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THE POSTEMBRYONIC DEVELOPMENT OF THE SPINNING APPARATUS IN
CRIBELLATAE SPIDERS, AND ITS UTILIZING IN SOLVING PHYLOGENETIC
PROBLEMS.

According to the classification of Kaestner (1965), three main groups of the Araneae are distinguished, suborders: Mesothelae, Ecribellatae, Cribellatae. All groups possess spinning organs, which are situated near the caudal end of the abdomen, on the ventral aspect, and consist usually of three pairs of spinnerets to which may be added another organ, the cribellum, or the non functional rudiment colulus.

In Kaestner's systematic classification, the characteristic feature of the last two suborders is presence or absence of cribellum or colulus.

However Lehtinen (1967), Levi (1982) and some other arachnologists merge cribellate and ecribellate spiders in common superfamilies and families, as presence or absence of the cribellum as such cannot be used in the limitation of families. Lehtinen accentuated, that group names /Cribellatae, Ecribellatae/ are widely used and convenient, but they do not refer to taxonomic categories. In the ancestor of all Araneomorphae the cribellum was homologous with the anterior median spinnerets and has been independently reduced in numerous lines of spiders' evolution. This is still in process in several recent groups.

Levi (1982) lastly distinguished Araneae into 3 suborders: 1. Mesothelae, 2. Orthognatha, 3. Labidognatha. Mesothelae show four pairs of spinnerets, they are located in the middle of the venter of the abdomen. The presence of four pairs of spinnerets, just as four pairs of dorsoventral muscles is plesiomor-

phic. In other spiders there are no anterior median spinnerets. Orthognatha have at maximum three pairs of spinnerets, the anterior laterals have two articles, which may be reduced or absent, the posterior medians are unsegmented, the posterior laterals have three articles. The Labidognatha possess three pairs of spinnerets and a cribellum or alternatively a colulus.

The definition of the colulus was largely different, nor have the different types of colulus been described. Theoretically, the size of a nonfunctional structure is not expected to exceed that of the corresponding functional homologue. In Loxoscelidae it is provided with a pair muscles. The loxoscelids threads look hackled, allegedly in cause of the action of the colulus on the emerging silk. The possible relations and transformations between the anterior median spinnerets and the colulus and the cribellum formulated Platnick (1977) are as follows: "Thus the only question is whether the cribellum and colulus are also homologous to each other; words, are there two separate transformation series (anterior median spinnerets to cribellum and anterior median spinnerets to colulus) or only one (anterior median spinnerets to cribellum to colulus or alternately, anterior median spinnerets to colulus to cribellum)? If the first model holds, then cribellate and colulate spiders could both represent monophyletic groups; if the second model holds, one or both groups are not phylogenetic."

In my work I have dealt with the spinning apparatus, its construction and postembryonic development. The phylogenetic development is thus reconstructed on the principle of ontogenetic recapitulation, together with problems of morphogenesis.

The spinning apparatus has been studied in eighteen species: *Filistata insidiatrix* Latr., 1810., *Eresus niger* (Petagna, 1787) *Stegodyphus lineatus* Latr., 1802., *Amaurobius ferox* Walck., 1830, *Amaurobius jugorum* L.K. 1869, *A. claustrarius* Hahn., 1831, *A. fenestralis* Ström., 1786, *Titanocea obscura* Walck., 1802., *T. schinerii* L.K. 1872, *T. veteranica* Herm., 1879., *Brigittea latens* (Fabr., 1775)., *Dictyna arundinacea* (L. 1758), *D. uncinata* Thor., 1856, *Nigma viridissima* (Walck., 1902)., *N. flavescens* (Walck.,

1825), *Lathys puta* (O.D. Cbr. 1863), *Hyptiotes paradoxus* (C.L.K., 1834)., *Uloborus walckenaerius* Latr., 1806.

In all the eighteen species of spiders belonging to eleven genera and six families (Filistatidae, Eresidae, Amaurobiidae, Titanocidae, Dictynidae, Uloboridae), the spinning apparatus is formed by three pairs of spinnerets, by cribellum and calamistrum. The research has further proved that there are 7 categories of glands participating in producing the web: glandulae ampullaceae, gl. piriformes, gl. aciniformes, gl. tubuliformes, gl. pseudoflagelliformes, gl. cribelli and cribellum-like glands. The last is found only in Dictynidae and Uloboridae. I consider the name of the last mentioned glands just as a working term. Similar glands on the median spinnerets of Uloboridae are called gl. paracribelli by Peters and Kovoor (1980). However, I found and described cribellum-like glands with Dictynidae (*Nigma flavescens*, *N. viridissima*, *Dictyna arundinacea*, *D. uncinata*, *Brigittea latens*) and I called them gl. pseudocribelli. I am not quite sure, whether they are quite equivalent to gl. paracribelli Uloboridae. I found small tubuliform glands with segmented external spigots also at the posterior spinnerets of the spiders family Titanocidae (*T. obscura*, *T. schinerii*). All the above described cribellum-like glands and their external spigots are reduced in adult males. There was described a praecribellum (only present in nymphae I. - II. instars) in the form of a protuberance with pair features, which I appraise as a primary colulus. The reduced cribellum represents, in my opinion, a colulus of secondary and uncertain phylogenetic value. The praecribellum is found in the above mentioned nymphae, whose spinnerets are capable of spinning activities.

Taking into account the primary colulus of Cribellatae Labidognathae it is possible to admit the transformation line of the anterior median spinnerets - colulus - cribellum. The colulus of Ecribellatae and the primary colulus of Cribellatae are considered as mutually homological formations, being a common feature of all labidognaths.

The cribellum could have phylogenetically developed from a colulus, by a secondary formation of the spinning area, where the spigots were centralized, originally not having a spinning function. The sclerotine plate of the spinning area, border-like limited basal fields, could have arisen by fusion of basal parts of the external spinning spigots in the way as it is indicated in pseudocribella of Dictynidae. The study has proved close functional and developmental connection between cribellum and median spinnerets and their glands. As to the cribellum: In young spiders of *Nigma viridissima* and *Nigma flavescens* there appear limited pores with segmented tubes near the basis of the back edge of the spinning area (beyond the perforated field) and it seems probable that the original position of the tubuli textorii of the cribellum glands is indicated here (Hajer 1980). During the ontogenesis the functional cribellum arises always later than functioning spinnerets provided with spigots and their glands. External tubes of cribellar glands of the 2-nd instar stage of nymphs of *Filistata insidiatrix* are not all segmented, and they have the ampoule-like shape.

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Figures

1. *Amaurobius fenestralis*. The spinning apparatus of first instar nymphs is formed by three pairs of segmented spinnerets with differentiated spigotes and functioning spinning glands attached to them. The Cribellum is not yet present, only the primary colulus is developed. The anterior spinneret (ant.) carries one spinning tube (1) which is connected with gl. ampullacea, and two small spinning tubes to which are connected gl. piriformes. The median spinneret (med.) and the posterior spinneret (post.) carry small spinning tubes to which the aciniform glands are connected.
2. *Amaurobius fenestralis*, 2nd instar stage of nymphs. At this stage the spinning apparatus is already complete including the cribellum and calamistrum that enable the construction of three-dimensional webs for catching animal food. On both, anterior and median spinnerets, appears one more gl. ampullacea (1,2). The number of small glands and their external tubes on all spinnerets also increased.
3. *Nigma flavescens*. The spinning apparatus of the first instar stage of nymphs. Cribellum and calamistrum are not present. Primary colulus is developed. 1,2 the spigots of gl. ampullacea.
4. *Nigma flavescens*, adult female. Topography of the external spinning structures. The spigot, marked by number 2, is reduced in the same way as the gl. ampullacea.

5. *Nigma flavescens*, adult male, posterior spinneret. 1-The spigot of gl. tubuliformis.
6. The location of the pseudocribellum on the surface of median spinnerets of dictynid spiders (genera *Nigma*, *Brigittea* and *Dictyna*).
7. Details of the pseudocribellum.

The development of cribellum and calamistrum during the ontogenesis *Filistata insidiatrix*

Cth (mm)	N.II	N.III	N.IV.	N.V	adult. ♀	adult. ♂
	0,64	1,15	1,57	2,63	4,62	2,82
Spinning area of crib./mm ² /	0,00027	0,00086	0,0039	0,0078	0,018	reduced
Number of tub.textorii	280	964	2 880	4 920	7 100	reduced
Length of met. IV.p. /mm/	0,38	0,96	1,76	2,78	3,20	4,63
Length of calamistrum	0,084	0,012	0,16	0,27	0,33	reduced
Number hairs of calamistrum	9	9	9	9	9-11	reduced

The number of spinning structures in the successive developmental stages in *Filistata insidiatrix* Latr. 1810, whose entire ontogenetic cycle was studied in laboratory conditions.

G l a n d s		Developmental stages					
		N. II	N. III	N. IV	N. V	adult. ♀	adult. ♂
anterior spinn.	gl. ampullaceae majores	1	2	2	2	2	2
	gl. piriformes	17	24	35	53	142	77
	Total for each spinneret	16	26	37	55	146	79
	Total for both spinnerets	34	52	74	110	292	158
middle spinn.	gl. aciniformes majores	3	3	3	3	3	3
	gl. aciniformes minores	2	2	2	2	2	2
	gl. ampullaceae majores	1	1	1	1	1	1
	gl. tubuliformes	1	1	1	1	1	1
	Total for each spinneret	7	7	7	7	7	7
	Total for both spinnerets	14	14	14	14	14	14
posterior spinn.	gl. tubuliformes	2	2	2	2	2	2
	gl. aciniformes	6	8	12	19	84	49
	Total for each spinneret	8	10	14	21	86	51
	Total for both spinnerets	16	20	28	42	172	102
Spinning apparatus total		64	86	116	166	478	274

The spinnerets and their glands of stages nymphae I. and II. instars, family Dictynidae

Spinnerets	Glands	Dictyna uncinata		Dictyna arundinacea		Nigma flavescens		Nigma viridissima		Brigittea latens	
		N.I.	N.II.	N.I.	N.II.	N.I.	N.II.	N.I.	N.II.	N.I.	N.II.
Anterior	Glandulae ampullaceae	2	2	2	2	2	2	2	2	2	2
	Glandulae piriformes	2	3	2	4	2	4	2	4	2	6
	Glandulae aciniformes	1	2	1	2	1	2	1	2	1	3
Middle	Glandulae ampullaceae	1	1	1	1	1	1	1	1	1	1
	Glandulae pseudocribelli	0	12/5	0	12/5	0	6/3	0	6/3	0	6/3
	Glandulae aciniformes	4	5	4	5	4	5	5	6	4	5
Posterior	Glandulae tubuliformes	0	0	0	0	0	0	0	0	0	0
	Spinning apparatus total	20	50	20	52	20	40	22	42	20	46

The spinnerets and their glands in subadult stages of spiders
family Dictynidae

Spinnerets	Glands	Dictyna unicata		Dictyna arundinacea		Nigma flavescens		Nigma viridissima		Brigittea latens	
		sub-ad. ♀	sub-ad. ♂	sub-ad. ♀	sub-ad. ♂	sub-ad. ♀	sub-ad. ♂	sub-ad. ♀	sub-ad. ♂	sub-ad. ♀	sub-ad. ♂
Anterior	Glandulae ampullaceae	2	2	2	2	2	2	2	2	2	2
	Glandulae piriformes	8	8	9	9	8	8	10	10	8	8
Middle	Glandulae ampullaceae	1	1	1	1	1	1	1	1	1	1
	Glandulae aciniformes	2	2	3	3	3	3	3	3	3	3
	Glandulae pseudocribelli	17/7	17/7	16/8	17/7	17/7	17/7	12/5	12/5	17/7	17/7
Posterior	Glandulae aciniformes	9	6	8	6	9	6	11	9	5	5
	Glandulae tubuliformes	0	0	0	0	0	0	0	0	0	0
	Spinning apparatus total	78	72	78	74	80	74	78	74	70	70

Spinnerets	Dictyna uncinata		Dictyna arundinacea		Nigma flavescens		Nigma viridissima		Brigittea latens	
	adult. ♀	adult. ♂	adult. ♀	adult. ♂	adult. ♀	adult. ♂	adult. ♀	adult. ♂	adult. ♀	adult. ♂
Anterior	Glands									
	Glandulae ampullaceae	1	1	1	1	1	1	1	1	1
	Glandulae piriiformes	14	11	16	12	14	11	21	12	8
	Glandulae ampullaceae	3	3	3	1	1	1	1	1	1
Middle	Glandulae aciniformes	3	3	6	3	6	3	5	6	3
	Glandulae pseudocribelli	18/8	reduced	17/8	reduced	19/7	reduced	17/5	reduced	reduced
	Glandulae aciniformes	14	4	12	4	15	9	14	9	5
Posterior	Glandulae tubuliformes	3	0	3	0	1	0	1	1	0
	Spinning apparatus total	114	40	116	62	114	50	120	92	36

The spinnerets and their glands in adult spider family Dictynidae.

Number of glands *gl.pseudocribelli* is expressed by a fraction, where the numerator indicates the number of external segmented tubes (=tubuli textorii), and the denominator indicates the number of basal parts from which segmented tubes reach out.