Barcode taxonomy at the genus level

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Abstract
DNA barcode sequencing has rapidly become one of the most powerful tools for biodiversity assessments. Beyond its original uses for the identification of animal species, including the discovery of cryptic diversity in difficult taxonomic groups, the growing public sequence datasets also offer opportunities for more wide-ranging applications. This contribution shows how barcode data can provide useful complementary information to assist taxonomic decision making at the genus level. An analysis of public barcode datasets for 10 diverse spider families, covering more than 3400 species and morphospecies, reveals numerous examples where sequence similarities either strongly support or convincingly refute recent controversial genus assignments. The following nomenclatorial changes are suggested based on a combined assessment of morphological evidence and the barcode analysis:

- Acantholycosa = Pardosa (syn. nov.);
- Piratula = Pirata (syn. nov.);
- Pulchelodromus, Philodromimus, Tibellomimus, Artanes, and Enargidromus = subgenera of Philodromus (stat. nov.);
- Cryptachaea riparia = Prasteatoda riparia (comb. nov.);
- Oblertidion = Heterotheridion (syn. nov.);
- Saaristoa = Aphileta (syn. nov.);
- Aphileta microtarsa = Euaira microtarsa (comb. conf.);
- Centromerita and Tallusia = Centromerus (syn. conf.);
- Obscuriphantes, Agnyphantes, and Acanthoneta = Poeciloneta (syn. nov.);
- Bolyphantes bipartitus = Poeciloneta bipartita (comb. nov.);
- Anguliphantes, Improphantes, Piniphantes, and Mansuphantes = Orymphantes (syn. nov.);
- Palliduphantes antroniensis = Orymphantes antroniensis (comb. nov.);
- Lepthyphantes nodifer = Orymphantes nodifer (comb. nov.);
- Hypositticus, Sittipub, Calositticus, Sittisax, Sittiflor, and Attulus = Sitticus (syn. nov.).

Key words: Araneae, DNA barcoding, cladistics, phylogenetic systematics.

Introduction
The large-scale determination of short, standardized, species-specific genetic sequences (“DNA barcoding”) has in recent years become one of the most versatile tools of biodiversity research, with applications ranging from biodiversity assessment by environmental DNA sequencing (e.g., Taberlet et al. 2012, Thomsen & Willerslev 2015, Goodwin et al. 2017) to ensuring the correct labelling of food products (e.g., Prosser & Hebert 2017, Raja et al. 2017, Willette et al. 2017, Hellberg et al. 2017). Several large barcode datasets have been assembled specifically for spiders (e.g., Astrin et al. 2016, Blagoev et al. 2013, 2016), and many more sequences are continually being deposited in the BOLD database of barcode sequences (Ratnasingham & Hebert 2007). Barcodes were originally introduced as a means to enable rapid identification of specimens at the species level (Barrett & Hebert 2005, Hebert et al. 2003), and they are particularly useful for identifying
cryptic species diversity (e.g., Fišer et al., 2018, Janzen et al. 2017, Ortiz & Francke 2016, Xu et al. 2015, Hamilton et al. 2011) and for identifying specimens in taxonomically difficult groups (e.g., Blagoev & Dondale 2014, Planas & Ribera 2015, Marusik et al. 2018, Mendoza & Francke 2017, Luong et al. 2016, Sim et al. 2014, Nadolny et al. 2016, Ballesteros & Hormiga 2018), including immature specimens of spiders, or matching males and females collected separately (e.g., Magalhães et al. 2017). However, species identification regularly fails for very recently diverged groups, possibly because of incomplete lineage sorting or as a result of hybrid introgression (e.g., Astrin et al. 2016, Spasojevic et al. 2016, Oxford & Bolzern 2018, and references therein), and it is also not suitable for elucidating relationships between widely diverged groups, where the much larger DNA datasets acquired by phylogenomic methods have recently enabled major advances (Wheeler et al., 2017, Hedin et al. 2018, Godwin et al. 2018, Kallal et al. 2018, Maddison et al. 2017, Hamilton et al. 2016, Garrision et al. 2016, Bond et al. 2014, Fernández et al. 2014). If barcodes fail at the lowest taxonomic level (separation of sibling species), as well as at the highest levels (identification of relationships between families), it is tempting to explore their potential for elucidating affinities at intermediate levels, specifically as a complementary source of data to validate or refute taxonomic decisions at the genus level (Coddington et al. 2016). For example, barcode information has recently been used to evaluate the controversial relationship between Micaria and Arboricaria (Gnaphosidae; Breitling 2017), and numerous analogous cases from various spider families might potentially benefit from a similar approach. This short note applies this idea to a few selected cases to determine the general potential and challenges of barcode taxonomy at the genus level. It uses a manual case-by-case approach, instead of a high-throughput automated pipeline like the one proposed by Porter & Hajibabaei (2018). The analysis does not aim for completeness, but rather focuses on particularly compelling or controversial examples (with an abundance of available data and unambiguous phylogenetic signal) that might help clarifying the underlying concepts and, hopefully, stimulate further data collection and analysis.

A number of formal taxonomic changes are suggested on the basis of the integrative analysis of the barcode data and previous morphological work. In each specific case, an attempt was made to minimize nomenclatural disruption by applying the stringent criteria proposed by Vences et al. (2013) for analogous cases. Importantly, no new names are introduced, and the vast majority of the proposed changes merely reconfirm earlier morphological results.

Materials and methods

Barcode sequences were downloaded in FASTA format using the public data portal of the BOLD database (www.boldsystems.org) in April 2018. All public records of Cytochrome Oxidase Subunit 1 5’ region barcodes (COI-5P) for specimens placed in the families Agelenidae, Araneidae, Gnaphosidae, Philodromiidae, Linyphiidae, Lycosidae, Salticidae, Tetragnathidae, Theridiidae, and Thomisidae were retrieved, covering 3419 species, including specimens identified only to genus level or using morphospecies codes, with an average of 17 sequences per species (Table 1). Sequences analysed using the DECIPHER package (Wright 2016) and custom-made scripts in R (R Core Team 2018). While plausibility checks were carried out for individual cases, taking into account photographic evidence provided in the BOLD database and zoogeographic patterns, no attempt was made at manually curating the barcode data by correcting obvious misidentifications. Instead, such misidentifications (where noticed) are highlighted in the discussion, and no nomenclatural changes are suggested for cases that are supported only by individual sequences for single species. Moreover, median pairwise interspecies barcode similarities were calculated using DECIPHER, which (when multiple sequences are available for each species involved) should be robust against a small number of misidentified specimens. These pairwise similarities were either directly examined, or visualized using multidimensional scaling using the MASS package (Venables & Ripley 2002) or by constructing neighbour joining trees using DECIPHER. Additional neighbour joining trees were reconstructed based on the distances between majority-rule consensus barcodes for each species, and maximum likelihood trees were reconstructed for subsets of the barcodes using phylogeny.fr (Dereeper et al. 2008) with default settings as described in Breitling (2017). None of the figures presented should be interpreted as a detailed phylogenetic hypothesis; the intention here is to visualize the barcode similarities between closely related groups at the genus level, rather than the exact evolutionary details of relationships within or between all genera – to elucidate the latter, additional sequences and, importantly, different tree reconstruction methods would be required. The trees and multidimensional scaling maps should be
considered merely as visual aids to explore the pairwise distance matrices, which underlie all discussions and taxonomic proposals presented in the text. Given the limited information content of the barcode data, the figures should not be over-interpreted; not all branches of the trees are equally well supported and consistent across analysis methods, and in particular the deeper relationships between distantly related groups are entirely unresolvable using this dataset. The two sets of neighbour-joining trees and multidimensional scaling results for each family, as well as the maximum likelihood trees for selected species groups, are available as electronic supplementary material (https://doi.org/10.13140/RG.2.2.22117.04324). The underlying distance matrices, barcode sequences and consensus sequences are available from the author upon request.

Table 1. Overview of available barcode information per family.

| Family         | No. of barcode sequences | No. of species |
|----------------|--------------------------|----------------|
| Agelenidae     | 1543                     | 315            |
| Araneidae      | 9196                     | 353            |
| Gnaphosidae    | 1414                     | 127            |
| Linyphiidae    | 16512                    | 810            |
| Lycosidae      | 8908                     | 314            |
| Philodromidae  | 2298                     | 69             |
| Salticidae     | 4299                     | 578            |
| Tetragnathidae | 4016                     | 128            |
| Theridiidae    | 6708                     | 460            |
| Thomisidae     | 3585                     | 265            |

Results and Discussion

Table 2 provides summary statistics for the median pairwise distances between barcodes of specimens within the same species, as well as between species with the same genus. It can be seen that, while there is some variation in the observed distances in different families, the values within families are very consistent, with narrow interquartile ranges. Table 3 shows details for the genetic distance between species in selected large genera, further illustrating the relatively narrow range of values observed. Exceptionally small distances are observed for species within a few genera of Lycosidae which have earlier been seen to contain a particularly large number of species pairs (or even species groups) with very small or even non-existent barcode gaps (e.g., Astrin et al. 2016, Nadolny et al. 2016). In most cases, the distances between members of the same genus are smaller than the distances to neighbouring genera. The subsequent analysis focuses on selected examples where this is clearly not the case and relates these to previous morphological assessments of phylogenetic relationships.

Table 2. Summary of median pairwise distance between specimens from the same species (intraspecies), and between species from the same genus (intragenus) in percent. Only species with at least 5 sequenced specimens, and genera with at least 5 sequenced species, are considered. The interquartile range is indicated in brackets, and the maximum and minimum values are highlighted.

| Family         | Median intraspecies distance | Median intragenus distance |
|----------------|-----------------------------|---------------------------|
| Agelenidae     | 0.4 (0.0–2.2), n=31         | 10.3 (9.0–11.7), n=17     |
| Araneidae      | 0.6 (0.2–1.3), n=132        | 11.4 (11.0–14.0), n=19    |
| Gnaphosidae    | 0.5 (0.2–1.0), n=57         | 10.2 (8.9–11.1), n=8      |
| Linyphiidae    | 0.5 (0.2–0.8), n=414        | 10.9 (9.6–12.9), n=47     |
| Lycosidae      | 0.5 (0.2–0.9), n=177        | 8.5 (7.0–9.2), n=12       |
| Philodromidae  | 0.8 (0.2–1.1), n=37         | 12.7 (11.7–14.2), n=4     |
| Salticidae     | 0.6 (0.2–1.2), n=117        | 10.6 (9.9–11.6), n=26     |
| Tetragnathidae | 1.2 (0.4–2.1), n=48         | 13.4 (12.0–14.5), n=8     |
| Theridiidae    | 0.4 (0.2–0.9), n=135        | 11.5 (9.9–12.7), n=15     |
| Thomisidae     | 0.8 (0.5–1.4), n=83         | 10.2 (9.7–11.0), n=11     |
Table 3. Median pairwise distance between species from the same genus. Only genera with at least 20 sequenced species are included. The interquartile range is indicated in brackets.

| Genus       | Family   | Median interspecies distance (%) | n  |
|-------------|----------|----------------------------------|----|
| Anoteropsis | Lycosidae| 4.8 (4.1-5.5)                    | 20 |
| Pardosa     | Lycosidae| 5.9 (5.2-7.1)                    | 101|
| Alopecesta  | Lycosidae| 7.3 (6.2-8.1)                    | 29 |
| Mecaphesa   | Thomisidae| 7.9 (6.5-9.1)                   | 26 |
| Spintharus  | Theridiidae| 8.1 (6.9-9.1)                  | 141|
| Xysticus    | Thomisidae| 10.2 (8.9-11.1)                  | 101|
| Myrmarchne  | Salticidae| 10.5 (9.2-12.6)                  | 26 |
| Pirenetega  | Agelenidae| 10.6 (9.6-11.4)                  | 29 |
| Walckenaeria| Linyphiidae| 10.8 (9.9-11.9)               | 44 |
| Habronattus | Salticidae| 10.9 (8.9-12.2)                  | 23 |
| Gnaphosa    | Gnaphosidae| 11.0 (8.5-12.5)                 | 21 |
| Argoipe     | Araneidae| 11.2 (9.9-12.3)                  | 44 |
| Hogna       | Lycosidae| 11.3 (10.2-12.1)                 | 26 |
| Philodromus | Philodromidae| 11.4 (9.9-13.2)               | 33 |
| Theridon    | Theridiidae| 11.5 (10.3-12.7)                | 44 |
| Anelosimus  | Theridiidae| 11.7 (9.9-13.6)                 | 38 |
| Eratigena   | Agelenidae| 11.7 (10.6-12.7)                | 14 |
| Scotinotylus| Linyphiidae| 11.9 (10.0-13.2)              | 21 |
| Draconarius | Agelenidae| 12.1 (11.0-13.3)                | 77 |
| Argyrode    | Theridiidae| 12.4 (11.3-13.5)                | 28 |
| Latrodectus | Theridiidae| 12.7 (11.1-14.8)               | 22 |
| Tegenaria   | Agelenidae| 12.9 (11.7-14.1)                | 23 |
| Agyneta     | Linyphiidae| 12.9 (11.4-14.3)                | 57 |
| Bathypthantes| Linyphiidae| 13.6 (12.0-14.7)                | 21 |
| Cyclosa     | Araneidae| 13.8 (11.9-15.1)                | 31 |
| Araneus     | Araneidae| 14.6 (13.4-15.7)                | 37 |
| Neriene     | Linyphiidae| 15.7 (14.5-17.2)               | 21 |
| Tetragnatha | Tetragnathidae| 16.3 (14.6-17.6)            | 50 |

Acantholycosa is a junior synonym of Pardosa. The wolf spider genus Acantholycosa Dahl, 1908, had been synonymized with Pardosa C. L Koch, 1847, by Wunderlich (1984), who pointed out that there are no reliable diagnostic characters distinguishing the two genera. This decision was, however, not followed by subsequent workers (e.g., Buchar & Thaler 1993, Kronestedt & Marusik 2002). The type species of Acantholycosa (A. norvegica sudetica) has not been barcoded yet, but barcodes are available for P. lignaria, one of three species included by Dahl 1908 in the original definition of Acantholycosa, as well as for the American A. solituda, which was formerly placed in Pardosa, but transferred to Acantholycosa by Kronestedt & Marusik (2002), thus reflecting the most recent understanding of the genus boundaries. The two barcoded Acantholycosa species are close to the type species of Pardosa, P. alacris, with a median pairwise distance of 4.4% and 5.9%, respectively, closer than the median distance between individual Pardosa species, which is already unusually low (Table 3). But, importantly, they are even more similar in their barcodes to members of the nigra and ferruginea species groups, which both Wunderlich (1984) and Kronestedt & Marusik (2002) had already highlighted as sharing important morphological diagnostic characters with Acantholycosa species, including a high number of ventral spines on the anterior tibia, a low thorax, and the position of the apical tooth on tarsal claw I. In neighbour-joining and maximum likelihood trees, the two Acantholycosa species are solidly embedded within a combined nigra/ferruginea group of
**Pardosa** (Figure 1). This excellent agreement of barcoding results and independent morphological analyses supports Wunderlich’s earlier conclusion that a removal of *Acantholycosa* from *Pardosa* would result in a seriously paraphyletic residual *Pardosa*, unless this morphologically and genetically very homogenous genus is split excessively. Wunderlich’s suggestion that this could be avoided by raising the current species groups of *Pardosa* to genus (or subgenus) rank seems impractical, as illustrated by the difficulty of distinguishing, e.g., members of the *nigra* and *ferruginea* species groups. This conclusion is not changed by the absence of the type species of *Acantholycosa* from the barcode dataset; even if *A. sudetica* would turn out to be placed outside *Pardosa* s. str., the drastic redelimitation of *Acantholycosa* that would be required to keep the genus monophyletic would destroy all practical usefulness of keeping the species in a separate genus. While the barcode analysis is not a comprehensive revision of the two genera, it does cover a representative selection of the Holarctic wolf spider diversity. It is therefore proposed that *Acantholycosa* is again considered a junior synonym of *Pardosa* (*syn. conf.*). This obviously raises some doubt about the status of other genera containing former members of *Acantholycosa* not represented by barcode data, i.e. *Mongolicosa*, *Sibiricosa*, and *Pyrenecosa*, all established by Marusik et al. (2004). However, none of these shows clear morphological affinities to either *Acantholycosa* s. str. or any of the species groups within *Pardosa* (Marusik et al. 2004), and it thus seems quite possible that they do indeed represent independent evolutionary lineages. Another genus containing former members of *Pardosa*, *Wadicosa* Zyuzin, 1985 (type species *W. fidelis*), is supported by barcode information as a potential sister group of *Pardosa* as defined here.

**Piratula** is a junior synonym of *Pirata*. The genus *Piratula* was erected by Roewer (1960) based on subtle differences in the eye arrangement. It was rejected by Dondale & Redner (1981) who argued that the type species of *Piratula* shared important derived characters of the pedipalp with the type species of *Pirata*, but resurrected by Omelko et al. (2011) on the grounds that it showed many differences in the male palps, as well as some differences in sternal patterns and leg spination in females, while also differing in overall size. Both genera are well represented in the barcoding dataset, including data on their respective type species, *Pirata piraticus* and *Piratula hygrophila*. The barcode sequences show quite clearly that a separation of the two genera is not tenable, not even at the level of subgenera (Figure 2). For instance, the type species of *Pirata* differs only by 3.4% from *Piratula canadensis*, and the type species of *Piratula* by 7.0% from *Pirata praedo*. This should be compared to median intrageneric distances of 7.3% between *Pirata piraticus* and *Pirata piscatorius*, 7.4% between *Piratula hygrophila* and *Piratula latitans*, or 10.9% between *Pirata piraticus* and *Pirata praedo*. Even the median distance between the two type species is only 9.1%, exactly
equal to the median of the pairwise distances between species within *Pirata*. The genetic data strongly support the conclusion that (a) *Pirata* s. lat. is a monophyletic group and (b) the two current genera *s. str.* are not. While some of the mix-up between the genera could be ascribed to lack of high-quality sequences (for several of the species only single barcodes are available), this is not the case for the specific examples discussed above, where each species is represented by at least a dozen sequences. It is therefore proposed to consider *Piratula* a junior synonym of *Pirata* (*syn. nov.*).

**Figure 2.** Extracts of (A) a multi-dimensional scaling plot and (B) neighbour-joining tree illustrating the close intermingling of members of *Pirata* and *Piratula* in terms of barcode distances.

**Tigrosa might be a junior synonym of Rabidosa.** An analogous situation seems to be present among the American lycosid genera *Tigrosa* Brady, 2012, and *Rabidosa* Roewer, 1960; again the barcodes show a considerable mixing of the two nominal genera (Figure 3). The type species of *Tigrosa* (*T. helluo*) is closer to *Rabidosa punctulata* (median pairwise distance 8.2%) than to any of the barcoded members of *Tigrosa* (*T. grandis* 9.0%, *T. aspersa* 9.2%, and *T. annexa* 10.3%), and each of these is considerably closer to the type species of *Rabidosa* (*R. rabida*; median pairwise distances between 7.6% and 8.0%). Moreover, both *Rabidosa* and *Tigrosa* show close barcode similarity to a number of *Geolycosa* species (in particular, *G. micanopy*, *G. pikei*, and possibly *G. vultuosa*), with a median pairwise distance of 10.1% (range 9.1%-12.1%), significantly smaller than the distance of each of these three species to other 12 barcoded members of *Geolycosa*: *G. micanopy* median 12.3%, minimum 10.1; *G. pikei* median 12.4, min. 10.0; *G. vultuosa* median 12.7%, min. 11.6). In neighbour-joining trees and multi-dimensional scaling maps of the barcode distances, the remaining *Geolycosa* species, which include the members of Wallace’s (1942) species groups 1–4, consequently form a compact and unrelated cluster, well separated from *Rabidosa*, *Tigrosa* and *G. micanopy* (Wallace’s species group 5), *G. pikei*, and *G. vultuosa*. This might indicate that *Tigrosa* is a junior synonym of a redelimited *Rabidosa*, which in that case should also include *G. micanopy*, *G. pikei*, and possibly *G. vultuosa*. The exact composition of this extended *Rabidosa* s. lat. will only be possible to determine following a comprehensive revision of the entire *Geolycosa/Hogna* complex in the widest sense, and no formal transfers or synonymies are proposed here. The results of the barcode analysis, however, strongly emphasize that genera largely based on differences colour patterns, behaviour or ecology are unlikely to be monophyletic in this group, and even genital affinities can be misleading in this morphologically rather conservative complex.

**Pulchellodromus is a subgenus of Philodromus.** The genus *Pulchellodromus* Wunderlich, 2012, was established for the *pulchellus* species group of *Philodromus* Walckenaer 1826. While most other genera established or resurrected in the same work for various species groups of *Philodromus* were not accepted by later workers, *Pulchellodromus* is currently considered a valid genus (Kastrygina & Kovblyuk 2014), as is
Rhysodromus Schick, 1965 (Kastrygina & Kovblyuk 2016). The two barcodes for Pulchellodromus pulchellus, the type species of the genus, are particularly close to Philodromus rufus (median pairwise distance 8.9%) and P. emarginatus (9.1%), both well below the 11.4% median distance between Philodromus species. The species could thus be placed in Tibellomimus Gertsch, 1933, sensu Wunderlich (2012, type species T. lineatus, and including the rufus group of Philodromus s. lat.), or Emargidromus Wunderlich, 2012 (type species E. emarginatus), but the median distances to the type species of Philodromus s. str., P. aureolus, and that to P. dispar (type species of Philodromus Wunderlich, 2012) are only 9.9% and 11.2%, respectively, both smaller than the median distance between species currently placed in Philodromus s. lat. It appears that the current Philodromus is quite homogeneous, genetically and morphologically, with somewhat ambiguous relationships between species groups. The situation is potentially different for other groups previously placed in Philodromus: most importantly, the barcode distances support an independent Rhysodromus (type species R. histrio), in good agreement with the morphology-based results of Muster (2009), Wunderlich (2012) and Kastrygina & Kovblyuk (2016). Even Artanes Thorell, 1870 (type species A. margaritatus) might be the sister group of Philodromus s. str., in contrast to Muster’s phylogenetic analysis, although support for this relationship is very low (Figure 4). Despite this possible discrepancy in detail, both the morphological and the genetic analysis agree that, unless a much more extensive splitting of the genus is proposed, Pulchellodromus (and, by implication, Philodromimus, Tibellomimus, Artanes, and Emargidromus) should be considered at most a subgenus within Philodromus (stat. nov.), as its removal would leave the remaining genus paraphyletic. The obvious alternative, i.e., accepting Wunderlich’s split of Philodromus into, at least, six genera (Philodromus s. str., Pulchellodromus, Philodromimus, Tibellomimus, Artanes, and Emargidromus), seems undesirable, as it would obscure the close relationship and monophyletic nature of the refined Philodromus s. lat. (i.e., without Rhysodromus and potentially some other species groups not represented in the barcoding dataset; see Muster 2009), while not providing additional information beyond that offered by the subgeneric divisions (see Wallach et al. 2009 for a detailed discussion of the benefits of a more widespread use of subgenera).

Figure 3. Extract of a neighbour-joining tree illustrating the close interrelationship of Rabidosa, Tigrosa and a number of Geolycosa species.

Gibbaranea, Agalenatea and Epeira might be subgenera of Araneus, while Atea is possibly a valid genus. Despite considerable revisionary work, it is obvious that the genus Araneus Clerck, 1957, as currently conceived is still polyphyletic. This is also suggested by the large intragenus distances in barcode sequences (Table 3). The type genus of Araneus, A. angulatus, twelve specimens of which have been barcode sequenced, differs by at least 11.8% median pairwise distance from all the remaining 36 Araneus species included in the barcode dataset. The type species of several other genera proposed, but not generally accepted, for members of Araneus s. lat. have also been barcoded and show the following median pairwise distances to A. angulatus: A. ventricosus (type species of Cathaistela Archer, 1958) 12.3%; A. detrimentosus (Cambridgepeira Archer, 1951) 14.9%; A. miniatus (Conepeira Archer, 1951) 16.0%; A. sturmi (Atea C. K. Koch, 1873) 17.3%; A. triguttatus (Mimaraneea Archer, 1951) 14.5%. As a result, the putative members of Atea, Cambridgepeira, and Conepeira are placed far from A. angulatus in neighbour-joining trees and multiple-scaling plots, as are several other small groups of species. Only A. ventricosus is found consistently close to a large homogenous group of species close to A. angulatus. As the exact relationships between Conepeira and Cambridgepeira, as well as their composition, are entirely unclear, no formal resurrection of these genera is proposed here, also in view of repeated objections by Levi (1973, 1991), who emphasized
that he could not find unambiguous diagnostic criteria distinguishing the groups proposed by Archer. The situation appears to be different for *Atea*, which has been much more widely used as an independent genus and is genetically particular far from *A. angulatus*. It has consistently been used only for *Atea sturmi* and *Atea triguttata*, but if resurrected as an independent genus, it should probably also include members of the *viperifer* group and related species, such as *A. auriculatus*, *A. borealis*, *A. gayongensis*, *A. hoshi*, *A. iriomotensis*, *A. nojimai*, *A. pseudosturmi*, *A. ryukyuanus*, *A. tsurasakii*, *A. viperifer*, *A. yasudai*, and *A. yuanminensis*. Diagnostic characters that distinguish the genus from the rest of *Araneus* could be the rather broad, triangular opisthosoma, small size and most importantly the tightly wound, serpentine form of the epigynal scapus and associated details of the pedipalp. However, considering the unclear limits of a revalidated *Atea* no formal new combinations are proposed here.

![Image of a neighbour-joining tree illustrating the position of *Pulchellodromus* within *Philodromus*, as well as the more distant relationship of *Rhysodromus* (including *R. histrio*, listed as *Philodromus histrio* in the barcode database).](image-url)
In view of the obvious paraphyly of *Araneus* s. lat., it might seem eccentric to suggest the transfer of an entire well-defined and clearly monophyletic genus into the genus *Araneus*, instead of moving individual species groups out of it. However, this is what the barcoding results suggest. They reveal a well-supported monophyletic group of core *Araneus* species, including the type species *A. angulatus* and members of the *diadematus* group, but also members of *Gibbaranea* (as a monophyletic subgroup) and the type species of *Agalenatea*, *A. redii*. The median pairwise distance to *Araneus diadematus* (a species long considered the type species of *Aranea* Linnaeus, 1758, and always treated as an undisputed member of the same genus as *A. angulatus*) is 14.1%, compared to 13.2% for *Agalenatea redii*, and distances between 14.1% and 14.5% for the three barcoded representatives of *Gibbaranea*, including the type species, *G. bituberculata*. Even Grasshoff (1976) who, subsequent to Archer, went farthest in the subdivision of the *Araneus* into separate genera, considered the species around *A. diadematus* as undisputed members of *Araneus* s. str. Maintaining *Agalenatea* and *Gibbaranea* as separate genera would necessitate disrupting the historically established unity of the genus, and obscure its monophyletic nature. It would therefore appear reasonable to instead consider *Agalenatea* and *Gibbaranea* as subgenera of *Araneus* s. str.. Curiously, the only formal name available specifically for the *diadematus* group seems to be *Epeira* Walckenaer, 1805, and for consistency it would be advisable to use this name for a subgenus of *Araneus* containing the members of the *diadematus* group, whenever subgeneric names are employed in this genus. Grasshoff (1976) had rejected the use of subgenera for the species groups within *Araneus* s. lat., as he had doubts regarding the monophyly of the genus in the widest sense. The barcode data show that these concerns were well justified for many of the groups formerly placed within *Araneus*, which clearly belong to distinct evolutionary lineages, e.g., *Araniella*, *Neoscona* or *Nuctenea* (plus *Larinioides*). For *Gibbaranea*, *Agalenatea* and *Epeira*, the concern would, however, not apply, as their close relationship to the type species of *Araneus* seems beyond doubt. Their treatment as subgenera within *Araneus* s. lat. would therefore make a clear phylogenetic statement: these groups form a monophyletic group with *Araneus* s. str. (the *angulatus* group). This is not as revolutionary as it might at first seem: e.g., Wiehle (1931) had placed *Gibbaranea* in his species group 2, immediately following the *angulatus* group and before the *diadematus* group, expressing (albeit implicitly) a similar relationship to that reflected in the barcode data. *Agalenatea*, on the other hand, had never been convincingly justified as a separate genus; in his description of the genus, Archer (1951) had indicated affinities to *Atea*, *Nuctenea* (sub *Chinestela*), and *Conepeira* – each of these is strongly refuted by the barcode sequences, as well as by morphology. In light of the fact that the problems with the current taxonomy of *Araneus* s. lat. are far more pervasive than can be meaningfully assessed on the basis of the current species sampling, no formal synonyms or transferred are proposed here for this case.

**Cryptachaea riparia belongs in the genus Parasteatoda.** The subdivision of the former genus *Achaearanea* into a large number of independent genera, initially by Archer (1946, 1950) and Saaristo (2006), but most extensively by Yoshida (2008, 2016), was one of the major achievements of recent spider taxonomy. The barcoding data raises doubts about the justification of some of this splitting; e.g., both *Parasteatoda* and *Cryptachaea* are rather widely dispersed across the neighbour-joining trees. However, some of this confusion might be attributable to the incomplete coverage and quality of the barcode data. For instance, the barcode of *Parasteatoda komprensis* is closer to that of *Nihonhimea japonica* (type species of *Nihonhimea* Yoshida, 2016: 1.2%) than to that of *Parasteatoda tepidariorum* (type species of *Parasteatoda* Archer, 1946: 12.0%). This seems to be the result of a misidentification of at least one of the sequenced specimens. For the time being, only one change in genus assignment seems to be strongly supported by the barcode data: *Cryptachaea riparia* differs by only 7.2% from the type species of *Parasteatoda*, *P. tepidariorum* (and by 7.3% from *P. simulans* and *P. culicivora*, and 7.6% from *P. lunata*), but by at least 7.7% from any of the numerous *Cryptachaea* species included in the analysis. It is thus closer to the type species of *Parasteatoda* than, e.g., *P. tabulata* (8.0%) or *P. lunata* (9.0%). In neighbour-joining trees it is consequently clearly placed within the genus *Parasteatoda*. The association with *Parasteatoda*, rather than *Cryptachaea* is also confirmed by the maximum likelihood analysis. *C. riparia* is currently the only endemic European member of an otherwise predominantly American genus. Neither Archer (1950) nor Yoshida (2008) provide an explicit discussion justifying the placement of this species in *Cryptachaea*, but its male and female genitalia are clearly more similar to those of *Parasteatoda* species than to American *Cryptachaea*, including the type species *C. porteri*. For example, *C. riparia* has a large and distinct epigynal depression, without a posterior lobe, and a large subtegulum and relatively small tegulum on the male palp; characters that according to
Yoshida (2008) distinguish *Parasteatoda* from *Cryptachaea*. While the genetic analysis raises more general doubts about the limits and diagnosability of the various genera derived from the former *Achaearanea* s. lat., for now only *C. riparia* is formally transferred to *Parasteatoda*, as *Parasteatoda riparia* (*comb. nov.*), based on its morphological, genetic and zoogeographic affinities.

![Multidimensional scaling plot illustrating the close relationship between *Crustulina* and *Asagena* and the *Steatoda* species. The particularly divergent *Steatoda grossa* is not included in the plot. *Steatoda* sp. 7GAB corresponds to American specimens of *S. nobilis.*](image)

**Figure 5.** Multidimensional scaling plot illustrating the close relationship between *Crustulina* and *Asagena* and the *Steatoda* species. The particularly divergent *Steatoda grossa* is not included in the plot. *Steatoda* sp. 7GAB corresponds to American specimens of *S. nobilis*.

*Crustulina* and *Asagena* are likely junior synonyms of *Steatoda*. The barcode sequences of the four species of *Crustulina* Menge, 1868, included in the dataset (including the type species, *C. guttata*) differ
from *Steatoda bipunctata* (type species of *Steatoda* Sundevall, 1833) by between 10.6% and 12.6%. The two species of *Asagena* Sundevall, 1833 (including the type species *A. phalerata*) differ from *S. bipunctata* by 13.3% and 14.1%, respectively. In contrast, the type species of the former genus *Lithypantes* Thorell, 1869, *S. albomaculata*, differs from *S. bipunctata* by 14.6%, that of *Teutana* Simon, 1881, *S. triangulosa* by 12.3%, and *Steatoda grossa* even by 16.9%. The members of *Crustulina* differ from these divergent *Steatoda* species by mean distances of only 13.4%, 12.0%, and 16.9, respectively, and from the *Asagena* species by a mean of 13.7%. This means that both *Asagena* and *Crustulina* are firmly embedded among the *Steatoda* species (Figure 5). Thus, if the genus *Steatoda* is maintained roughly in its current form, it would need to be extended by including *Asagena* and *Crustulina*. For the former, this has long been suggested (see, e.g., Levi & Levi 1962, Murphy & Roberts 2015). Several members of the latter, including the type species, have repeatedly been placed in *Steatoda* by early authors. Its sexual biology, according to Knoflach (1994), is most similar to that of the *Steatoda* species. Nevertheless, the distinct habitus and genital morphology (see, e.g., Levi 1957, Levy & Amitai 1979, Knoflach 1994) have lead all modern (and most early) authors to accept *Crustulina* as an independent, albeit closely related, genus in the Asagenni. However, while *Crustulina* is clearly defined by a number of distinct synapomorphies, nobody seems to have identified consistent synapomorphies unique to *Steatoda*. While the barcoding data do indeed confirm that *Crustulina* is monophyletic, it places the group as a derived clade deep within an equally monophyletic *Steatoda* s. lat. However, given the potential medical and ecological relevance of some of the species involved, no formal synonymy is proposed here.

**Ohlertidion** is a junior subjective synonym of *Heterotheridion*. One of the unexpected results of the barcode analysis is the close relationship between *Ohlertidion* and *Heterotheridion*. These two genera were established by Wunderlich (2008) for two groups of species originally placed in *Theridion* Walckenaer, 1805, but morphologically sufficiently distinct from the type species *T. pictum* to justify separation from this genus in the narrow sense. The median barcode distances (12.3% and 13.5% between *T. pictum* and *Ohlertidion ohleri* and *Heterotheridion nigrovariegatum*, respectively) do not strongly argue against this separation, when compared to the typical interspecies distances within *Theridion* (Table 3). However, surprisingly, the type species of the two genera have notably similar barcode sequences (median distance 8.2%, interquartile range 7.7%-8.6%). They are thus considerably more similar than seen for average congeneric species pairs (Table 2), not just in Theridiidae, but in most spider families. As *Heterotheridion* is a monotypic genus and the three species of *Ohlertidion* are morphologically clearly related, the barcode data do not provide an immediate compelling reason to synonymize the two genera. Their relationship is analogous to that between *Larinioides* and *Nuctenea* (Araneidae) in the present dataset. However, given the undesirability of monotypic genera (Platnick 1976) and the otherwise completely obscure relationships of the two genera – Wunderlich (2008) is unable to identify any close relative for either of the two –, it would appear that only a formal synonymy will be a sufficiently strong expression of the phylogenetic hypothesis suggested by the barcode similarity. Clarifying the relationship in this way is also justified by the fact that Knoflach (2004) describes strikingly different copulatory behaviour for the two type species – leading to the corollary that behavioural traits might not always be good indicators of phylogenetic affinities in this group. The two genus names were published simultaneously; I here give precedence to *Ohlertidion* over *Heterotheridion*, as First Reviser according to Article 24.2.2 of the International Code of Zoological Nomenclature, and consider *Ohlertidion* as its junior subjective synonym (syn. nov.).

**Saaristoa** is a junior synonym of *Aphileta*. The genus *Saaristoa* was established by Millidge (1977, 1978) for two species that had formerly been placed in *Oreonetides*, but which he considered members of his *Aphileta* group. He distinguished *Saaristoa* (and *Maro*) from *Aphileta* on the basis of its more complex male genitalia. While Millidge was thus aware of the close relationship between *Saaristoa* and *Aphileta*, later authors do not seem to have explored the relationship in more detail, and in some cases even expressed doubt about the possible affinity (e.g., Crawford 1988, Thaler 1981). In its barcode sequences, *Aphileta misera* is more closely similar to typical members of *Saaristoa* (*S. abnormis*, *S. firma*, and *S. sammamish*) than to the other barcoded member of *Aphileta* (median intergenus distances between 8.0% and 11.4%, compared to an intragenus distance of 13.6%). A fourth species of *Saaristoa*, *S. ebinoensis*, is represented by a partial barcode sequence only and thus appears as more distantly related to either of the two groups, with a difference of 19.1% from *A. misera*, and 15.5% from *S. abnormis*. The two species originally placed in *Saaristoa*, *S. abnormis* and *S. firma*, show a 10.5% median pairwise barcode distance, compared to distances...
of 8.4% and 11.4% to *A. misera*. Consequently, in neighbour-joining trees, *A. misera* is firmly embedded with *Saaristoa* (*Figure 6*), while *A. microtarsa* shows much closer affinities to *Eulaira* (*E. arctoa* and *E. obscura*). *A. microtarsa* has previously been included by multiple authors in *Eulaira*, an endemic genus of North America, and therefore a formal transfer back to this genus is fully justified (the species name thus should be *Eulaira microtarsa*, **comb. conf.**). The species was already listed in *Eulaira* by Buckle et al. (2001), who also provide details on earlier references supporting this placement. Regarding *Saaristoa*, the barcoding results leave little doubt that this genus should be placed in synonymy of *Aphileta* (**syn. nov.**). The confusion about the placement of *A. microtarsa* and *S. ebinoensis* clearly supports the notion that so far a certain level of oversplitting has obscured the genus-level relationships within this group.

![Figure 6. Extract of a neighbour-joining tree illustrating the close affinity of *Agyneta* and *Saaristoa*, and the placement of *A. microtarsa* in *Eulaira.*](image)

**Gnathantes** is a valid genus for the *fillmorana* species group of *Agyneta*. *Agyneta* Hull, 1911, is one of the genetically most diverse large genera in this analysis (**Table 3**). Indeed, the barcode distances reveal a deep split in the genus, with a group of species (*A. darrelli*, *A. fillmorana*, *A. bucklei* and *A. flibuscrocus*, approximately the *fillmorana* group of Duperré 2013) clearly separated from the rest of the genus, forming a separate clade with unclear affinities. For this group, the name *Gnathantes* Chamberlin & Ivie, 1943 (type species *Gnathantes ferosa* = *G. fillmorana*), is available and is here resurrected from its synonymy with *Agyneta* (**stat. rev.**), as the valid genus for the members of Duperré’s *fillmorana* group plus *A. flibuscrocus*.

The remaining large group of barcoded species, including the species closest to the type species *Agyneta decora*, form clearly a homogeneous group. The type species itself is unfortunately not represented in the dataset, but morphologically closely related members of the *decora* group sensu Duperré are: *A. allosubtilis*, *A. olivacea*, *A. watertoni*, *A. protrudens* and *A. perspicua*. The species of the former genus *Meioneta* s. str. (the *rurestris* group of Duperré) do not form a distinct subgroup within the genus, but are scattered throughout. The genus *Tennesseellum*, represented by its type species *T. formica*, has a median pairwise distance from barcoded members of the *decora* group (*Agyneta* s. str.) of 12.2%, *Mesasigone mira* (type species of the monotypic *Mesasigone*) 12.1%, *Nippononeta coreana* (one of the original members of *Nippononeta*) 12.6%, and *Parameioneta tricolorata* 14.0%, compared to a median distance of 14.3% between members of the *decora* group and *Gnathantes*. While this supports the separation of *Gnathantes* from *Agyneta*, it raises obvious concerns about the validity of all these genera, which might more informatively be considered subgenera of *Agyneta* s. lat (Wallach et al. 2009). The median distance of *A. rurestris* (type of *Meioneta*) to the barcoded representatives of *Tennesseellum*, *Mesasigone* and *Nippononeta* is 10.6%, 10.1% and 9.9%, compared to a median distance of 10.4% between *A. rurestris* and members of the *decora* group. In neighbour-joining trees the latter two are consistently placed within *Agyneta*, and in a maximum likelihood tree both *Tennesseellum* and *Parameioneta* are embedded within *Agyneta.*
Mesasigone was erected by Tanasevitch (1989) as a monotypic genus of unclear affinities, but the supposed (senior) synonym of its type species, *M. beijianensis*, was described in Meioneta. Wunderlich (1995) emphasized its similarity with Agyneta, despite a lack of processes on the cymbium and tibia of the male pedipalp, the absence of a lamella caracteristica and a shorter embolus in Mesasigone, but also discusses possible relationships to Parameioneta, Oreonetides, Theonina, Oreophantes, and Microneta. Except for *Theonina*, all of these are included in the barcode dataset, and in contrast to *Agyneta*, none of them shows any particularly close affinity to *Mesasigone* (minimum pairwise distance: 13.3% to *Parameioneta*).

*Nippononeta* was established by Eskov (1992) for former members of *Meioneta*, distinguished by the lack of a conical elevation of the cymbium, an L-shaped paracymbium, a notable splitting of the lamella caracteristica, a sharply constricted scapus and a dorsal pattern on the abdomen. Yan et al. (2015) performed a detailed analysis of the genus and suggested that *Nippononeta* is the sister group of a clade combining *Agyneta*, *Tennesseellum*, and *Anibontes* (not barcoded). The barcoding distances do not support this hypothesis and instead place *Nippononeta* as a derived group within *Agyneta*; however, the barcode for *Nippononeta* is incomplete, and this placement is therefore tentative.

As the number of sequences for the relevant type species is rather small and some of the barcodes are incomplete, no formal taxonomic changes are suggested beyond the separation of *Gnathant*es, which is strongly supported by the sequence data.

**Centromerita** and **Tallusia** are junior synonyms of **Centromerus**. Both *Centromerita* and *Tallusia* Lehtinen & Saaristo, 1972, have been repeatedly synonymized with *Centromerus* (e.g., Locket et al. 1974, Millidge 1977, Saaristo & Tanasevitch 1996). The barcode sequences of the type species, *Centromerus bicolor* and *Tallusia experta*, however, unequivocally support the synonymy, placing both genera not only in close proximity to each other, but also deeply nested within *Centromerus*, close to typical *Centromerus* members, such as *C. pabulator* and *C. incilium* (the type species of *Centromerus*, *C. brevipalpus*, has not been barcoded yet). As in many of the previously discussed cases, these two small genera represent derived members of a monophyletic larger genus, which would become paraphyletic upon their removal. Thus, both *Centromerita* and *Tallusia* are here confirmed as synonyms of *Centromerus* (*syn. conf.*).

The erection of a large number of independent genera for the various species groups of the large and obviously polyphyletic genus *Leptophyantes* has been one of the most ambitious and controversial recent developments in spider taxonomy (e.g., Saaristo & Tanasevitch 1996, 2000, 2003, 2004, Tanasevitch 1992, 2001, Wunderlich 1992). The new genera have been widely accepted, but the barcode data indicate the mixed success of the morphology-based definition of micronetine genera. Some genera, most importantly *Palldiphantes*, *Bathyphantes*, and *Tenuiphantes*, are indeed well-defined monophyletic groups that clearly deserve the status of independent genera. In many other cases, the splitting of *Leptophyantes* s. lat. has been far less successful in identifying valid evolutionary lineages, and the resulting, much diminished *Leptophyantes* s. str. seems to be still far from being monophyletic, as demonstrated not only by the extreme interspecies barcode distances in the genus, but also by its widely scattered appearance in neighbour-joining trees and multidimensional scaling maps based on the barcode distances. Despite covering a large number of species, the barcode data will obviously not be able to fully resolve the taxonomy of *Leptophyantes* and its relatives. Instead, only a couple of particularly clear examples are highlighted, to illustrate the extent of the remaining taxonomic challenges.

**Obscuriphantes, Agnyphantes, and Acanthoneta** are junior synonyms of **Poeciloneta**. The barcoding data clearly reveal that *Poeciloneta* as currently conceived is polyphyletic (Figure 7). To achieve monophyletic coherence, the genus has to be considerably extended, to include the genera *Obscuriphantes*, *Agnyphantes* and *Acanthoneta* (all represented by their type species in the barcode dataset). All of these are therefore considered junior synonyms of *Poeciloneta* Kulczyński, 1894 (*syn. nov.*). The close relationship between these genera is not entirely surprising; *Acanthoneta* was originally considered a subgenus of *Poeciloneta* and *Obscuriphantes* as “close to *Poeciloneta*” (Saaristo & Tanasevitch 2000). Nevertheless, the degree to which the morphologically defined subdivisions fail to correspond to evolutionary units is rather astonishing. The extended *Poeciloneta* should also include *Poeciloneta bipartita* (*comb. nov.*), currently placed in the closely related genus *Bollyphantes*, This species is closer to the type species of *Agnyphantes* (*A. expunctus*, 9.6%)
and Poeciloneta (P. variegata, 10.8%), than to that of Bolyphantes (B. luteolus, 11.7%). The revised placement is also confirmed by the genitalic similarity to the type species of Poeciloneta.

Figure 7. Neighbour-joining tree illustrating the polyphyletic nature of Poeciloneta s. str. and its close affinity to Obscuriphantes, Acanthoneta, Agnyphantes and Bolyphantes bipartitus.

Anguliphantes, Improphantes, Mansuphantes, and Piniphantes are junior synonyms of Oryphantes. The situation revealed by the barcode analysis is even more confused in this example. The clearly monophyletic group containing the type species of Anguliphantes (A. angulipalpis) and Mansuphantes (M. mansuetus), as well as uncontested members of Improphantes (I. complicatus and I. nitidus) and an unidentified Oryphantes species (annotated as O. angulatus, the type species of the genus, in the BOLD database, but not in the sequence files), shows a confused mixture of the members of the various nominal genera. The detailed discussion of the four genera by Saaristo & Tanasevitch (1996), when they established these for the first time, already indicated some of these close relationships, considering Anguliphantes as “very closely related to Oryphantes” and vice versa, but no close relationship was indicated for Mansuphantes, while Improphantes was considered as “closely related to Piniphantes”, which is not represented in the barcode dataset. The median interspecies distance between members of different genera in this cluster is only 10.3% (range: 7.6%–12.2%), obviously compatible with a placement in a single genus. Where multiple species are included from the same genus, they do not cluster together in the multidimensional scaling maps or neighbour-joining and maximum likelihood trees (Figure 8), with the exception of the two barcoded Mansuphantes species, which differ by only 1.5%, thus raising doubts about their species status. This indicates that these four genera are not only difficult to diagnose, but also para- or polyphyletic, and cannot be maintained even at the subgenus level. Following the same reasoning as in the cases discussed before, this implies that these four genera should be considered as synonyms, with Oryphantes Hull, 1932, having priority over Anguliphantes, Mansuphantes, and Improphantes Saaristo & Tanasevitch, 1996 (syn. nov.). For consistency, this extended Oryphantes should also contain the species currently placed in Piniphantes (syn. nov.), a group closely related to the members of Improphantes, even if this assessment is for now based merely on morphological evidence. The expanded genus should also include Oryphantes antroniensis (comb. nov., currently in Palliduphantes) and Oryphans nodifer (comb. nov., currently in Lepthyphantes). The latter had already been placed in close neighbourhood to the type species of Anguliphantes (A. angulipalpis) in the original description (Simon 1884), and by all subsequent authors (e.g., Miller & Kratochvil 1938, Wielie 1965, Thaler & Buchar 1993), and its transfer is probably overdue. O. antroniensis was listed as a member of the angulatus group of Lepthyphantes s. lat. by Heimer & Nentwig (1991) and only “tentatively placed in Palliduphantes” by Saaristo & Tanasevitch (2004). A comparison to Heimer & Nentwig’s arrangement of Lepthyphantes s. lat. reveals that the expanded Oryphantes almost exactly corresponds to their angulatus group, which contains L. nodifer, L. antroniensis, L. angulipalpis, L. pinicola, L. improbulus and L. angulatus and their closest relatives, plus the mansuetus group, which combines species from Mansuphantes with some of those currently placed in Improphantes (L. decolor, L. geniculatus, L. holmi, L. nitidus). In addition, Heimer & Nentwig place two rather divergent species in the same groups: L. lepthyphantiformis (currently the only member of the monotypic Formiphantes) and L. notabilis (currently in Lepthyphantes, but “very isolated” in this genus; Thaler 1982). A conclusive decision about their status can probably only be made after their barcode data become available, but at the moment there is no clear
justification for a transfer to *Oryphantes* s. lat. The detailed and very specific agreement between barcode results and earlier morphological subdivisions, just like in the case of *Acantholycosa*, adds strong support to the validity of the genetic approach to genus-level taxonomy. At the same time, it reinforces the point that systematic decisions based on a detailed analysis of the genitalia do not escape the risk of resulting in artificial classifications, if they are not accompanied by a careful phylogenetic analysis.

*Figure 8. Extracts of a neighbour-joining tree (A) and multidimensional scaling plot (B) showing the close intermingling of barcode sequences for species related to *Oryphantes* but currently assigned to six different genera.*

**Hypositticus, Sittipub, Calositticus, Sittiflor, and Attulus are junior synonyms of *Sitticus***. The genus *Sitticus* s. lat. was recently split into a number of separate genera (Prószyński 2016, 2017), following an earlier subdivision of the European members into several subgenera by Lohmander (1944). This action was part of a larger series of revisions that has recently come under severe criticism (Kropf et al. 2019). The question to ask in the context of the barcode analysis is obviously whether this extensive splitting of *Sitticus* is justified. The barcode dataset includes the type species of *Sitticus* s. str. (*S. terebratus*), *Attulus* (A. *distinguendus*), *Calositticus* (C. *caricos*), *Sittiflor* (S. *floricola*), and *Hypositticus* (=*Sittipub*) (*S. pubescens*), as well as a number of other species, including other representatives of *Sitticus* s. str. (*S. fasciger*, *S. finschi*, and possibly *S. albolineatus*, which was not treated in Prószyński’s revision), *Calositticus* (C. *rupicola*, C. *cutleri*, C. *striatus*, C. *zimmermanni*), *Attulus* (A. *ammophilus*, A. *avocator* A. *penicillatus*, A. *saltator*), as well as a putative member of *Sitiab* (*S. concolor*) and specimens labelled as “*S. rainieri*”, presumably a misspelling for *Sittisax ranieri*. The barcoding data show *S. concolor* to be quite distinct from the rest of the genus (minimal median distance 10.9%, and 13.5% median distance from *S. terebratus*), justifying, at least provisionally, the maintenance of *Sitiab* as a separate genus. *S. pubescens*, in contrast, is amongst the species most similar to *S. terebratus* in their barcode sequence, with a median distance of 7.3%; only *S. fasciger* (6.9%) and *S. cutleri* (7.1%) being more similar. *S. finschi* (10.9%) and *S. albolineatus* (10.7%), the other two members of Prószyński’s *Sitticus* s. str. are considerably further from the type species of the genus. This most strongly refutes the validity of *Hypositticus* (=*Sittipub*) as an independent genus. With the possible exception of *Calositticus* (=*Sittiflor*), none of the other suggested genera included in the dataset receives support as a monophyletic group in neighbour-joining trees or multidimensional scaling plots (*Figure 9*). In contrast, following the removal of *S. (Sitiab) concolor*, the remaining genus *Sitticus* s. lat. is clearly monophyletic. Therefore, *Hypositticus, Sittipub, Calositticus, Sittisax, Sittiflor, and Attulus* are collectively placed in the synonymy of *Sitticus* Simon, 1901. The reversal of precedence in favour of *Sitticus* over the older name *Attulus* seems preferable in the interest of stability, but would probably require a formal approval by the ICZN in the future.
Figure 9. Multidimensional scaling plot (A) and extract of a neighbour-joining tree (B) illustrating the barcode affinities between members of *Sitticus* s. lat.

**Conclusions**

The examples presented here show that barcode sequences can make an important contribution to genus-level taxonomic decision making. Some of the suggested nomenclatorial changes will be at least as controversial as the current placements, but it is hoped that the bold hypotheses expressed by the proposed changes will stimulate future data collection, both regarding traditional character systems and additional DNA sequence information. They might also motivate a more tightly reasoned phylogenetic justification of genus-level splitting, as well as more explicit and testable genus definitions, especially in cases where the barcode data either contradict current subdivisions or suggest new and unexpected relationships. While the overall excellent congruence of barcode similarities and traditional genus-level taxonomy in many specific details is reassuring, it would nevertheless be very interesting to validate the observations reported here on the basis of different genome regions, including various nuclear genes. Additionally, the barcode dataset discussed here covers less than 10% of global spider diversity. For many species, only single incomplete sequences are available, increasing the risk of misidentifications and underestimating the diversity across the geographic range of each species. In any case, once a broader barcode coverage of the entire order has been achieved, it seems realistic that barcode sequences will make a major contribution to the integrative taxonomy required for filling in the dense phylogenetic scaffold provided by recent phylogenomics projects.

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