the proposal meets with any well-founded resistance". It is difficult to disagree with Mey that the species normally found on *Regulus regulus* should have the name that has been assigned to it throughout the last 180 years, even if by capricious fate the specimens to which this name was originally attached are now known to represent a different species, which may not be identifiable. Regardless of anything else, Mey's goal here is laudable, and should perhaps be emulated more widely to secure nomenclatural stability among poorly identifiable species of lice.

The case for stability would be that the *Philopterus* species naturally occurring on *R. regulus* in Europe has been assumed to be *Ph. reguli* since Denny (1842) first described the species. Both Najer et al. (2020) and Mey (2020) listed some instances where this name has been applied to the species of *Philopterus* living on *R. regulus* and *R. ignicapilla*, but a casual search revealed many more; these are listed in Table 3, but this list may also not be exhaustive. In total, at least 30 publications over the last 180 years have used the name *Ph. reguli* for the species of *Philopterus* that occurs naturally on *R. regulus* and *R. ignicapilla*. In contrast, the name *Ph. gustafssoni* has so far only been used by members of the same research team as Najer et al. (2020) (Table 3).

If a request was put to the Commission to set aside any name-bearing types of *Ph. reguli* and recognize a neotype, this list of usages may be used to establish prevailing usage in favour of the petition. In general, more published usages of a name would suggest that stability of nomenclature would be disrupted if action is not taken to designate a neotype. However, it should be noted that the Commission does not operate on a principle of precedence, and each case is judged on its own merits. There is therefore no "magic number' of usages that are needed to establish prevailing usage. Moreover, it is ultimately up to the louse research community which name will be used, as the Commission has no enforcing capabilities if researchers are dissatisfied with their ruling.

COLLECTION HISTORY OF *PH. REGULI*

The first publications that report specimens of *Ph. reguli* other than the Denny specimens were Balát (1958) and

Table 3 (continued next page). Summary of published uses of the name *Docophorus/Philopterus/Docophorulus reguli* (Denny, 1842) or *Philopterus gustafssoni* Najer et al. (2020) based on references provided by Najer et al. (2020) and Mey (2020), as well as some sources omitted by these authors; list is not necessarily complete. Two sources listed by Najer et al. (2020) were not seen: 1) Kravtsova (1998) is an unpublished PhD thesis; 2) Fedorenko (1987) is a volume in a series on the fauna of Ukraine. Judging from other entries in Fedorenko (1987), there may be illustrations and a description of *Ph. reguli* in this publication similar to that of Złotorzycka (1977). These two publications are not listed below. Records of "*Philopterus subflavescens*" listed by Najer et al. (2020) are also not listed, as these records have no influence on the present case. For each publication, the following data is listed: 1) Information provided (i.e., what data about the lice of *Regulus regulus* is given?); 2) Data used (i.e., does this publication rely on examined specimens or is it a list of previous literature record etc.?); 3) Method of identification (i.e., were published sources or comparisons with type specimens used to establish identity of the lice? Note that only sources explicitly referring to the identity of *Ph. reguli/gustafssoni* are listed here, even if other sources were used to identify other species mentioned. If no method is explicitly given for *Ph. reguli/gustafssoni*, but Material and Methods include references that include descriptions of *Ph. reguli/gustafssoni*, these are listed here under the assumption that this is the method used); 4) Problem with changing name? (i.e., would changing the name from *Ph. reguli* to *Ph. gustafssoni* have effects beyond just the name change, e.g., by disconnecting published data other than locality records from the published name?). If the only change necessitated by the taxonomic acts of Najer et al. (2020) is a change of name in a regional, national or taxonomic checklist, this is not here considered a problem. A problem, as defined here, only appears if a publication contains any amount of secondary data (e.g., descriptions, measurements, host associations, prevalence data, etc.). This includes e.g., morphological data, ecological data, or life-history data.

Source	Region	Information provided	Data used	Method of identification	Problem with changing name?
Philopterus reguli					
Denny (1842)	UK	original description and illustration	specimens	original description	yes
Gervais (1844)	–	listed in global list of lice	description	Denny (1842)	no
Gray (1852)	UK	Included in list of specimens obtained	–	Denny (1842)	no
Giebel (1874)	–	included in a list of species the author did not examine	–	Denny (1842)	no
Piaget (1880)	–	listed in global list of lice	–	Denny (1842)	no
Harrison (1916)	–	listed in global checklist of lice	literature record	–	no
Thompson (1937)	–	included in list of specimens	london syntype?	–	no
Séguy (1944)	France	listed in list of species presumably occurring in France	–	–	no
Hopkins & Clay (1952)	–	listed in global checklist of lice	london syntype?	specimen	no
Negru (1958)	Romania	national records; measurements; new host record	specimens	Denny (1842)?	yes
Balát (1958)	Bulgaria	national records	specimens	none stated	no
Ash (1960)	Sweden	national records; prevalence data	specimens	none stated	yes
Bechet (1961)	Romania	national records	specimens	none stated	no
Złotorzycka (1964b)	Poland	redescription and illustration	specimens	none stated	yes
Rékási (1973)	Hungary	national records	specimens	none stated	no
Eichler & Hackman (1973)	Finland	listed in national checklist	specimens	none stated, possibly Złotorzycka (1964b)	no
Złotorzycka & Lucińska (1976)	Poland	redescription and illustration	specimens	none stated	yes
Balát (1977)	Czechoslovakia	listed in national checklist	specimens	none stated	no
Złotorzycka (1977)	Poland	redescription and illustration	specimens	none stated	yes
Rékási (1993)	Hungary	listed in national checklist	literature record	none stated	No

Table 3 (continued).

Source	Region	Information provided	Data used	Method of identification	Problem with changing name?
Hackman (1994)	Finland	listed in national checklist	literature record	previous record accepted	No
Mey (2003)	Germany	listed in national checklist	literature record	none stated	No
Price et al. (2003)	–	listed in global checklist	literature record	–	No
Adam & Sandor (2004)	Romania	national records	specimens	presumably Złotorzycka (1977)	No
Palma & Jensen (2005)	Faroe Islands	listed in regional checklist	specimens	none stated	No
Martín Mateo (2006)	Spain	listed in national checklist	literature record?	none stated	No
Ilieva (2009)	Bulgaria	listed in national checklist	literature record	previous record accepted	No
Vas et al. (2012)	Hungary	listed in national checklist	literature record	previous record accepted	No
Dik et al. (2017)	Turkey	national records	specimens	Złotorzycka (1964b)	No
Rékási et al. (2018)	Romania	listed in regional checklist	literature record	previous record accepted	No
Malysheva & Tolstenkov (2018)	Russia	regional and national record	specimens	none explicitly stated, possibly Fedorenko (1987)	No
Gustafsson et al. (2019b)	Sweden	listed in national checklist	literature record	previous record accepted	No
Philopterus gustafssoni					
Najer et al. (2020)		redescription	specimens	specimens	Already changed
Najer et al. (2021)	Azores, Czechia	phylogenetic data	specimens	Najer et al. (2020)	Already changed
Mey (2020)		redescription	specimens	Specimens; Najer et al. (2020)	yes
Oslejskova et al. (2020)	Azores	regional records; prevlence data	specimens	Najer et al. (2020)	already changed
Oslejskova et al. (2021)	Slovakia	listed in national checklist	specimens	None stated; presumably Najer et al. (2020)	Already changed

Negru (1958). Balát (1958) collected nymphs and eggs from the type host of *Ph. reguli*, whereas Negru (1958) collected both adults and nymphs from at least two host birds, both of which were the non-type host *R. ignicapilla*. After that, Ash (1960) collected a small number of specimens from the type host in Sweden, and Bechet (1961) reported an unknown number of specimens from the type host from Romania. None of these authors included any description or illustration of their specimens, nor any indication as to how their specimens were identified.

For all these publications, the only available illustrations and descriptions were those of Denny (1842), and the only known specimens were those allegedly at the NHML (Hopkins & Clay 1952). As none of these authors indicated that they examined the London syntype or any other specimen at the NHML, and it is clear from Denny's illustration and description that his species is not conspecific with the species normally found on *R. regulus* and *R. ignicapilla*, it must be concluded that these early records were identified based on host associations and a mistaken conflation of type host and natural host. This is particularly obvious in the case of Balát (1958), as he only collected nymphs, and Denny (1842) only described and illustrated the adult.

Złotorzycka (1964b) made the first attempt to redescribe *Ph. reguli* based on specimens she had obtained in Poland. Złotorzycka (1977) and Złotorzycka & Lucińska

(1976) also redescribed *Ph. reguli*, and these descriptions can be treated together. In the 1964b description, only the dorsal anterior plate is illustrated (Złotorzycka 1964b: fig. 5i) and the text description is short and useless for identification even to genus level. Złotorzycka & Lucińska (1976) had access to more specimens, which resulted in a more thorough attempt to illustrate and describe the species, but the lack of detail still makes it largely impossible to identify other specimens definitely from this account. Nevertheless, the 1976 illustrations are largely congruent with the more detailed illustrations of Najer et al. (2020) and Mey (2020). The 1977 account largely reuses the same illustrations as the 1976 account, but adds illustrations of the trabecula, parts of the mouthparts, and some of the tergopleurites. The text, in the form of a dichotomous key, is more detailed than previous accounts. Both Najer et al. (2020) and Mey (2020) agreed that the species illustrated in these three publications, and the specimens Złotorzycka used for those illustrations, are conspecific with the Brno species. Najer et al. (2020) examined most of these specimens in person, and there seem to be no reason to doubt this judgement.

Fedorenko (1987) may also have illustrated and redescribed *Ph. reguli*, but I have not seen this publication, and cannot judge whether this publication is useful. Based on other drawings by Fedorenko, any potential redescription of *Ph. reguli* in this book may be similar to that of Złotorzycka (1977).

Starting in 1964, it is thus theoretically possible to identify a species identified as *Philopterus reguli* without reference to Denny's illustrations or description. However, it is clear that Złotorzycka did not examine the London syntype, nor examine the published description and illustration well. For instance, Złotorzycka (1977) illustrated a long, typically shaped trabecula for *Ph. reguli*, which (as discussed above) are explicitly stated to be small in this species by Denny (1842). These trabeculae are also visible in the head outlines published by Złotorzycka & Lucińska (1976) and Złotorzycka (1977). Złotorzycka's illustrations must thus be assumed to be based on specimens she had identified by host-association, not by morphology. Here, if not earlier, the idea that any *Philopterus* specimens found on *R. regulus* must be *Ph. reguli* creeps into the usage of this name, thus establishing the pattern of misidentification that eventually led to the disagreement between Najer et al. (2020) and Mey (2020).

Three other publications during the 1970s are based on collected specimens (Rékási 1973; Eichler & Hackman 1973; Balát 1977). Of these, Eichler & Hackman (1973) and Balát (1977) merely list species present in previous collections (P. Krüger's and K. Pfleger's, respectively) and provide no data on how many specimens are present, the age and sex distribution of these, and how they were identified. Eichler & Hackman (1973) mistakenly refer to the author of *Docophorulus* [= *Philopterus*] *reguli* as "Złotorzycka 1964[b]". Rékási (1973) stated that he found one adult and three nymphs on a single host, and that this was a new record for Hungary, but did not state how these specimens were identified.

Two subsequent uses of the name *Ph. reguli* from Hungary (Rékási 1993; Vas et al. 2012) are updates of Rékási's (1973) checklist, which also do not contain any data on how these specimens were identified and appear to mainly refer back to the original record by Rékási (1973). Similarly, the usages of Hackman (1994), Mey (2003), Ilieva (2009), Rékási et al. (2018), and Gustafsson et al. (2019) are merely inclusions in national checklists that accept previous literature records, and do not attempt to detail how these previous records were identified. The usage by Martín Mateo (2006) also appears to fall into this category. Palma & Jensen (2005) evidently studied novel specimens purportedly of *Ph. reguli*, but did not detail in their checklist how many specimens were examined, nor how specimens were identified.

The next records that include actual specimens purported to be *Ph. reguli* are Adam & Sandor (2004; Romania), Dik et al. (2017; Turkey), and Malysheva & Tolstenkov (2018; Kaliningrad exclave of Russia). None of these publications are explicit in how the specimens were identified, but all cite sources that include illustrations and descriptions of *Ph. reguli sensu* Złotorzycka (1964b). It may thus be safe to assume that the specimens reported in these publications, as well as those by, for example, Palma & Jensen (2005) and Martín Mateo (2006), also represent the Brno species; however, this needs to be verified.

DATA PROVIDED

It is clear from this brief overview of the published record of *Philopterus reguli* that almost all data provided are just new locality (or national) records. *Philopterus reguli* is listed in national checklists for Bulgaria, "Czechoslovakia", Finland, Hungary, Romania, and Sweden, and for regional checklists of the Danube delta, the Faroe Islands, and the Community of Madrid (references in Table 3). In some of these cases, no detailed collection data was provided in the checklists or their sources, and inclusion of *Ph. reguli* in national or regional checklists is thus sometimes asserted rather than demonstrated. Almost invariably, no specific specimen slides, with deposition data, are included in the checklists or their primary sources.

Apart from geographical distribution, the only additional data given by the authors listed in Table 3 is the following: Negru (1958) added some measurements, noted a co-occurrence of *Ph. reguli* and *Ricinus frenatus* (Burmeister, 1838) on the same host, and added *R. ignicapilla* as a host species; Ash (1960) added some prevalence data; Złotorzycka (1964b, 1977), Złotorzycka & Lucińska (1976) and possibly Fedorenko (1987) added illustrations and redescriptions, but these are not of the

same species as *Ph. reguli* as described by Denny (1842). Beyond that, 180 years of research has not added anything to our knowledge of *Philopterus reguli*, and most of the data we have applies to a different species than *Ph. reguli sensu* Denny (1842).

In contrast, under the name "*Philopterus gustafssoni*", the Brno species has been provided with a complete description (Najer et al. 2020), many illustrations and photos (Najer et al. 2020; Mey 2020), new regional records (Oslejskova et al. 2020, 2021), genetic data (Najer et al. 2020, 2021), prevalence data (Oslejskova et al. 2020), and new host associations (Najer et al. 2020). It is fair to say that the majority of the data we have on the Brno species, whatever it is named, has either been published under the name *Ph. gustafssoni*, or could easily be redirected to this name without problem.

The question becomes: what is the disruption of stability if Denny's species is considered a *nomen dubium* that cannot be identified until any other potential extant syntype specimens are rediscovered, and the name *Ph. gustafssoni* is used for the Brno species? This question has no clear answer. However, there is no secondary literature on the Brno species (e.g., ecology, life-history, phylogenetics, behaviour) that would be easily overlooked by non-taxonomists if there was a change in name. The species is not used as a model organism, and it appears to be comparatively rare, given the few specimen-based records that have been published. Finally, both Balát (1977) and Oslejskova et al. (2021) published checklists of the "Czechoslovakian" louse fauna. Both checklists include the Brno species, but different names are used for it. This suggests that for most of the known uses of *Ph. reguli*, there will be no problem substituting one name for the other.

PUTTING THE CART BEFORE THE HORSE

It is clear that the present conundrum is the direct result of a conflating of the concepts of type host and natural host, and an overreliance on extrinsic characters such as host associations rather than intrinsic characters such as morphology. Any of the many researchers who have either worked at the NHML, visited this museum, borrowed specimens from this museum, or who has otherwise worked with *Philopterus* could at any time have noticed that neither the London syntype nor the Figure 4 specimen is conspecific with the species of *Philopterus* normally found on *R. regulus*. Instead, the assumption of host specificity and taxonomic laziness perpetuated a mistake that could have continued for another 180 years if Najer et al. (2020) had not decided to examine the London syntype and discovered that there was a problem with its identity.

A large part of the blame for this problem must of course be laid at the feet of Jadwiga Złotorzycka, who redescribed and illustrated *Ph. reguli* three times in less than two decades without ever consulting type specimens or, apparently, the original description and illustration. Instead, her adherence to Fahrenholz's rule and the Eichlerian methodology (*sensu* Gustafsson & Najer 2022) made her assume that any and all specimens of *Philopterus* collected from *R. regulus* must be *Ph. reguli*. That is, because the *type host* of *Ph. reguli* is *R. regulus*, she assumed that the *natural host* of *Ph. reguli* is *R. regulus*. The only way to ascertain whether a type host is also the natural host is to compare specimens from multiple collections from that host with the holotype (or equivalent). This was not done, or it would have been discovered already in the 1960s that the London syntype was not conspecific with the species whose natural host is *R. regulus*.

Any subsequent researchers who identified their specimens – implicitly or explicitly – based on the redescriptions of *Ph. reguli* by Złotorzycka may be partially forgiven for acting in good faith, assuming that Złotorzycka's description was accurate. If the Brno species is the only *Philopterus* species naturally occurring on *R. regulus* in Europe, and that species is the one illustrated by Złotorzycka (1964b, 1977), then fresh collections that correspond to Złotorzycka's illustrations would reinforce the impression that her illustrations depict the correct species.

However, the fact that multiple researchers have drawn the wrong conclusion does not automatically mean that that conclusion should be retroactively validated when this is revealed. The name "*Philopterus reguli* Denny, 1842" does not refer to any and all specimens of *Philopterus* that are found on the type host of this species. Instead, in the absence of a validly designated neotype, the name *Ph. reguli* applies strictly, precisely, and exclusively to the specimen(s) that can reasonably be said to have been considered type specimens by Denny at the time of the publication of his monograph, as well as any specimens considered conspecific with these based on intrinsic characters. To put it more generally, specific names do not apply to hypothetical concepts of what a researcher believes they are dealing with, nor to hypothetical concepts of what they believe another researcher was dealing with.

This is precisely what makes judgements on whether designating a neotype for *Ph. reguli* that corresponds with the Brno species so difficult. Rewarding impreciseness and laziness for the sake of formality and expedience is, in principle, deleterious to the study of chewing lice. There is of course appeal in retaining the name *Ph. reguli* to the species of *Philopterus* that occurs on *Regulus regulus*, especially as that has been assumed to be the case for 180 years. However, in the overview of the history of the use of this name above (and in Table 3), I cannot see that changing the names would cause such a catastrophic upheaval in louse taxonomy, that it is worth

doing. In almost all cases, the name is used as just a name in a list of species collected in or known from a region, with almost no significant extra information added to the original description in almost 180 years, until Najer et al. (2020) added more data under a different name.

In short, I do not agree with Mey (2020) that "stability and universality is threatened" to any significant degree by following the taxonomic recommendations published by Najer et al. (2020). Naturally, other researchers may evaluate the published data differently, and more opinions on this topic would be welcomed, especially if, as suggested by Mey (2020), the Commission needs to be called upon to settle this matter.

GOING FORWARD

There is no doubt that additional cases similar to this one may be discovered in the future. As a general rule of thumb, any louse publication that includes new taxa where there are not clear, complete illustrations, detailed descriptions, and comparisons with other taxa in the same group may be suspected of harboring parallel cases to *Philopterus reguli*. This is not least the case with older authors such as Burmeister, Denny, Giebel, Piaget, Kellogg, Mjöberg, Uchida, and others, but also with authors who habitually omitted meaningful morphological data from their descriptions and assumed species limits based on host associations. Apart from Eichler and Złotorzycka, this may include any author contemporary with them who did not completely illustrate or describe their species. More work clearly needs to be done in the spirit of the four publications by Clay & Hopkins (1950, 1951, 1954, 1960), who systematically went through older publications and sorted out species identity and limits, and erected neotypes to stabilize the nomenclature of the louse species described between 1758 and 1818.

As such, the present case may be seen as a "community precedent", to examine how louse researchers should approach cases of mistaken identity in the future. It should be clear that the kind of detailed analysis that is necessary to sort out some of these issues may be substantial, but much of this can be avoided if decisions on taxonomy, typification, and identity are sorted out carefully *before* publication rather than after.

MISTAKES WERE MADE

There is no doubt that Najer et al. (2020) made several substantial mistakes in their study, which caused more subsequent problems than they solved. For instance, the London syntype was not described, illustrated, or photographed, which would have shown unequivocally that it is not conspecific with the Brno species. They mistakenly called the London syntype a holotype, when Denny used no such term, and Denny had access to multiple specimens. Najer et al. (2020) could have designated either the London syntype or the Figure 4 specimen as the lectotype, thus simplifying the case considerably as the identity of *Philopterus reguli* would then have been unequivocal. They could also have designated any of the specimens they examined of the Brno species as the neotype of *Ph. reguli* and recommended that any previous name-bearing types were set aside by request to the Commission.

Similarly, Mey (2020) was too hasty to assign a neotype without analyzing the case adequately. This has caused problems with the neotype designation that invalidates it. In particular, the neotype designation violates the following Articles of the Code:

75.3.4 – a valid neotype designation needs to include "the author's reasons for believing the name-bearing type specimen(s) […] to be lost or destroyed, and the steps that had been taken to trace it or them". This was not included by Mey (2020), who merely asserted that "[a] part from the doubtful individual mentioned above [i.e., the London syntype], nothing of the original material of *Philopterus reguli* Denny has apparently been preserved". This is not known; moreover, it has not been established that the London syntype is not a genuine syntype. No attempts to trace other specimens were detailed by ether Najer et al. (2020) or Mey (2020); however, I could easily find a potential location of additional syntype specimens in the Jenyns collection, which may still be extant at the Museum of Zoology, Cambridge, UK (see above).

75.3.5 – a valid neotype designation needs to include "evidence that the neotype is consistent with what is known of the former name-bearing type from the original description and from other sources". This is clearly not the case. Not only is the Halle neotype morphologically different from the London syntype, but even if the syntype status of this specimen is dubious, the Halle neotype is also different from the Figure 4 specimen (Table 2), which is the only specimen we can tell for certain is (or was) a syntype. Mey (2020) stated that "Denny's copper engraving […] is at least consistent with the habitus of *P. reguli* as we know it today", but this is not true, as the Figure 4 specimen is drawn without *pronotal submarginal setae* and without trabeculae, both of which are clearly present in both the Brno species and the Halle neotype.

75.3.6 – a valid neotype designation must come "as nearly as practicable from the original type locality […] and, where relevant, from the same […] host species as the original name-bearing type". This is clearly not the case. Denny's description does not include any locality data for any of the specimens of *Ph. reguli* he examined, but his monograph is on species of lice from Great Britain, and his correspondent L. Jenyns mainly collected specimens in the Cambridge area (Suarez Ferreira 2021). In contrast, the Halle neotype is from northern Germany.

While there seems to be little genetic variation among the Brno species collected from Czech Republic and the Azores, there is some variation (Najer et al. 2020, 2021); moreover, specimens from Great Britain have not been analyzed. It is therefore not established that the population of *Philopterus* that naturally occur on *R. regulus* in Great Britain is conspecific with that of the continent, although this is of course exceedingly likely.

These three aspects alone are sufficient to consider the neotype proposed by Mey (2020) invalid, regardless of the identity of the London syntype and the Figure 4 specimen, and regardless of issues of stability of nomenclature. Following Article 75.4, this means that if the louse community decide that a neotype of *Ph. reguli* is the best way to go forward, the choice of a neotype is not limited by Mey (2020), as his neotype was not validly designated in accordance with Article 75.3.

RECOMMENDATIONS

Following this discussion, I would like to recommend the following guidelines :

1. Do not conflate "type host" with "natural host". In essence, "type host" is a taxonomic concept which is more or less only relevant in taxonomic papers where issues of neotype selection are or may be concerned. In almost all cases when discussing, for example, behaviour, ecology, evolution, phylogenetics, or life history of lice, the term that should be used is "natural host", which is the only biologically relevant one.
2. Do not assume louse identity based on host associations, but consult published descriptions, illustrations, photos, or keys, or confer with other experts who may be able to identify specimens. Enough data has been published in the last few decades to show that lice may be generalists, that straggling and host-switching occurs, and that host associations may not be reliable (summarized by Gustafsson & Najer 2022). Fahrenholz's rule and the Eichlerian methodology are invalid methods for species identification and should be discarded in favour of examination of intrinsic characters of the lice themselves.
3. Be clear and explicit about how each species collected or examined was identified and be clear and explicit about when there is reason for doubt about the species identity. In faunal lists, the sources (keys, descriptions, illustrations, museum specimens) that have been consulted should ideally be listed individually for each genus or species, so that there is no mistake about the level of certainty in the identification. If no published accounts of a species are adequate for identification, specimens may be identified to genus level only. Alternatively, it may be stated that specimens are tentatively identified by host association, but that a revision of the group is necessary. Whenever possible, consult experts in identification if there are any doubts at all.
4. Do not publish accounts of, for example, phylogenetics, life-history, ecology, or behaviour of lice without detailing how these lice were identified. If they cannot be reliably identified, do not use species-level names but confine your study, analysis and discussion to taxonomic levels that can be identified (e.g., genus level).
5. Whenever there is doubt about the identity of an older name you come across, consider devoting some time to analyzing the matter in detail, and perhaps track down any remaining types, examine them, and revise the species (or group) so that future researchers may benefit from your observations. Taxonomy, including revisionary taxonomy, is easier than commonly perceived, and needs input from more people.
6. If doing taxonomic work, make sure your taxonomic decisions follow the Code, and do not create additional unnecessary work for future taxonomists. In particular, when dubious cases of identity are discovered, great care must be taken not to cause more problem than necessary. Describing new louse species from hosts that are type hosts of congeneric louse species must be approached very carefully, and if there is the slightest doubt about the identity, it may be better to clarify the identity of the older names before publishing new names.

THE NAME OF THE LOUSE ON *R. REGULUS*

So, which name should be used for the species of *Philopterus* that evidently lives on *Regulus regulus* and *Regulus ignicapilla* across much of the range of these species?

For a start, the name of this species cannot presently be said to be *Philopterus reguli*. Based on our current knowledge, it seems likely that the description and illustration of *Ph. reguli* published by Denny (1842) refers to the Figure 4 species, whereas the only known extant supposed syntype associated with this name is the London syntype. Neither of these species has been shown to be conspecific with the species that naturally occurs on *R. regulus* and *R. ignicapilla*, which is the Brno species. Moreover, regardless of the identity of these specimens, the Halle neotype was not validly designated, and thus the taxonomic acts of Mey (2020) do not imply that the name *Philopterus reguli* should henceforth be used for the Brno species.

Going forward, as things stand today, the name *Ph. gustafssoni* must be used for the Brno species, as this is the only name for this species for which a validly des-

ignated name-bearing type is unequivocally designated. At the same time, the name *Philopterus reguli* must for the present be considered a *nomen dubium* (i.e., "a name of unknown or doubtful application"; the Glossary of the Code), as neither of the known specimens associated with this name (the London syntype and the Figure 4 specimen) can unequivocally be considered conspecific with the Brno species.

However, as the arguments on stability of nomenclature can only be settled by the louse community as a whole, and has no clear, unambiguous solution beyond an application to the Commission, this may change if it is felt that a neotype needs to be validly designated to retain the usage of *Ph. reguli* for the Brno species. This would depend on whether the community considers that the change from *Ph. reguli* to *Ph. gustafssoni* for the Brno species would cause too much instability to be warranted. Personally, I am not presently convinced that that is the case, but this may change if better and more extensive arguments are put forward that those presented by Najer et al. (2020) and Mey (2020).

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