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"Morphological" and "molecular" systems of araneoids: an attempt at harmonization with a subsequent testing of the obtained cladogram using web-building characters (Aranei: Araneoidea)

«Морфологическая» и «молекулярная» системы аранеоидов: попытка согласования с последующим тестированием результирующей кладограммы сетестроительными признаками (Aranei: Araneoidea)

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КЛЮЧЕВЫЕ СЛОВА: Araneae, система Araneoidea, морфологические и молекулярные признаки, 'тетрагнатоидная' и 'аранеоидная' ветви, эволюция сетестроения.

ABSTRACT: The 'three step protocol' is proposed here for the purposes of practical taxonomy: (1) choosing the initial cladogram of a taxon, based on morphological characters; (2) correcting it using molecular characters (however, only that new 'molecular clades', which can be confirmed by independent — i.e., non-molecular — methods, should be accepted); (3) testing the obtained 'harmonized morpho-molecular cladogram', using independent behavioral (e.g., web-building) characters (and if they are harmonized too, such a cladogram may be adopted as a 'natural system of the taxon'). For applying this protocol to the superfamily Araneoidea (22 families), the morphological cladogram by Griswold *et al*. [1998] was chosen as the basis; it was subsequently corrected using the well-supported molecular clade 'enlarged Tetragnathoidea' established by Dimitrov *et al*. [2017]. The resulting 'harmonized morpho-molecular cladogram' implies a splitting of a basal araneoid stock into the two principal branches: the 'tetragnathoid branch' (the malkaroid and tetragnathoid lineages) and the 'araneoid branch' (the araneoid, symphytognathoid, linyphioid, cyatholipoid, and theridioid lineages). Web-building characters strongly support such a division, and it seems to be a 'natural system' of the Araneoidea. Two opposite principal trends are evident in the evolution of web-building in the two principal superfamily branches: the transformation of the primary orb-web in 'araneoids' and its complete abandonment in 'tetragnathoids'. The main general evolutionary trend in the araneoid branch is the replacing of the primary orb-web by various versions of sheet-webs: from the basal araneoid lineage (orb-webs only) to the terminal 'araneoid sheet web builders clade' (sheet-webs only), via the intermediate symphytognathoid lineage (both orb- and sheet-webs). The primary sheet-web is probably but a horizontal orb-web reduced up to a central hub lacking the edging spiral, and with radii transformed into vertical support-lines. Such a simplification of the web architecture allows the spiders to simplify their spinning apparatus too, as well as to minimize the required silk volume; both seem critically important during miniaturization, the key evolutionary trend in the symphytognathoid lineage. In addition, Pararchaeidae Forster et Platnick, 1984, Micropholcommatidae Hickman, 1944 and Comaromidae Wunderlich, 2004 are restored as independent families; Sinopimoidae Li et Wunderlich, 2008 is revalidated in the rank of a subfamily of the family Linyphiidae; Oarcinae Simon, 1890 is returned to Mimetidae from Araneidae; Taphiassinae Rix et Harvey, 2010 and Gigiellinae Rix et Harvey, 2010 are relocated to Anapidae from Micropholcommatidae; the placement of *Holarchaea* Forster, 1955 in Anapidae and of *Gaucelmus* Keyserling, 1884, *Hamus* Ballarin et Li, 2015, and *Nescina* Ballarin et Li, 2015 in Synotaxidae are confirmed by new data.

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РЕЗЮМЕ: Для целей практической таксономии (т.е. построения стабильной системы таксона) здесь предлагается «трехшаговый протокол» обращения с комплексами морфологических, молекулярных и поведенческих признаков: (1) выбор исходной морфологической кладограммы таксона; (2) корректировка ее молекулярными данными (при этом принимаются только те новые «молекулярные клады», которые могут быть подтверждены независимыми, т.е. немолекулярными, методами); (3) тестирование результирующей «согласованной морфо-молекулярной кладограммы» поведенческими (например, сетестроительными) признаками (и если согласуются и они, то можно говорить о «естественной системе таксона»). Применительно к надсемейству Araneoidea (22 семейства) за основу выбрана морфологическая кладограмма Griswold *et al.* [1998], которая затем откорректирована введением в нее хорошо поддержанной молекулярной клады «расширенных тетрагнатоидов» (‘enlarged Tetragnathoidea’) по Dimitrov *et al.* (2017). «Согласованная морфо-молекулярная кладограмма» отражает разделение базового ствола аранеоидов на «тетрагнатоидную ветвь» («малкароидная линия» и «тетрагнатоидная линия») и «аранеоидную ветвь» («аранеоидная», «симфитогнатоидная», «линифиоидная», «циатолипоидная» и «теридиоидная» линии). Фундаментальное разделение надсемейства на «тетрагнатоидов» и «аранеоидов» четко поддерживается и сетестроительными признаками, и может быть аттестовано как «естественная система» Araneoidea. Два прямо противоположных основных направления сетестроительной эволюции в двух основных ветвях надсемейства — это трансформация исходной колесовидной сети в «аранеоидах» и полный отказ от нее в «тетрагнатоидах». Главное направление эволюции в аранеоидной ветви — это замещение исходной колесовидной сети различными вариантами покровных сетей: от базальной «аранеоидной линии» (только колесовидные сети) к терминальной «кладе строителей покровных сетей (‘araneoid sheet web builders clade’)» (только покровные сети), через переходную «симфитогнатоидную линию» (есть и колесовидные, и покровные сети). Первичная покровная сеть — это, вероятно, просто горизонтальная колесовидная, редуцированная до центрального хаба, лишенного обрамляющей спирали, и с радиусами, превращенными в вертикальные поддерживающие тяжи. Подобное упрощение сетевой архитектуры позволяет упростить также и паутинный аппарат, а также минимизировать объем используемого паутинного шелка; оба эти фактора критически важны при миниатюризации — ключевом эволюционном тренде в «симфитогнатоидной линии». Кроме того, в настоящей работе восстановлен статус Pararchaeidae, Micropholcommatidae и Comaromidae как самостоятельных семейств; Sinopimoidae восстановлены в ранге подсемейства Linyphiidae; Oarcinae возвращены в Mimetidae из Araneidae; Taphiassinae и Gigiellinae перемещены в Anapidae из Micropholcommatidae; помещение *Holarchaea* в Anapidae, а *Gaucelmus*, *Hamus* и *Nescina* в Synotaxidae подтверждено новыми данными.

1. Introduction

After three (or even four) decades of large-scale using of molecular methods in taxonomy, the taxonomist community had to admit a disagreeable fact: “One important but surprising observation is that morphology, the backbone of museum-based comparative biology, and behaviour, almost uniquely informative in orb-web weaving spiders […], correlates poorly with molecular data. Most of the clades named in this study cannot be corroborated, as far as currently known, by non-molecular data” [Scharf *et al*., 2020: 16]. Malicious gossip has it that the taxonomic samples of quite good coordination between morphological and molecular data seem to be lucky accidents rather than regular occurrences.

The problem of coordination between molecular data and morphological and behavioral ones have been discussed repeatedly (e.g., Lopardo *et al*. [2011]; Frick & Scharff [2014]); however, the results of so-called ‘combined analyses’, as a rule, seem controversial and cannot be presented in the form of conventional hierarchal systems of taxa. Therefore, a formalized protocol is badly needed: how should a taxonomist operate, step by step, constructing the system of a taxon, if morphological and molecular data are antagonistic ‘edge against edge’ and lead to mutually exclusive results? Which witness testimony should considered by default as more convincing in such a trail?

At first glance the following ranking of these character classes seems clear: the modern phylogenetic paradigm is based on undoubted supremacy of molecular methods, and morphology may be permitted only to seek corroborations for an already generated molecular cladogram. Moreover, even such ‘morphology corroborations’ are estimated as optional (“If it works, it’s fine, and if it doesn’t, it will do anyway”), whereas ‘morphology objections’ may (or should) be ignored. This view is postulated sometimes with a shocking straightforwardness. As a result, we are facing a lot of ‘virtual clades’: “Few of these groups [clades newly established by molecular methods] are currently corroborated by morphology, behavior, natural history, or biogeography" [Scharff *et al*., 2020: 1].

However, for the tasks of practical taxonomy (in contrast to those of molecular genetic as such), the 'morphological' systems have such a serious advantage as stability; they are at least not altered beyond recognition every two or three years, as it happens quite frequently with their 'molecular' competitors. So, the protocol proposed here for constructing the system of a taxon is based on the harmonization of three character complexes (morphological, molecular, and behavioral), but with some sort of 'positive discrimination' of morphological data. There are three steps:

First, a cladogram is based on morphological characters only. 'Morphological characters' we have in mind here are all that can be touched-and-felt (by means of a microscope, microtome, *etc*.) and preserved as a photograph.

Second, this initial morphological cladogram is tested and corrected by molecular methods. The most important thing is that the newly recognized 'molecular clades' should not be taken in account until they are supported by independent (i.e., non-molecular) synapomorphies better than competitive clades of an earlier, purely morphological, cladogram. Drawing a parallel with law: in a criminal case of *Molecules vs. Morphology*, the 'morphological' party takes its positions by default, 'under natural law'; accordingly, it is a 'defendant' protected by the presumption of innocence, and the burden of proof is on the 'accuser', i.e., the 'molecular' party.

Here is yet another legal parallel. Let us say the police got its hands on a wiretap detailing all the dirty work of a mafia boss. However, that material will be of no value in a court of law unless it is backed up by evidence, witness statements, *etc*. So, the molecular sequences in question (even if they are read correctly) are just such a 'wiretap'; they are just a reason to launch a 'proper criminal investigation', which might (or might not) find some 'admissible evidence': that is, SEM-images, histological sections, *etc*.

Finally, the resulting 'harmonized morpho-molecular' cladogram is tested by the third independent group of characters, behavioral ones. And if they seem harmonized too, the proposed cladogram may be appreciated as a 'natural system of the taxon'. The spiders are especially good subjects in this respect due to such a remarkable complex of behavioral characters as web-building.

2. Harmonization of 'morphological' and 'molecular' systems of the superfamily Araneoidea

Let us apply the proposed 'three step protocol' to a system of araneoids. Araneoidea is the largest superfamily in the order Araneae, comprising 22 families and more than one third of spider species; its monophyly is strongly supported by both morphological and molecular data. There is a conventional morphological system of the superfamily [Griswold *et al*., 1998], revised recently by molecular methods [Dimitrov *et al*., 2017]. In addition, the webs and web-building behavior of araneoids are extremely diverse, and thus seem a remarkable tester for the 'harmonized morpho-molecular' cladogram of the superfamily.

2.1. System of Araneoidea, general outline: the fundamental division into 'tetragnathoids' and 'araneoids'

To avoid terminological debates focusing on the ranks of subordinated taxa (the 'Linnaean rank system': [Agnarsson, 2004]), we prefer to use here, following to Griswold *et al*. [1998], the taxonomically neutral terms 'lineages' and 'branches' for the main monophyletic units of Araneoidea ranking higher than family (e.g., 'linyphiod lineage' or 'linyphioids': Linyphiidae + Pimoidae).

Four new araneoid clades and their rankings were recognized by Griswold *et al*. [1998: fig. 7]: the 'cyatholipoid lineage' (Cyatholipidae plus Synotaxidae *s.l.*), the 'spineless femur clade' ('theridioid lineage' plus 'cyatholipoids'), the 'araneoid sheet web builders' ('linyphioids' plus the 'spineless femur clade'), and the 'reduced piriform clade' ('symphytognathoids' plus 'araneoid sheet web builders'). This, terminal, branch of the araneoid tree is accepted by us without serious changes. Araneidae have been stated as the sister group to the rest of the araneoids, the 'derived araneoids' clade, and we support this ranking too.

However, Tetragnathidae (including nephilins) is nested by Griswold *et al*. [1998: fig. 7] in the 'derived araneoids' clade, and it was refuted later by molecular methods quite convincingly [Dimitrov *et al*., 2017]. Moreover, several families (Mimetidae, Micropholcommatidae, Holarchaeidae, Pararchaeide, and Malkaridae) have remained without any treatment by Griswold *et al*. [1998], because at that time they were listed in the 'enlarged Palpimanoidea' [Forster, Platnick, 1984; Platnick, Forster, 1987]. Later, Schütt [2000, 2003] refuted the concept of the 'enlarged Palpimanoidea' and returned the above families to Araneoidea, but their relations with other araneoids were still obscure for a long time.

New molecular data, summed by Dimitrov *et al*. [2017], demonstrated first of all a low nodal support for interfamilial relationships in Araneoidea (in comparison with other entelegyne spider lineages): "Nodal support for interfamilial relationships is generally low across Araneoidea, except in a few instances: the clade of Mimetidae plus Arkyidae + Tetragnathidae and the clade of Malkaridae plus Pararchaeidae. […] Nephilidae plus Araneidae form a well-supported clade, and although both groups appear reciprocally monophyletic in some analyses, nodal support for Araneidae is low whereas it is high for the clade of *Nephila* and its closest relatives" [Dimitrov *et al*., 2017: 229].

So, on the one hand, "Only some of the interfamilial groupings, such as the clade [Mimetidae + (Arkyidae + Tetragnathidae)], were recovered with high support" [Dimitrov *et al*., 2017: 229], and such groupings are accepted here. But, on the other hand, those authors, basing on molecular data, declared the polyphyly of Symphytognathoidea, and placed symphytognathoid families in various, very distant, araneoid clades (e.g., mysmenids appeared coupled with tetragnathoids, theridiosomatids with synotaxids, *etc*.) [Dimitrov *et al*., 2017: fig. 2]. In this case the morphological and the molecular data provides mutually exclusive results, and we are faced with a choice (according to the protocol above).

The proposed 'new molecular clades' (e.g., mysmenids + tetragnathoids) have not been supported by any non-molecular synapomorphies; moreover, Dimitrov *et al*. [2017: 228] acknowledged themselves: "The symphytognathoid families constitute a polyphyletic group, although all the nodes involving these interfamilial relationships receive low support values". Therefore, we are following here the traditional, 'morphological' point of view on the 'symphytognathoid lineage' as a monophyletic taxon.

As result, we recognize here the majority of the main araneoid lineages (i.e., 'symphytognathoids,' 'linyphioids,' 'theridioids,' and 'cyatholipoids'), following Griswold *et al*. [1998]; however, 'araneoids' (including nephilids) and especially 'tetragnathoids' and 'malkaroids' are accepted here according to the new molecular data [Dimitrov, Hormiga, 2011; Dimitrov *et al*., 2017]. Thus, superfamily Araneoidea is divided here into two principal branches: the tetragnathoid branch ('tetragnathoid' and 'malkaroid' lineages) and the araneoid branch ('araneoid', 'symphytognathoids', 'linyphioids', 'cyatholipoids', and 'theridioid' lineages); such a 'harmonized morpho-molecular cladogram' is presented at Fig. 1. Nicodamoidea is accepted as the sister-group to Araneoidea in the majority of modern phylogenies [Kallal *et al*., 2018: fig. 1B–F].

2.2. Proposed system of the superfamily Araneoidea, down to subfamilies

Detailed elaboration of the familial/subfamilial composition of the araneoid lineages is presented here; abbreviations of lineage and family names are the same, as in Fig. 1.

1. 'Malkariod lineage' (MA).
1.1. Pararchaeidae Forster et Platnick, 1984 (Par).
1.2. Malkaridae Davies, 1980 (Mal).

Malkaroids are small-sized cryptozoic cursorial araneophages of so-called 'Gondwanan' distribution (Australia, New Zealand, New Caledonia and southernmost South America) and controversial taxonomic position. Its members were in former times listed in various, very distant, spider families, belonging to different superfamilies/infraorders: Palpimanidae, Zodariidae, Archaeidae, Mecysmaucheniidae, Mimetidae, and Araneidae (see review in Hormiga & Scharff [2020]). Finally, Dimitrov *et al*. [2017] united, basing on molecular data, pararchaeids with malkarids in a common lineage and nested it into the superfamily Araneoidea as the sister group of 'tetragnatoids'; the family Pararchaeidae was ranked by them as a subfamily of Malkaridae.

However, pararchaeids are distinguished from the other malkarids by a number of important apomorphies (i.e., the elevated chelicerae arising from a distinct, fully sclerotized foramen in the prosoma; pars cephalica steeply elevated from pars thoracica above level of coxae III or IV; the presence of cheliceral peg teeth and the absence of a tarsal claw on the female pedipalp). Due to the fact that both taxa "turned out to be reciprocally monophyletic" [Hormiga, Scharff, 2020: 348], we prefer to conserve for them ranks of independent sister families.

No suprageneric taxa were distinguished in the family Pararchaeidae by Rix [2006]. Malkarids were divided by Hormiga & Scharff [2020] to the subfamilies Sternoidinae Moran, 1986, Tingotinginae Hormiga et Scharff, 2020 and Malkarinae Davis, 1980.

2. 'Tetragnathoid lineage' (TE).
2.1. Mimetidae Simon, 1881 (Mim).
2.2. Arkyidae L.Koch, 1872 (Ark).
2.3. Tetragnathidae Menge, 1866 (Tet).

'Tetragnathoids' (sensu Dimitrov & Hormiga [2011] and Dimitrov *et al*. [2017]) are the sister group of 'malkaroids' [Hormiga, Scharff, 2020: fig. 2].

Mimetids ('pirate spiders') are known as webless specialized araneophages with sophisticated foraging behavior named 'aggressive mimicry' [Benavides *et al*., 2017]. Their taxonomic position in the superfamily was still controversial for a long time; Forster & Platnick [1984] even attempted to relocate them from Araneoidea to Palpimanoidea, but it was refuted by Schütt [2000] and subsequent authors. Currently, three subfamilies are recognized in Mimetidae: the globally distributed Mimetinae Simon, 1881, the Neotropical Gelanorinae Mello-Leitão, 1935 and the endemic for southernmost South America Oarcinae Simon, 1890 [Platnick, Shadab, 1993].

Recently, Benavides & Hormiga [2020], basing on molecular data and following to Dimitrov *et al*. [2012], nested oarcins in araneids, but we disagree with this relocation. In addition to the webless lifestyle and leg spination with the typically mimetid 'capture basket' [Platnick, Shadab, 1993: figs. 10, 11], the chelicerae of both oarcin genera, *Oarces* Simon, 1879 and *Gnolus* Simon, 1879, possess pore-bearing gland mounds and promarginal peg teeth replacing true teeth [Platnick, Shadab, 1993: figs 16–18 and 21–23], i.e., the key synapomorphies of Mimetidae never reported in Araneidae. Trichobothrial bases in Oarcinae also seem rather 'mimetid' than 'araneid' [Eskov, Marusik, *in prep.*, a].

Arkyids were formerly considered an araneid subfamily, comprising two endemic Australian genera, *Arkys* Walckenaer, 1837 and *Demadiana* Strand, 1929 [Scharff, Coddington, 1997; Framenau *et al.*, 2010]. Later they were re-ranked and relocated: "The arkyines (which we rank at the family level in our revised classification), represented here by nine terminals, are monophyletic and well supported but do not fall within Araneidae (where they are currently classified); instead, the arkyine clade is sister group to Tetragnathidae and this lineage is sister to Mimetidae" [Dimitrov *et al.*, 2017: 229].

The orb-weaving Tetragnathidae were divided by Dimitrov & Hormiga [2011] into five subfamilies: Tetragnathinae Menge, 1866, Leucauginae Caporiacco, 1955, Metainae Simon, 1894, Diphyainae Simon, 1894, and Nanometinae Forster et Forster, 1999. The rank of Diphyaini Simon, 1894 varied in different tetragnathid classifications (cf. Álvarez-Padilla *et al.* [2009] and Dimitrov & Hormiga [2011]); we support the later opinion and consider Diphyainae as a separate subfamily.

3. 'Araneoid lineage' (AR).
3.1. Araneidae Clerck, 1757 (Ara).
3.2. Nephilidae Simon, 1894 (Nep).
3.3. Zygiellidae Simon, 1929 (Zyg).

Araneidae were usually considered formerly (i.e. before the recognizing of 'enlarged Tetragnathoids' by Dimitrov *et al.* [2017] as a sister group of the other Araneoidea (e.g., Scharff & Coddington [1997]; Griswold *et al.* [1998]).

In classification of araneids, we prefer to follow here Scharff & Coddington [1997], who recognized six subfamilies in the family (Araneinae Clerck, 1757, Argiopinae Simon, 1890, Cyrtophorinae Simon, 1895, Cyrtarachninae Simon, 1895, Gasteracanthinae O. Pickard-Cambridge, 1871 and Micratheninae Simon, 1895), mainly corresponding to the araneid subfamilies recognized by Simon (1894); the cyrtarachnin tribe Mastophorini Mello-Leitão, 1931 (the 'bolas spiders,' possessing a unique foraging behavior) are sometimes elevated to the subfamilial rank (see Scharff & Hormiga [2012]). Several new suprageneric clades were recently distinguished in the family cladogram by molecular methods, but the authors frankly reserved: "Few of these groups are currently corroborated by morphology, behaviour, natural history or biogeography" [Scharff *et al.*, 2020: 1]. Kuntner *et al.* [2023] established the new family Paraplectanoididae Kuntner, Coddington, Agnarsson et Bond, 2023 for the monotypical araneid genus *Paraplectanoides* Keyserling, 1886, but its status need clarification.

Nephilids ('golden orbweavers') were for a long time considered a sister-group of Tetragnathidae or even included in tetragnathids as a subfamily (e.g., Levi & Eickstedt [1989]; Zhu *et al.* [2003]), but recently they were with certainty nested into the 'areneoid lineage' [Álvarez-Padilla *et al.*, 2009; Dimitrov *et al.*, 2017; Kuntner *et al.*, 2019].

Zygiellinae was many times relocated from araneids to tetragnathids and vice versa (see review in Gregorič *et al.* [2015]), and finally has been nested in the 'araneoid lineage' too and was elevated to family by Kuntner *et al.* [2019: 563] under the name Phonognathidae Simon, 1894; the latter name was not accepted for reasons of stability by Scharff *et al.* [2020], and we support this opinion.

Kuntner *et al.* [2019: 557 and 563] listed the genera attributed by them to Nephilidae and Zygiellidae (=Phonognathidae) but have not divided these taxa into subfamilies or tribes.

4. 'Symphytognathoid lineage' (SY).
4.1. Anapidae Simon, 1895 (Ana).
4.2. Micropholcommatidae Hickman, 1944 (Mic).
4.3. Comaromidae Wunderlich, 2004 (Com).
4.4. Synaphridae Wunderlich, 1986 (Syn).
4.5. Mysmenidae Petrunkevitch,1928 (Mys).
4.6. Theridiosomatidae Simon, 1881 (Ths).
4.7. Symphytognathidae Hickman,1931 (Sym).

Forster [1959] united the minute, mainly apneumonic spiders of the families Symphytognathidae, Anapidae, Textricellidae, Micropholcommatidae, and Mysmenidae in his Symphytognathidae *s.l.* Later Forster & Platnick [1984] attempted to relocate micropholcommatids with textricellids from Araneoidea to their enlarged Palpimanoidea, but this hypothesis was refuted by Schütt [2000] and subsequent authors. Coddington [1986a, b] suggested that Anapidae, Mysmenidae, and Symphytognathidae form a monophyletic taxon and comprise the sister group of Theridiosomatidae; since then, Symphytognathoidea ('the micro-orbweaver clade' by Miller *et al.* [2009]) of this composition was listed in the majority of spider classifications (e.g., Griswold *et al.* [1998]; Schütt [2003]; Lopardo & Hormiga [2015]). In addition to morphological characters, the monophyly of symphytognathoids seems strongly supported by data on the web structure and web-building behavior (e.g., Coddington [1986a]; Miller *et al.* [2009]). A cladogram of Symphytognathoidea was presented by Lopardo *et al.* [2011] as Theridiosomatidae (Mysmenidae (Synaphridae (Symphytognathidae (Anapidae *s.l.* (Anapinae + Micropholcommatinae))))).

But recently Dimitrov *et al.* [2017: fig. 2], based on molecular data, declared the polyphyly of Symphytognathoidea and distributed symphytognathoid families over various, very distant, araneoid clades: mysmenids appeared coupled with tetragnathoids, theridiosomatids with synotaxids, anapids were divided into 'Anapidae I' and 'Anapidae II' (sic!) and coupled with theridiids and cyatholipids, respectively. However, these 'new molecular clades' are lacking not only morphological, but also a sufficient molecular support: "The symphytognathoid families constitute a polyphyletic group, although all the nodes involving these interfamilial relationships receive low support values" [Dimitrov *et al*., 2017: 228]. Due to these reasons, we conserve here Symphytognathoidea in the traditional status, as a monophyletic taxon.

Regarding symphytognathoid subtaxa, the 'Godwanan' micropholcommatids (ranged in Australia, Tasmania, New Guinea, New Zealand, New Caledonia, Lord Howe Island, and southernmost South America, but with a single fossil member in the Eocene of Europe: [Penney *et al*., 2007; Rix, Harvey, 2010a]) are accepted here as an independent family (see Eskov & Marusik [*in prep.*, b]) in the composition suggested by Platnick & Forster [1986], who united Micropholcommatidae Hickman, 1944 with Textricellidae Hickman, 1945. Later Schütt [2003] synonymized Micropholcommatidae under Anapidae Simon, 1895; Lopardo *et al.* [2011] confirmed the above synonymy and fixed a new rank of micropholcommatids as a subfamily of anapids: "Anapidae is monophyletic and includes a distal clade grouping the micropholcommatid taxa […]. Although Micropholcommatidae could be monophyletic […], treating the latter lineage at the family rank renders Anapidae paraphyletic" [p. 307]. Rix & Harvey [2010a] supported the close relatedness of the two above lineages too; however, they regarded micropholcommatids as not a 'distal clade' of anapids but a sister group of ones and, respectively, considered both lineages as separate families; we support the later point of view.

Anapidae *s.l.* (by Eskov & Marusik [*in prep.*, b]) is a monophyletic clade that comprises three families: (1) Micropholcommatidae Hickman, 1944, with subfamilies Micropholcommatinae Hickman, 1944 and Textricellinae Hickman, 1945; (2) Anapidae *s.str.* Simon, 1895 with subfamilies Taphiassinae Rix et Harvey, 2010 and Gigiellinae Rix et Harvey, 2010 (transferred from micropholcommatids), Holarchaeinae Forster et Platnick, 1984 and Anapinae Simon, 1895 (the rest of the anapid genera, including the basal monotypic *Acrobleps* Hickman, 1979); (3) the well supported 'teutoniellid taxa clade' by Rix & Harvey [2010a], which should be formalizing as an independent family. The key diagnostic characters of the main anapid taxa (i.e., unambiguous synapomorhies found in all of a clade without exception members and never outside it) are as follows: the cheliceral gland mound fussed with a proximal promarginal tooth, and a particular 'key-lock' mode of fixation the bulbus in the naturally expanded condition (Anapidae *s.l.*); the cheliceral promargin with peg teeth replacing true teeth, and a pair of fused setal sockets adjacent to the fang base (Micropholcommatidae); and a pair of pore-bearing carapace depressions strictly above the maxilla (Anapidae *s.str.*).

The case of Holarchaeidae is particularly interesting. The family was established by Forster & Platnick [1984] to accomodate a single genus *Holarchaea* Forster, 1955 from New Zealand and Tasmania. Its taxonomic position was still enigmatic until Dimitrov *et al*. [2017] found that *Holarchaea* is close, according to molecular data, to the anapid genus *Acrobleps* Hickman, 1979, and on this ground synonymized Holarchaeidae under Anapidae. Surprisingly, it turned to be a 'direct hit': our own study of *Holarchaea* microstructures [Eskov, Marusik, *in prep*., b] confirmed that it really is none other than a very aberrant anapid. It possesses the complete set of anapid diagnostic characters, including vestiges of the pore-bearing carapace supramaxillary depression, and should be treated as Anapidae: Holarchaeinae Forster et Platnick, 1984.

Comaromidae was established by Wunderlich [2004a] as an anapid subfamily to comprise the controversial genus *Comaroma* Bertkau, 1889, nested in Anapidae by Kropf [1990a], and later elevated to family rank [Wunderlich, 2011]. The status of Comaromidae Wunderlich, 2004 as a separate symphytognathoid family was supported recently by Eskov & Marusik [2022]. *Comaroma* appeared to lack both of the two unique synapomorfies of Anapidae *s.l*., i.e., the cheliceral gland-mound fused with the proximal promarginal tooth and the pore-bearing depressions at the edge of the carapace, while retaining the lateral paracymbium, the male epiandrous spigots and the suprapedicellar setae, lost in all anapids and symphytognathids. Thus, comaromids seem to be the sister-group of at least the Symphytognathidae + Anapidae *s.l.* branch [Rix, Harvey, 2010a: fig 2, 'EbCY clade'; Lopardo, Hormiga, 2015: fig. 160, 'C-112 clade'], or even of the all other symphytognathoids (including theridiosomatids), united by the presence of a ciliate setae row on the cheliceral retromargin [Forster, 1959; Platnick, Forster, 1989: figs 9–10].

The position of Synaphridae in araneoids was still controversial for a long time. This taxon was established by Wunderlich [1986] as a subfamily of anapids, then elevated to family rank and restricted to a couple of genera, *Synaphris* Simon, 1894 and *Cepheia* Simon, 1894, by Marusik & Lehtinen [2003]. It was nested in Symphytognathoidea [Schütt, 2003], rejected from this lineage by Marusik & Lehtinen [2003] and Lopardo *et al*. [2007] (who place it together with Theridiidae and Cyatholipidae, respectively), and finally returned to symphytognathoids [Lopardo *et al*., 2011; Lopardo, Hormiga, 2015].

Regarding the rest of the symphytognathoid families, they are accepted here within traditional boundaries. Coddington [1986b] has divided theridiosomatids into four subfamilies (Platoninae Coddington, 1986, Epeirotypinae Archer, 1953, Ogulninae Coddington, 1986, and Theridiosomatinae Simon, 1881), and Lopardo & Hormiga [2015] distinguished two subfamilies in mysmenids (Mysmeninae Petrunkevitch, 1928 and Mysmenopsinae Lopardo et Hormiga, 2015), leaving several genera unclassified; Symphytognathidae Hickman,1931 is still undivided to subfamilies or tribes.

5. 'Linyphioid lineage' (LI).
5.1. Linyphiidae Blackwall, 1859 (Lin).
5.2. Pimoidae Wunderlich, 1986 (Pim).

The 'linyphioid lineage,' forming, together with the 'cyatholipoids' and 'theridioids,' a distal branch of the superfamily Araneoidea (i.e., 'clade 12', or 'araneoid sheet web weavers,' according to Griswold *et al*. [1998: 16]) and represents the sister-group of the latter pair (Griswold *et al*., 1998: fig. 7).

Linyphiidae, the second most speciose spider family, comprises four subfamilies: the Holarctic Stemonyphantinae Wunderlich, 1986, the cosmopolitan Erigoninae Emerton, 1882 and Linyphiinae Blackwall, 1859 (divided into the tribes Linyphiini Blackwall, 1859 and Micronetinae Hull, 1920, sometimes regarded as separate subfamilies), and the South Hemisphere Mynogleninae Lehtinen, 1967 [Arnedo *et al*., 2009; Frick, Scharff, 2014].

Interestingly, in linyphids, perfectly characterized and outlined by morphology, molecular data seem controversial: "Most recently, Arnedo *et al*. (2009) have published phylogenies based on both morphology and molecules and with a broader representation of all subfamilies, and this study is currently the most comprehensive in terms of data and taxa for a family level phylogeny of Linyphiidae. The monophyly of the family Linyphiidae is well supported by morphological data (Miller and Hormiga, 2004) and almost all combined analyses (morphology and molecules) of Arnedo *et al*. (2009). However, when molecular data are analysed separately, they do not support the monophyly of Linyphiidae (Arnedo *et al*., 2009)" [Frick, Scharff, 2014: 69–70].

The family Sinopimoidae Li et Wunderlich, 2008 was established for the monotypical genus *Sinopimoa* Li et Wunderlich, 2008, the minute crown-dwelling linyphioid from tropical China [Li, Wunderlich, 2008]. Dimitrov *et al*. [2017] declared that *Sinopimoa* (not included in their analysis) is a linyphiid (and, consequently, Sinopimoidae is a junior synonym of Linyphiidae), and nested it in erigonines: "In addition, *Sinopimoa* shares two Erigoninae synapomorphies (Hormiga, 2000; Miller and Hormiga, 2004): absence of the female palpal claw and a retrolateral tibial apophysis in the male palp, and like many erigonines, is of very small size and has only one dorsal tibial spine in legs III and IV" [Dimitrov *et al*., 2017: 246].

Wunderlich [2020a] resurrected the family Sinopimoidae, and his arguments seem quite convincing to us. Furthermore, besides such unique characters of the male plap as the tegulum, expanded backward up to the patella, and the tibial apophyses, almost twice as long as the tibia itself and provided with a couple of trichobothria, *Sinopimoa* possesses a pointed conical paracymbium completely fussed with the cymbium (in contrast to all the linyphiids), and leg spination with the femoral and metatarsal bristles (in contrast to erigonines) (see Li & Wunderlich [2008: figs. 3, 9, 10, 12]). We are not insisting on the family rank of Sinopimoidae, but in any case it seems to be a separate high-ranking linyphioid taxon, provisionally the subfamily Linyphiidae: Sinopimoinae.

Pimoidae Wunderlich, 1986 was established as a linyphiid subfamily to comprise the controversial genus *Pimoa* Chamberlin et Ivie, 1943 with a relict disjunct distribution (mountains of southern Europe, Himalaya, southern China and western Nearctic), previously transferred by Wunderlich [1979] to Linyphiidae from Metidae (= Tetragnathidae). Hormiga [1993] elevated it to a separate family, the sister-group to Linyphiidae.

Several linyphiid taxa were replaced (mainly due to molecular data) to Pimoidae: "These [molecular] results could support a transfer of *Weintrauboa* and *Putaoa* to Linyphiidae, as members of the subfamily Stemonyphantinae (which would need a significant revision of its morphological diagnosis) and re-circumscribe Pimoidae to include only *Pimoa* and *Nanoa*. Such a hypothesis is in conflict with the results of morphological analyses (e.g., Hormiga, 2008; Hormiga and Tu, 2008). […] Preliminary analyses of the combined and molecular data robustly support pimoid monophyly including *Weintrauboa* and *Putaoa*, and linyphiid and linyphioid monophyly (Hormiga and Dimitrov, 2010)" [Dimitrov *et al*., 2017: 246]. But a short time later these genera were returned to Linyphiidae: Stemonyphantinae [Hormiga *et al*., 2021].

Presently a single member of Pimoidae, except of *Pimoa*, is an enigmatic monotypical genus *Nanoa* Hormiga, Buckle et Scharff, 2005 from California and Oregon [Hormiga *et al*., 2005]. Its taxonomic position remains ambiguous. Wunderlich [2008a: 127] attributed *Nanoa* to the extinct family Pumiliopimoidae Wunderlich, 2008; it probably deserves the status of an independent linyphioid family or subfamily. By the way, the trichobothrial bases of *Pimoa* and *Nanoa* sharply differ from each other [Eskov, Marusik, *in prep*., a].

6 'Cyatholipoid lineage' (CY).
6.1. Synotaxidae Simon, 1894 (Syt).
6.2. Physoglenidae Petrunkevitch, 1928 (Phy).
6.3. Nesticidae Simon,1894 (Nes).
6.4. Cyatholipidae Simon, 1894 (Cya).

The 'cyatholipoid lineage' (Cyatholipidae + Synotaxidae *sensu* Forster *et al*. [1990]) and the 'theridioid lineage' (Theridiidae + Nesticidae) were stated by Griswold *et al*. [1998: fig. 7] as sister-groups forming the terminal clade of the araneoid cladogram: the 'spineless femur clade', Clade 10. Ramírez *et al*. (2022: fig. 1), according to both morphological and molecular data, replaced nesticids from 'theridioids' to 'cyatholipoids'. Kulkarni *et al*. (2021), basing solely on molecular data, nested cyatholipids together with Linyphiidae + Pimoidae, but this nesting lacks any morphological support.

Forster *et al*. [1990] united the monotypical tribe Synotaxini Simon, 1894 (from theridiids), subfamily Physogleninae Petrunkevitch, 1928 (from pholcids) and numerous newly described southern temperate (New Zealand, Australia and southern South America) taxa in the 'enlarged Synotaxidae' with three subfamilies (Synotaxinae Simon, 1894, Physogleninae Petrunkevitch, 1928, and Pahorinae Forster, 1990), and recognized the Cyatholipidae Simon, 1894 as its sister-group.

However, Dimitrov *et al*. [2017] redelimited Synotaxidae to a single Neotropic genus, *Synotaxus* Simon, 1895, and united all the other synotaxids [by Forster *et al*., 1990] in Physogleninae, elevated the latter to the family rank and dividing it into subfamilies Physogleninae and Pahorinae. "We distinguish Synotaxidae and Physoglenidae as separate families to recognize the separate affinities on our [molecular] tree and to make each family easier to diagnose" [Dimitrov *et al*., 2017: 241]. Moreover, Synotaxidae s.str. and Physoglenidae were nested by them in distant araneoid branches, as the sister-groups of theridiosomatids and linyphioids, respectively [Dimitrov *et al*., 2017: fig. 2], although they noted themselves: "Support values for most nodes at the base of linyphioids (Linyphiidae plus Pimoidae) are low, as well as that of the node that indicates that the sister group of 'linyphioids' is the Physogleninae plus Pahorinae synotaxid clade" [Dimitrov *et al*., 2017: 229].

And finally, Ramírez *et al*. [2022], based on both morphological and new molecular data, transferred the controversial theridiid genus *Tekellina* Levi, 1957 and three nesticid genera, *Gaucelmus* Keyserling, 1884, *Hamus* Ballarin et Li, 2015, and *Nescina* Ballarin et Li, 2015, into Synotaxidae *s.str.* It should be noted that all the three relocated nesticid genera are sharply distinguished by the trichobothrial bases from all the rest of the members of Nesticidae, and are very similar to each other and to *Tekellina* and *Synotaxus* [Eskov, Marusik, *in prep*., a]. In addition, Physoglenidae and such 'newly enlarged' Synotaxidae were recognized as independent but sister families [Ramírez *et al*., 2022: fig. 1].

According the same data, both morphological and new molecular, Nesticidae are the sister group of the couple Synotaxidae + Physoglenidae, not of Theridiidae [Ramírez *et al*., 2022: fig. 1]. Lehtinen & Saaristo [1980] established two tribes (instead of subfamilies) in family Nesticidae, Nesticini Simon, 1894 and Nesticellini Lehtinen et Saaristo, 1980, but left the well-known Nearctic genera *Gaucelmus* and *Eidmannella* unclassified. *Gaucelmus* (as well as the recently described nesticid genera *Nescina* and *Hamus*) is already transferred to Synotaxidae (see above); *Eidmannella* differs from the all 'typical nesticids' (F. Ballarin, pers.com.) and can be listed as an '*Eidmannella* clade'.

The South Hemisphere Cyatholipidae (South Africa, Australia, and New Zealand; the other supposed locality, Jamaica, seems to be erroneous) is still undivided into conventional subfamilies or tribes [Griswold, 2001].

7. 'Theridioid lineage' (TH).
7.1. Theridiidae Sundevall, 1833 (Thr).

After the relocation of Nesticidae by Ramírez *et al*. [2022] to 'Cyatholipoids', the sister lineage of the 'spineless femur clade,' Theridiidae remained the only member of the 'rheridioid line' [Griswold *et al*., 1998: fig. 7].

Agnarsson [2004] recognized six theridiid subfamilies: Argyrodinae Simon, 1881, Hadrotarsinae Thorell, 1881, Latrodectinae Petrunkevitch, 1928, Pholcommatinae Simon, 1894, Spintharinae Simon, 1894 and Theridiinae Sundevall, 1833. Hadrotarsines were formerly described as an independent family or listed in Haplogynae (see discussions in Forster *et al*. [1990] and Agnarsson [2004]), but nowadays they are universally recognized as a subfamily.

2.3. Extinct araneoid families

Araneoids appeared in the fossil record in the Triassic, as Araneoidea *incertae sedis* [Selden *et al*., 1999]. In addition to the fossil members of the extant araneoid families (e.g., theridiosomatids from Lower Cretaceous deposits of Siberia [Selden, 2010] and Middle Cretaceous ambers of France [Penney, 2014], micropholcommatids from Paleogene ambers of France [Penney, 2007]), ten extinct araneoid families were established:

1. Jurassic
1.1. † Juraraneidae Eskov, 1984 from the Upper Jurassic deposits of Siberia [Eskov, 1984; Selden, 2012].

2. Cretaceous: all from Middle Cretaceous ambers, Burmese and Jordanian [Wunderlich, 2008b, 2012, 2015, 2020b; Wunderlich, Müller, 2018, 2021, 2022].
2.1. † Burmascutidae Wunderlich, 2008.
2.2. † Cretamysmenidae Wunderlich in Wunderlich et Müller, 2018.
2.3. † Leviunguidae Wunderlich in Wunderlich et Müller, 2018
2.4. † Megasetidae Wunderlich in Wunderlich et Müller, 2021.
2.5. † Zarqaraneidae Wunderlich, 2008.

3. Paleogene: all from European ambers, Baltic and Bitterfeld [Wunderlich, 2004b, 2008a, b].
3.1. † Baltsuccinidae Wunderlich, 2004.
3.2. † Praetheridiidae Wunderlich, 2004.
3.3. † Protheridiidae Wunderlich, 2004.
3.4. † Pumiliopimoidae Wunderlich, 2008.

The monotypical Juraraneidae was established by Eskov [1984] for an adult male araneoid *Juraraneus rasnitsyni* Eskov, 1984 from Jurassic deposits of Transbaikalia, on account of it showing a unique mosaic of characters also found in other araneoid families. *Juraraneus* was later redescribed by Selden [2012], who considered it "a cribellate araneoid, and thus forms

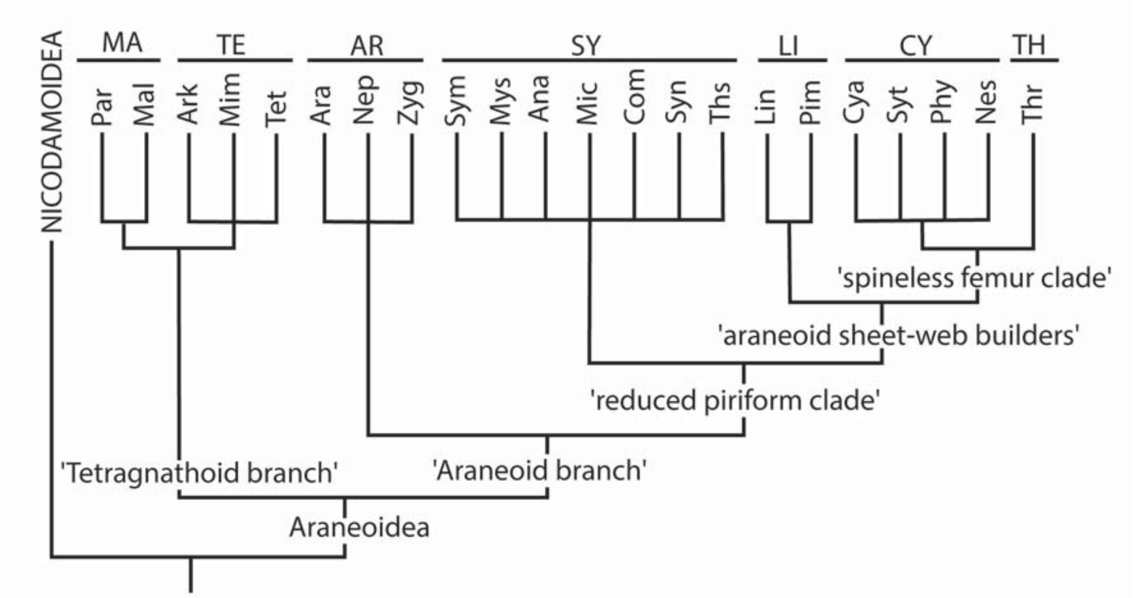

Fig. 1. 'Harmonized morpho-molecular cladogram' for Araneoidea, with main clade names.

Abbreviations of clades: AR —Araneoid, CY — Cyatholipoid, LI — Linyphioid, MA — Malkaroid, SY — Symphytognathoid, TE — Tetragnathoid, TH — Theridioid. Abbreviations of families: Ana — Anapidae, Ara — Araneidae, Ark — Arkyidae, Com — Comaromidae, Cya — Cyatholipidae, Lin – Linyphiidae, Mal — Malkaridae, Mic — Micropholcommatidae, Mim — Mimetidae, Mys — Mysmenidae, Nep — Nephilidae, Nes — Nesticidae, Par — Pararchaeidae, Phy — Physoglenidae, Pim — Pimoidae, Sym — Symphytognathidae, Syn — Synaphridae, Syt — Synotaxidae, Tet — Tetragnathidae, Thr — Theridiidae, Ths — Theridiosomatidae, Zyg — Zygiellidae.

Рис. 1. «Согласованная морфо-молекулярная кладограмма» Araneoidea с названиями всех клад.

part of the cribellate stem-group orbweavers which pre-dated the ecribellate araneoids found today" [Selden, 2012: 315]. It should be noted, however, that the cribellum as it is indistinguishable in *Juraraneus*, while the structure interpreted as a 'calamistrum' is situated on metatarsi-4 strictly ventrally, i.e., conversely of the known calamistrums (see Selden [2012: figs. 2–3]). Interpretations of the male palpal structures of *Juraraneus* by Eskov [1984] and Selden [2012] differ in details but are consistent in stating that the palp is complex and has a distinct basolateral paracymbium, typical of araneoids (see Selden [2012: figs. 5, 6]). Therefore, if *Juraraneus* 'calamistrum' (by Selden [2012]) will turn out to be a real calamistrum, Juraraneidae would be considered a 'cribellate araneoids', a basal sister group of all the other, ecribellate araneoids.

It should be confessed that the listed extinct taxa do not seem to be supported by unique synapomorphies as certainly as the extant taxa of the family level; some of them (e.g., Zarqaraneidae or Protheridiidae) are undoubtedly polyphyletic, artificial groups. Therefore, at present we refrain from nesting these taxa in the proposed cladogram (Fig. 1).

3. Testing the presented 'harmonized morpho-molecular cladogram' using web-building characters

Griswold *et al*. [1998: fig. 7] used in their cladogram the web architecture and other behavioral characters alongside with morphological ones (15 characters of 93), and even named one of the clades according to web shape (the 'araneoid sheet web builders', Clade 12). We, however, regard the behavior (in particular, the web-building) as a separate complex of characters, independent of both morphological and molecular ones, and due to this reason available to testing them. So, let us estimate, according to the above-proposed 'three step protocol,' the correspondence of the araneoid web-building characters with the presented 'harmonized morpho-molecular cladogram' of the superfamily (Fig. 1).

3.1. Big picture of web-building trends

First of all, each of the main clades in the 'morpho-molecular cladogram' is strongly supported by some web-building character (Fig. 2). These are as follows: (1) origin of an ancestral orb-web — for Araneoidea (Clade 28 by Griswold *et al*. [1998]); (2) origin of sheet-webs, replacing (at least partially) horizontal orb-webs — for the 'reduced piriform clade' (Clade 20 by Griswold *et al*. [1998]); (3) complete abandonment of orb-webs — for the 'araneoid sheet web builders' (Clade 12 by Griswold *et al*. [1998]); and (4) origin of sticky silk wrap attack behavior (character 93 by Griswold *et al*. [1998]) — for the 'spineless femur clade' (Clade 10 by Griswold *et al*. [1998]).

The first splitting of the basal araneoid stock into two principal branches, 'araneoids' and 'tetragnathoids',

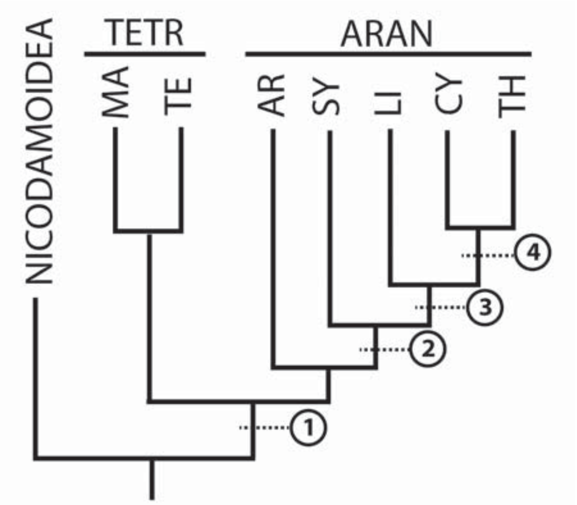

Fig. 2. Main web-building characters of main clades of the ‘harmonized morpho-molecular cladogram’ for Araneoidea. Abbreviations of lineage names as in Fig. 1.

1 — origin of the ancestral orb-web; 2 — origin of the sheet-webs, replacing (at least partially) horizontal orb-webs; 3 — complete abandonment of orb-webs; 4 — origin of sticky silk wrap attack behavior.

Рис. 2. Главные признаки сетей основных клад «гармонизированной морфо-молекулярной кладограммы» Araneoidea.

1 — происхождение анцестральной колесовидной сети; 2 — происхождение покровных сетей, заменяющих (как минимум частично) горизональные колесовидные; 3 — полная утрата колесовидных сетей; 4 — происхождение атакующего поведения с опутыванием жертвы клейкими паутинными нитями.

is perfectly confirmed by web-building data too. The general evolutionary trend in the araneoid branch is their replacing of the primary orb-web by various versions of sheet-webs: from the basal araneoid lineage (orb-webs only) to the terminal ‘araneoid sheet web builders clade’ (sheet-webs only), via the intermediate symphytognathoid lineage (both orb- and sheet-webs). The general evolutionary trend in the tetragnathoid branch is their complete abandonment of the primary orb-web, retained only in Tetragnathidae, and the emergence of a great number of webless cursorial and sit-and-wait predators — all the rest of the members of the ‘tetragnathoid lineage’ (Arkyidae and Mimetidae) and all members of the malkaroid lineage.

At the same time, there are no cases of replacing the primary orb-web by à capture web of any other type in tetragnathoid branch. And vice versa: webless cursorial and sit-and-wait predators are completely absent in the araneoid branch. Several ‘araneoids’ abandoned web-building, indeed, but all these cases are caused by particular lifestyles (kleptoparasitism, etc).

3.2. Particular cases of web-building: deviations from the mode usual for a family

Thus, the big picture seems quite consistent: the web-building characters really support the main clades of the proposed cladogram, especially the fundamental splitting of the superfamily Araneoidea into the two principal branches, ‘araneoids’ and ‘tetragnathoids.’ Moreover, these characters seem even more convincing in this respect than strictly morphological ones. But could it be that the devil is in the details, and ‘exceptions to the rules’ will turn out as numerous and serious, that devalues such a ‘rule’?

Let us therefore look into the ‘exceptions’. Let us pay a particular attention to the deviations from the web-building mode (or web abandonment) usual for a lineage or family, and search regularities in such deviations. These cases are summed in Figs 3 and 4; the numbers of the cases in the cladograms are as in text bellow.

(1) Mimetids (‘pirate spiders’ or ‘cannibal spiders,’ which, more aptly, can also be named ‘werewolf spiders’) are well known as webless specialized araneophages, using the so-called ‘aggressive mimicry’: they invade spider webs and imitate the movements of a prey ensnared on the host web or the courtship movements of the conspecific male to attract the resident female and then attack it. In addition to such web-invading, mimetids are actively searching for prey, cursorial spiders and insects [Kloock, 2001; Benavides, Hormiga, 2020]. And the unusual mode of using silk by these webless spiders was discovered in two Neotropical *Mimetus* Hentz, 1832 species: the females guard the eggs and juveniles in a ‘nursery web’ consisting of non-sticky silk lines [Benavides *et al*., 2017: 392, fig. 18D].

(2) Arkydae reportedly “spin no web at all (or very little)” [Scharff, Coddington, 1997: 405]. *Demadiana* Strand, 1929 and at least partially *Arkys* Walckenaer, 1837 (= *Archemorus* Simon, 1893) species are webless sit-and-wait predators [Mascord, 1968; Heimer, 1984; Framenau *et al*., 2010]. However, some *Arkys* species use during the hunting a single non-sticky horizontal silk line: “I observed webs and associated behaviour of *Arcys* and some prey. For want of a more convenient term ‘web’ is used here to denote the silk line (interpreted as a reduced web) made by *Arcys*. It is not a web in the sense of a snare” [Main, 1982: 425], and further: “The non-viscid, horizontal, single-line suspension web of *Arcys* appears to be a previously unrecorded variant in the reduction sequence of the orb web. It may represent the primary horizontal strand of an araneid orb web frame” [Main, 1982: 430].

(3) There are several cases of the abandonment of web-building activity in the orb-weaving family Tetragnathidae. There is the monophyletic ‘spiny leg clade’ in the genus *Tetragnatha* Latreille, 1804, comprising 12 endemic Hawaiian species, all members of which use various webless lifestyles: “Some are very active, cursorial predators, while others behave as more typical sit-and-wait foragers, spending long periods hanging in mid-air, legs outstretched” [Gillespie, 1992: 176]; in addition, individuals of certain *Tetragnatha* species are optionally capable of capturing prey without the use of a web [Dąbrowska-Prot, Łuczak, 1968; Levi,

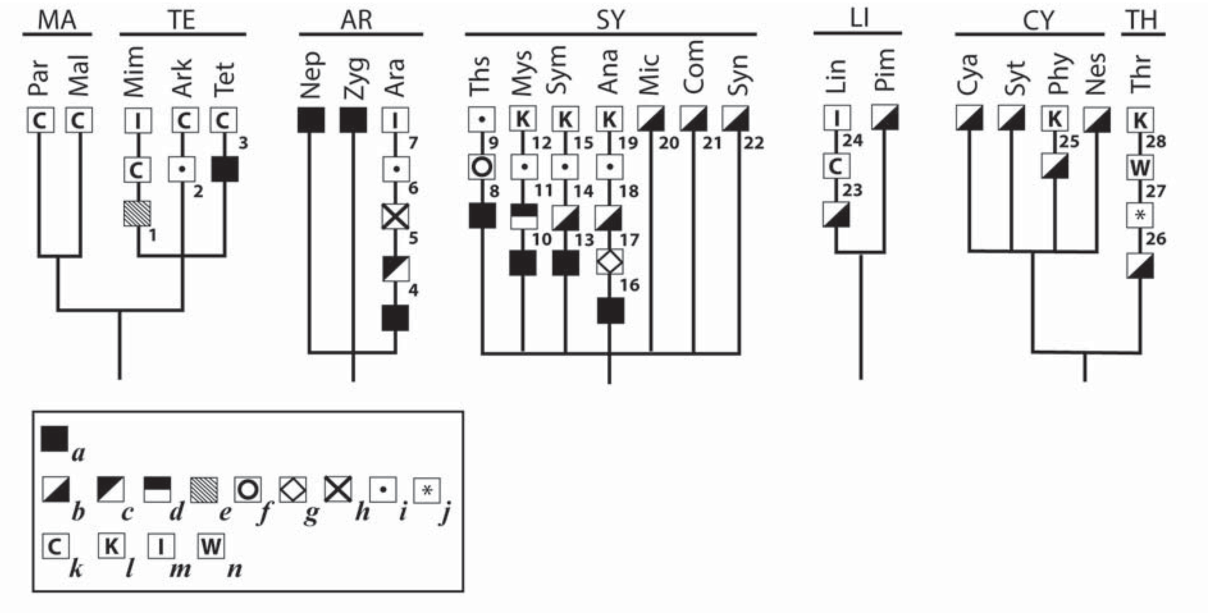

Fig. 3. Transformations and abandonments of the ancestral orb-web in various araneoid lineages (detailed). For numbers of cases, see text (section 3.2).

a — basal type (orb-web), *b–j* — intermediate types (another webs), *k–n* — terminal types (complete abandonment of webs): *a* — orb-webs (including 'spherical webs' of mysmenids, 'ladder web' of *Scoloderus*, 'star-shaped web' of *Wixia*, *etc*.); *b* — sheet-webs (including tangle-webs, 'chicken-wire web' of *Synotaxus*, 'H-shape webs' of spintharines, *etc*); *c* — 'basilica web' of cyrtophorines; *d* — 'intermediate orb-sheet' microweb of *Trogloneta granulum*; *e* — 'nursery web' of *Mimetus*; *f* — vertical 'water-touching web' of *Wendilgarda*; *g* — horizontal 'floating web' of *Conculus lyugadinus*; *h* — 'bolas' of mastophorines; *i* — non-sticky 'single line webs'; *j* — sticky 'single line web' of *Phoroncidia*; *k* — cursorial predators; *l* — kleptoparasites; *m* — web-invaders; *n* — wrap-attacking webless theridiids.

Рис. 3. Трансформация и утрата анцестральной колесовидной сети в разных кладах (в деталях). Нумерация — см. пекст (раздел 3.2).

a — колесовидные сети (включая «сферические сети» мизменид, «лестничную сеть» *Scoloderus*, «звездообразную сеть» *Wixia*, и т.п.); *b* — покровные сети (включая сети-путанки, «цыплячий садок» *Synotaxus*, «Н-образные сети» спинтарин, и т.п.); *c* — «купольные сети» циртофорин; *d* — «промежуточная колесовидно-покровная» микросеть *Trogloneta granulum*; *e* — «колыбельная сеть» *Mimetus*; *f* — вертикальная «водокасающаяся сеть» *Wendilgarda*; *g* — горизонтальная «плавучая сеть» *Conculus lyugadinus*; *h* — «аркан» арканщиков-мастофорин; *i* — неклейкая «сеть из одной нити»; *j* — клейкая «сеть из одной нити» *Phoroncidia*; *k* — бродячие охотники; *l* — клептопаразиты; *m* — охотники на пауков-сетестроителей; *n* — атакующие добычу клейкими нитями теридииды.

1981]. The case of *Pachygnatha* Sundevall, 1823 is particularly interesting. Its adults have lost the ability to make webs: they have reduced accessory claws needed for handling silk and lack aggregate glands, which produce the viscid droplets on silk. At the same time, young *Pachygnatha* build small horizontal orb-webs; they have more distinct accessory claws than adults, and possess aggregate and flagelliform glands like other ecribellate orb-weavers [Levi, 1980: 50].

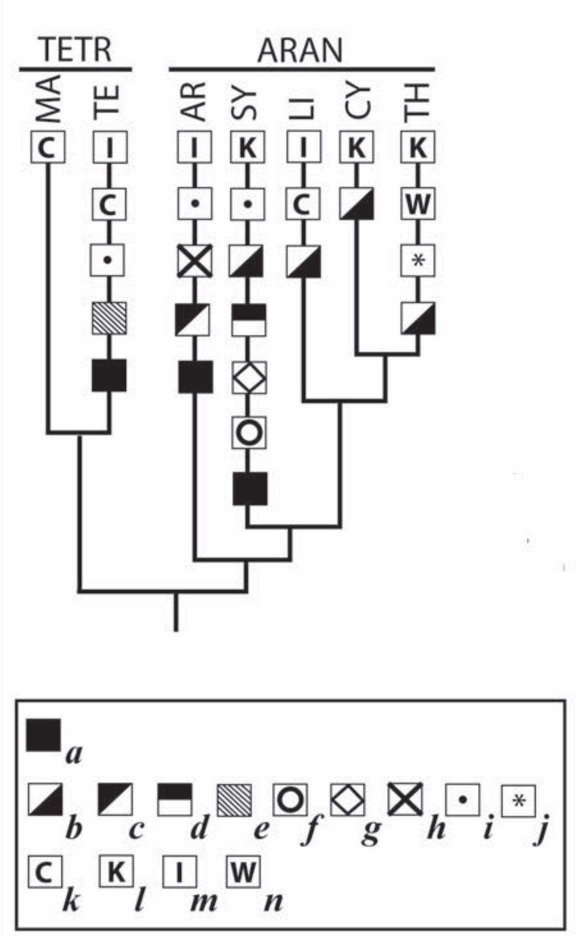

Fig. 4. Transformations and abandonments of the ancestral orb-web in various araneoid lineages (generalized). Abbreviations and symbols as in Fig. 3.

Рис. 4. Трансформация и утрата анцестрального типа колесовидных сетей у разных филогенетических ветвей аранеоидов (обобщенно). Сокращения и обозначения как на Рис. 3.

(4) ‘Basilica spiders’ is a common name (reflecting the domed design of the web) of the araneid genera *Mecynogea* Simon, 1903, *Manogea* Levi, 1997, *Kapogea* Levi, 1997, and *Cyrtophora* Simon, 1864, commonly referred to as tent-web spiders due to the unique shape of their orb-webs. “The orb weavers placed in the genera *Mecynogea* and *Cyrtophora* form a distinct group in the family Araneidae: their webs are horizontal, often dome-shaped, and supported by a tangled webbing. They are believed to lack viscid silk in the web […], and the dome has an extremely small, dry silk mesh […]. Unlike other orb weavers, they do not reconstruct the web on a daily basis and may not remove old webs but build a new one above the old […]. Whereas their silk glands differ from those of other araneids […], the external appearance of these spiders is not as distinct from other araneids as one might expect” [Levi, 1997: 215].

(5) The ‘bolas spiders’ comprise four genera (*Mastophora* Holmberg, 1876, *Ordgarius* Keyserling, 1886, *Cladomelea* Simon, 1895, and *Exechocentrus* Simon, 1889), forming a tribe Mastophorini Mello-Leitão, 1931 in Cyrtarachninae (or even a separate araneid subfamily Mastophorinae: see Scharff & Hormiga [2012]) possess a unique foraging behavior. “At night, the bolas spider feeds on male moths attracted by the spider”s scent; the scent mimics the sex attractant of the female moth. […] All late-instar and adult female bolas spiders spin a horizontal line composed of multiple threads, and then attach a bolas to it. The bolas consists of one, rarely several, balls of sticky glue drops on a line. A moth attracted by the spider’s scent is caught by a swing of the leg holding the bolas; the adhesive is strong enough to hold moths. […] The bolas of spiders in the genus *Mastophora* is held with the first leg and swung at prey. Members of the Australasian genus *Ordgarius* and the African genus *Cladonielea* use the second leg and whirl the bolas” [Levi, 2003: 309–310]. Interestingly, that juveniles of *Mastophora* do not use a bolas, but attract prey and grab it by their first two pairs of legs; instead of male moths, attracting by adults, they preying psychodid flies [Yeargan, Quate, 1996].

(6) Two genera of the araneid subfamily Cyrtarachninae, *Taczanowskia* Keyserling, 1879 and *Celaenia* Thorell, 1868, use, as well as the abovementioned *Arkys*, a single non-sticky line instead of an orb-web: “[*Taczanowskia* female] had no web, but hung on a horizontal line head down, with legs one and two partly spread. [...] A passing insect was seized with a sudden grab, embraced, then wrapped. The spider”s prey were pyralid moths, which seemed to fly toward the spider, suggesting that *Taczanowskia*, like *Mastophora*, uses an attractant” [Levy, 1996: 186]. The same mode of foraging was described in *Celaenia* [Forster, Forster, 1973; Main, 1982].

(7) In another cyrtarachnin genus, *Chorizopes* O. Pickard-Cambridge, 1871, the foraging behavior is amazingly similar to the mimetid one: web-invading with ‘aggressive mimicry’. These webless araneids are “preying on other orbweavers, provoking them from the periphery of the web and attacing the web’s occupant when they investigate” [Kallal, Hormiga, 2019: 473].

(8) The ‘water-touching web’ of the genus *Wendilgarda* Keyserling, 1886 is a reduced vertical theridiosomatid orb-web. “The web is peculiar, consisting of a horizontal non-sticky line from which vertical sticky lines adhere with considerable tenacity to the surface film of flowing tropical streams” [Coddington, 1986b: 89, fig. 202]; the spider’s lifestyle was termed by Eberhard [2001] ‘trolling for water striders.’ Horizontal non-sticky line is the vestige of a frame, while vertical sticky lines are vestiges of a spiral.

(9) A further step in the reduction of an initial orb-web is supposedly found in another theridiosomatid genus, *Chthonos* Coddington, 1986: “Collectors have found the animals walking in leaf litter or on single dry threads between foliage (the animal may have spun the thread, or it may have used the drag line of another spider). Apparently *Chthonos* are wandering predators that do not spin prey-catching webs. […] I collected one *Chthonos* individual adjacent to the web of another spider; perhaps like mimetids, *Chthonos* also eats other spiders. No direct evidence, however, supports either of these speculations” [Coddington, 1986a: 35]. We, however, prefer to classify this aberrant theridiosomatid as a ‘single-line web’ builder.

(10) The majority of Mysmenidae build so-called ‘spherical orb-webs’. However, the web of *Trogloneta granulum* Simon, 1922, described in detail by Hajer [2000], was considered by Lopardo *et al*. [2011: 321] as a sheet-web, representing an intermediate stage between more typical orb webs and webs like those of theridiids or *Comaroma* Bertkau, 1889.

(11) In some other *Trogloneta* Simon, 1922 species, the initial orb-web may be reduced in another way than in *T. granulum*. At least several undescribed Australian species were collected from single threads [Lopardo *et al*., 2011: 321].

(12) There are two webless kleptoparasitic genera of mysmenids, *Isela* Griswold, 1985 and *Mysmenopsis* Simon, 1898, forming the purely kleptoparasitic subfamily Mysmenopsinae. The kleptoparasitic lifestyle seems to have a single origin within mysmenids caused by complete or partial absence of the ‘araneoid triad’ of the spinnerets in Mysmenopsinae and the concomitant loss of the ability to spin sticky silk [Lopardo *et al*., 2011; Hormiga, 2015]. Interestingly, almost all species of both *Isela* (two African species) and *Mysmenopsis* (52 Neotropical species) inhabit the funnel-webs of the web-building mygalomorph family Dipluridae [Griswold, 1985; Dupérré, Tapia, 2020].

(13) Symphytognathids, as a rule, build horizontal orb-webs. However, in *Symphytognatha globosa* Hickman, 1931 from Tasmania, observed by V.V. Hickman both in the field and in the laboratory, “the web consists of a few irregular threads in a more or less horizontal plane. The spider rests below them in an invert-

ed position. […] The threads do not appear to be adhesive" [Forster, Platnick, 1977: 3]. At the same time, at least one *Symphytognatha* Hickman, 1931 species, the South African *S. imbulunga* Griswold, 1987, makes a horizontal orb-web typical for the family [Griswold, Yan, 2003]. The web of *Anapistula ataecina* Cardoso et Scharff, 2009 from Portugal caves is sheet-like, horizontal, with a number of vertical threads suspending this structure from above [Cardoso, Scharff, 2009: fig. 2B], whereas other *Anapistula* Gertsch, 1941 species have usual to the family horizontal orb-webs [Griswold *et al*., 1998: fig. 3C]. Such a coexistence of orb-weavers and sheet-weavers in the same genera, viz. *Symphytognatha* and *Anapistula*, seems unique throughout araneoids.

(14) In addition, some other *Symphytognatha* Hickman, 1931 species have been collected from single threads [Lopardo *et al*., 2011: 321]. Thus, a series of as many as three web types exists in the same genus, *Symphytognatha*.

(15) Kleptoparasitic webless symphytognathids are represented by *Curimagua bayano* Forster et Platnick, 1977. It has been collected on the webs of diplurid mygalomorphs in Panama, and kleptoparasitic mysmenids *Mysmenopsis* Simon, 1898 are also frequently found in that habitat [Forster, Platnick, 1977: 3].

(16) In contrast to the'aquatic web' of *Wendilgarda* Keyserling, 1886, originated from a vertical theridiosomatid orb-web (see above), the 'aquatic webs' of some anapid genera are less modified horizontal orb-webs, typical for Anapidae: "The aquatic webs made by *Sheranapis villarrica* are not so specialized as those of the Japanese anapid *Conculus lyugadinus* [...], but still have a particular specialization. The orb is placed at a very short distance from the water surface, whereas [its] terrestrial webs are never so close to the substrate. […] All this variability points out that some details of web architecture of phylogenetic interest (e.g., presence/absence of supplementary radii) would be better taken from several specimens rather than one or two" [Ramírez *et al*., 2004: 7]. The 'floating web' of *Conculus lyugadinus* Kishida, 1940, crowning this web-building trend, is "basically a horizontal orb-web, but the sticky spirals were hung down and reach onto the water surface. In this modified orb-web, the attachment of the sticky spiral on the water surface had many fine threads. After spinning the sticky spirals, the spider broke every radius part between the hub and the inner loop of sticky spirals and extended every radius toward the periphery of web. As the radii were reluxed, distal parts of the sticky spirals of the modified orb-web were floating on the stream" [Shinkai, Shinkai, 1988: 1, fig. 1c–d].

(17) The webs of *Taphiassa* Simon, 1880 remain undescribed, but the biology of the closely related genus *Olgania* Hickman, 1979, the second member of Anapidae: Taphiassinae Rix et Harvey, 2010, has now been studied quite well: "Spiders build small, horizontal sheet-webs on the walls or floor of limestone caves […]. The webs are held in position by vertical support-lines […]. The web is composed of an extremely fine mesh of silk, and some webs have two parallel layers of silk. […] Both adult males and females can be found sitting in their own webs, and the spiders seem to be at least loosely colonial, with several webs usually found in close proximity" [Rix, Harvey, 2010a: 92]. Furthermore, "At least one undescribed anapid [i.e. Anapidae: Anapinae Simon, 1895 in the accepted here classification] species from Madagascar builds a horizontal sheet web, like those of cyatholipids, with the animals walking upside down, under the sheet" [Lopardo *et al*., 2011: 320]. So, sheet-weavers are presented in two anapid subfamilies, Anapinae and Taphiassinae.

(18) The natural history of the anapid subfamily Holarchaeinae Forster et Platnick, 1984 remains poorly known. *Holarchaea globosa* (Hickman, 1981) was found in a Tasmanian rainforest "close to midnight, during persistent rain, with the male seen hanging from a single line of silk between the fern leaves" [Rix, 2005: 150]. Thus, it seems to represent yet another, fifth case of a 'single line web' in araneoids.

(19) The family Anapidae Simon, 1895, as well as mysmenids and symphytognathids, includes at least one kleptoparasitic member: the Chilean *Sofanapis antillanca* Platnick et Forster, 1989 inhabits the webs of the 'hypochiloid' genera *Austrochilus* Gertsch et Zapfe, 1955 and *Thaida* Karsch, 1880 [Ramírez, Platnick, 1999]. It should be noted, however, that the another, undescribed, *Sofanapis* Platnick et Forster, 1989 species was collected in Chile (Alerce Costero National Park) outside of any large-sized spider webs, in epiphytic moss (personal observation by the senior author of this study).

(20) Orb-weavers are completely absent in the large family Micropholcommatidae Hickman, 1944, in contrast to its sister family Anapidae Simon, 1895. Moreover, the transforming of the ancestral orb web has led to the two different web types, i.e., the sheet- and tangle-webs, in the two micropholcommatid subfamilies, Textricellinae Hickman, 1945 and Micropholcommatinae Hickman, 1944: "All studied species of Textricellini build very small, horizontal, platform sheet-webs, often between leaflets of moss, on top of which they sit and wait for prey. […] The silk appears to be sticky. Species of *Micropholcomma*, in contrast, have been shown to build irregular, three-dimensional tangle-webs, not unlike those constructed by certain Theridiidae" [Rix, Harvey, 2010a: 105].

(21) The web of the European comaromid, *Comaroma simonii* Bertkau, 1889, has been described in detail by Kropf [1990b]. It is an irregular threedimensional web with long threads containing sticky silk at their distal ends attaching to the substrate, similar to the typical theridiid cob-webs.

(22) Synaphrid webs were described in *Synaphris lehtineni* Marusik, Gnelitsa et Kovblyuk, 2005 from south-eastern Europe: "The spiders spin very thin sheet webs over the hollows, underneath stones. The webs

cover small saucer-like depressions. In one 10 cm depression there can be up to 5–7 contiguous occupied webs, but in some cases the spiders are alone [Marusik *et al*., 2005: 129]. Thus, a 'loosely colonial' life-style, as in taphiassine *Olgania* Hickman, 1979 (see above), may be supposed in this species.

(23) Abandonment of web-building is almost unknown in linyphiids [Hormiga, Eberhard, 2023]; even obligate myrmecophils inhabiting ant nests retain capture webs [Cushing, 1995, 2012]. Surprisingly, two linyphiid species, *Neomaso defoei* (F.O. Pickard-Cambridge, 1899) and *Laminacauda gigas* Millidge, 1991, both endemics of the south Pacific Archipelago of Juan Fernandez, turned out to be webless predators: "The largest species in the genus, and possibly the largest known erigonine, is *Laminacauda gigas*, with females that can reach close to 1 cm in body length. This species has abandoned weaving foraging webs and is found mainly under rocks and logs [...] *Neomaso defoei* n. comb., previously classified in the genus *Laminacauda*, is very large (females reach more than 7 mm of body length, comparable in size to those of *Laminacauda gigas* which reach over 9 mm), has abandoned foraging webs in exchange for a cursorial lifestyle and is usually found under rocks and fallen logs (again, the same habitat where *Laminacauda gigas* is found)" [Arnedo, Hormiga, 2021: 335]. All the other *Neomaso* Forster, 1970 and *Laminacauda* Millidge, 1985 species are small to medium-sized sheet-weavers; thus, such parallel web abandonment, combined with gigantism and some other convergent somatic similarities [Arnedo, Hormiga, 2021], in the two unrelated but sympatric linyphiid species seems to be an amazing effect of island isolation.

(24) One more endemic Juan Fernandez *Neomaso* Forster, 1970 species has abandoned web-weaving too, and became a web-invader, attacking other linyphiids in their webs: "The most striking case is that of the long-legged *Neomaso*, another undescribed species [...] Our field observations suggest that this species does not build foraging webs but instead invades the webs of other spiders to prey on their hosts. This species is rare and we have been able to collect only a few specimens, two of them in *Laminacauda* sheet webs and two in or adjacent *Dubiaranea insulana* webs" [Arnedo, Hormiga, 2021: 336]. Thus, there is a third case of undoubtedly independent evolving of such a specialized foraging behavior in araneoids, in addition to mimetids and the araneid genus *Chorizopes* O. Pickard-Cambridge, 1871 (see above).

(25) The only known case of commensalism or kleptoparasitism in the 'cyatholipoid lineage' is an undescribed New Zealand physoglenid that inhabits the webs of the cyatholipid genus *Tekella* Urquhart, 1894 and mimics the web host; however, this physoglenid (initially identified as a theridiid) was later found also in stiphidiid and hexathelid webs, with dissimilar web hosts [Forster, 1988: 8–9; Dimitrov *et al*., 2017: 242].

(26) The 'single line web' of the theridiid genus *Phoroncidia* Westwood, 1835 sharply differs from all the previous cases of using a single horizontal line for the spider hanging (see above), which is supposed to be an orb-web reduced to its non-sticky frame. In contrast, a single thread of *Phoroncidia* is adhesive, not used by spider for hanging [Agnarsson, 2004: fig. 97B–D], and flies stick to it due to prey attractant [Eberhard, 1981]. So, it seems to originate not from an orb-web, but from a platform of sheet-web.

(27) At least some species of the theridiid genus *Euryopis* Menge, 1868 are specialized myrmecophges; they do not build any sort of capture webs but use the sticky silk wrap to attack ants [Carico, 1978; Cushing, 2012]; such a hunting style may be more widely spread in theridiids, especially in hadrotarsines.

(28) Agnarsson [2004: 448] noted that no other family includes so many kleptoparasites as Theridiidae; however, they all belong to the huge genus *Argyrodes* Simon, 1864 *s.l.* (more than two hundred species), elevated now to the subfamily rank, Argyrodinae Simon, 1881, and divided into several genera [Agnarsson, 2004: 476]. Highly diverse kleptoparasitic behavior, including attacking of web hosts during their molting and capture of their young, has been recorded in *Argyrodes* s.l. [Whitehouse *et al*., 2002]. *Argyrodes* have been recorded on the webs of 29 host genera from eight families (Ageienidae, Amaurobiidae, Araneidae, Linyphiidae, Pholcidae, Psechridae, Theridiidae, and Uloboridae), and some species have many hosts [Elgar, 1993: 419].

3.3. Discussion: detailed elaboration of the big picture

The first question is whether the listed details contradict the above-described big picture of the fundamental splitting of the superfamily: 'orb-web transformations, no abandonments' in 'araneoids' vs. 'orb-web abandonments, no transformations' in 'tetragnathoids'? How frequent and serious are the exceptions?

There are only two cases of any use of silk (except for the egg-sac) in 'tetragnathoids': the 'single-line web' in some *Arkys* Walckenaer, 1837 species (Arkyidae) and the 'nursery web' in some tropical *Mimetus* Hentz, 1832 species (Mimetidae). Benavides & Hormiga [2020: 144] consider the later sheet-web-like construction as 'rudimentary', but in our opinion it is rather newly originated by the multiplication of non-sticky silk lines used for hanging an egg-sac. Similar 'egg sac webs' evolved also in some synotaxids and theridiids [Agnarsson, 2004: fig. 95B, C, E], and exist simultaneously with their capture webs.

Regarding the 'single-line web', it turned out to be a unique web type, common for both principal branches: it is recorded in 'tetragnathoids' (Arkyidae) and as many as five times in 'araneoids' (Araneidae, Theridiosomatidae, Mysmenidae, Symphytognathidae, and Anapidae). We fully agree with Main's interpretation of such non-sticky line for a spider hanging as the last remnant of reduced orb-web, a horizontal portion of the frame: "The non-viscid, horizontal, single-line suspension web of *Arcys* appears to be a […] variant in the reduction sequence of the orb web. It may represent the primary horizontal strand of an araneid orb web frame, i.e. the ultimate stage in the reduction of the orb web. If *Arcys* and [webless] *Archemorus* are indeed closely related as is generally considered then the *Arcys* web represents a 'stage' prior to complete abandonment of the web as an aid to prey capture" [Main, 1982: 430]. The 'bolas web' seems originated from the 'single-line' one, especially because both 'bolas' and 'single-line' araneid genera belong to the same subfamily Cyrtarachninae Simon, 1895.

Thus, there are six events of independent evolving of this web type in all three orb-web lineages of the superfamily (i.e., the tetragnathoid, araneoid, and symphytognathoid lineages), and never outside them (Fig. 4), easily explained by the parallel reduction of an initial orb-web. It should be emphasized that the 'sticky single-line web' recorded in the non-orb-web theridioid lineage (genus *Phoroncidia* Westwood, 1835) is only a superficially similar structure. It is used by the spider for quite another hunting mode than the 'non-sticky' one [Eberhard, 1981], and seems evolved due a reduction too, but rather from the sticky platform of a theridiid sheet-web.

The web abandonment occurs in both branches but is drastically different in each one. There are numerous cursorial and sit-and-wait predators in 'tetragnathoids' (the malkaroid lineage consists entirely of them), but no kleptoparasites; mimetids are known to use sometimes the prey of consumed web host [Benavides, Hormiga, 2020], but it is not a kleptoparasitism in generally accepted sense, of course. And conversely, there are numerous kleptoparasites in 'araneoids', but no proven cursorial predators, except of the couple amazing linyphiid species, sympatric endemics of Juan Fernandez Islands [Arnedo, Hormiga, 2021], in which a web abandonment is combined with an island gigantism and may be caused by the latter.

Capture web is absent in at least some *Euryopis* Menge, 1868 species (and, probably, in some other Hadrotarsinae), but they practice the 'sticky silk wrap attack' on their prey [Carico, 1978; Cushing, 2012]; thus, the sticky silk, using during the theridiid wrap attack, may be regarded as a 'portable capture web' replacing a 'stationary' one. It should be emphasized that in Linyphiidae, which are incapable of the sticky silk wrap attack, even obligate myrmecophils inhabiting ant nests retain webs: "*Masoncus pogonophilus* builds prey capture webs inside nest chambers and females deposit small silken egg sacs each containing up to seven eggs in depressions in the walls of the chambers (Cushing, 1995)" [Cushing, 2012: 9].

It should be noted that araneoid kleptoparasitism in the symphytognathoid lineage on the one hand and in the 'spineless femur clade' (the cyatholipoid plus the theridioid lineages) on the other differ from each other in the respect of web hosts. Symphytognathoids, such as Mysmenidae and Symphytognathidae, inhabit almost exclusively webs of diplurid mygalomorphs [Forster, Platnick, 1977; Griswold, 1985; Dupérré, Tapia, 2020], or, such as Anapidae, webs of another archaic spider group, the 'hypochiloids' [Ramírez, Platnick, 1999], whereas the 'spineless femur clade' members (Physoglenidae and Theridiidae) inhabit webs of numerous genera of at least 11 families, mainly araneoids [Forster, 1988; Elgar, 1993].

The complete absence of kleptoparasites in 'tetragnathoids' and cursorial predators in 'araneoids' is especially surprising if we take in account the origin in both branches of such sophisticated webless foraging behavior as web-invading araneophagy. It evolved as a general lifestyle in the tetragnathoid family Mimetidae [Benavides, Hormiga, 2020], and twice in 'araneoids': in the araneid genus *Chorizopes* O. Pickard-Cambridge, 1871 [Kallal, Hormiga, 2019] and in one species of the linyphiid genus *Neomaso* Forster, 1970 [Arnedo, Hormiga, 2021]. The undoubtedly independent origin of such highly specialized web-invaders, using aggressive mimicry, in such unrelated families as Mimetidae, Araneidae and Linyphiidae (see Fig. 4) is a remarkable, 'textbook' example of convergent evolution.

Two opposite principal trends in the evolution of the primary orb-web in the two principal superfamily branches, i.e. its transformation to a sheet-web in 'araneoids' and its complete abandonment in 'tetragnathoids', may be traced sometimes even at the generic level. 'Araneoids' sometimes demonstrate the coexistence of both orb-weavers and sheet-weavers in same genera (*Symphytognatha* Hickman, 1931 and *Anapistula* Gertsch, 1941), whereas 'tetragnathoids' sometimes demonstrate the coexistence of both orb-web-building and webless species in the same genus (*Tetragnatha* Latreille, 1804) and orb-web-building and webless age stages in the same species (*Pachygnatha* Sundevall, 1823). And the coexistence of the webless sit-and-wait predators and the species using 'single line web' (which is just the ultimate stage of an orb-web reduction) in the genus *Arkys* Walckenaer, 1837 seems a perfect 'freeze frame' of this evolutionary trend.

The general trend to orb-web transformation into sheet-web, detected previously for the araneoid branch of the big picture, seems supported by its details too. The araneoid lineage, basal for the branch, lacks other capture web types except the basal one, the orb-web (on the cyrtophorine 'basilica webs' — see below). The most advanced clade, the 'araneoid sheet-web builders' (the linyphioid, cyatholipoid, and theridioid lineages), completely lost an ancestral orb-web, and even such its remnants as the 'non sticky single-line web' (see above). In the mainly orb-web symphytognathoid lineage results of parallel replacing the orb-web by sheet- and tangle-webs are traceable as 'non orb-web' families (Micropholcommatidae, Comaromidae, and Synaphridae), 'non-orb-web' genera in mainly orb-web families (Symphytognathidae and Anapidae), and even 'non-orb-web' species in mainly orb-web genera (*Anapistula* Gertsch, 1941) (Fig. 3).

How and why sheet-webs has arose instead of orb-webs? The primary sheet-web may be supposed to be but horizontal orb-web, reduced to the central hub lacking the edging spiral, and with radii transformed into vertical support-lines. Precisely the symphytognathoid lineage seems to be the main field of evolution experiments with such a radical web transformation.

The case of the mysmenid *Trogloneta granulum* Simon, 1922 web is of particular interest. It was considered by Lopardo *et al*. [2011] as a sheet-web, represents an intermediate stage between more typical orb webs and theridiid webs. "The so-called 'radial threads', regarded in the original description (by Hajer, 2000) as homologous to the orb radii, are used for prey capture, that is, they are covered by sticky silk (as also are the 'transverse threads'), and are attached to the substrate, conforming the frame of the web. Typical orb webs result from stereotyped behavior in the construction of the hubs, and the radii are usually attached to the frame of the web, not to the substrate, and do not posses sticky silk" [Lopardo *et al*., 2011: 321]. We agree that the web of *Trogloneta granulum* is an important intermediate stage in web-build evolution from orb- to sheet-webs, but suppose this structure [Hajer, 2000: figs 1–5] to be rather a vestigial horizontal orb-web, reduced up to a minute (ca. 1 mm) irregular central hub, edged by a few vestigial fragments of a spiral.

Such a simplification of the web architecture (compared with the initial orb-web) allowed the spiders to simplify also the spinning apparatus: the clade uniting symphytognathoids and 'araneoid sheet web builders,' both able to construct sheet-webs, is aptly named by Griswold *et al*. [1998] the 'reduced piriform clade' (Fig. 1). A reduction of some components of the spinnerets (piriform, and also aciniform gland spigots), as well as minimization of the spending silk volume, seems critically important during miniaturization, which is the key evolutionary trend in the symphytognathoid lineage (see discussion in Griswold *et al*. [1998: 20]).

The single case of the emergence of a sheet-like web in araneoid lineage, in the 'basilica spiders,' should be noted in this connection: the horizontal, dome-shaped web lacking viscid silk and the absence of flagelliform silk glands in *Cyrtophora* Simon, 1864 [Coddington, 1989] seems clearly correlated characters. The modified horizontal orb-web of another araneid, *Paraplectanoides crassipes* Keyserling, 1886, reduced to the central hub with radii, both non-viscid, and without vestiges of a spiral [Hickman, 1975; Kuntner *et al*., 2023], may have been the initial stage of this trend.

If the hypothesis about the origin of araneoid sheet-webs as a consequence of miniaturization is correct, the absence of such webs in the tetragnathoid branch is easily understandable, due to the absence of miniaturization trends in this branch too. Even the smallest tetragnathoids (e.g., some *Dolichognatha* O. Pickard-Cambridge, 1869) belong to the size-class of 'small spiders,' and none of them belong to size-class of 'minute spiders' (ca. 1 mm, as the majority of symphytognathoids).

Tetragnathid webs are generally very uniform [Álvarez-Padilla, Hormiga, 2011]: not only orb-web transformations (to sheet- and cob-webs, *etc*), but even their modifications (as araneid 'ladder web' of *Scoloderus* Simon, 1887, 'star-shaped web' of *Wixia* O. Pickard-Cambridge, 1882, the web of *Paraplectanoides* Keyserling, 1886 which may be named 'trampoline web', *etc*) are absent in this family. By contrast, the lifestyles of webless 'tetragnathoids' are very diverse; in particular, there are numerous araneophages, specialized in different ways: ones use the 'aggressive mimicry' (Mimetidae), whereas others (Pararchaeidae) are sit-and-wait predators [Rix, 2006]. Malkaroids, due to their webless lifestyle, lost the 'triad' on the posterior lateral spinnerets, an important synapomorphy of the superfamily Araneoidea [Hormiga, Scharff, 2020], and Rix & Harvey [2010b] even have argued, on this base, that Pararchaeidae belong to araneoids.

4. Conclusions

1. The initial morphological cladogram of the superfamily Araneoidea [Griswold *et al*, 1998] is supplemented by the molecular clade of the 'enlarged tertagnathoids' [Dimitrov *et al*., 2017]. Harmonized in such a way, our 'morpho-molecular cladogram' implies a splitting of the basal araneoid stock into the two principal branches: the 'tetragnathoid branch' (the malkaroid and tetragnathoid lineages) and the 'araneoid branch' (the araneoid, symphytognathoid, linyphioid, cyatoliphoid, and theridioid lineages).
2. Web-building characters strongly support the main clades of the proposed 'harmonized morpho-molecular cladogram'; so, the latter may be appreciated as a 'natural system of the superfamily Araneoidea'.
3. The two opposite principal trends in the evolution of web-building in the two principal superfamily branches are the transformation of the primary orb-web in 'araneoids' and its complete abandonment in 'tetragnathoids'. There are no cases of replacing the primary orb-web by à capture web of any other type in the tetragnathoid branch. And vice versa: webless cursorial and sit-and-wait predators are completely absent in the araneoid branch; several araneoids abandoned web-building, but all these cases are caused by particular lifestyles (kleptoparasitism, etc).
4. A general evolutionary trend in the araneoid branch is the replacing of the primary orb-web by various versions of sheet-webs: from the basal araneoid lineage (orb-webs only) to the terminal 'araneoid sheet web builders clade' (sheet-webs only), via the intermediate symphytognathoid lineage (both orb- and sheet-webs). Precisely symphytognathoids seem to be the main field of evolutionary experiments with parallel orb- to sheet-web transformations.

5. The primary sheet-web may be supposed to be but a horizontal orb-web, reduced to the central hub lacking the edging spiral, and with radii transformed into vertical support-lines. Such a simplification of the web architecture allows the spiders to also simplify the spinning apparatus. A reduction of some components of the spinnerets (piriform, and also aciniform gland spigots), as well as the minimization of the spent silk volume, seems critically important during miniaturization, which is the key evolutionary trend in the symphytognathoid lineage.

6. If the hypothesis about the origin of araneoid sheet-webs as a consequence of miniaturization is correct, the absence of such orb-web transformation in the tetragnathoid branch is easily understandable, due to the fact miniaturization trends in this branch are also absent.

Disclosure statement

No potential conflict of interest was reported by the authors.

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