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What's a Spider? Designation of the Neotype for the First Animal Species Ever Described, *Araneus angulatus* Clerck 1757 (Araneae: Araneidae) †

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Abstract

We designate a neotype for the Eurasian spider species *Araneus angulatus* Clerck, 1757, thereby fixing the objective application of the species name, the genus name *Araneus* Clerck 1757, the family name Araneidae Clerck 1757, and the superfamily name Araneoidea Clerck 1757. By etymology and arachnological tradition, it also unofficially fixes the application of the ordinal name Araneae Clerck 1757 and thus answers the uncontroversial question, "What's a spider?" *A. angulatus* also happens to be historically the first animal species ever described because Clerck (1757) has priority over Linnaeus (1758). Neotype designation is justified for three reasons: the syntypes of *A. angulatus* are lost; "*A. angulatus*" contains significant COI sequence divergence, potentially representing intraspecific variation, misidentifications, or as many as four undescribed species; and, with the neotype anchored via a COI barcode to a reference genome, future researchers can use this species as the "exemplar spider" in analyses, knowing that their results will not be compromised in the future by nomenclatural changes. Because all 1757 Clerckian names are spiders, should the considerably less uncontroversial question ever arise, "What's an animal?" one objective answer is, "It's a spider, and probably the neotype of *A. angulatus*."

Keywords: Clerck; Linnaeus; ICZN; nomenclatural typification; DNA barcodes; cryptic species

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1. Introduction

All taxonomic names are proper names, in that they ultimately apply objectively to the name-bearing type specimen (or series) cited in the original species description. As in humans, they objectively denote just one organism, in taxonomy called the "holotype." The assignation of their name to other organisms, hypothesizing conspecificity, is subjective. If disputed, the only objectively based resolution ultimately resides in interpretation of

the holotype, because the holotype ostensively defines the name. Holotypes are housed in museums, herbaria, and other collection-oriented institutions, and, by some criteria, are the most valuable biological scientific collections [1]. Holotypes are especially valuable because they serve as permanent, name-bearing reference specimens. Unfortunately, holotypes are fragile. Like all mortal remains, they degrade. For this reason, 21st century biology increasingly relies on the interpretation of DNA sequences to identify species and to define conspecificity and phylogenetic relationships, which require genome quality tissues and DNA. Because sequences provide permanent, reproducible, distributable, and widely accessible records, DNA sequences have been proposed as alternatives to physical holotypes, particularly for environmentally detected organisms [2].

For the vast majority of Earth's species, the intractability of sequencing their historical holotypes versus the tractability of sequencing their modern conspecifics bottlenecks biodiversity science and much else [3,4]. Current scientific standards could reasonably wish that all holotypes were objectively linked to genome quality collections. In the case of the species *Araneus angulatus* Clerck 1757, this redefinition is possible, because its 269-year-old syntype series is lost [5,6].

When types are lost and there is exceptional need, taxonomists can designate a neotype. Most name-bearing types representing the names of the approximately 644 animal Orders [7] are degraded beyond the reach of financially reasonable genomics [8,9], to say nothing of degrading the type (most animal species are small), so the opportunity to fix objectively the meaning of "spider" is unusual (assuming, as arachnologists have for the past 200 or so years, that an *Araneus* species would play that role). This event is even more curious, because the official spider nomenclature antedates Linnaeus [10] by a year, giving Carl Alexander Clerck's 1757 early discovery and hypothesis new, 21st century meaning. The ICZN [11] disregarded this historical fact and set the date of publication for both works as 1 January 1758 but gave Clerck [12] priority over Linnaeus [10]. This Solomonic decision caused confusion. While the ICZN opines that all taxonomists should refer to *Araneus angulatus* Clerck 1757 as *Araneus angulatus* Clerck 1758, because they said so (admittedly, a valid argument), we and most arachnologists (especially see WSC's 450+ word FAQ 10 on the topic [13]) prefer historical fact to "deeming provisions" (see below). In this article we refer to the author of *Araneus angulatus* as "Clerck 1757," except in strictly nomenclatural and legalistic contexts.

Here, we designate a neotype for the Eurasian spider *Araneus angulatus* Clerck 1757 and therefore fix the application of the species name *Araneus angulatus* Clerck 1758, the genus name *Araneus* Clerck 1758, the subfamily name Araneinae Clerck 1758, the family name Araneidae Clerck 1758, the superfamily Araneoidea Clerck 1758, and, albeit unofficially, the ordinal name Araneae Clerck 1757, commonly known as spiders. No neotype has been designated since Thorell [14] was the last to see the syntype series for several reasons. First, the identity of *A. angulatus* has not been in doubt until recent molecular work (e.g., [15]). Second, Article 12.2.7 [16] states that illustrations can make a species name available, and Clerck's illustrations were diagnostic (Figure 1).

Third, it now appears that *A. angulatus* may contain as many as four undescribed species (see below). It will require thorough study of the species complex using modern methods to decide how many exist and whether the non-*angulatus* species have available names. However, the morphological and COI evidence is sufficiently compelling to warrant designation of the neotype now, as allowed by Article 75 of the International Code of Zoological Nomenclature [16]. Given the widespread use of spiders as exemplars in phylogenetic work (e.g., [17–21]) and the ever-larger availability of annotated spider genomes [22] including a chromosome-level genome from a British specimen of *A. angulatus* [23], it is important to clarify objectively what the name *A. angulatus* means. Finally, this act intends

to help alleviate species misidentifications when more genomes become available (e.g., [24]; see [25,26]).

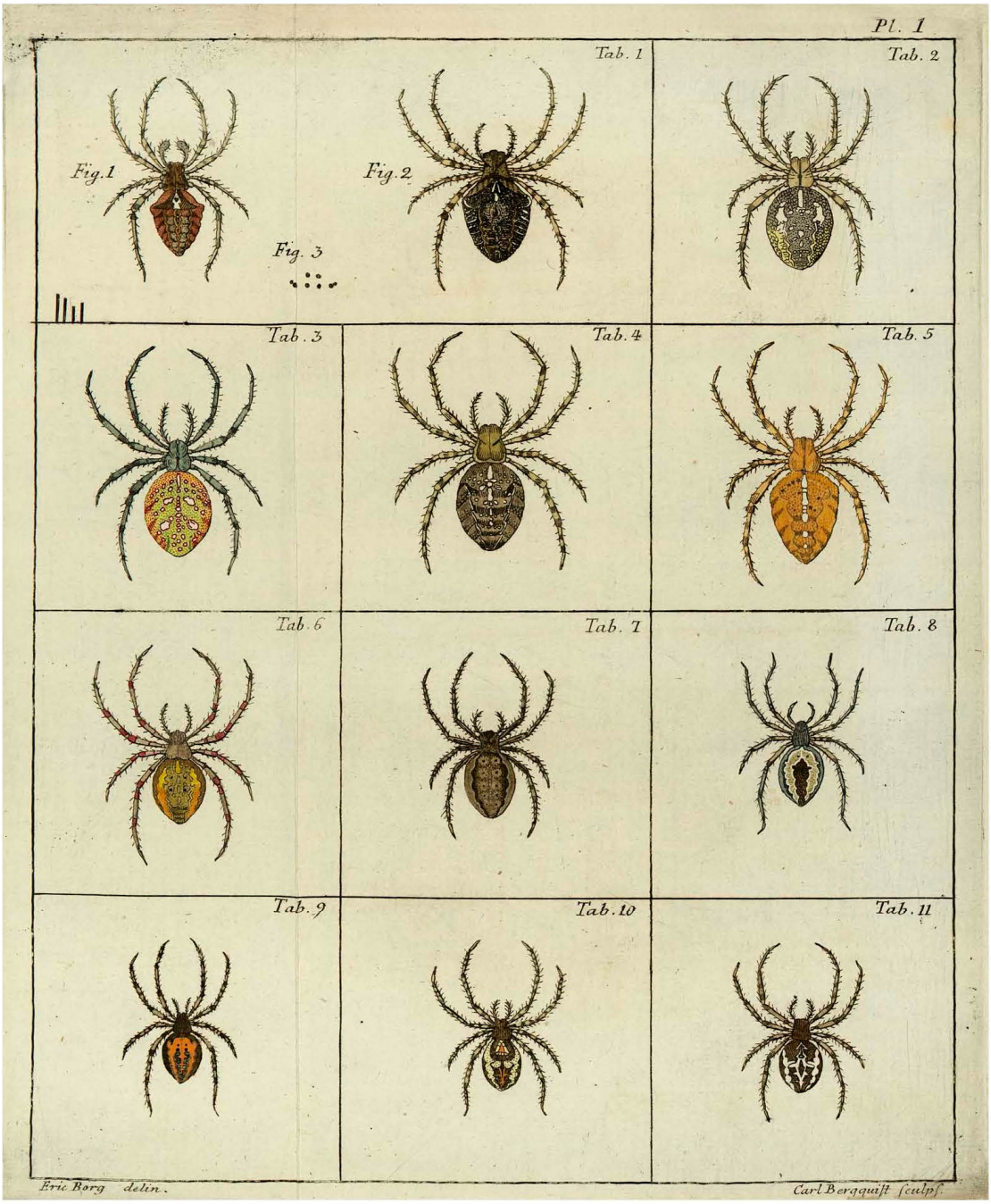


Figure 1. Plate 1 of Clerck [12]. Tab 1 is *Araneus angulatus*, fig. 1, male, fig. 2, female, fig. 3, eyes.

The Zoological Code [16] does not regulate fixation of names above the family-group rank, and therefore the name used for any order or higher rank will always be the choice of the researcher. In the case of the name Araneae, by etymology and tradition arachnologists generally agree that the prototypical spider is an *Araneus* species, often *A. diadematus* Clerck 1757, perhaps following Linnaeus [10] (p. 619), Petrunkevitch [27] (p. 136), and Bonnet [28] (p. 408). But *A. angulatus* is objectively the type species of *Araneus*, not *A. diadematus*. To guide usage of an "exemplar spider" in higher level systematics, phylogenetics, and many other kinds of work, it is important that *A. angulatus* be unambiguously defined.

2. Materials and Methods

2.1. Specimens

Matjaž Gregorič obtained two males of *Araneus angulatus* from Montenegro (2025), one female from Serbia (2024), and four females from Slovenia (2011, 2023, 2025) from which tissue was stored at −80 °C. Raul Vicente collected three adult males, four females, and one juvenile in 2026 in Gotska Sandön National Park, Gotland, in southern Sweden about 125 km from Stockholm, presumably Clerck's original type locality. A male from this series is designated as neotype. The cold chain protocol involved storing specimens at −20 °C within 8 h after death, shipping to Slovenia for species description and COI sequencing. Six of those (RV01-03, RV05-07) were then shipped to the Smithsonian for deposition and two, including the neotype male (RV04) and a co-collected female (RV08), were shipped to the Swedish Museum of Natural History for deposition. Shipping took 2–2.5 days, at ambient temperatures, but specimens at all locations were stored at −20 °C, except for the time necessary for description and imaging. The following museum and institution abbreviations are used: NIB—National Institute of Biology, Ljubljana, Slovenia, NHRS—Swedish Museum of Natural History, Stockholm, Sweden, USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, and ZRC—The Research Centre of the Slovenian Academy of Sciences and Arts, Ljubljana, Slovenia. Anthropic [29] was used to write R scripts to collate data from GenBank (accessed 30 September 2026), BOLD (accessed 30 September 2026), and GBIF (GBIF.org (23 September 2026) GBIF Occurrence Download https://doi.org/10.15468/dL.fsbhsp [7] to produce Table S1 and the map (Figure 2). Country centroids are used when a country would otherwise have no records. Several points lacked exact localities and were approximated. Red dots have associated COI sequences; blue dots do not.

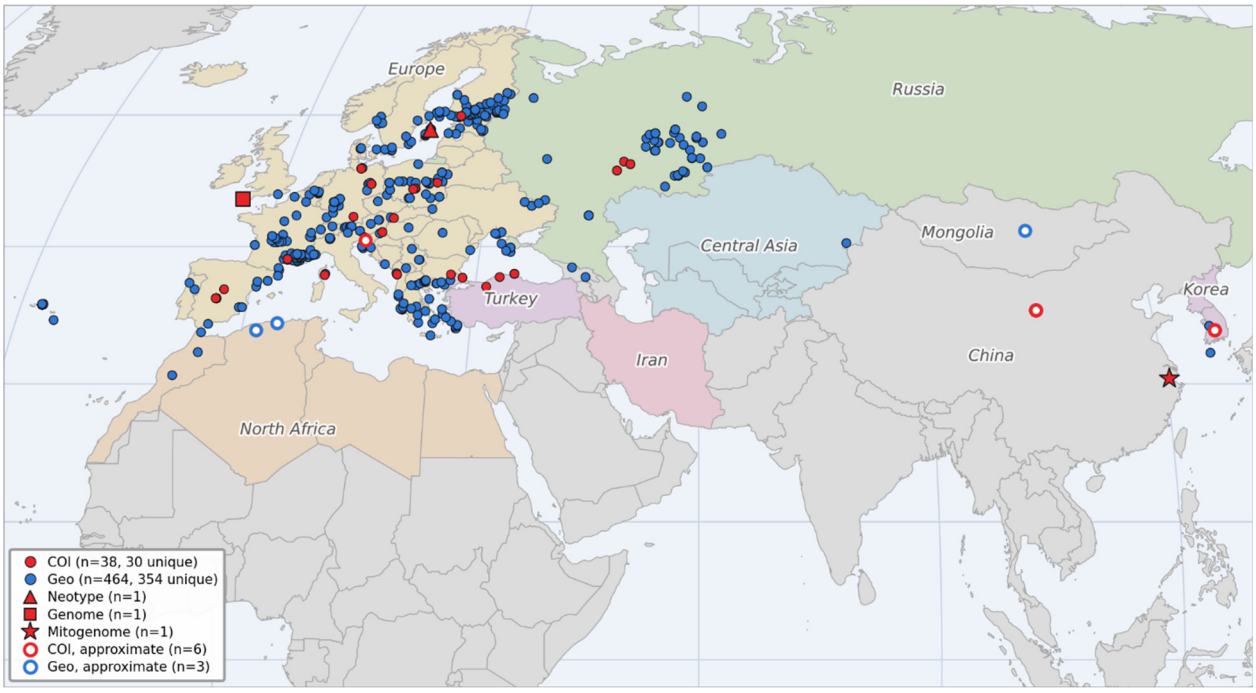


Figure 2. Robinson projection map of 514 *Araneus angulatus* specimens identified as such in 391 localities. Red dots are BOLD + GenBank, blue dots are non-barcoded GBIF records of preserved specimen or material citation/sample localities. Shaded regions are the WSC [13] distribution (Europe, North Africa, Turkey, Russia (Europe to Far East), Iran, Central Asia, Republic of Korea). Country centroids, inferences,

or approximations are used when a country would otherwise have no records. The red square is the locality of the complete genome [23], the red star the complete mitogenome and the red triangle of the neotype. Map produced by the authors in Python 3.11 using Matplotlib 3.10, GeoPandas 1.2 and PyProj 3.7 (Robinson projection, central meridian 60° E). Country boundaries are from Natural Earth 1:50 m Admin 0—Countries (https://www.naturalearthdata.com), which is in the public domain. Occurrence records are from GBIF (GBIF.org (23 September 2026) GBIF Occurrence Download https://doi.org/10.15468/dL.fsbhsp [7]), BOLD Systems (https://www.boldsystems.org, 23 September 2026), GenBank (https://www.ncbi.nlm.nih.gov/genbank/, 23 September 2026) and specimens examined in this study. The map is original to this article and no permission is needed to reproduce it.

2.2. Morphological Methods

Specimens were examined, measured, and imaged using a Leica M205C stereomicroscope and a Keyence VHX7000 digital microscope. Z axis images were combined using Zerene Stacker T2026-05-04-0750 and thereafter minimally adjusted using Adobe Photoshop 2025. All measurements are given in millimeters. Anatomical terminology follows the previous taxonomic revision and the morphological homology framework for Nephilidae and Orbipurae [30]. The following abbreviations appear in the text and figures: ALE, anterior lateral eye(s); AME, anterior median eye(s); B, base; BH, basal hematodocha; BL, basal lamella; CB, cymbium; CO, copulatory opening; DH, distal hematodocha; G, gonopore; MA, median apophysis; PC, paracymbium; PLE, posterior lateral eye(s); PME, posterior median eye(s); R, radix; ST, subtegulum; STA, subterminal apophysis A; STB, subterminal apophysis B; Sc, scape; T, tegulum; TA, terminal apophysis.

2.3. Molecular Procedures

A total of 75 Cytochrome Oxidase 1 (COI) sequences were downloaded from GenBank [31] and BOLD [32] including 43 putative *A. angulatus* and 32 araneid outgroups (Supplementary Materials, Table S1). In addition, we obtained three original COI sequences of *A. angulatus* from Sweden, Slovenia, and Montenegro following the pipeline in Gregorič et al. [26], for a final matrix containing 78 taxa (Supplementary Materials, Table S1). We chose outgroup taxa representing putative close relatives (e.g., *A. andrewsi* (Archer, 1951), *A. bicentenarius* (McCook, 1888), *A. circe* (Audouin, 1826), and *A. grossus* (C. L. Koch, 1844), other representatives of *Araneus* (*Araneus* s.s.), a number of species in multiple genera previously placed in *Araneus*, and more distant araneid outgroups. Sequences were compiled and managed in Mesquite 4.03 [33]. Matrices were also exported for analyses from Mesquite, resulting trees imported, visualized, and edited, and graphic tree files were exported from Mesquite to Adobe Illustrator 24.0.3 for final aesthetic manipulation. The sequences were aligned—a trivial task as COI is a protein coding gene resulting in unambiguous alignment without any gaps—using the Needleman–Wunsch algorithm in ClustalW [34], via Mesquite. The final aligned matrix consists of 1262 characters with 31% missing data, mostly in the region that is not amplified with typical DNA barcoding markers. The appropriate models for the phylogenetic analysis were selected with jModelTest2 on XSEDE (2.1.6) [35] using the Akaike information criterion (AIC) [36].

The best model was GTR+I+Γ. Phylogenetic analyses were undertaken using Bayesian and Maximum Likelihood methods. We used MrBayes 3.1.2 [37], running for 10,000,000 generations (nchains 4) under invgamma, sampling a tree every 1000 generations, and posterior probabilities were determined from a majority rule consensus after 50% burn-in. Maximum Likelihood was performed in MEGA11 [38], implementing GTR+I+Γ with initial trees made with neighbor joining and using "extensive" subtree-pruning-regrafting and "very strong" branch swap filter, with support estimated through 1000 bootstrap replicates.

A more sophisticated analytical approach seems unwarranted given the severe limits of the simple (single gene) and gappy (missing data) available sequences, and the simple point we wish to test: *A. angulatus* as currently circumscribed may represent multiple species. Analytical sophistication will not yield more robust results on this dataset; better testing of phylogeny and species limits with more robust datasets (100s/1000s of loci) are needed. We calculated evolutionary divergence—the number of base substitutions per site between sequences using MEGA11 [39].

Species delimitation analyses using bPTP and GMYC [40,41] were performed through the bPTP and GMYC web servers (https://species.h-its.org/ptp/, https://species.h-its.org/gmyc/, accessed on 30 September 2026) and ABGD [42] and ASAP [43] through the Spart explorer (https://spartexplorer.mnhn.fr/, accessed on 30 September 2026), all with default settings.

3. Results

3.1. Nomenclatural History

The history of the nomenclatorial status of Clerck's names and his collection is curious ([44], best summary; [6,14,45–49]). Clerck [12] used binomial names and diagnostic illustrations to describe 66 spider species [6,49], of which 53 are still recognized as valid, and 23 are the type species of genera [13]. Taxonomists (including to some extent Linnaeus) used Clerck's names for the next 135 years. However, the Second International Zoological Congress in Moscow in 1892 decided that zoological nomenclature would commence with the 10th edition of Linnaeus published in 1758 [10], deemed to have been published on 1 January 1758, thereby rejecting Clerck's names. Arachnologists objected and at the 13th International Congress of Zoology in Paris in 1948 they were able to pass a motion to make an exception for Clerck's 1757 publication [11,50]. This is the only such exception zoological nomenclature has ever made and is now enshrined in ICZN Article 3.1 [16], and by Direction 104 [11]:

> *"Article 3. Starting point. The date 1 January 1758 is arbitrarily fixed in this Code as the date of the starting point of zoological nomenclature.*
>
> *3.1. Works and names published in 1758. Two works are deemed to have been published on 1 January 1758:*
>
> *-Linnaeus's Systema Naturae, 10th Edition;*
>
> *-Clerck's Aranei Svecici.*
>
> *Names in the latter have precedence over names in the former, but names in any other work published in 1758 are deemed to have been published after the 10th Edition of Systema Naturae."* [16]

and

> "*RULING.-(1) In accordance with a decision of the Thirteenth International Congress of Zoology, Paris, 1948 (Bull. zool. Nomencl. 5: 33-35, 98-100), the generic name Araneus (Class Arachnida) and the specific names published in combination with it in C. A. Clerck's Aranei Svecici are hereby ruled to be available as though they had been published subsequent to the starting point of zoological nomenclature and are to have priority as though they had been published in 1758 prior to the publication of the 10th edition of Linnaeus's Systema Naturae."* [11]

The key verb in Article 3.1 is "deemed." In law, deeming provisions bypass complex factual investigations to create a fixed rule, and the ICZN simply borrowed the trick. To non-lawyers it may seem absurd to stipulate that a work published in 1757 is to be regarded "as though" published in 1758, but it preserved the stable date for the start of zoological nomenclature while giving arachnologists what they needed.

Kluge [51] (case 3371) proposed, and the ICZN [52] (opinion 2224) confirmed, that the name *Araneus* Clerck 1758 is the type genus of the family group name Araneidae (Clerck 1758), and the name *Araneus angulatus* Clerck 1758 is the type species of the genus group name *Araneus* Clerck 1758, as subsequently designated (Article 69.1) by Simon [53] (p. 829) and enshrined in Article 3.1.

By fiat, therefore, *Araneus angulatus* Clerck, 1757 is the first animal species ever described. Likewise, the first plant species ever described is *Canna indica*, Linnaeus, 1753 [54] but no controversy clouds this fact.

The priority of Clerck [12] over Linnaeus [10] raises an interesting, currently fanciful implication. By ICZN Article 3.1, all of Clerck's spider names have equal priority. Fifty-three are still valid. These are the first available names published in zoological nomenclature. If the ICZN ever did decide to typify higher ranks of Metazoa and protists, what would the type specimen of the type species of the type genus be? Recommendation 69A.10, "All other things being equal, preference should be given to the nominal species cited first in the work, page or line ("position precedence")" provides an answer. If the question should ever arise, "What's an animal?" a nomenclaturally reasonable and objectively defined answer is, "It's a spider, and probably the neotype of *Araneus angulatus*."

3.2. History of the Collection

The history of Clerck's collection is also tangled. Apparently, the collection was rarely accessed at its location at the Bergius Botanical Garden in Stockholm, as Thorell, who was an experienced Swedish arachnologist, did not learn of its existence until after Thorell [48]. Clerck collected in the historical province of Uppland, and probably only in the environs of Stockholm [48]. He illustrated an adult male, female and a juvenile male of *A. angulatus*, which he reared to maturity [12] (p. 25). Thorell [14] found specimens of 50 of Clerck's species, but the collection was in poor shape, with the spiders pinned, many in fragments, and with only numbers as labels. Thorell surmised that the numbers reflected a list, subsequently lost. At this time the collection still included syntypes of *A. angulatus*: " Of *Epeira angulata* there are three specimens, ♂et ♀ad. and ♂jun.; no other species with angulated abdomen occurs." The collection was again forgotten, but rediscovered in 1965 [46,55]. By this time, specimens of *A. angulatus* were absent, indicating that the syntype series was lost between 1858 and 1965. The Clerck collection has since been incorporated into the collections of the Swedish Museum of Natural History [6,46].

As part of his review of the *Araneus diadematus* group in North America, Levi [5] illustrated *A. angulatus* and was the first to state that the types were lost. Breitling et al. [56] synonymized ten subspecies under two species, *A. angulatus* s.s. (five synonymies), and *Araneus pallidus* (Olivier, 1789) (five synonymies). Breitling [57] summarizes some of the issues involved in *Araneus* taxonomy. *Araneus angulatus* is a well-known European species with excellent illustrations and keys [58,59].

3.3. Distribution

The distribution of *A. angulatus* sensu lato (Figure 2) shows that specimen-based localities (blue) far outnumber barcoded localities (red). Shaded regions are the WSC [13] distribution (Europe, North Africa, Turkey, Russia (Europe to Far East), Iran, Central Asia, Republic of Korea). Of course, one cannot rely on unverified identifications. However, pending more detailed work, this map reflects known localities of *A. angulatus* based on GBIF, GenBank, and BOLD.

3.4. DNA Evidence

The Darwin Tree of Life project sequenced the genome of an *A. angulatus* adult male [23]. The *A. angulatus* genome is 2.980 Gb, scaffolded into 14 haploid chromosomes, and the mitochondrial genome 15.53 Kb. Wang et al. [60] published the complete mitochondrial genome (14.205 KB) from an "*Araneus angulatus*" specimen in Zhejiang Province, China. Our COI results (Figure 3) suggest it may be *Araneus ventricosus* (L. Koch, 1878) or possibly an undescribed species.

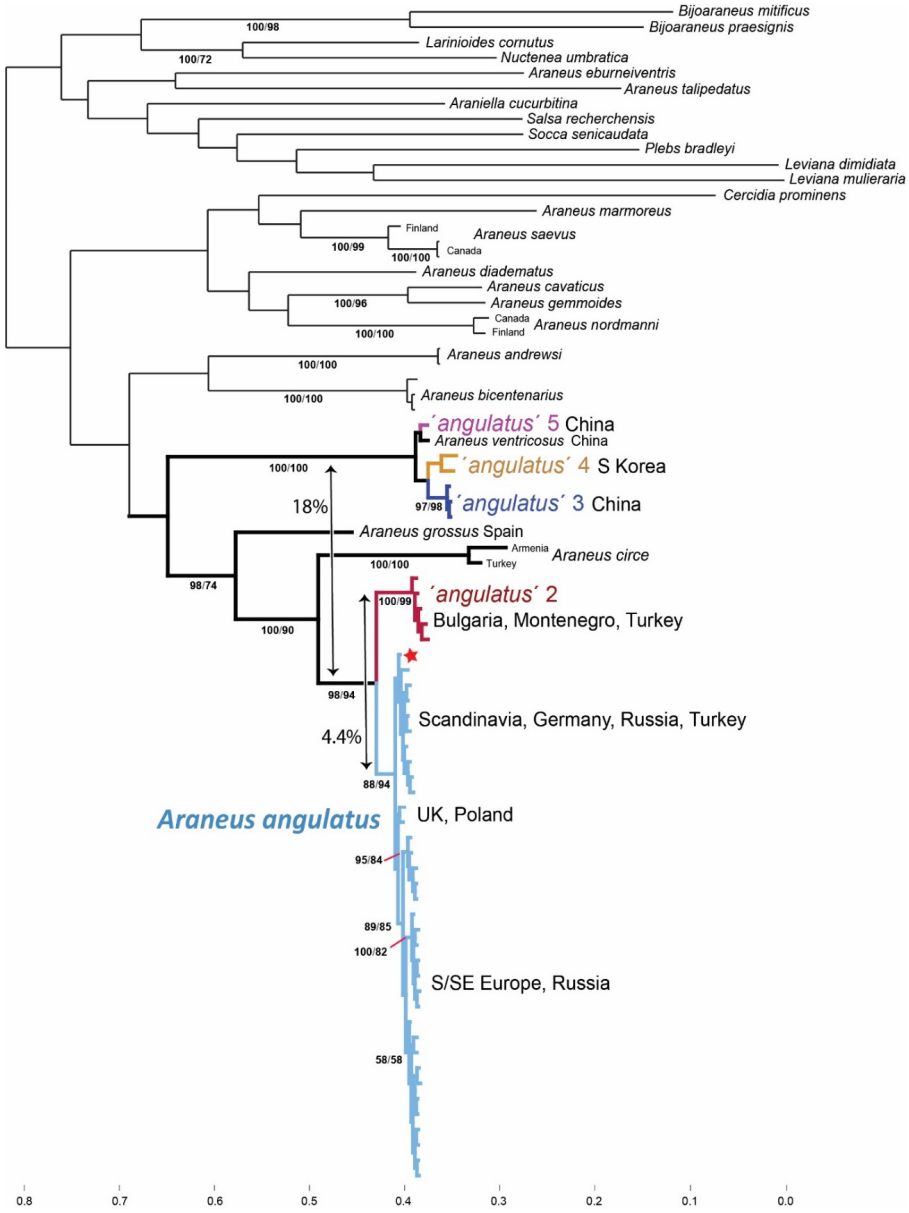


Figure 3. Bayesian Phylogeny using Cytochrome Oxidase 1 (COI) sequences downloaded from GenBank and BOLD, in addition to the three specimens sequenced here, including 46 *A. angulatus* and 32 araneid outgroup sequences. The optimal phylogeny separates *A. angulatus* into 5 clades (*angulatus* sensu stricto clade 1 (light blue) northern-southeastern Europe (red star marks the neotype), *angulatus* clade 2 (red) southeast Europe, *angulatus* clade 3 (dark blue) China, *angulatus* clade 4 (yellow) Republic of Korea, *angulatus* clade 5 China (purple). Numbers below clades are posterior probabilities/ML Bootstrap support values, displayed for major clades when both are above 50%. Scale bar shows expected substitutions per site.

The optimal Bayesian and ML phylogenies separate *A. angulatus* into five clades (*angulatus* northern-southeastern Europe, '*angulatus'* 2 southeast Europe, '*angulatus*' 3 China, '*angulatus*' 4 Republic of Korea, '*angulatus*' 5 China), but support is generally modest and three of the clades contain genetically variable taxa, with some apparent geographical structuring within *A. angulatus* (Figure 3). Three groups are clearly differentiated based on distance (4.4-19%), *A. angulatus*, '*angulatus*' 2, and the group containing '*angulatus*' 3–5. The distance between *A. angulatus* and '*angulatus*' 2 is on par with typical sister species pairs (4.4%), but variation within the clades is also considerable (1.1%) within *A. angulatus*. Distances among the three Asian clades ('*angulatus'* 3–5) are 2–2.5%. Results from the single locus species delimitation analyses bPTP, ABGD, and ASAP [40,41] agree in supporting *A. angulatus*, '*angulatus*' 2, and '*angulatus*' 4 (Figure 3) but vary in delimitation and support for other putative species ('*angulatus*' 3 and 5). Support for *A. angulatus* is modest (PP/Bootstrap = 88/94) though its sister group, clade 2, is well supported (100/99). These two are clearly separated from the Asian taxa, but the boundaries among the latter group are unclear (2–4 species, all poorly supported).

The species is supported by delimitation analyses, except for GMYC (Figure 3). The *Araneus angulatus* specimen collected in 2026 in Sweden (accession # NHRS-TOBI000005697) pertains to true *angulatus* s.s. (clade 1) a species ranging at least from Scandinavia to Russia, to southern Europe and Turkey (Figure 3). This widespread species has considerable genetic variability (1% within group mean genetic distances), and is sister to a clade ('angulatus' 2, southeastern Europe) separated by 4.4% mean genetic distance.

Taxonomy

Order Araneae Clerck, 1757
Family Araneidae Clerck, 1757
Araneus angulatus Clerck, 1757
"Angular Orb Weaver"
Figures 4–6

Neotype: Neotype male deposited in NHRS (NHRS-TOBI000005697) from Gotska Sandön National Park, Gotland, Sweden, N58.37031, E19.22951, 2vi2026, Coll. R. Vicente (RV04). Sandy old-growth pine forest with sparsely scattered old pines.

We designate a neotype for *Araneus angulatus* Clerck, 1758 in accordance with Article 75.3 of the International Code of Zoological Nomenclature [16] in order to clarify the taxonomic status of *A. angulatus*, which as currently applied includes several distinct mitochondrial lineages, so that the precise molecular identity of the neotype is crucial (Article 75.3.1). We provide a diagnosis (Article 75.3.2), and a description (Article 75.3.3). The original syntype series was last seen in 1858 and numerous searches in his collection now in NHRS and formerly in the Bergius Botanical Garden (Stockholm) have failed to find these specimens [5,6,14,46] (Article 75.3.4). The neotype is consistent with Clerck's original description and illustrations (Figure 1, Figure 5a,b, Article 75.3.5). The precise locality of Clerck's original collecting locality is vague. He said "…when in the neighbourhood of Stockholm alone, I have found more than sixty," [12] (Preface), which roughly agrees with the number of species described in that publication. Gotska Sandön is a National Park and protected area 125 km from Stockholm. Article 75.3.6 states "…evidence that the neotype came as nearly as practicable from the original type locality…" *A. angulatus* is uncommon in southern Sweden, and Clerck's original collecting locality is probably now urban Stockholm. Although its preferred habitat, old growth pine forests are not that rare in the Stockholm region, *A. angulatus* remains very rare there. In Sweden, it is seemingly more common in sandy pine forests, especially on Gotland. The neotype (and its co-collected specimens) is almost certainly conspecific with other northern European *A. angulatus*, especially given its

continuous, if sparse, distribution in that region (Figure 2). Although the neotype itself was not sequenced to avoid damage, COI data from a co-collected male (RV05) provide a molecular reference for the population from which the neotype was selected.



Figure 4. *Araneus angulatus* habitus. Female (left, RV07, USNMENT02419120) and male (right, RV05, USNMENT02419112) of specimens sympatric with the neotype.

Additional material examined: Montenegro, Valdanos, N41.952848, E19.178847, 2025, Coll. Žarković L., ♂(ZRC-ARA9459); Sutorman, N42.150441, E19.109695, 2025, Coll. Žarković L., juv. ♂(ZRC-ARA9447); **Serbia**, Belgrade, Višnjica, N44.834292, E20.566711, 29vii2024, Coll. Žarković L., ♀(ZRC-ARA8328); **Slovenia**, Sežana, Griže, N45.750600, E13.950900, 10v2011, Coll. Gregorič M., Čandek K., ♀(ZRC-ARA168); **Slovenia**, Sežana, Griže, N45.755806, E13.946639, 29v2026, Coll. Čandek K., Turk E., Kuntner M. ♂(NIB-A_ang_SLO_26); **Slovenia**, Maribor, Tezno, N46.516817, E15.688687, 3ix2023, Coll. Gregorič M., ♀(ZRC-ARA8115); **Sweden**, Gotland, Gotska Sandön National Park, Coll. R. Vicente: (RV08), N58.38691, E19.22512, 7vi2026, ♀(NHRS-TOBI000005698); (RV03), N58.35198, E19.26279, 2vi2026, ♀(USNMENT02419100); (RV06), N58.38521, E19.19935, 4vi2026, ♀(USNMENT02419102); (RV07), N58.38841, E19.21833, 7vi2026, ♀(USNMENT02419120); (RV01), N58.38532, E19.25607, 1vi2026, ♂(USNMENT02419110); (RV05), N58.38521, E19.19935, 4vi2026, ♂(USNMENT02419112); (RV02), N58.38521, E19.19935, 4vi2026, juv. (USNMENT02419104).

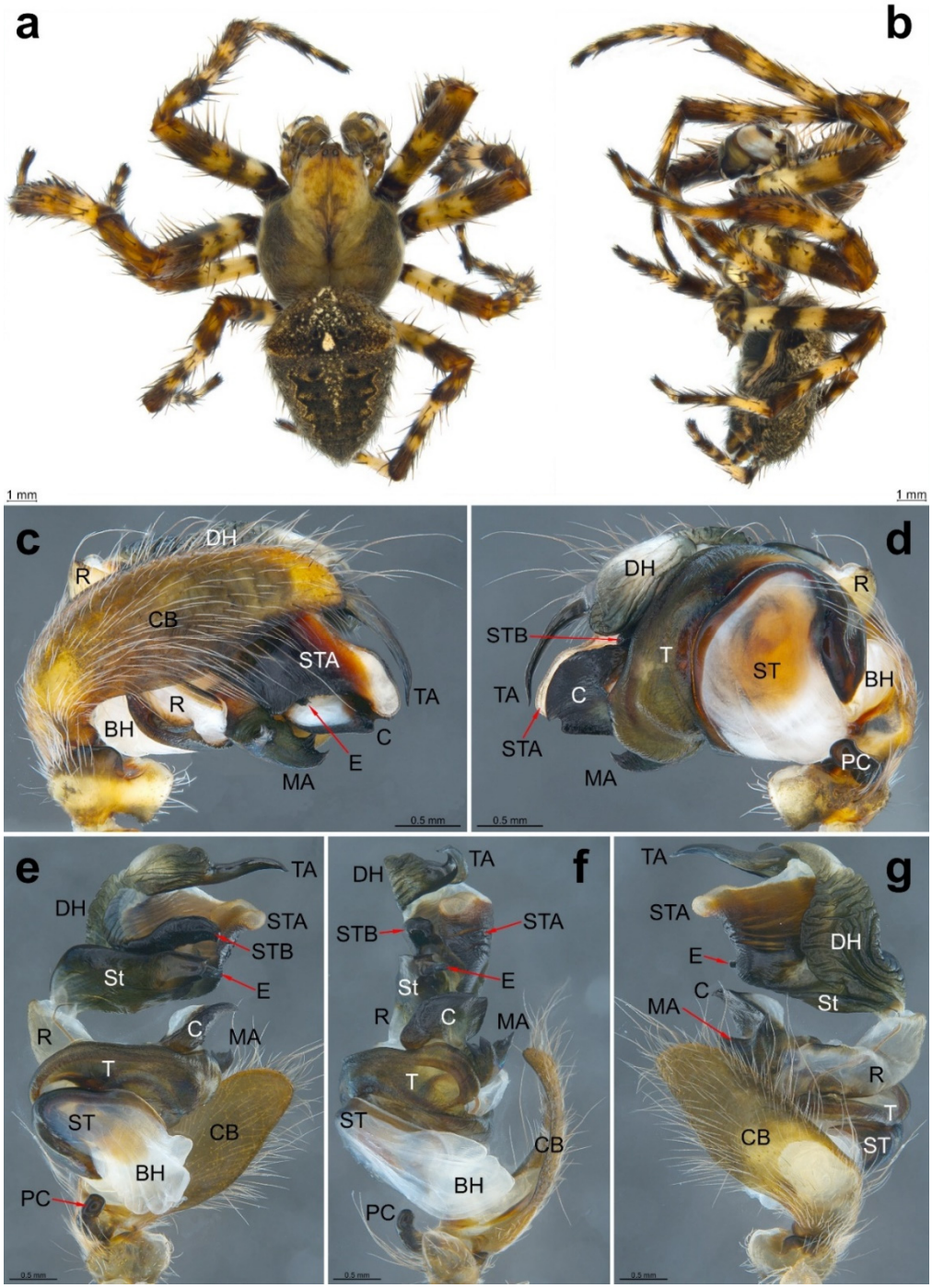


Figure 5. *Araneus angulatus* male. Neotype male (RV04, NHRS-TOBI000005697) habitus (**a**) dorsal, (**b**) lateral. Right male palp of co-collected specimen (RV01, USNMENT02419110), (**c**) prolateral, (**d**) retrolateral; expanded (**e**) ventral, (**f**) prolateral, (**g**) dorsal. Abbreviations: BH, basal hematodocha; C, conductor; CB, cymbium; DH, distal hematodocha; E, embolus; MA, median apophysis; PC, paracymbium; R, radix; ST, subtegulum; STA, subterminal apophysis A; STB, subterminal apophysis B; T, tegulum; TA, terminal apophysis.

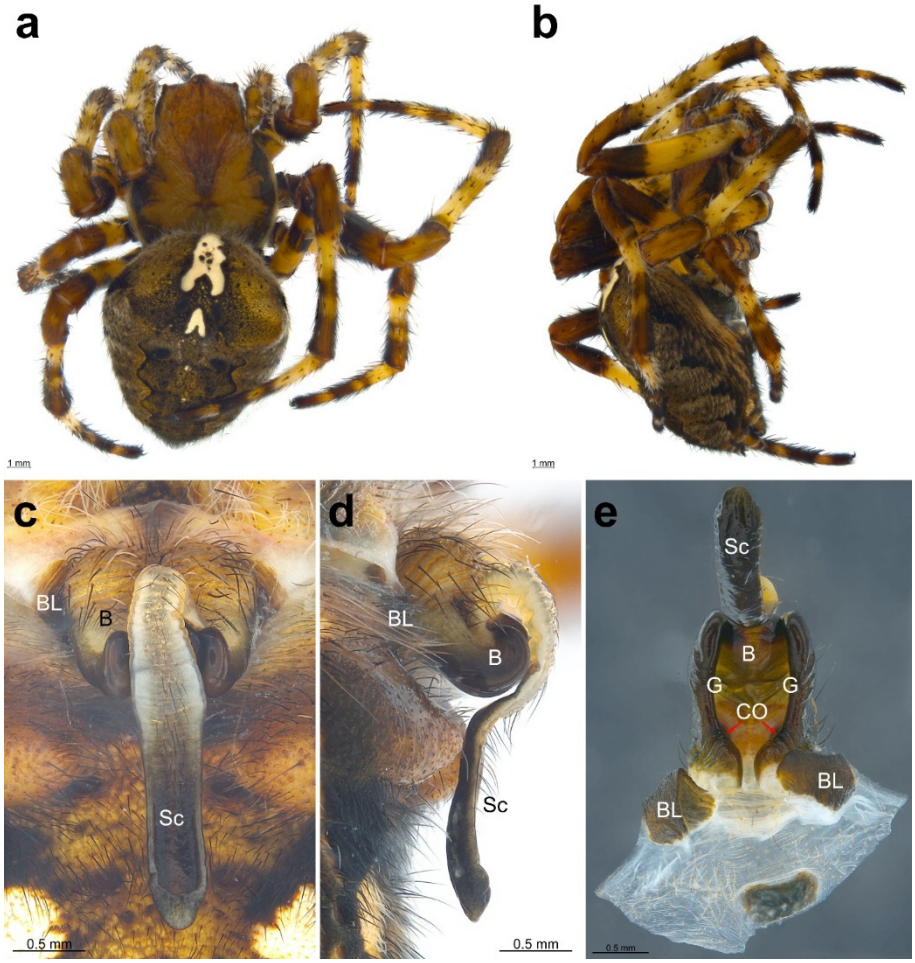


Figure 6. *Araneus angulatus* female habitus and epigynum (RV08, NHRS-TOBI000005698). Dorsal (**a**) and lateral (**b**) habitus. (**c**) ventral, (**d**) lateral, and (**e**) posterior epigynum. Abbreviations: B, base; BL, basal lamella; CO, copulatory opening; G, gonopore; Sc, scape.

Diagnosis: Both sexes of *A. angulatus* differ from the remaining *Araneus* species in Europe by the combination of these easily observed features: (i) large body size (>11 mm in both sexes); (ii) paired humps on anterior part of abdomen; (iii) white patch on frontal dorsum (Figure 4). When dissected or expanded, the male palp reveals an additional sclerite termed by Thaler [61] (figs. 24–26) as subterminal apophysis B (see STB in Figure 5d–f). This sclerite was not specifically labeled as distinct from the subterminal apophysis by other authors. In *A. angulatus*, STB is distinctly tubular (Figure 5e). For further putative diagnostic features, consult prior work on *A. angulatus* [58,59,62–65].

Description: Male (neotype, Figure 5). Total length 11.21. *Prosoma* 5.10 long, 3.28 wide. Sternum 2.94 long, 1.91 wide. AME diameter 0.27, ALE 0.15, PME 0.24, PLE 0.15. AME separation 0.27, PME separation 0.15, PME-PLE separation 0.89, AME-ALE separation 0.71, AME-PME separation 0.17, ALE-PLE separation 0.02. Clypeus height 0.21. *Appendages* Leg I length 20.26 (Fe 6.14, Pa 2.69, Ti 5.53, Me 4.33, Ta 1.57). *Opisthosoma* with paired lateral humps and a white patch on frontal dorsum, 6.52 long, 4.61 wide, 3.03 high. Female (RV08; Figures 4 and 6). Total length 17.12. *Prosoma* 9.57 long, 6.90 wide. Sternum 3.36 long, 3.00 wide. AME diameter 0.30, ALE 0.19, PME 0.27, PLE 0.22. AME separation 0.36, PME separation 0.30, PME-PLE separation 1.39, AME-ALE separation 1.25, AME-PME separation 0.29, ALE-PLE separation 0.04. Clypeus height 0.48. *Appendages* Leg I length 26.55 (Fe 7.33, Pa 3.08, Ti 7.18, Me 6.58, Ta 2.38). *Opisthosoma* 11.40 long, 8.46 wide, 6.25 high.

Both sexes have 4 prolateral and 3 retrolateral teeth on the chelicerae.

Variation: Male total body length from 11.21 to 13.72 (N = 3), female total body length from 11.50 to 17.12 (N = 4).

Natural History: *Araneus angulatus* s.s. is a well-known European species, which is found in dry habitats on pines and junipers [64]; juveniles and females construct their orb webs mostly on tree trunks, in forest edges in the lowland, rarely in low mountain range, also on buildings [58,59,63,64]. iNaturalist [66] lists 5284 verifiable or research grade records of its distribution and phenotypic variation and phenology.

Distribution: The World Spider Catalog [13] summarizes the range of *A. angulatus* as Europe, North Africa, Turkey, Russia (Europe to Far East), Iran, Central Asia, and Republic of Korea. Figure 2 maps records from GBIF, GenBank, and BOLD.

4. Discussion

Given the nomenclatural importance of the name *Araneus angulatus* Clerck (1757) in spider taxonomy, it is surprising the species has received so little attention in the taxonomic, phylogenetic, and evolutionary literature. It is not common in Fennoscandia, being confined to warm pine forests, occasionally oak forests, and most often barren pine forests. In Sweden, it is red listed as Near Threatened (NT) [67], also in Finland and Norway.

It was also surprising to realize that the name has lacked a type specimen or series since at least 1965 and at most 1858 [14,55]. The lack of type material made important spider names at the species, genus and family rank at best ambiguous, and given the plethora of subspecies until recently, indecisive. It is also surprising to note that landmark publications in araneid phylogeny omitted *A. angulatus* as an exemplar [68], although Scharff et al. [15] did say "the identity of *Araneus angulatus* and its relatives should be an urgent research priority."

The concept of the name *Araneus angulatus* was further obscured by the description of numerous subspecies. Franganillo [69–71] described ten subspecies of *A. angulatus* and Simon [72] described two more. Breitling et al. [56] synonymized nine of them and designated one as a *nomen dubium* and Sherwood et al. [73] synonymized the last. Many of these subspecies names have existing type specimens but all are irrelevant to the typification of *A. angulatus*. In particular, WSC [13] lists a syntype of *A. a. personatus* Simon 1929 in the Muséum national d'Histoire naturelle in Paris under the "Type Repository" section of the *A. angulatus* page, but they are types of the subspecies *personatus*, not of the nominate *A. angulatus*. None of the authors concerned with its subspecies designated a neotype for the nominotypical form. When the ICZN in 1892 settled on Linnaeus [10] as the start of zoological nomenclature, zoology assigned the burden of nomenclatural typification to *diadematus*, not *angulatus*.

We cannot say with certainty that any of the non-*angulatus* clades in Figure 3 are valid species, because we have not seen vouchers for their sequences (if they exist). This paper simply designates a neotype and offers preliminary data and comments for the proper analysis of the *angulatus* species complex in the future. The COI data do imply that true *A. angulatus* and the southeastern European "clade 2" forms are distinct and possibly sympatric in Turkey. The Asian group is clearly geographically structured, but the distances are small for among species (2–2.5%) and large for within species [74]. They may be misidentified *A. ventricosus* but both names have been repeatedly used in the Chinese literature (see below).

Current data show that *A. angulatus* s. lat. is widely distributed. Country centroids or approximations used in Figure 2, if correctly identified, point to areas that are undercollected and that could be more undescribed species of "*A. angulatus*."

Raper and Sivell's chromosome level assembly is an important addition to our knowledge of *A. angulatus* [23]. The genome quality metrics are impressive (see above). COI data indicate that this specimen is conspecific with the neotype (Figure 3). Their paper contains an ambiguity

as to the sex, and therefore which animal was sequenced, but it does not affect these results: "We present a genome assembly from an individual female *Araneus angulatus* (orb-weaver spider; Arthropoda; Arachnida; Araneae; Araneidae)." (p. 1). "The high-quality genome of *Araneus angulatus* was sequenced from a single male (NHMUK014537398; SAMEA11024980) from Kings Wood, St Austell, England (Figure 1)" (p. 3). "The specimen used for genome sequencing was an adult male *Araneus angulatus* (specimen ID NHMUK014537398, ToLID qqAraAngu1; Figure 1), collected from Kings Wood, St Austell, England, United Kingdom (latitude 50.3045, longitude –4.8001) on 2021-06-28" (p. 4). Their fig. 1 (p 2) is a female.

The complete mitogenome provided by Wang et al. [60] is from Tongxiang County (E120.57, N30.64), Zhejiang Province, China. Given the COI results (Figure 3), and as mentioned above, that specimen may be an undescribed *Araneus* species lurking under the name *A. angulatus* or a misidentification.

The identity of East Asian specimens reported as *Araneus angulatus* also warrants investigation. The specimens illustrated by Zhang [75] (fig. 46.1–3) and Yin et al. [76] (fig. 74a–d) are difficult to assess from the available illustrations, although the male palp in Zhang [75] appears broadly similar to that of *A. angulatus* s.s. The latter figures were seemingly reproduced by Song et al. [77] and Kim & Kim [78].

A second Chinese/Korean form, illustrated by Hu & Wu [79] (fig. 61.1–2), Namkung [80,81] (fig. 19.3a–c) and Kim & Lee [82] (fig. 7A–C), is distinct from *A. angulatus* s.s. in the illustrated genital morphology and habitus. Its scape is shorter and distinctly divided into a proximal wrinkled and distal smooth, spatula-shaped region, and the epigynal base is longer and narrower than in *A. angulatus* s.s. The male palp has a broader terminal apophysis, apparently lacks a pronounced dorsal hook, and differs in the shape of the conductor, which appears either distinctly bifurcate or to have a broad, pronounced subterminal branch (STB). The habitus further differs in its more reddish-brown coloration, pattern of the prosoma and opisthosoma, leg annulation, and possibly also in being less setose (e.g., [81]). The illustrated morphology indicates that these specimens do not represent *A. angulatus* s.s.

Both the nomenclatural history of *A. angulatus* and of its syntype series have been turbulent. This paper serves to clarify the concept of the name, and to provide increased stability to a uniquely important taxon in araneological and zoological systematics.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/taxonomy6040071/s1, Table S1, including GenBank, BOLD, and GBIF accession codes and ancillary data, as well as coordinates, used in Figures 2 and 3. Complete COI tree including all sequences in Figure 3.

Author Contributions: Conceptualization, J.A.C., I.A., M.K. and M.G.; methodology, J.A.C., I.A., M.K. and M.G.; software, J.A.C., I.A., K.-P.Y. and M.G.; validation, J.A.C., I.A., M.G., M.K., K.-P.Y. and R.V.; formal analysis, J.A.C., I.A., M.G., M.K. and K.-P.Y.; investigation, K.-P.Y. and R.V.; resources, J.A.C., I.A., M.G. and M.K.; data curation, J.A.C., I.A., M.G., M.K. and K.-P.Y.; writing—original draft preparation, J.A.C.; writing—review and editing, J.A.C., I.A., M.G., M.K., K.-P.Y. and R.V.; visualization, K.-P.Y. and T.R.L.; supervision, J.A.C.; project administration, J.A.C.; funding acquisition, J.A.C. and M.K. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The original data (GenBank accession codes) are openly available in GenBank https://www.ncbi.nlm.nih.gov/genbank/, 23 September 2026 and the publication is registered in ZooBank: urn:lsid:zoobank.org:pub:C77DAFE1-4468-4654-B680-0BC0A41CE1CC.

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Conflicts of Interest: Although Raul Vicente is employed by the company Pro Natura, Sweden, his contribution to this article was conducted in the absence of any commercial relationship to Pro Natura that could be construed as a potential conflict of interest. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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