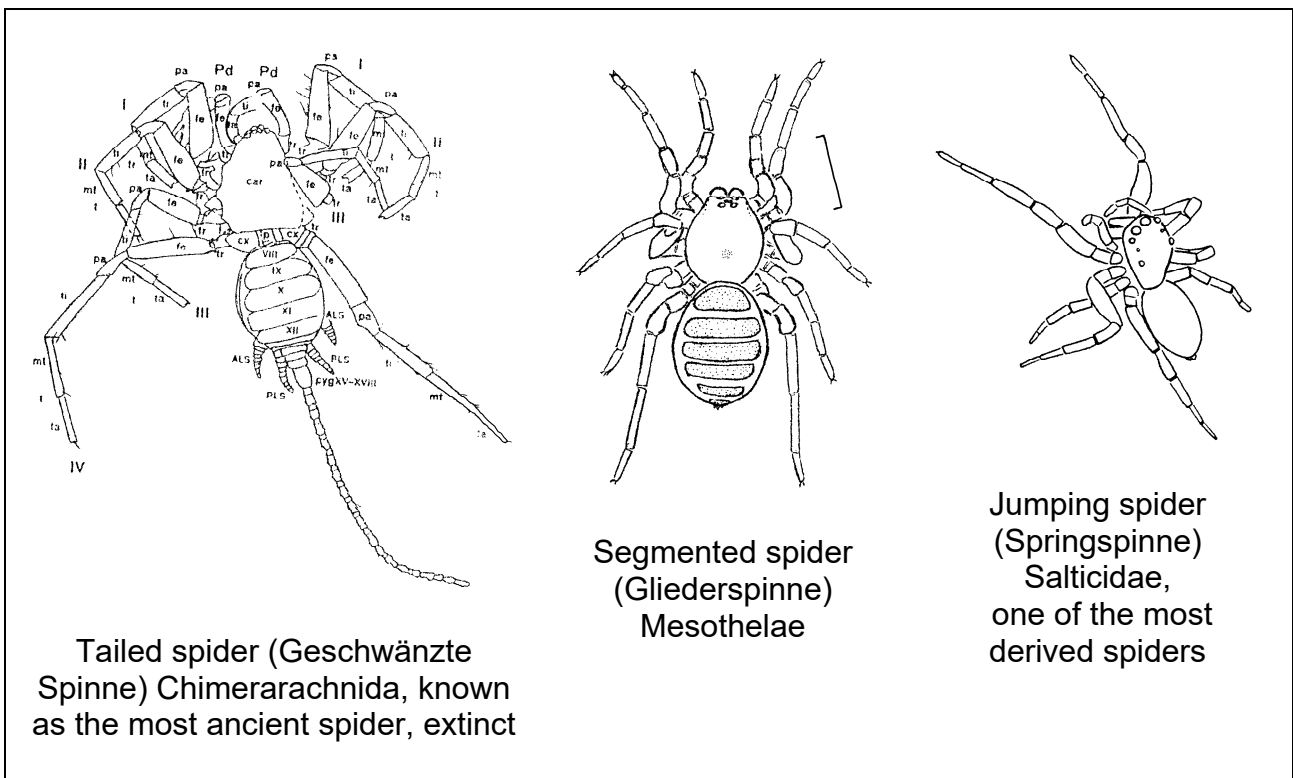


WHAT IS A SPIDER?

CRETACEOUS FOSSILS MODIFY STRONGLY PHYLOGENETICS AS WELL AS DIAGNOSES OF FAMILIES, SUPERFAMILIES AND EVEN SUBORDERS OF SPIDERS (ARANEIDA) AND OTHER ARTHROPODS

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CRETACEOUS FOSSILS MODIFY STRONGLY PHYLOGENETICS AS WELL AS DIAGNOSES OF FAMILIES, SUPERFAMILIES AND EVEN SUBORDERS OF SPIDERS (ARANEIDA) AND OTHER ARTHROPODS

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Abstract: The basal branchings of spider evolution are treated, based on selected characters of extinct and extant taxa. The orders Uraraneida (extinct) and Araneida (in a new sense) have been united in the superorder Serikodiastida by GARWOOD & DUNLOP 2014. A strongly modified classification of the order Araneida is presented, including the extinct order Chimerarachnida WUNDERLICH 2018, based on the Chimerarachnidae **n. fam.**, and its sister suborder, the Araneae. The taxon Araneae is used in the traditional sense; it includes all Araneida (except the Chimerarachnida): The suborders Mesothelae and Opisthohelae, see fig. A. Opisthohelae includes (a) the Basalhaplogynae (Synspermiata - e. g. Dysderidae and Pholcidae - and Filistatidae) and (b) its sister group, the Neocribellatae (**new sense**): The Hypochilidae and its sister group, the "Praeentelegyne" (**new name**): The Austrochiloidea and its sister group, the Dipneumonomorpha (= Entelegynae): All the remaining taxa like Archaeidae, Oecobiidae, Araneidae and taxa of the RTA-clade (e.g. Lycosidae and Salticidae). The taxon Cleistospermiata WUNDERLICH 2015 has to be deleted. - Further main ideas/results of this study regard the evolution of spiders: (1) The posterior pair of lungs was lost three times; (2) the anterior pair of median spinnerets were displaced two times by a cribellum (in the Neoribellatae and in the Filistatidae; a reversal is unknown to me) and were probably displaced DIRECTLY by a colulus in the Synspermiata which ancestor did not possess a cribellum; (3) the mediognath position of the basal cheliceral articles evolved at least three times separately: In the Mesothelae, within certain Mygalomorpha as well as in the Araneomorpha; (4) the labidognathy evolved two times: In the Basalhaplogynae and in the Dipneumonomorpha. - The phylogeny of the Mesothelae is discussed, the translocation of the

spinnerets in the anterior direction during the evolution of the Mesothelae is documented by fossils. The diagnoses of the Mesothelae and of certain spider families have to be strongly modified if fossil taxa are included and mainly apomorphic characters are used. The Cretaceous mesothelid **new family** Eomesothelidae - based on *Eomesothele noninclinata* **n. gen. n. sp.** - and the probably confamilial *Intermesiothele pulcher* **n. gen. n. sp.** are described. Notes are given on faunistic changes, relic and extinct taxa, as well as additions and corrections regarding vol. 11 (2018) of the Beitr. Araneol.

Key words: Amber, anal tubercle, Arachnida, Araneae, Aranei, Araneida, Araneoclada, Araneomorpha, Austrochilidae, Austrochiloidea, Basalhaplogynae, Burmite, Chimerarachnida, Chimerarachnidae, chronocladogram, classification, Cleistospermiata, colulus, coxal glands, Cretaceous, cribellum, Dipneumonomorpha, Eomesothelidae, evolution, extinctions, fauna, Filistatidae, Fillistatomorpha, flagellum, heart ostia, Haplogynae, Hypochilidae, Hypochilomorpha, labidognathy, Liphistiidae, mediognathy, Mesothelae, Mesozoic, “missing link”, Mygalomorpha, Neocribellatae, Opisthothelae, orthognathy, Palaeocribellatae, Palaeozoic, perenniality, phylogenetics, plesion, Praeentelegynae, RTA-clade, relics, segmentation, Serikodiastida, spiders, spinnerets, Synspermiata, tarsal organ, taxonomy, telson, trichobothria, Uraraneida.

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CONTENTS: In this paper I treat **(1)** shortly few modified diagnostic characters of selected families and superfamilies of spiders (p. 4), **(2)** modified diagnostic characters of few spider taxa higher than the superfamily level, including new taxa of the Mesothelae and the extinct Chimerarachnida, and remarks on their phylogeny (p. 5), **(3)** the proposal of a modified new classification of spiders (p. 9), **(4)** phylogenetics, main evolutionary steps as well as cladograms of higher basal taxa of the Araneida (p. 10), **(5)** the new Cretaceous family Eomesothelidae of the Mesothelae as well as previously unpublished mesothelid material in Burmite kept in the collection of the author (CJW) (p. 18), **(6)** notes on the fauna as well as relic and extinct spiders (p. 22). - Additions and corrections regarding vol. 11 (2018) of the Beitr. Araneol. are given (p. 26). Drawings and photos are presented at the end of the paper.

Mainly during the last 15 years researchers of arthropod taxa of the tropical Mid Cretaceous Burmese amber – the corresponding amber forest existed in Myanmar (Burma) ca.100 million years ago – published a remarkable number of peculiar higher taxa. Some of these taxa are of special interest: they can be regarded as models of “missing” or “connecting” links, e. g., of the Araneae, see below and WUNDERLICH

(2015ff), the Blattaria, the Siphonaptera and the Lepidoptera/Trichoptera, see ROSS (2017f). The discovery of such fossils gives rise to discussions concerning the cladograms, the diagnoses, the levels and the names of various taxa. Chronocladograms as well as diagnoses of families and some higher taxa have to be strongly modified if fossil taxa are included; see the Leptoneoid/Araneoid branch in the sense of WUNDERLICH in WUNDERLICH & MÜLLER (2018). – Certain taxa of fossil Arachnida in Mid Cretaceous Burmese amber modify greatly the view of the phylogeny of spiders, e. g., the genus *Chimerarachne* WANG et al. 2018 – which I like to call “the *Archaeopteryx* among spiders” - and various taxa of the Mesothelae like the ancient new family Eomesothelidae. In the present paper I focus on the basal branchings of high spider taxa and the quite remarkable segmented Mesothelae which connects as “connecting link” the ancestral tailed Chimerarachnida and derived spiders like Jumping spiders (Salticidae), see the figs. p. 1.

(1) Modified characters concerning the family and superfamily levels

(A) The superfamily DEINOPOIDEA:

Extant members of the deinopoid family ULOBORIDAE possess femoral trichobothria which in contrast are absent in certain Mid Cretaceous taxa in Burmite, see WUNDERLICH (2008f), the lateral eyes are widely spaced from each other in the extant taxa of this family but they are close together in certain fossil taxa; the absence of poison glands - like in the extant taxa – has not yet been investigated in the fossils. – DEINOPIDAE: The position of the eyes of the fossil *Eodeinopes longipes* WUNDERLICH 2017, which I consider to be an unusual member of the family DEINOPIDAE, is distinctly different from the highly specialized eye position of extant taxa of this family: It possesses two eye rows and SMALL posterior median eyes.

(B) The superfamily LEPTONETOIDEA:

The extant members of the LEPTONETOIDEA possess only six eyes like several fossil spiders but certain ancient taxa in Burmite possess eight eyes, see WUNDERLICH (2018: Fig. 68). Some ancient fossil taxa of the same superfamily possess a cribellum which exists only in a single extant genus (*Archoleptoneta* GERTSCH 1974) of the diverse family Leptonetidae in which also a very large colulus may exist: In the Telemidae and in the Leptonetinae, see WUNDERLICH (2018: Figs. 75 and 86).

Note: Fossil taxa point to close relationships of Leptonetoidea and Araneoidea but not of Leptonetoidea and the RTA-clade, see WUNDERLICH (2018).

(C) The superfamily ARANEOIDEA:

Members of the diverse extinct Mid Cretaceous family ZARQARANEIDAE possessed a peculiar large and erect paracymbium which I regard as an ancient character of the superfamily Araneoidea, see WUNDERLICH (2018: E. g. figs. 113, 129). This kind of paracymbium exists also (a) in extinct ancient cribellate members of the superfamily Leptonetoidea as a synapomorphy of both taxa, (b) in extinct Eocene taxa of the fam-

ily Protheridiidae, see WUNDERLICH (2004: 1151, fig. 26), and (c) in certain Eocene as well as extant members of the family Tetragnathidae.

The characters of the only two known Mid Cretaceous genera (*Cretotheridion* WUNDERLICH 2015 and *Burmatheridion* WUNDERLICH 2018) of the family THERIDIIDAE are quite remarkable: Only few diagnostic family characters existed (apparently the most basal ones): The not rebordered labium, the reduced leg bristles, the absence of a retrolateral paracymbium and the typical structures of the tibia of the male pedipalpus which is flat and widened/elongated and bears a transverse subapical row of strong (bristle-shaped) hairs, see WUNDERLICH (2018: Figs. 217, 221). Other typical characters of certain - or even most - extant Theridiidae - like a ventral hair comb of tarsus IV or a prosomal-opisthosomal stridulatory organ - were still absent in the fossils and evolved later on, in my opinion step by step.

(2) Modified diagnostic characters of few spider taxa higher than the superfamily level, including new taxa of the Mesothelae and the extinct Chimerarachnida, with remarks on their phylogeny

(A) SERIKODIASTIDA, ARANEIDA, CHIMERARACHNIDA (including the CHIMERARACHNIDAE) (see the figs. A and B and the new classification below):

Undoubtedly members of two taxa – of the Chimerarachnida and of the Mesothelae – represent most important keys for solving questions of spider phylogeny besides Hypochilidae and Filistatidae. The most spectacular recent discovery within the Arachnida in Burmite is the discovery of the tailed spider *Chimerarachne yingi* WANG et al. last year, see the fig. on p. 1: A monotypic taxon, which has been regarded as a spider (Araneae) by WANG et al. (2018) and by WUNDERLICH (2018: 6) but in contrast as a member of the related extinct order Uraraneida by HUANG et al. (2018) (*).

The characters of this taxon provides the question: WHAT IS A SPIDER?

Mainly because of the existence of opisthosomal silk glands I previously (2015) regarded the tailed Palaeozoic Uraraneida as a spider, to be its most basal suborder. The recent discovery of the also tailed – but much more derived and younger - Mesozoic *Chimerarachne* changed my opinion: These animals possessed (a) a typical spinning apparatus like extant spiders – four pairs of spinnerets placed ventrally in a group at the end (**) of the opisthosoma – and (b) a male pedipalpus proper for sperm transfer, see WANG et al. (2018). I regard these as apomorphic characters of the Araneida (spiders) in a new sense, see fig. A. The SPECIAL KIND of a slender flagellum is regarded as a synapomorphy of the Uraraneida + Araneida, of the superorder Serikodiasida (***) ; its further diagnostic characters: see fig. A. The telson is known as an ancient arachnid character. So a spider (order Arachnida, see below) is a member of the Tetrapulmonata, which – in the sense of the present author - possesses basically (a) four pairs of spinnerets placed in a group ventrally at the end of the opisthosoma (apomorphy) and (b) a male pedipalpus proper for sperm transfer (apomorphy). In the Chimerarachnida WUNDERLICH 2018: 6 furthermore a flagellum exists (plesiomorphy) which was lost in most parts – reduced to an anal tubercle - in the remaining spider taxa (Araneae). Another plesiomorphic character of the Chimerarachnida is the existence of two pairs of lungs, see fig. A. The median spinnerets

are quite small in all spiders, the posterior medians are lost in *Chimerarachne*, the anterior medians are lost or replaced by a cribellum or by a colulus in numerous taxa of the Araneae, see below. The loss of the posterior median spinnerets and the small size of the male pedipalpus - which bears slender articles - may be the apomorphic characters of the Chimerarachnida, see the Chimerarachnidae and below, figs. A-B.

(*) *Uraraneida* SELDEN possesses a quite different spinning apparatus: Spigots situated in a row on the lateral margin of the opisthosoma. Spinnerets are not documented by the fossils, the function of the male pedipalpus is unknown.

(**) A similar plesiomorphic position of the spinnerets near the end of the opisthosoma exists in most extinct Mesothelae: See below and figs. 5-6.

(***) This palaeoDB taxon is regarded here as superorder, considered as the sister group of the Schizotarsata (*Xenarachne* GARWOOD et al. 2016). In the dubious extinct genus *Idmonarachne* DUNLOP & POSCHMANN 1997 a flagellum and spinnerets are absent.

CHIMERARACHNIDAE n. fam. (fig. in fig. A), photo p. 1

Etymology: See WANG et al. (2018) (*Chimerarachne*). – Note: The greek origin of the term is chimaer- but not chimer-.

Type genus (by monotypy): *Chimerarachne* WANG et al. 2018.

Diagnosis (male; female not surely known) (see figs. A and B): (a) apomorphies: Posterior median spinnerets absent, anterior median spinnerets strongly reduced, pedipalpus small and articles quite slender (a possible apomorphy); (b) plesiomorphies (see above, Chimerarachnida): Opisthosoma bearing a long and slender telson; eyes (POSSIBLE plesiomorphies): Position fairly wide, tubercle absent, no triads; apical article of the pedipalpus simple, bearing two apophyses. - Venom glands, epandrous glands/spigots and tarsal organs have not yet been studied.

Note: Probably a “traumatic insemination” existed in the Chimerarachnidae - or already in the earliest extinct Arachnida - as the most ancient kind of sperm transfer in the Araneida, similar to the pattern which “regained” in the extant species *Harpactea sadistica* (Dysderidae).

Relationships: See above, Chimerarachnida, and the figs. A and B.

Distribution: Mid Cretaceous amber forest of Myanmar (Burma).

(B) MESOTHELAE:

Today only the extant families Heptathelidae and Liphistiidae exist. In 2017 I added the extinct families Burmathelidae (juv.), Cretaceothelidae (juv.) and Parvithelidae (ad. male unknown) from Mid Cretaceous Burmese amber. In this paper I add the new family Eomesothelidae (juv.) which may include the new genus *Intermesothele* (juv.). From the Palaeozoic the plesion *Eothele* SELDEN 2000 has been described in

stone in which BOTH margins of the fang furrow bear teeth in contrast to extant taxa and Cretaceous fossils in Burmite except probably the Eomesothelidae.

The main diagnostic characters of the EXTANT Mesothelae – see the photos and the diagnosis at the end of this paragraph - are the existence of tergites of the distinctly segmented opisthosoma (plesiomorphy), the prognath position of the basal cheliceral articles (plesiomorphy), the mediognath position of the fangs (apomorphy in my opinion), four pairs of spinnerets (plesiomorphy), strongly pseudosegmented lateral spinnerets (plesiomorphy), a position of the spinnerets near the middle of the opisthosoma or somewhat posteriorly (e. g. in *Vinathela nahang*) - see WUNDERLICH (2015: 40f, 48), (2017: 87f) – (apomorphy, existing in the extant and several extinct taxa), an inclination of coxa IV (apomorphy, existing in the extant and some extinct taxa) and peculiar structures of the male copulatory organ (apomorphy). A narrow sternum exists only in adult extant spiders but to my knowledge in adult AND juvenile Mid Cretaceous spiders. Regarding several characters the mesothelid families in Burmite differ strongly from extant families: In the members of the extant families of the Mesothelae the position of the spinnerets is near the centre of the opisthosoma (similar to fig. 1) or somewhat behind it in contrast to the Mid Cretaceous taxa in Burmese amber in which a quite variable position of the spinnerets exists: Near the middle of the opisthosoma (in the Burmathelidae, fig. 1), near the end of the opisthosoma (in the Eomesothelidae, figs. 4-5) and between both positions (in the Cretaceothelidae and in the Parvithelidae, fig. 2; in fig. 7 more posteriorly). In the Carboniferous plesion *Eothele* SELDEN 2000 from France (not assigned to a family) the position of the spinnerets on the deformed opisthosoma is more posteriorly, especially of the posterior lateral spinnerets, see fig. 3 in SELDEN (1996). In the Permian “Araneae incertae sedis” from Kazakhstan – in my opinion most probably also a member of the Mesothelae - apparently spinnerets at the end of the opisthosoma exist, see SELDEN et al. (2014: figs. 4a-b). According to the posterior position of the spinnerets in these oldest members of the Mesothelae - the same position of the spinnerets in the ancient Chimerarachnida and the same position in certain Mid Cretaceous taxa - I regard the terminal position of the spinnerets as a plesiomorphic character of the Mesothelae. In the mesothelid taxa of the Burmese amber forest the ancient almost terminal position of the spinnerets in certain taxa (figs 4-5) were retained and the spinnerets were translocated more or less anteriorly in other taxa (figs. 1-2, 7). Today only taxa of the advanced families Heptathelidae and Liphistiidae outlived in which a spinneret position near/in the middle of the opisthosoma exists similar to the Cretaceous Burmathelidae (fig. 1). It is remarkable that we find various stages of the position of the spinnerets – as well as of other structures, see tab. 1 – within a single period, the Mid Cretaceous, in Burmite. Also worth mentioning are the huge gaps in the fossil record of the Mesothelae: (a) more than 200 million years between the Carboniferous and the Mid Cretaceous Burmite and (b) 100 million years between the Mid Cretaceous and today. - The four extinct Mid Cretaceous families (+ an unsure genus) of the Mesothelae and its two extant families show a mixtum of characters, see tab. 1, and indicate a mosaic-like evolution. According to the plesiomorphic existence of teeth of the retromarginal fang furrow, the posterior position of the spinnerets - and probably also the absence of an inclination of coxa IV (fig. 3) - the extinct Eomesothelidae is the most ancient mesothelid family in Burmite; according to the anterior position of the spinnerets, the existence of an inclination of coxa IV and the absence of retromarginal teeth of the fang furrow the extinct Burmathelidae and the extant Heptathelidae and Liphistiidae are the most derived families, see tab. 1. Nothing is known about the existence of venom glands in the fossil taxa; I do not want to exclude that the tiny glands known from extant spiders evolved during the mesothelid

evolution but see fig. B. The digging behaviour and a trap door evolved probably a taxon of the ancestor of the Mesothelae.

In short: The diagnostic characters of extant and fossil Mesothelae differ distinctly from each other. The occurrence of two derived mesothelid characters is remarkable: (1) the spinnerets' position near the middle of the opisthosoma exists in all (two) extant families but only in one (Burmathelidae) of four known extinct Cretaceous families, see tab. 1; (2) a narrow sternum of adult spiders (it is wider in juveniles) exists only in the two extant families in contrast to the wide sternum – see WUNDERLICH (2015: 246, fig. 6) - of all fossil taxa. - If Mid Cretaceous taxa are included I regard as sure APOMORPHIC somatic diagnostic characters of the Mesothelae only the median position of the fangs and the peculiar structures of the COMPLICATED male copulatory organ, e. g., the spiny outgrowths of tibia and cymbium, see fig. A.

Character	Liphisti-idea	Heptathelidae	Burmathelidae	Cretaceothelidae	Eomesothelidae (*)	Parvithe- lidae
pseudo-pulvillus	--	--	--	--	--	+ (fig. 9)
opisthosoma: spinnerets position	near the middle or posteriorly	near the middle or posteriorly	near the middle (fig. 1)	in the poste- rior half (fig.2)	near the end (figs. 4-5)	in the pos- terior half (figs. 7-8)
narrow sternum	+	+	--	--	--	--
inclination of coxa IV (fig.10)	+	+	+	--	-- (?)	+
clubshaped leg trichobo- thria	+(!) (fig. 11)	--	--	--	--	--
two-rowed teeth of the paired tarsal claws	-- (fig. 12)	--	+ (!)	--	--	--
small/short teeth of the paired tarsal claws	--	--	--	+ (!)	+ (!)	--
anterior med. spinnerets replaced by a colulus	--	+ (!)	--	--	--	--
teeth of the fangs' retro- marg. furrow	--	--	--	--	+ (?)	?
distribution	extant, SE-Asia	extant, SE-Asia	Burmite	Burmite	Burmite	Burmite
genera	<i>Liphistius</i>	several	<i>Burmathele</i>	<i>Cretaceothele</i>	<i>Eomesothele</i> , <i>?Intermesothele</i>	<i>Parvithele</i> , <i>Pulvillothele</i>

Tab. 1. Selected characters of the Mesozoic and extant families of the Mesothelae.
(*) See also the new genus *Intermesothele* in Burmite which is not included here.

(3) Proposal of a modified new classification of the Araneida (spiders):

Remark: Spider phylogeny is tricky. Previous classifications – see, e. g., taxa like “Cribellatae”, “Haplogynae”, “Dionycha” as well as synonyms (see MARUSIK (2018)) – were controversially discussed, modified or even removed during my scientific life time of more than fifty years. They were partly based, e. g., on the number of lungs, the presence/absence of a cribellum/colulus, the haplogyne/entelegyne stage, the pattern of the chelicerae, the presence/absence of an unpaired tarsal claw, genetic patterns and (recently) the kind of spermia; see LEHTINEN (1967: 277-280). Certain classifications were regarded as useful by various authors and repeated for a certain time – an example for CONFIRMATION BIAS, see HOSSENFELDER (2018). Recent studies refer to a quite complicated situation of spider phylogeny: A mosaic-like evolution which differs from former opinions. Fossils surely can help to answer certain questions of spider phylogeny.

- Order Araneida (1)
 - Suborder † Chimerarachnida (2)
 - Suborder Araneae (3)
 - Infraorder Mesothelae (4)
 - Infraorder Opisthothelae (5)
 - Microorder Mygalomorpha (6)
 - Microorder Araneomorpha
 - Clade Basalhaplogynae
 - Branch Synspermiata (7)
 - Branch Filistatomorpha (8)
 - Clade Neocribellatae (8)
 - Branch Hypochilomorpha (9)
 - Branch Austrochiloidea (10)
 - Branch Dipneumonomorpha (11)

-
- (1) Spiders (in German: Spinnen) in a new wide sense, including two suborders: the extinct monotypic Chimerarachnida and the very diverse Araneae. The orders Araneida (under Araneae) (*) and Uraraneida are united in the Serikodiastida; this name was coined by GARWOOD & DUNLOP (2014) and is ranked here as a super-order. This classification is based on fig. A. See above and ESKOV & ZONSHTEIN (1990).
 - (2) Chimerarachnida WUNDERLICH 2018: 6: Tailed spiders (in German: Schwanztragende Spinnen). Only the Mid Cretaceous extinct *Chimerarachne yingi* WANG et al. 2018; see WUNDERLICH (2018: 5-6) and above, the new family Chimerarachnidae.
 - (3) Tailless spiders (in German: Schwanzlose oder <Eigentliche> Spinnen) = spiders (Spinnen) in the traditional sense. All extinct and extant spiders except *Chimerarachne*. Its anal tubercle is regarded here as remains of the flagellum of the Chimerarachnida. See Aranei in the sense of MARUSIK (2018: 44).
 - (4) Segmented spiders (in German: Gegliederte Spinnen).

- (5) Unsegmented spiders (in German: Ungegliederte Spinnen).
- (6) Mygalomorphs (in German: Längskiefernspinnen).
- (7) = Dysderoidea s. l., Pholcoidea (Scytoidea) etc. See MICHALIK & RAMIREZ (2014), and Scytodiformes in the sense of MARUSIK (2018: 45) (!). – If a branching really existed in this way an unknown extinct taxon should have existed in which the posterior pair of lungs was probably lost and the anterior pair of median spinnerets still existed. The chelicerae may **BASALLY** have been fused.
Note: Like in the Synspermiata the anterior median spinnerets are convergently replaced by a colulus in the Mesothelae: Heptathelidae. I will call this directly replacing structure the “PRIMARY COLULUS”, and the structure replacing the cribellum – like in numerous members of the Dipneumonomorpha – I will call the “SECONDARY COLULUS”.
- (8) Filistatids (in German: Sternnetzspinnen). Only the family Filistatidae. Lorum/ petiolar segments as a plesiomorphic character: See ESKOV & ZONSHTEIN (1990: 132). The mating position, the perenniality, the thick articles of the male pedipalpus and - to my knowledge – the existence of several small metatarsal trichobothria (in my opinion probably a regain) are plesiomorphic “relic character” of the Mygalomorpha. In the ancestor of the Neocribellatae evolved a different kind of a cribellum. - The remaining taxa - which are basically cribellate - are united here under the name Neocribellatae CAPORIACCO in a **new sense** (Filistatidae and Synspermiata are excluded, Hypochilidae are included), see fig. A.
- (9) = Palaeocribellatae. Only the family Hypochilidae. Its sister group – Austrochiloidae + Dipneumonomorpha are united here under the **new name** Praeentelegynae.
- (10) Its high taxa and some important characters: See below.
- (11) ~ Cleistospermiata WUNDERLICH 2015 (part.), without the “Hypochilomorpha” s. l. which possesses no cleistospermia. The term Cleistospermiata has to be deleted. The remaining spiders - the Dipneumonomorpha (≠ Araneoclada) – are “entelegyne”; they may be named ENTELEGYNAE and include many superfamilies/branches, like Archaeoidea, Oecobioidea, Deinopoidea, Araneoidea and the RTA-clade. In my opinion the “entelegyne stage” developed much more than three times. e. g. within the Synspermiata, the Austrochilomorpha and the Dipneumonomorpha (see the “protoentelegyne” Leptonetoidea). A three-dimensional capture web evolved convergently within certain Synspermiata like the Pholcidae. A reversal of a short life cycle exists in the perennial family Eresidae. See also below, ESKOV & ZONSHTEIN (1990) and WUNDERLICH & MÜLLER (2018: 12).
-

(*) The numbers four/eight is in a unique fourfold way characteristic of Araneida (spiders): 4 pairs of legs, **BASICALLY** 4 (2 pairs of) lungs, basically 8 (4 pairs of) eyes and basically 4 pairs of spinnerets. 4 pairs of legs exist also in almost all of the remaining Arachnida (their number is less in larvae of Acari and Ricinulei and in certain adult Acari). Except of the legs numerous losses of the basic numbers exist.

(4) Phylogenetics: Main evolutionary steps and branchings of spider evolution; cladograms.

The existence, the losses and the origin/evolution of selected innovatory characters of higher spider taxa. See p. 9-10, 16 and the cladogram fig. A.

Numerous – partly strongly controversial - cladograms regarding high spider taxa can be found on the internet. Fig. A shows my ideas concerning the branchings of the basal groups of spiders which appear most logical to me. I used characters which I regard as most special, rare within their kin and/or innovative, e. g., the origin of a cribellum (Filistatidae, Neoribellatae), of a colulus, of different positions of the fangs, of cuspules of the mouth parts (Mygalomorpha), the origin/loss of tarsal trichobothria and feathery hairs; losses see below. - In this connection it is very important to find out close relationships of the peculiar cribellate families Hypochilidae and Filistatidae, see p. 10, notes 8, 10. According to its characters – e. g. the simple structures of the bulbus – Filistatidae is close to the Synspermiata and to the Mygalomorpha as well, but not to the Hypochilidae as regarded by certain authors like LEDFORD. ESKOV & ZONSHTEIN (1990) regarded the Filistatidae even as sister group of the Mygalomorpha.

In the following certain structures are discussed which I regard as most important:

LUNGS: In the ancient Chimerarachnida, the Mesothelae, the Mygalomorpha as well as in the cribellate Hypochilidae, Gradungulidae and certain Austrochilidae 2 pairs of lungs exist. The posterior pair of lungs has been lost in the Austrochilinae, Basalhaplogynae and Dipneumonomorpha and are set posteriorly in the Hypochilidae and Austrochiloidea. See fig. A and WUNDERLICH & MÜLLER (2018: 64, fig. D) (in which the word “lungs” near the bottom has to be replaced by “posterior pair of lungs”).

SPINNERETS, CRIBELLUM AND COLULUS: In my opinion the anterior median pair of spinnerets – existing reduced in its size especially in the ancient Chimerarachnida and in most Mesothelae – has **(a)** DIRECTLY been replaced by a colulus (a “knob”, the single functionless remains of spinnerets) in the family Heptathelidae of the Mesothelae and – suggested by me - probably in the Synspermiata (Dysderoidea, Pholcoidea etc.), see the note (7) p. 10 (it even may be lost) or **(b)** was replaced by a cribellum, in my opinion two times (see fig. A): In (the ancestor of) the Filistatidae and in (the ancestor of) the Neocribellatae. Within the Dipneumonomorpha a colulus replaced “secondarily” the cribellum or got lost, e. g., in the Araneoidea and numerous times within the RTA-clade. A quite large colulus exists, e. g., in the Telemidae, in certain Oecobiidae (the extinct Mizaliinae) and in some extinct Leptonetoidea (in certain taxa it may be a functionless cribellum), see WUNDERLICH & MÜLLER (2018). A reversal – a secondary origin of the cribellum - is unknown to me. The posterior pair of median spinnerets is absent (lost in my opinion) in *Chimerarachne*. The special position of the spinnerets in the Mesothelae: See above and below. A position of the spinnerets slightly to fairly set forward exists, e. g., in the family Filistatidae, too.

POSITION OF THE BASAL CHELICERAL ARTICLES AND THE FANGS: Their plesiomorphic position is regarded as orthognath (protruding basal articles and parallel fangs) like in the Chimerarachnida and sister group of the Araneida, the Uraraneida. This position still exists in most (!) Mygalomorpha with several exceptions: A mediognath position (oblique position of the fangs) evolved in several families like the Migidae. A mediognath position evolved in the ancient Mesothelae (see above and the photo) as well as – in my opinion convergently - in the Araneomorpha in which the position of the basal cheliceral articles is vertical but not protruding horizontally. The most advanced labidognath position (a nippers-shaped position of the fangs placed on the basal cheliceral articles in a vertical position) evolved in the Dipneumonomorpha and basically in the Basalhaplogynae (with few modifications in the Synspermiata, e. g., in *Dysdera*). The position of the basal cheliceral articles and of the fangs are connected or not, in my opinion both evolved independently, see fig. A. See the discussion and terms published by ESKOV & ZONSHTEIN (1990: 131) which don't appear useful to me. See also p. 16 (plagiognathy).

FEATHERY HAIRS (see fig. A) originated to my knowledge in (the ancestor of) the Praeentelegynae. Recently I found this type of hairs in the family Austrochilidae, see MICHALIK & WUNDERLICH (2017: Fig. 4). This type of special hairs on body and/or legs and/or pedipalpi is completely absent in the Chimerarachnida, the Mesothelae, the Mygalomorpha, the Hypochilidae, Filistatidae and Synspermiata. These hairs have apparently been lost numerous times within the Dipneumonomorpha, for example in the the Archaeoidea (= Palpimanoidea), in certain Deinopoidea, in the Leptonetoid-Araneoid branch – see WUNDERLICH & MÜLLER (2018) -, and several times within the RTA-clade like in the Ageleninae.

TARSAL TRICHOBOTHRIA exist in the Chimerarachnida, see WANG et al. (2018). They are lost in the Araneomorpha (see fig. A), and evolved again (regained) in the RTA-clade as well as “sporadically” in certain other taxa of the Synspermiata like the Caponiidae and the Dipneumonomorpha: The Lagonomegopidae of the Archaeoidea (= Palpimanoidea).

PERENNIALITY (see ESKOV & ZONSHTEIN (1990: 133)) and MOULTING OF ADULTS: A perennial life cycle (a long life span) is considered as a plesiomorphic character of the Araneida (and Arachnida as well) (in contrast to males of the Mygalomorpha which may live only for a short time). Basalhaplogynae: I keep a female *Filistata* sp. (Filistatidae) from Amman (Jordan) for 12 years which is still alive in I 2019. In several (or even in most) members of the Synspermiata - e.g., in the genus *Ariadna* (Segestriidae) – a perennial life style exists, according to my observations only in the female sex. Within the Austrochiloidea the Gradungulidae is said to be perennial. According to observations by COYLE a member of the Hypochilidae possesses only a two-year (!) life cycle. A short life cycle probably evolved in the ancestor of the Cribellatae; it evolved convergently in certain or numerous Synspermiata like the Pholcidae. Perenniality was regained in certain Dipneumonomorpha like in the Eresidae. Frequently perenniality is connected with moulting of adults, e. g., in Mygalomorpha, probably in certain Synspermiata, in Filistatidae and in Eresidae.

THE ENTELEGYNE STAGE: See chapter 3, note (11), p.10.

Results (see also the abstract) and discussion

Fig. A shows my ideas concerning the branchings of the basal groups of spiders. Several steps in fig. A are *losses*, however – see the previous paper by WUNDERLICH (2015: 287, fig. G) important “*innovations/novelties*” exist: The origin of a cribellum, the labidognathy, the short sequence of generations resp. of the life span/cycle, the entelegyne stage, a well developed capture web which may possess sticky droplets (Araneoidea, Pholcidae), of olfactory leg hairs, and - again after a previous loss - the “development” of tarsal trichobothria, e. g., in the Dipneumonomorpha.

A large to huge pedipalpus in both sexes is generally regarded as an ancient/ plesiomorphic character of the class Arachnida, see, e. g., Scorpiones, Telephonida and Amblypygi. Also as plesiomorphic considered – and in my opinion a quite important taxonomic character! - are the thick articles of the male pedipalpus of certain basal Araneae: Of the Mesothelae (also a large – almost leg-shaped – female pedipalpus), of the Mygalomorpha (also a long female pedipalpus), and of the Basalhaplogynae (e. g. Filistatidae, Dysderidae, Pholcidae) which do NOT possess an enlarged FEMALE pedipalpus. In the ancestral spiders including the Hypochilidae the bulbus is attached near the end to the cymbium. In the more advanced Araneomorpha – including, e. g., families like Austrochilidae, Leptonetidae, Araneidae, Agelenidae and Salticidae – the long(er) cymbium bears the bulbus usually not at its end and the pedipalpus is basically not enlarged in both sexes. Articles of the male pedipalpus are secondarily thickened in certain families, for example in the Palpimanidae and the enigmatic Eresidae. – See the cladograms published, e. g., by ESKOV & ZONSTEIN (1990: Fig. 1), GARRISON et al. (2016), JOCQUE & DIPPENAAR-SCHOEMANN (2007), LEDFORD et al. (2016) (which in my opinion contains various dubious/unlikely “alternative” facts/results/conclusions), MICHALIK & RAMIREZ (2014).

Falsifiability. Regarding my hypothesis of the origin of the colulus of the very diverse colulate Synspermiata (Segestriidae, Dysderidae, Pholcidae etc.) (if Synspermiata is really a monophyletic group): In the case that in an early stage of development of a member of this clade special structures similar to a cribellum would be discovered the direct displacing of the anterior median spinnerets by a colulus must be wrong.

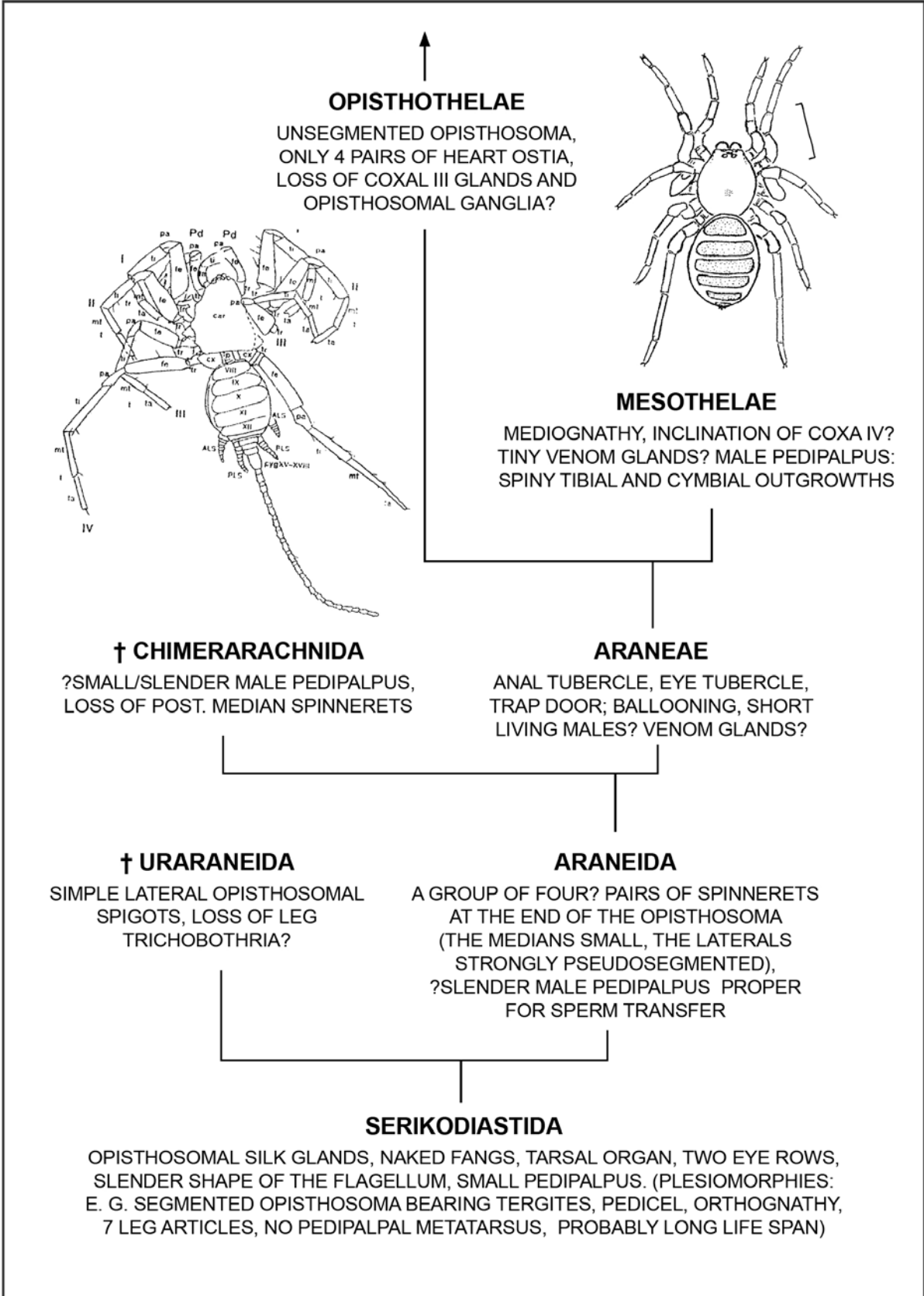
PARSINOMY concerning the most important characters used here; autapomorphies of high taxa which occurred more than one time (see fig. A):

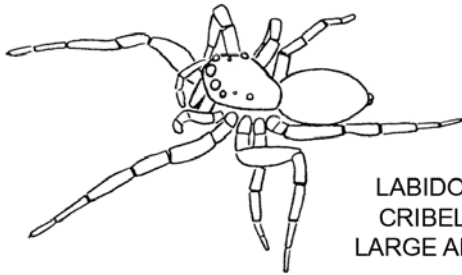
(a) numbers of origins:

- the cribellum: 2 times: Filistatidae and Neocribellatae;
- the mediognathy: 3 times;
- the labiognathy (after the development of mediognathy): 2 times;
- endocephalic venom glands: 2 times: Basalhaplogynae and Praeentelegynae.

(b) numbers of losses and displacings:

- loss of the posterior pair of lungs: 3 times;
- displacings of the anterior median spinnerets: 3 times: 2 times displacings by a cribellum, one time (Synspermiata) displacing by a colulus.





DIPNEUMONOMORPHA

LABIDOGNATHY, LOSS OF THE POSTERIOR PAIR OF LUNGS, CRIBELLUM DIVIDED, ONLY 3 HEART OSTIA? TENDENCY TO LARGE ANTERIOR MEDIAN EYES AND A LARGE/WIDE CYMBIUM

evolution of characters step by step from an extinct unknown species of the Austrochiloidea (1) to an extinct unknown species of the Dipneumonomorpha via several unknown extinct taxa, e. g., in the following order: Labidognathy, loss of the posterior pair of lungs, loss of one heart ostium (the entelegyne stage evolved probably several times).

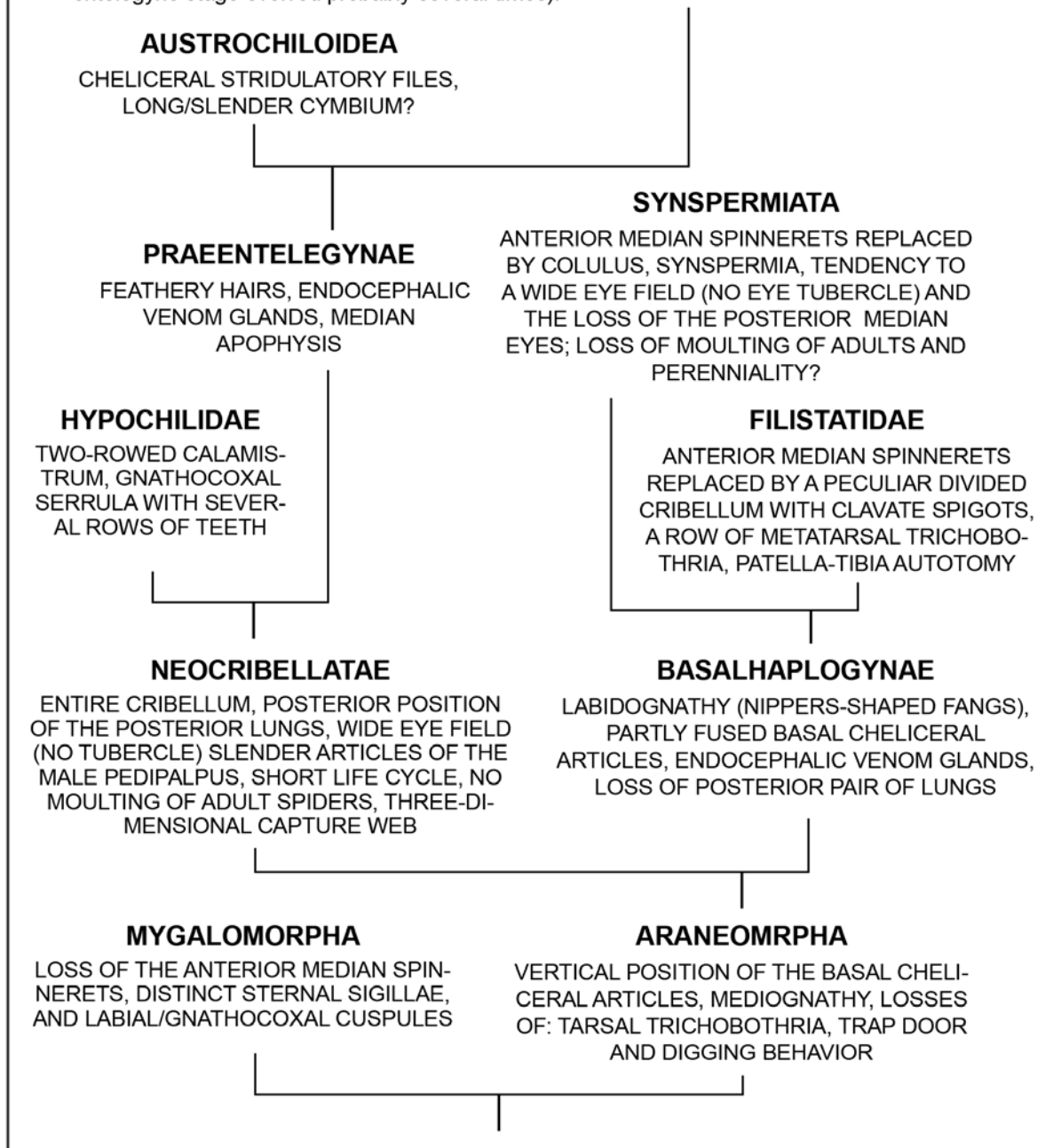


Fig. A. Proposed **branchings of high taxa** of spiders (Araneida) and Uruaraneida based on selected characters including BEHAVIOURAL patterns.

 (1) Austrochiloidea – fossils are still unknown! – is a small but fairly diverse taxon of two or three relic families (*Hickmania* is usually regarded as a genus of the Austrochilidae) in which – as a mixture of characters – a cribellum, the posterior pair of lungs and the entelegyne stage exist or are absent. See the tab. directly below and fig. A.

Four characters of the the ancient families Hypochilidae (*Hypochilus* of North America and *Ectatosticta* of South-East Asia), Austrochilidae s. l. (*Austrochilus* and *Thaida* of South America and *Hickmania* of Tasmania) and Gradungulidae (7 genera of Australia and New Zealand) (see FORSTER et al. (1987):

Genus	pairs of lungs	haplogyne/ entelegyne	cribellate	median apophysis
Hypochilidae	2	haplogyne	+	- (!)
<i>Austrochilus</i>	2	entelegyne	+	+
<i>Thaida</i>	2	entelegyne	+	+
<i>Hickmania</i>	1-2 (!)	entelegyne	+	+
Gradungulidae	2	haplogyne	+/- (!)	+

Note on certain further characters: Some further remarkable characters of these taxa are: Several rows of teeth and two rows of metatarsal trichobothria (in certain taxa) exist in the Hypochilidae in which cheliceral files are completely absent (in contrast to the Austrochiloidea), and strongly dissimilar paired tarsal claws I-II as well as a strongly reduced unpaired tarsal claws exist in the Gradungulidae, see FORSTER et al. (1987) and JOCQUE & DIPPENAAR-SCHOEMAN (2007).

Notes on plagiognathy and eye triads: Both are considered as plesiomorphic patterns in spiders by KRAUS & KRAUS (1993) but the ancestral *Chimerarachne* possesses an orthognathous position of the chelicerae and no eye triads.

(5) Descriptions of the new taxa and previously unpublished material of the Mesothelae in Burmite

See also above, the paragraph on the Mesothelae.

EOMESOTHELIDAE n. fam.

Etymology: See below.

Type genus: *Eomesothele* n. gen. Further genus probably the new *Intermesothele*.

Diagnostic characters (juv.): Spinnerets (figs. 4-5): Position near the end of the opithosoma (more anteriorly in *Intermesothele*, see the photos 2-4), anterior median spinnerets large in the type genus in which the posterior median spinnerets are unknown, anterior lateral spinnerets larger than the posterior laterals in the type genus (lateral spinnerets apparently retracted in its single known specimen); retromargin of the fang furrow probably bearing teeth, inclination of coxa IV most probably absent (fig. 3); pseudopulvillus absent.

Relationships (see tab. 1): According to the position of the spinnerets near the end of the opisthosoma, the existence of teeth of the fangs retromargin and the most probably absence of an inclination of coxa IV (ancestral characters; see the Cretamesothelidae) Eomesothelidae is the most ancient family of the known Cretaceous and extant Mesothelae. – According to their documented characters the Carboniferous *Eothele* SELDEN (= *Palaeothele* SELDEN) and the Permian Araneae indet./incertae sedis (see above) are most related. Because of their insufficient preservation unfortunately the most important characters of these fossils – they are preserved in stone – are not observable with certainty.

Distribution: Mid Cretaceous amber forest of Myanmar (Burma).

Eomesothele n. gen.

Etymology: From Eos (gr.) the dawn, referring to the high age of the Mesothelae, the name of a taxon which is included the new name.

The gender of the name is feminine.

Type species (by monotypy): *Eomesothele noninclinata* n. sp.

Diagnosis and distribution: See above.

Relationships: See below, the genus *Intermesothele*.

***Eomesothele noninclinata* n. gen. n. sp.** (figs. 3-5, photo 1)

Etymology: The species name refers to the coxa IV which is not inclined in contrast to most Mesothelae species, from non (lat.) not, and inclinatio (incision, notch).

Material: Holotype juv. in Mid Cretaceous Burmite, F3428/BU/CJW.

Preservation and syninclusions: The spider is completely and well preserved in a small block of yellowish amber, most mouth parts are hidden by small bubbles. – A long part of an insect's antenna is placed in a transverse position below the sternum, two plant hairs are lying on the left legs I and II.

Diagnosis, relationships and distribution: See above and ?Parvithelidae sp. 2.

Description (juv.):

Measurements (in mm): Body length 1.9; prosoma: Length 1.0, width 0.9; opisthosoma: Length 1.0, width 0.7; leg I: Femur 0.7, patella 0.28, tibia 0.38, metatarsus 0.32, tarsus ca. 0.3; tibia IV 0.57.

Colour light brown, legs not annulated.

Prosoma slightly longer than wide, fovea hidden, 8 eyes (partly hidden) on a hump in a narrow field, basal cheliceral articles well developed, fangs long, retromargin of the fang furrow probably bearing some teeth, sternum wide, similar to *Cretaceothele lata* WUNDERLICH 2015: 246, fig. 6, opisthosoma and spinnerets (figs. 5-6), see above. – Pedipalpus fairly long. – Legs rather short, bearing numerous thin bristles, IV longest, inclination of femur IV (fig. 3) most probably absent, pseudopulvillus absent, tarsal claws with small to tiny teeth. – Opisthosoma 1.4 times longer than wide, spinnerets: See above (the new family).

Questionable Eomesothelidae: Intermesothele n. gen.

Etymology: the name refers (1) to the phylogenetic relationships between two families, from inter (lat.) = between and (2) to the well-known taxon Mesothelae.

The gender of the name is feminine.

Type species (by monotypy): *Intermesothele pulcher* n. sp.

Diagnostic characters (juv.; probably subadult according to the existence of 8 tergites): Spinnerets (photos): Large, their position more posteriorly, inclination of coxa IV apparently absent, pseudopulvillus absent, a single row of few short teeth of the paired tarsal claws, existence of retromarginal teeth of the fang furrow unknown.

Relationships: According to the existence of only few small teeth of the paired tarsal claws and (most probably) the absence of an inclination of coxa IV the families Cretamesotheididae and Eomesotheididae are most related, the position of the spinnerets is even more posteriorly in the type genus of the Eomesotheididae in which the anterior median spinnerets are smaller and the lateral spinnerets are stouter (apparently retracted). I regard *Intermesothele* as a questionable genus of the Eomesotheididae.

Distribution: Mid Cretaceous amber forest of Myanmar (Burma).

***Intermesothele pulcher* n. gen. n. sp.** (figs. 6a-b, photos 2-4)

Etymology: The species name refers to the excellent preservation of the holotype, from pulcher (lat.) = beautiful.

Material: Holotype (juv.) in Mid Cretaceous Burmite, coll. of Patrick Müller, BUB-3417.

Diagnosis, relationships, and distribution: See above.

Preservation and syninclusions: The spider is excellently and almost completely preserved in a small clear block of yellowish amber; the retroventral parts of the basal cheliceral articles are lost and the unpaired claw of the right tarsus III is broken off near its base and lost. The thick opisthosoma of the spider may well be caused by decomposatory gas; a forked outgrowth in front of the spinnerets (see the photo) and a stalk running from the left ventral part of the opisthosoma to the surface of the piece of amber may also have been caused by such gas. – A small bubble is preserved between the left femur I and the left pedipalpus, a particle of detritus is preserved on the right leg III.

Description (juv., probably subadult: 8 of the 10 mesothelid tergites exist already): Measurements (in mm): Body length 2.3; prosoma: Length 1.1, width 0.85; labium: Width 0.7, length 0.18; sternum: Length 0.5, width 0.42; opisthosoma: Length 1.15, width 0.9, height 0.9; leg I: Femur 0.6, patella 0.25, tibia 0.4, metatarsus 0.37, tarsus 0.3, leg IV: Metatarsus 0.47, tarsus 0.44; pedipalpal femur ca. 0.43.

Colour (photo): Prosoma and legs light to medium brown, legs not annulated, opisthosoma light, tergites dark brown.

Prosoma (figs. 6a-b, photos) 1.4 times longer than wide, finely rugose, hairless, fovea low, apparently very wide (0.3 mm) and strongly recurved (?), 8 eyes on a tubercle, clypeus short, basal cheliceral articles large, stout and protruding, fangs slender, 0.3 mm long, their position mediognath, anterior margin of the fang furrow with a row

of at least 8 small teeth, posterior margin unknown (lost), gnathocoxae stout, labium short and wide, 1.9 times wider than long, not much smaller than the sternum, both separated by a deep furrow, sternum wide, 1.2 times longer than wide, rounded posteriorly, bearing few short hairs. – Pedipalpus large and spiny, tarsus bearing a long claw, its teeth unknown. – Legs (photos) stout, IV the longest, I-III about equal in length, bristles numerous and thin, femora 1 dorsally in the distal half and usually a dorsal one near the middle and a dorsal pair near the end, patellae about half a dozen; I: Tibia about a dozen, metatarsus about half a dozen laterally and ventrally, tarsus 1 ventrally (hair-shaped), trichobothria thin, unpaired tarsal claws probably smooth, paired claws large, bearing ca. 4 short teeth in a single row. – Opisthosoma (photos) 1.3 times longer than wide, finely rugose, bearing 8 tergites which bear 2-4 bristles, epigaster sclerotized, a larger plate exists between the epigaster and the spinnerets, anal tubercle large, 4 pairs of spinnerets, the lateral ones apparently expanded, both pairs quite similar in length, the median ones also similar in length, the anterior ones not larger.

(b) **Previously unpublished material**

Family BURMATHELIDE: *Burmathele* WUNDERLICH 2017:

Burmathele sp. indet., juv., F3389/BU/CJW.

The spider is almost completely and fairly well preserved (parts are deformed or hidden) in a yellowish piece of amber in which also two Acari and the larva of a Hemiptera are preserved. The body length of the spider is 3 mm, the retromargin of the fang furrow bears no teeth, the position of the spinnerets is near the middle of the opisthosoma.

Family PARVITHELIDAE: *Parvithele* WUNDERLICH 1017:

Parvithelidae indet. 1, juv., F3388/BU/CJW (fig. 7):

The spider is well (the spinnerets very well) preserved in a yellowish piece of amber, the dorsal part of the opisthosoma is cut off within the amber, the prosoma is strongly deformed. The body length is 5 mm, the legs are fairly stout, the paired claws bear long teeth, the long pseudopulvillus is apically distinctly divided. The four pairs of spinnerets (fig. 7) are well observable and in a more posterior position, the posterior lateral ones are quite long.

?Parvithelidae indet. 2, juv., F3427/BU/CJW (fig. 8):

The spider is well and almost completely preserved in a clear yellowish piece of amber, dorsal parts of the prosoma are cut off within the amber, some leg articles are

lost. The body length is 2.8 mm, the distinct fovea is slightly procurved, the 8 eyes are situated on a distinct hump close together, the anterior median eyes are tiny, the anterior margin of the fang furrow bears at least 7 teeth, the posterior margin is hidden, the wide labium is a free sclerite. The legs are fairly stout, the coxal IV inclination is well developed, paired and unpaired tarsal claws bear long teeth, the pseudopulvillus is well developed (comp. fig. 9). Four pairs of spinnerets exist in an only fairly posterior position a bit similar to *Eomesothele* (fig. 5), the laterals are fairly stout.

Parvithelidae indet. 3, juv., F3038/BU/CJW:

The spider is rather badly preserved in a small yellowish piece of amber, deformed and darkened; some leg articles are cut off, the dorsal-posterior part of the opisthosoma is cut off within the amber, the legs are fairly stout, the paired tarsal claws bear long teeth, the pseudopulvillus is only fairly large and slender. The spinnerets are placed in a rather posterior position, the posterior laterals are long.

(c) Note on *Cretaceothele lata* WUNDERLICH 2015 (Cretaceotheidae)

I do not want to exclude the existence of 2 pairs of tiny epiandrous gland spigots in the male holotype of *Cretaceothele lata* but such tiny structures are difficult to study under the magnification of 150x although the epigaster is well preserved in this juvenile specimen.

(6) Notes on faunistic changes, relic and extinct spider taxa

The great importance of the Mid Cretaceous Burmese amber is documented by the report of about 40 families of which by far most are extinct, see WUNDERLICH (2015, 2017: 80f, 2018: 6f). Regarding the extinct families only Lagonomegopidae, Mongolarachnidae and Spatiatoridae are known from other deposits and periods, too.

Burmite is the only Mesozoic kind of amber which offers a lot of pieces and contains remains of a diverse fauna. The spider fauna of the Mid Cretaceous Burmese amber forest - including gaps, relics and extinct taxa - was previously already been treated by me, see WUNDERLICH (2008ff). In the following I will add some further notes.

I consider a specified supraspecific taxon – like Mesothelae or Segestriidae, see (b) and (d) - to be surely a relic taxon under the condition that today the worldwide number of its families resp. genera is lower than their number known in Burmite. “Gaps” of the fauna: The absence of a taxon in the known fauna of the Burmite – e. g. of the Hypochilidae or of the diverse mygalomorph families - does not indicate its absence at that time or in the Burmese amber forest but only that it has yet not been found

because, e. g., of its large size or of its special habitat. (It furthermore has well been existed in a quite different region). - Questions regarding new discoveries of fossil spiders in Burmite during the last years as well as remarkable gaps of the fossil Burmese spider fauna – and of other Mesozoic Lagerstaetten - have still to be discussed. In the following I treat selected higher spider taxa.

(a) CHIMERARACHNIDA: The only genus *Chimerarachne* WANG et al. 2018 has recently been described as a unique tailed extinct taxon in Burmite, see the fig. p. 1. This ancient model of a “missing link” possesses a “tail” (flagellum) similar to the Palaeozoic order Uraraneida but furthermore true spinnerets near the end of the opisthosoma like other spiders. It shares the segmented opisthosoma with the extinct Uraraneida and with the most ancient extant spiders, the Mesothelae. In the Burmese amber forest – 100 million years ago – *Chimerarachne* was apparently already a relic which probably became extinct latest at the KT-events, apparently displaced by vagile members of the RTA-clade. A similar taxon has never been found elsewhere. See figs. A and B.

(b) MESOTHELAE: The ancient members of this taxon existed already in the Palaeozoic; they were probably the only spiders of this period besides the Chimerarachnida, see SELDEN et al. (1996, 2014). Mesozoic Mesothelae were unknown for a long time. Recently mesothelid spiders have been discovered in Mid Cretaceous Burmite (see above): Taxa of four families and a further genus are known from a single (!) Mesozoic forest, preserved in Burmite, but only two mesothelid families – Heptathelidae and Liphistiidae - survived as relics in tropical regions. Members of both families were absent in the Burmese amber forest and thus apparently are relatively young.

(c) MYGALOMORPHA in Burmite is still insufficiently known. Juveniles are not very rare; adult females live mainly in tubes in the ground and will only rarely be captured in amber; I don't know a single female in this kind of amber in contrast to several males (CJW) which may leave their tubes searching for tubes of fertile females. Therefore – based on the Burmese amber fauna - nothing can be said today about relic mygalomorph taxa. A single extinct endemic family - the Fossilcalcaridae WUNDERLICH 2017 has been described in Burmite; certain other spiders (CJW) may represent taxa of further undescribed extant or extinct families. The family Atypidae may well be a relic; its oldest report goes back to the Eocene Baltic amber forest.

(d) FILISTATOMORPHA AND SYNSPERMIATA (see above): No member of the ancient FILISTATIDAE has been found in Burmite. Spiders of this ancient family are not typical forest spiders today. – SYNSPERMIATA represents one of the quite diverse taxa of spiders in the Burmese amber forest, see WUNDERLICH (2015, 2017: 80f, 2018: 6f). Members of the cosmopolitan family Segestriidae were quite frequent and diverse in the Burmese amber forest: 6 genera have been described but today only 4 genera (only 2 are diverse, 2 are poor in species and may be relics) are known worldwide. Therefore Segestriidae is clearly a relic family. - A remarkable “gap” in Burmite concerns a part of the family Oonopidae: Only a single subfamily (Orchestininae) and a single genus – *Burmorchestina* WUNDERLICH 2008 - of this very diverse family has been described in Burmite. Most Oonopidae occur not in higher strata of the vegetation in contrast to certain extent and fossil Orchestininae. In the Eocene Baltic amber a similar situation of this subfamily exists as in Burmite. - Today Pholcidae is a diverse cosmopolitan family; spiders occur in higher strata of the vegetation, too, but not a single member has been found in Burmite up to now in contrast to re-

lated families like the Tetrablemmidae: A remarkable gap of the fauna in Burmite (and the whole Mesozoic period as well?).

(e) AUSTROCHILOIDEA and HYPOCHILIDAE: This ancient (“primitive”) branches of spiders are regarded as a relic but not a single fossil member has ever been reported – a remarkable gap of the ancient faunas! I do not want to exclude that a “hidden” austrochiloid taxon in Burmite may exist among published taxa, e. g., within the family Pholcochyroceridae: The fangs’ position of the long-legged and most probably cribellate *Spinipalpus veta* WUNDERLICH 2015 may be mediognath like in the Austrochiloidea, a pectunculus and a calamistrum are absent, I found feathery hairs (on the left femur I), I did not find cheliceral stridulatory files.

(f) DIPNEUMONOMORPHA is the most derived and most diverse group of the today’s described 110-120 spider families; ca. 82 dipneumonorph families exist today but only ca. a dozen is known in Burmite. Most families of the diverse superfamily Araneoidea and the very diverse RTA-clade are relatively young and radiated strongly apparently first after (or around the) the KT-events 65 million years ago. The most prominent RELIC taxa of this clade are the family Archaeidae and the superfamilies Deinopoidea and Leptonetoidea, see below. Regarding the number of its genera Oecobiidae is a relic family, too, see WUNDERLICH (2015).

FURTHER NOTES ON EXTINCTIONS, RELICS, GAPS OF THE FAUNA AND DISPLACINGS. See also WUNDERLICH (2008 ff) and directly above.

We still do not know the reasons for the “MASS EXTINCTION“ of the haplogyne families of the Synspermiata around the end of the Cretaceous and we do not know the reasons (the advantages) which caused the LATE AND EXPLOSIVE radiation of the taxa of the superfamily Araneoidea and of the taxa of the RTA-clade which happened after the KT-events. Both were diverse only ca. 25 million years later in the Eocene Baltic amber forest, see WUNDERLICH (2004, 2008). The reasons for the absence of members of the RTA-clade (so far known) in the Cretaceous (before the KT-events) and its huge radiation around or after the KT-events are still unknown. I suppose that the strong diversification of the RTA-clade – after the loss of the cribellum and the capture web - started on the ground of an open habitat (not a forest!), probably grassland, as a vagile hunter and fast runner, which developed a jumping behaviour and a well functioning visual system for diurnal prey capturing. Most of these “innovations” – at least its combination - are absent in the more ancient spider groups: Most members of the Synspermiata are capture web builders (Dysderidae is one of the exceptions) and possess a weak visual system; most Mygalomorpha are tube dwellers and possess a weak visual system, too. Most members of the Archaeoidea (= Palpimanoidea) (of the Dipneumonomorpha) are sit-and-wait predators; only certain/few archaeoid spiders like Spatiatoridae and certain - short-legged - Lagonomegopidae were probably vagile hunters. I do not want to exclude that the RTA-clade originated by a species close to the Oecobioidae or the Archaeoidea. Remarkably a retro-lateral tibial apophysis (RTA) of the male pedipalpus existed in the archaeoid family Lagonomegopidae. Hopefully (I am sure) we will discover - and recognize!? - an ancient/“primitive” fossil taxon of the RTA in the future, probably in Burmite. Fossil re-

mains of quite questionable taxa of the RTA-clade in Burmite: See WUNDERLICH (2017: 238-239, 2018: 123).

Several questions have to be discussed in the future, e. g., (1) why did the RTA-clade evolve and radiate so late - only within the last quarter - of the evolution of spiders? (2) Spiders of which groups were ground hunters in the Cretaceous? Were such spiders unknown and extinct members of the Mygalomorpha which were displaced by members of the RTA-clade? (3) Why does no comparable distinctive situation in megaorders of flying insects exist – in Coleoptera, Diptera and Hymenoptera? The extinction of several Cretaceous families – like the family Lagonomegopidae which was diverse and widely distributed on the Northern Hemisphere for probably far more than 70 million years – at about the same era around the KT-events as the strong radiation of the RTA-clade may not be an accident but caused by displacing: I suggest that the Lagonomegopidae was displaced by other sit-and wait predators like the Sparassidae and Thomisidae of the RTA-clade; see WUNDERLICH (2015: 242). I call the Lagonomegopidae the “dinosaurs of fossil spiders” which were displaced by advanced spiders. Regarding the Vertebrates: The extinction of the dinosaurs was the beginning of the strong radiation of the derived placental mammals. – Another and comparable example concerns the two branches of orb web weavers: (1) Today only the families Deinopidae and Uloboridae of the CRIBELLATE superfamily Deinopoidea exist, but 7-8 families have been described in Burmese amber (all families besides the Uloboidae and questionable Deinopidae are extinct). So Deinopoidea is doubtlessly a relic superfamily. (2) In contrast to the cribellate Deinopoidea about 15 families of the ECRIBELLATE superfamily Araneoidea exist today (and it was quite diverse in the Eocene Baltic amber forest, too, see WUNDERLICH (2004 and 2008)) but only three families have been reported in Burmite: The peculiar diverse Zargraneidae which may be polyphyletic, one specimen of the extinct family Cretamysmenidae WUNDERLICH 2018 and two specimens and genera of the extant family Theridiidae. It is a remarkable Cretaceous gap of the superfamily Araneoidea in the Cretaceous which radiated explosively after the KT-events. I suggest that most taxa of the Deinopoidea were displaced by taxa of the Araneoidea which evolved threads bearing sticky droplets in its capture web as a very important “innovation”. The strong radiation of the family Zargraneidae which is documented by fossils of the Burmese amber forest – see WUNDERLICH & MÜLLER (2018: 69-98) - point to a competition between these ecribellate spiders and cribellate spiders of the Deinopoidea at that era and area, the Mid Cretaceous Burmese amber forest. – The relic superfamily Leptonetoidea has been treated by WUNDERLICH & MÜLLER (2018: 40-62): Its ancient cribellate Cretaceous taxa have been displaced today by ecribellate taxa of the same superfamily (except one genus) and by ecribellate Araneoidea. - The family Archaeidae represents a further typical example of a relic family: Today the family is restricted to the Southern Hemisphere and only 4 genera are known, but at least 4 genera existed in a single Mid Cretaceous forest of the Northern Hemisphere, the Burmese amber forest, and 5 genera are known from the Eocene Baltic amber forest of the Northern Hemisphere; see WUNDERLICH (2004). – The extinct family Spatiatoridae PETRUNKEVITCH 1942 (Archaeoidea = Palpimanoidea) - a single species of the genus *Spatiator* is known from the Mid Cretaceous Burmese amber forest – survived only up to the Eocene Baltic amber forest (3 described species).

How many ancient spider families of the Cretaceous would have survived if they had not been displaced by the advanced members of the Araneoidea and the RTA-clade?

Additions and corrections regarding vol. 11 (2018) of the Beitr. Araneol.

P. 2, line 4 from below: The correct family names are Cyrtaucheniidae and Nemesiidae.

P. 3 in the middle: read “2011” instead of “2911”.

P. 38: Add to the diagnosis of the family Alteruloboridae: “Dense hairs on tarsus and metatarsus I”.

P. 64, line 2 from below: read “posterior lungs” instead of “lungs”.

P. 69, lines 7-8 from below and p. 75, line 9 from below: delete “and *Spinipalpitibia* n. gen.”.

P. 85: The figs. 118-119 refer to *Groehnianus*, the fig. 120 refers to *Hypertheridiosoma*.

P. 128 (Index): Add “*Autotomiana* 29”

P. 135, line 2 of the text (figs.): Read “19” instead of “10”.

Selected references; see also WUNDERLICH & MÜLLER (2018: 125-127)

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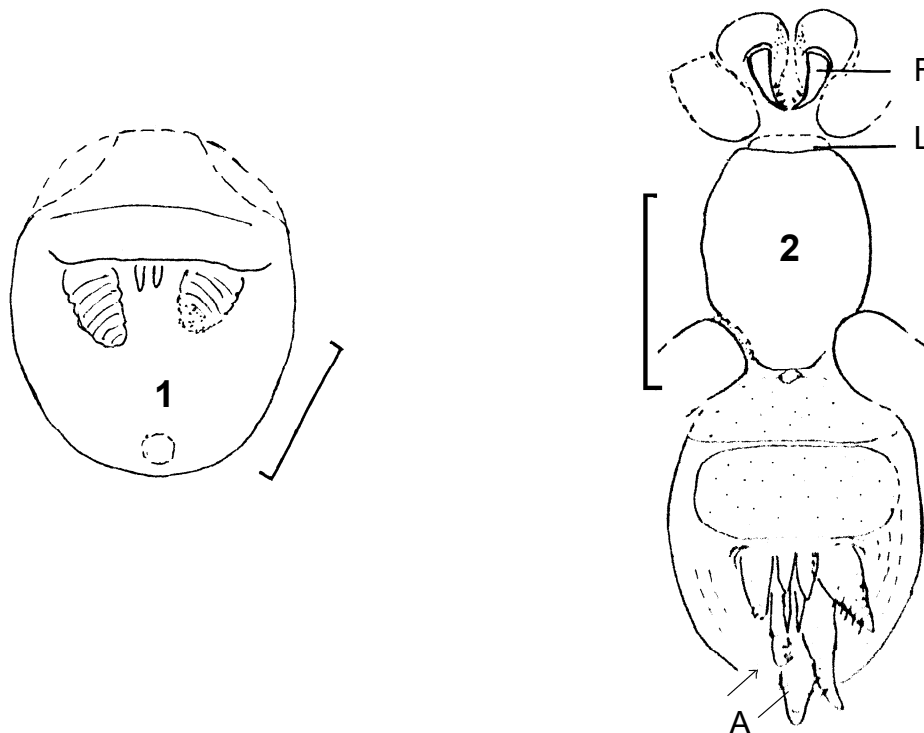
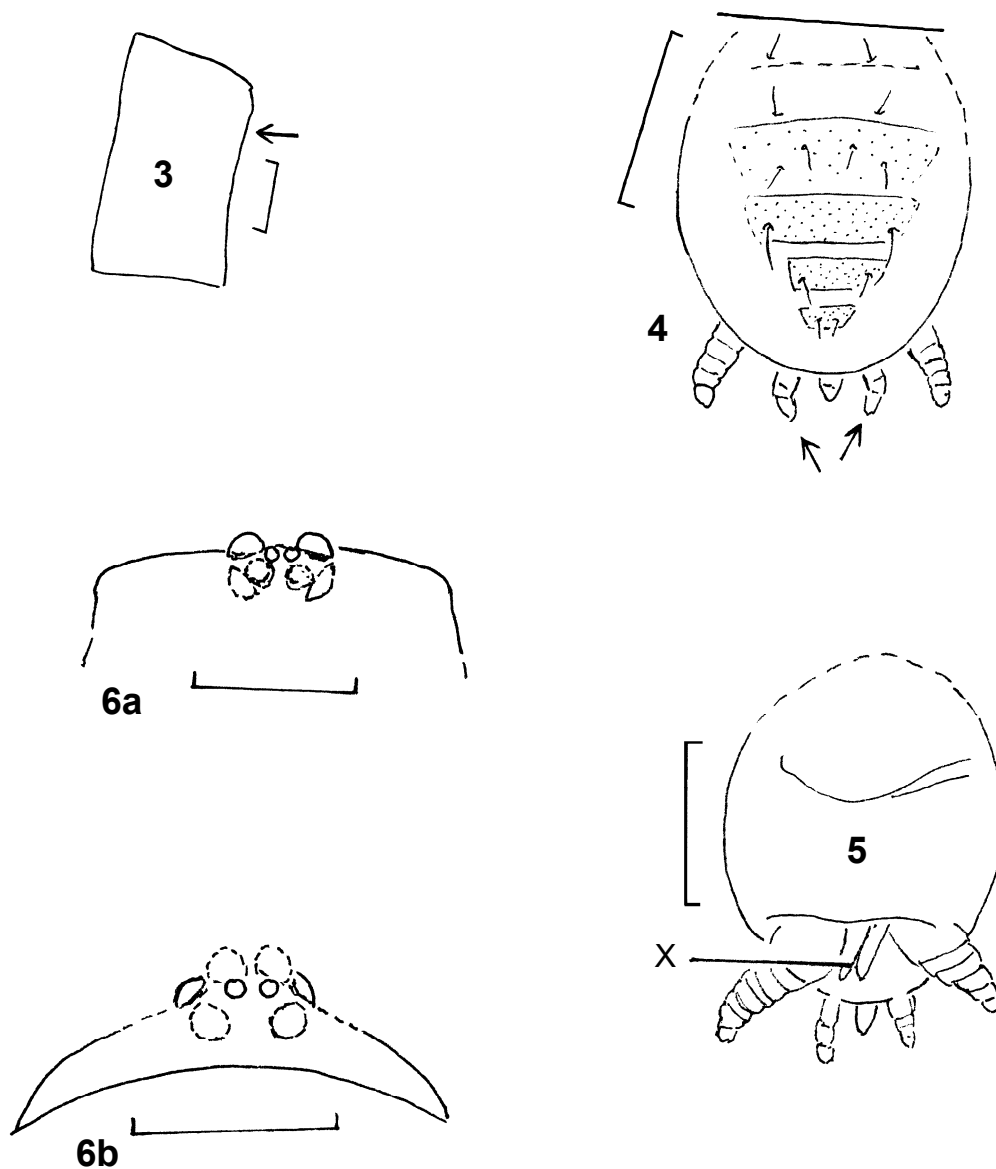


Fig. 1) *Burmathele biseriata* WUNDERLICH 2017 (Burmathelidae), paratype, juv., ventral aspect of the partly deformed opisthosoma. Only the anterior pairs of the spinnerets are well observable and drawn. Scale bar = 0.5 mm.

Fig. 2) *Cretaceothele lata* WUNDERLICH 2015 (Cretaceotheidae), holotype, juv., ventral aspect of the opisthosoma. Scale bar = 0.5 mm. The arrow points to the deformed posterior lateral spinneret.



Figs 3-5: *Eomesothele noninclinata* n. gen. n. sp. (Eomesothelidae n. fam.), holotype, juv.; 3) ventral aspect of the right coxa IV. The arrow points to the position in which an inclination in most Mesothelidae exists (see fig. 10) but apparently not in this species; 4) dorsal aspect of the opisthosoma. Note the quite posterior position of the posterior lateral spinnerets (arrows) which are placed almost laterally of the anal tubercle. The anterior part of the opisthosoma is partly hidden; 5) ventral aspect of the opisthosoma. Parts are hidden (e. g. the posterior median spinnerets) or deformed. Note the relatively long anterior median spinnerets (x); the lateral spinnerets may be retracted. Scale bars 0.1 and 0.5 mm.

Fig. 6a-b: *Intermesothele pulcher* n. gen. n. sp. (questionable Eomesothelidae), juv., dorsal and anterior aspects of the eyes which are deformed and partly covered with an emulsion. Scale bar 0.2 mm.

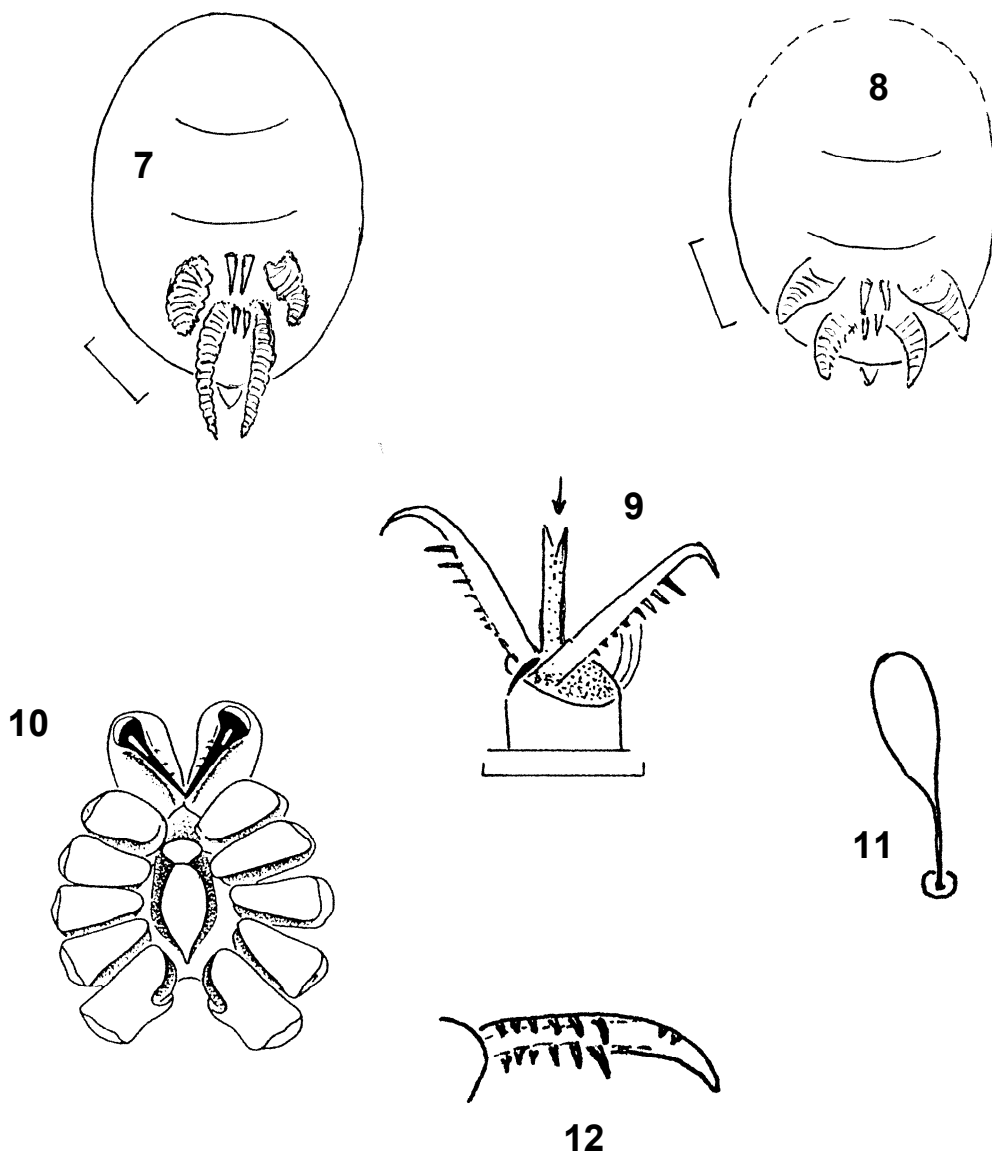


Fig. 7) Parvithelidae indet. 1, juv., F3388/BU/CJW, ventral aspect of the opisthosoma. Note the two pairs of quite small median spinnerets and the pair of quite long posterior lateral spinnerets. Scale bar = 0.5 mm.

Fig. 8) ?Parvithelidae indet. 2 (or sp. near the Eomesothelidae?), juv., F3427/BU/ CJW, ventral aspect of the opisthosoma which anterior part is hidden. Scale bar = 0.5 mm.

Fig. 9) Pulvillothele haupti WUNDERLICH 2017, tarsal claws with pseudopulvillus (arrow). Scale bar = 0.5 mm.

Fig. 10) Mesothelae sp. (extant), ventral aspect of the prosoma. Note the inclination of coxa IV. Taken from JOCQUE & DIPPENAAR-SCHOEMAN (2007).

Fig. 11) Liphistius sp. (extant, Liphistiidae), Club-shaped trichobothrium of a tarsus.

Fig. 12) Burmthelidae sp., paired tarsal claw with two-rowed teeth.

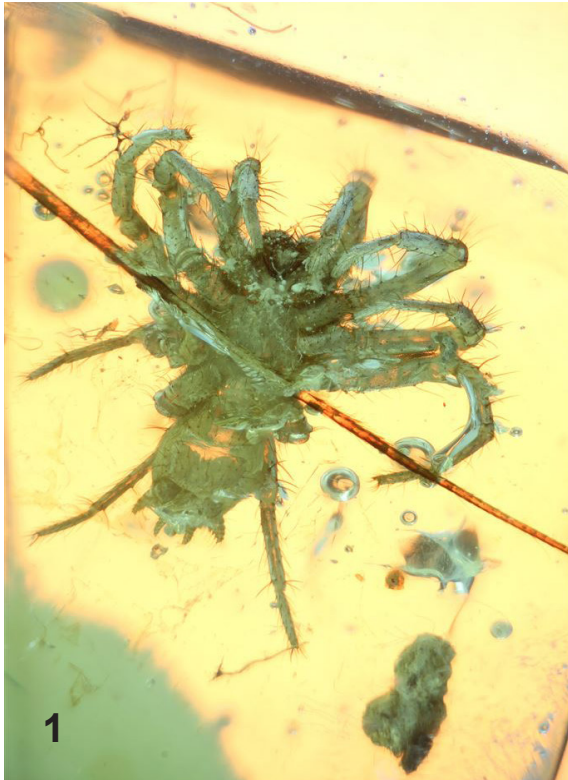


Photo 1: *Eomesothele noninclinata* n. gen. n. sp. (Eomesothelidae n. fam.), juv., body length 1.9 mm, ventral aspect of the spider.

Photos 2-4: *Intermesothele pulcher* n. gen. n. sp. (questionable Eomesothelidae n. fam.), juv., body length 2.3 mm; 2) dorsal aspect of the spider; 3) ventral aspect of the spider; 4) spinnerets enlarged. – All photos taken by Patrick Müller.

In this paper I have connected recent discoveries of fossil spiders with new ideas to new conclusions concerning the phylogeny of spiders, of high basal taxa.

JW