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The Convergent Development of Orb-webs in Cribellate and Ecribellate Spiders

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SYNOPSIS. Orb-webs are highly developed and can be understood as the best technical solution of the problem how to place capture-threads in the most efficient and economical way. They are built by cribellate and ecribellate spiders. Phylogenetical relations between some families of Cribellatae and Ecribellatae cannot be ignored, but for some important reasons it is difficult to imagine that on the level of orb-weaving cribellate spiders became ecribellate by reducing the cribellum. Thus, these specialized webs must have developed on both sides independently and are the result of a convergent evolution. Steps leading from primitive use of threads for capturing insects to the typical and later modified orb-webs of Cribellatae and Ecribellatae can be discerned.

Amongst the numerous types of spider webs, without any doubt the orb-webs are highly developed. They are the results of specific innate motor patterns; their product is a geometrical arrangement of different kinds of threads, ordinary ones and capture-snares.

Peculiarities of orb-webs:

1) With little spinning material they cover a great area and are flexible as well as strong; thus, their efficiency in capturing flying insects is enormous.

2) They require only a few points of attachment in their environment; they can be positioned in all directions: vertically, horizontally and diagonally.

3) Signals from a moving insect, when caught, are transferred to the spider directly; the same threads can be used for the approach.

4) The placing of capture-threads in a geometrical system makes it possible that the spider moves without touching and disturbing the arrangement. Considering their evolution, the most interesting fact is that orb-webs are built by cribellate as well as ecribellate spiders; these webs are identical in their way of construction and are composed of the same elements: frame-threads, radial threads, and spiral threads (first an auxiliary spiral, which afterwards has to be replaced by the more permanent, adhesive one).

Concerning their evolution, two possibilities come to mind: the development of the orb-web-type happened either on the cribellate or ecribellate side; hence, on the level of orb-weaving, either cribellate spiders must have become ecribellate or vice versa. The first solution has been considered often but not the second because there are enough reasons to believe that — phylogenetically — cribellate spiders became ecribellate and not the other way around. A third possibility (Kullmann, 1958, 1970/71) has been discussed: the probability of a separate evolution leading to the orb-web-type; in this case the orb-web of Cribellatae and Ecribellatae have to be considered as convergent achievements — an astonishing fact indeed regarding the remarkable correspondences. In Figures 1 and 2 the center of a cribellate web (*Uloborus plumipes*) can be compared with that of an ecribellate web (*Cyclosa insulana*). The fine white spots on the radial threads are the remaining attachment-points of the auxiliary spiral. Also, bands of silk (called "stabilimentum") turning round or crossing the hub of the orb are to be found in cribellate and ecribellate orb-webs. Kaston (1964) followed these ideas but — more than

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FIG. 1. Central part of a cribellate orbweb (*Uloborus plumipes*). The spiral consists of capture-snares produced by the cribellum (wool of elementary fibers and spinnerets (two warps). The small white dots on the radial threads are the remaining attachment-points of the destroyed auxiliary spiral.

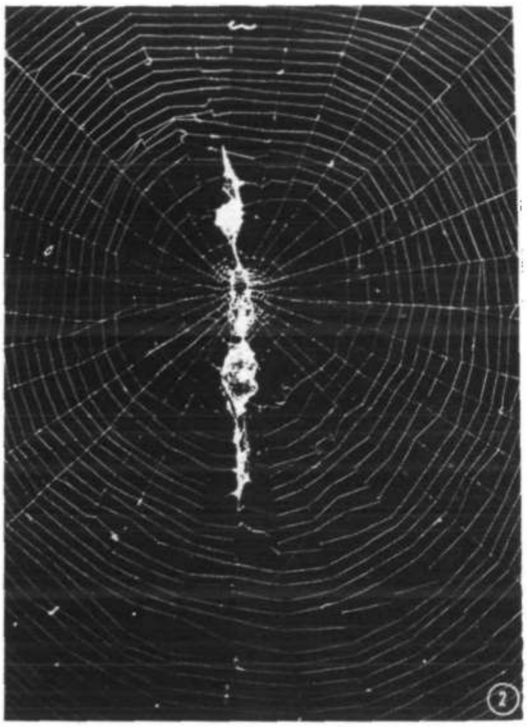


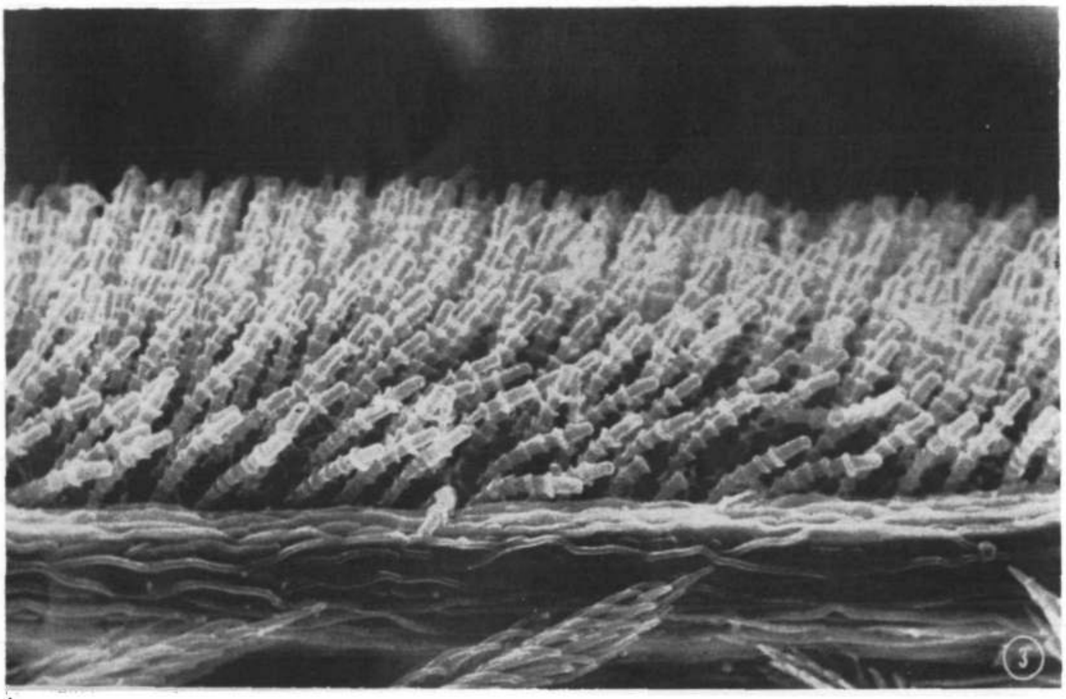
FIG. 2. Central part of an ecribellate orbweb (*Cyclosa insulana*). The construction of the web corresponds to the cribellate orbweb, but the spiral is produced merely by the spinnerets and consists of two warps plus gum-material.

that — he proposed a classification of all cribellate and ecribellate spiders based on differences or correspondences in web-construction. He has been sharply criticized by Lehtinen (1967): "Kaston totally failed in trying to compile an evolutionary classification of spiders on the basis of ethological characters." Saying this, however, he published a systematic revision based on principles of numeric taxonomy only! Both authors take extreme views: Kaston apparently believes in a totally separate development of cribellate and ecribellate spiders, whereas Lehtinen postulates more than 30 transitions.

There are reasons to believe that some ecribellate families arose from cribellates. For a long time such "twin-families" have been discussed. Based on close examination, however, until now only two cases may be considered as proven: Kraus and Baum (1971) investigated correspondences between Oecobiidae and Urocteidae regarding their spinning apparatus and sexual organs (these two families had been taken for "twin-families" before because of similarities in their behavior); Homann (1971) defined relations between Amaurobiidae and Lycosidae based on conformities in the structure of their eyes.

Cribellate Uloboridae and ecribellate Araneidae had been taken for relatives before, because most representatives of both families construct typical orb-webs. Again, they have been combined by Lehtinen (1967) irrespective of the possibility of morphological and ethological convergences; he united Uloboridae and "Araneidea" (Araneidae, Theridiidae, Linyphiidae and some others) within the "Araneides."

To make understandable why orb-webs



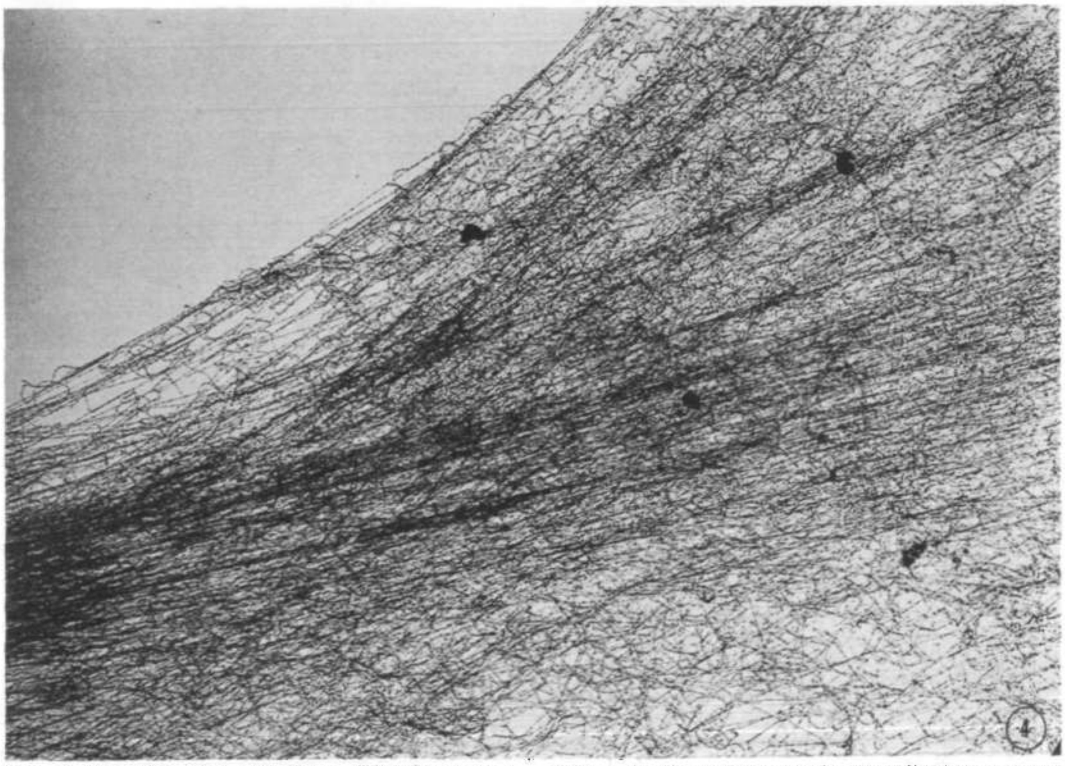
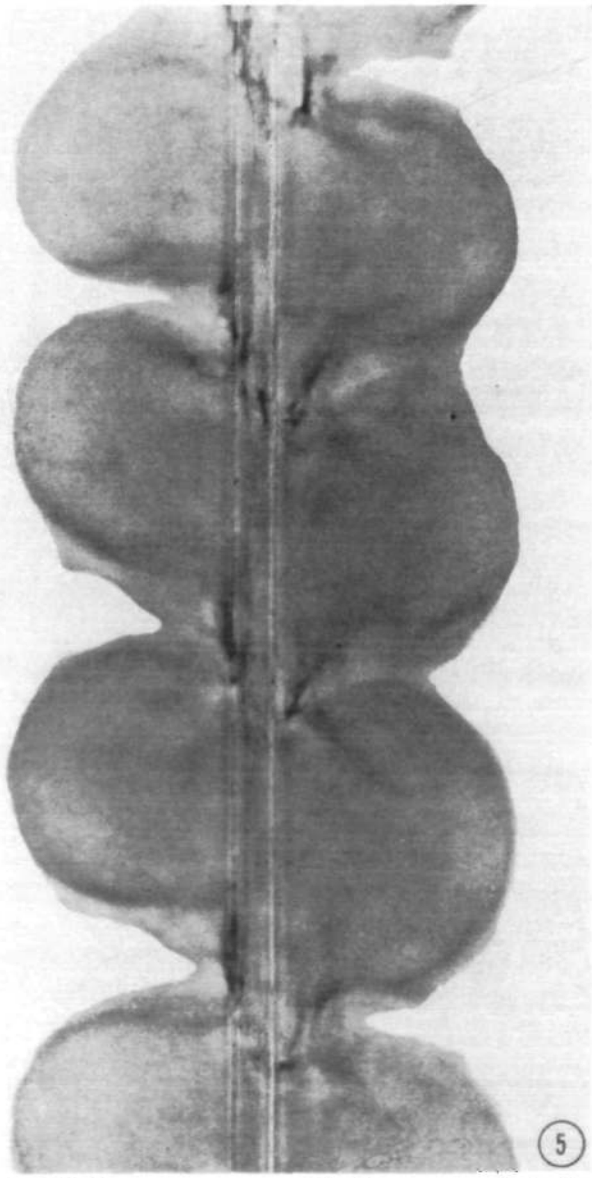


FIG. 3. Side-view of a cribellum (*Hyptiotes paradoxus*) photographed in a scanning-electron-microscope and showing the large amount of delicate spigots (tubuli textorii). (Magnification: 3100X).

FIG. 4. Section of the wool of a cribellate capture-snare (*Hyptiotes paradoxus*) demonstrating the large number of elementary fibers and their structure. (Electron-micrograph; magnification: 19,850X).

of Uloboridae and Araneidae cannot be regarded as homologous, some remarks on the differences between cribellate and ecribellate spiders are necessary.

Cribellate spiders possess a cribellum and a calamistrum. The cribellum (Fig. 3) is a spinning plate immediately in front of the three pairs of normal spinnerets; the calamistrum is a comb of specially structured hairs on the metatarsus of the fourth pair of legs. When in action it moves rhythmically over the plate, thus fixing a wool of fine cribellum-fibers on two warps produced by the spinnerets (Figs. 4, 5). Electron-microscopy made it possible to study the surface of the cribellum, the fine



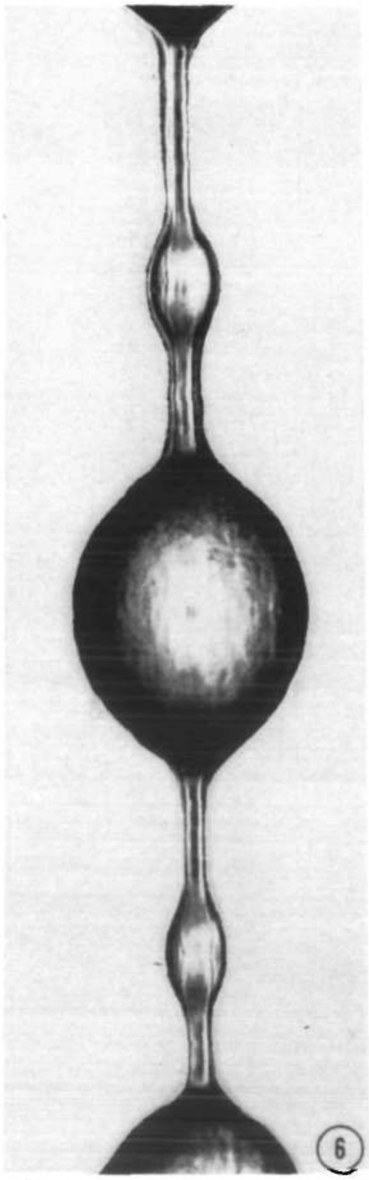


FIG. 5. Cribellate capture-snare (*Hyptiotes paradoxus*) consisting of two warps and the cribellum-wool. The elementary fibers are so thin that they cannot be seen in a light-microscope; the dry wool looks like a liquid.

FIG. 6. Ecribellate capture-snare (*Achaearanea tepidariorum*) consisting of two warps and droplets of gum-material.

structure of the calamistrum, and the highly specialized cribellate snares (Lehmensick and Kullmann, 1956*a,b*; Kullmann 1968, 1969; Friedrich and Langer, 1969; Lehtinen, 1971; Kullmann et al., 1971/72). Figures 3 and 4 show the delicate spigots of a cribellum and a short piece of the capture thread from *Hyptiotes paradoxus* (Uloboridae). In other families (Amaurobiidae, Dictynidae, Eresidae), the two parallel warps and the sticky woof are accompanied by one, two, or even three pairs of curled threads.

Cribellate spiders live stationary. Their snares have to be placed in the surroundings of the spider for catching insects; this happens in a way characteristic for the different genera and even species.

Ecribellate spiders possess only normal spinnerets, mostly three pairs. Many of them show in front of the first pair, or in between, instead of a cribellum, a small hillock called colulus. Very often relations have been discussed between cribellum and colulus, suggesting that the latter is a reduction of the first.

A high percentage of ecribellate spiders catch insects without the help of threads by chasing, jumping, or waylaying. Primitive web-builders use their webs only for getting information about the position of approaching insects. Others produce ordinary snares in such a way that the victims have scarcely a chance to escape. If they do not lay special capture-threads, a lot of spinning material is needed and the webs appear rather complicated and irregular; they are three-dimensional. A good example of these space-webs is the highly specialized constructions produced by members of the families Linyphiidae, Nesticidae, and Theridiidae and of the genus *Cyrthophora* (fam.: Araneidae): an adult female of *Cyrtophora citricola* needs up to four nights to finish her work. Similar webs are constructed by the genus *Allepeira*, but up to now not enough is known about the relations between these two interesting genera.

A gain which influenced decisively the evolution of ecribellate spiders was the production of ecribellate capture-threads. They are produced by the spinnerets and differ essentially from those of the cribellates; their efficiency is based on a thin layer of gum broken up into a series of fine droplets (Fig. 6). More primitive is the utilization of such glutinous silk during the capture of prey; more highly developed is their suspension in a frame.

When comparing the capture-threads of cribellate and ecribellate spiders, we find that their function is the same but their origin is different: they are not homologous but analogous; they — and those parts of webs composed of these threads — have to be considered the result of convergent evolution.

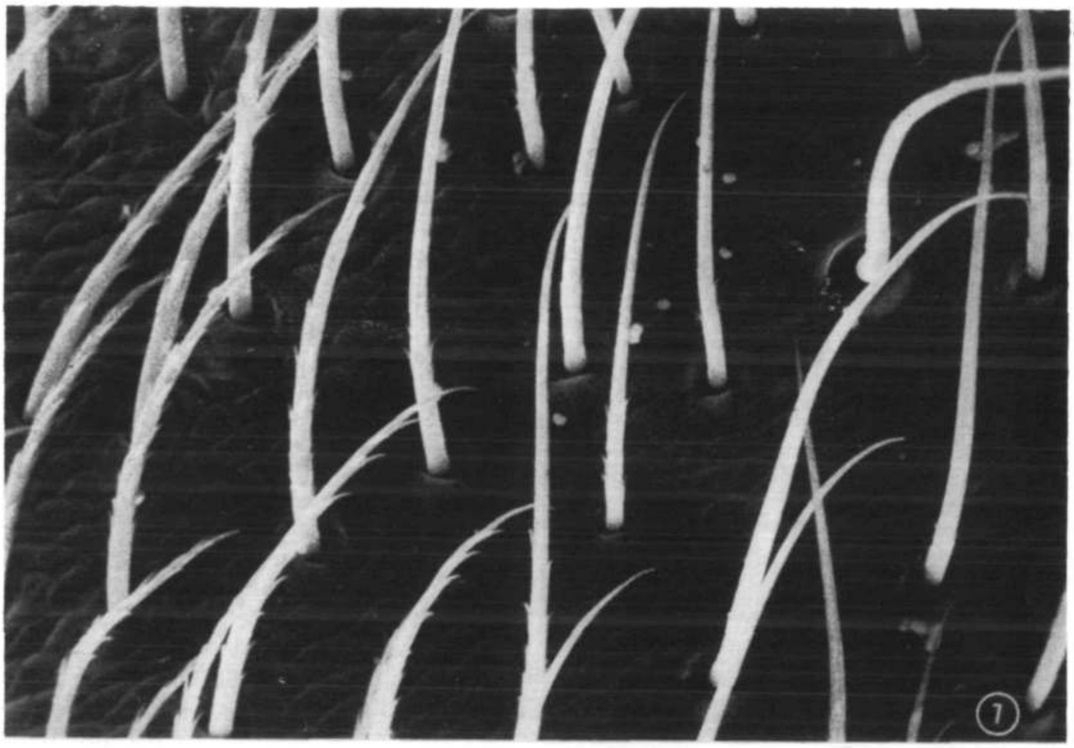
With the increasing use of viscid threads as part of the webs, the necessity arose to arrange them in a certain order; while on the other hand among ecribellate spiders, voluminous, three-dimensional constructions became useless.

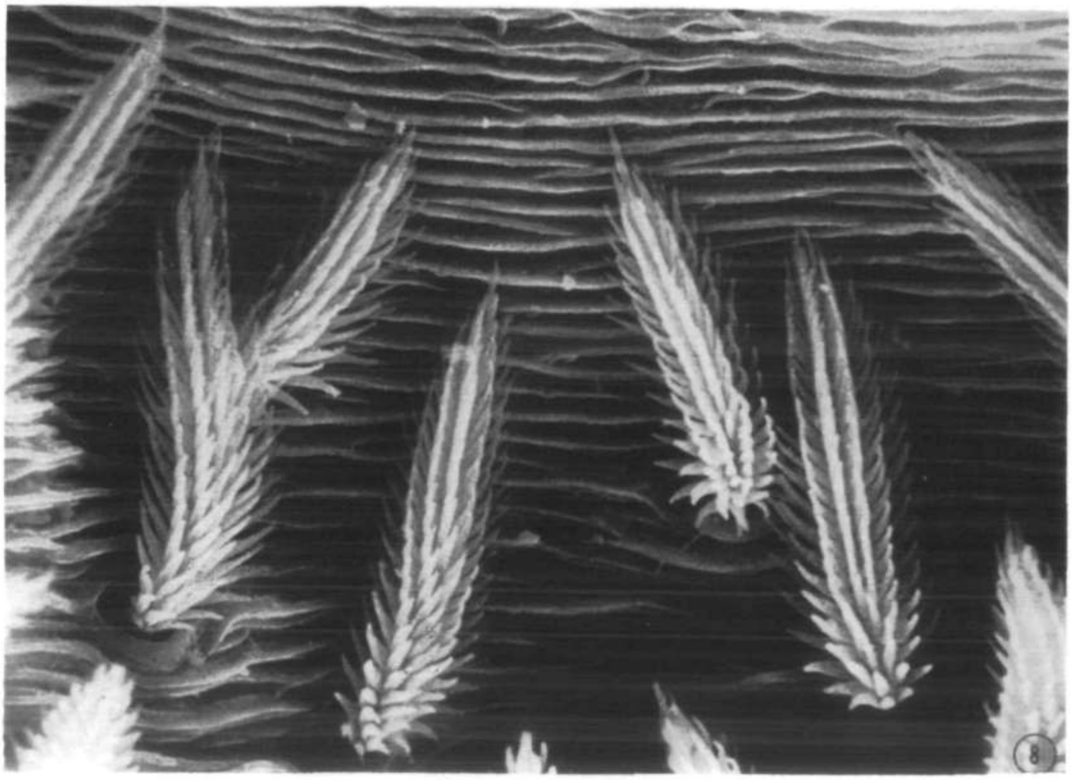
As they had to deal with similar problems concerning adhesive threads, these principles apply also to cribellate spiders Space-webs are only known from very primitive Cribellates (Palaeocribellata).

But Ecribellates had to solve one more problem: the gum-material dries up. For this reason the web has to be renewed more often, at least the viscid threads have to be replaced even when they have not been destroyed by capture. Cribellate capture-snares seem to be more economical.

Whereas Cribellatae because of so many conformities may belong to a monophyletic group, it is difficult to believe the same for Ecribellatae which are defined negatively by the non-existence of organs, which are typical for another group. The lack of cribellum and calamistrum may have different reasons. Ecribellates could be derived by reductions from cribellates as well as they could have descended from ancestors which did never possess such organs.

Before a concept of a double, independent evolution of orb-webs will be outlined, it should be explained why it is incredible that on the level of orb-weaving cribellate spiders became ecribellate. The





great difference between adhesive and viscid capture-threads and the fact that they cannot be homologous has been explained before.

1) It is improbable that, while preserving the same method of capture, the highly developed and extremely efficient dry cribellate snare is merely exchanged for the ecribellate viscid capture-thread. Simultaneously, the behavior of weaving cribellate threads plus the typical cribellate organs must have been reduced while being replaced by new spinning-organs plus necessary motor patterns.

2) Since orb-webs without any capture-threads are totally useless, in the time of transition either spiders which simultaneously produced cribellate and ecribellate capture-threads must have existed, or the change from one system to the other happened suddenly. Both ideas are fantastic.

3) One absurdity more — the Uloboridae are the only spiders without poison glands. Since they are not primitive, they must have descended from other spiders; these organs obviously have been reduced. After becoming ecribellate, they must have regained them, as all Araneidae are poisonous.

4) The typically structured hairs covering the body differ in both families. The Uloboridae have hairs like all cribellates — they are plumose (Fig. 8). Those of Araneids are smooth or more or less serrated only (Fig. 7); they are identical with those of other ecribellate families, especially Theridiids and Linyphiids. There is no doubt that these three families are related, but it is difficult to imagine that cob-webs of Theridiids and sheet-webs of Linyphiids developed via orb-webs of Araneids from those of Uloborids.

Through the last remark one thing should be clear — if someone tries to find a phylogenetical way leading to the ecribellate orb-web-type, he has to pay attention to the Theridiidae and Linyphiidae.

In Figures 9 and 10 hypothetical steps of two phylogenetic ways leading from primitive web-constructions to orb-webs on the cribellate and ecribellate side have been outlined. The stages on the cribellate side are in accordance with the suggestions made by Wiehle (1937) for the first time.

In stage I the web-types look similar but their function is different. Spiders living like *Amaurobius* and *Filistata* catch prey by means of capture-threads; spiders like *Segestria* catch the prey directly — the threads placed around their retreat serve to alarm the spider and disclose the position of an insect. There is, however, one correspondence as both live in "primary" retreats. They search for natural holes in the ground, on walls, between stones, and so on; others dig tubes. The threads for alarming or catching are placed around the entrance of their tube. With these webs only walking insects can be caught.

Stage II shows sheet-like webs, which lead from the primary retreat into the surrounding. The catching range is extended. The sheet can be an elongation of the ceiling or the floor of the retreat. In the first case the spiders, i.e., Theridiids, Linyphiids, and some Araneids, move under their sheet; in the second case, i.e., Agelenids and Eresids, they move on the sheet. In Eresids the sheet covers the ground; in some Theridiids (like *Lithyphantes*) they are arranged between plants and have to be fixed in the surrounding by scaffolding threads, the upper ones having the function of stopping threads. The result is a three-dimensional web on the ecribellate side.

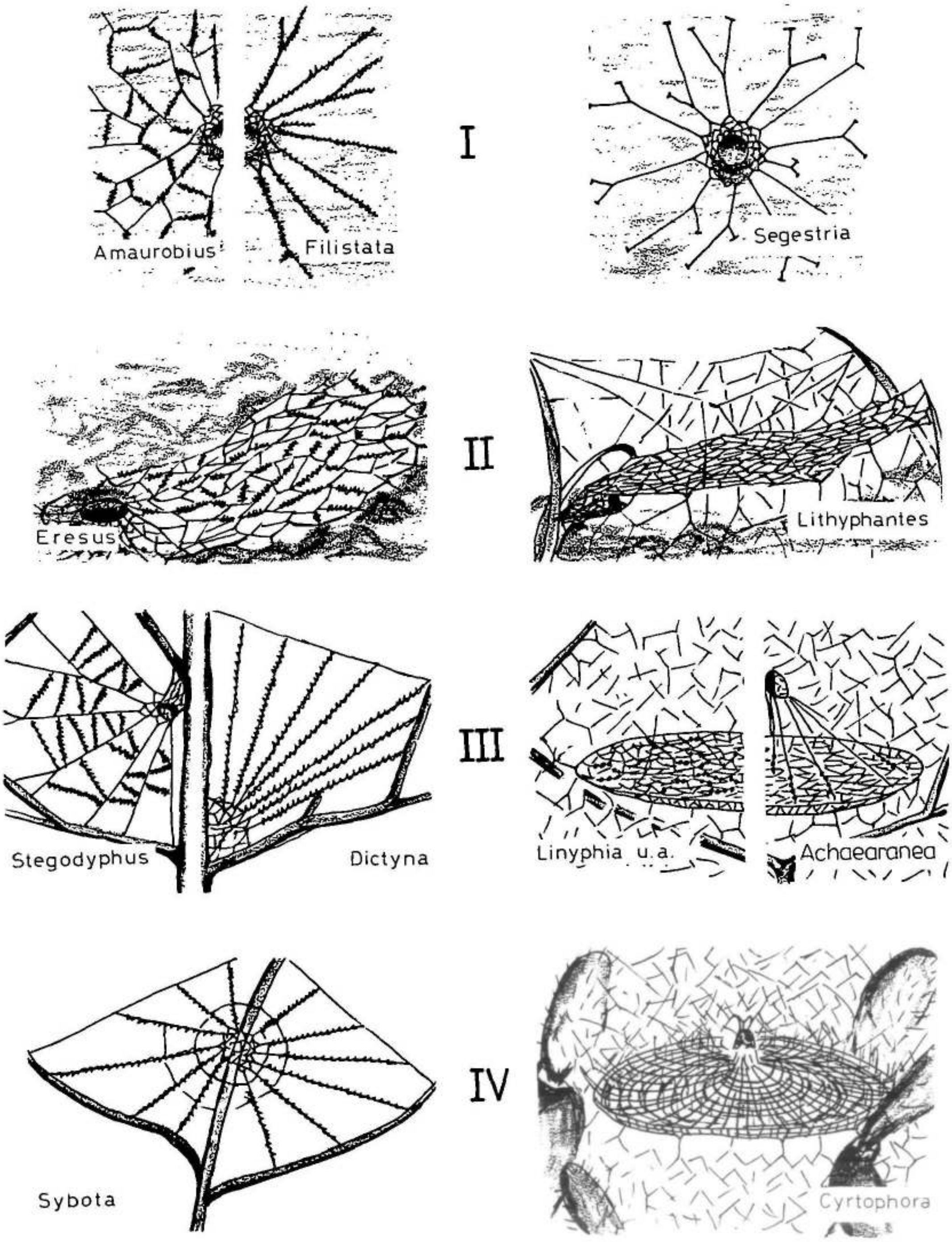
Step III is characterized by the abandonment of the primary retreat. Either the spiders do without any hiding place or build "secondary" retreats. These can be built on the margin of the webs on plants and so on (as with Eresids and Dictynids) or they are installed inside the webs without any direct connection with the environment. Still another way of development is that instead of constructing hiding-

FIG 7. Typical hairs of ecribellate spiders (*Cyrtophora citricola*) which are rather smooth and show only few, fine branches. (Magnification: 475X).

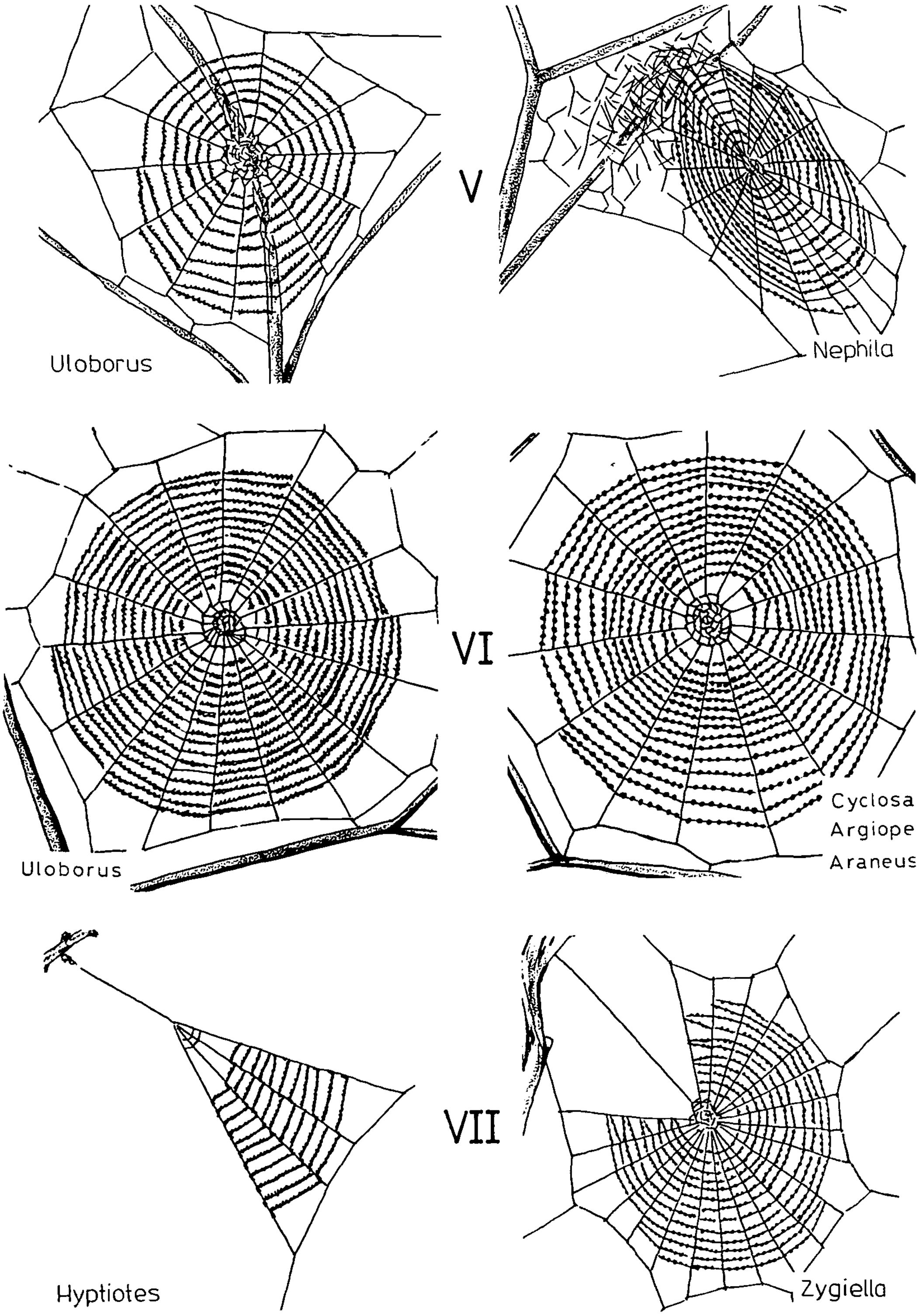
FIG. 8. Typical plumose hairs of cribellate spiders (*Uloborus plumipes*). (Magnification: 2200X).

places, the spiders hide by adapting to the color or objects of their surroundings.

Many Linyphiidae and Theridiidae utilize viscid threads. The webs of this type



FIGS. 9 and 10. Hypothetical, schematic outline of the convergent development of cribellate and ecribellate spiders.


V
Uloborus
Nephila
VI
Uloborus
Cyclosa
Argiope
Araneus
VII
Hyptiotes
Zygiella

serve in capturing flying insects. This function is improved in step IV which is superior through the centric arrangement of threads. The spiders stay in the center. In *Sybota* the radial capture-threads are connected with a spiral leading from the hub towards the periphery. A similar order is to be seen in the web of *Cyrtophora*. Phylogenetically, this most interesting genus undoubtedly belongs to the family Araneidae, but they construct webs functioning and looking like those of many Linyphiidae and some Theridiidae. Comparable with the web of the cribellate side is only the horizontal sheet, which is regularly meshed and consists of radial threads and a spiral running from the center to the periphery. But *Cyrtophora* does not lay capture-threads. A similar web is constructed by the genus Allepeira, but too little is known about this spider to take it into consideration.

Stage V shows first orb-webs, characterized by the existence of an adhesive spiral turning back from the periphery to the center. Primitive attributes of the *Nephila*-type are the existence of a reduced space-web, the transversal direction of the sheet and — last but not least — the fact that the primary spiral is not destroyed during the production of the viscid spiral. A primitive type of an *Uloborus*-web (*Uloborus plumipes* from Afghanistan) in this stage can be seen on the cribellate side. The spiders of this species sometimes construct their orbs in such a way that the hub is located on a twig, a blade of grass, or something else. In these cases the web is without a natural "stabilimentum." When these spiders build free-hanging webs, they produce bands of silk and arrange them across the center or around it, thus constructing the typical kind of stabilimentum as known from cribellate and ecribellate orb-web-spiders (Figs. 1, 2).

Step VI shows typical orb-webs. The hub is not directly attached to the environment, the three-dimensional ecribellate web is reduced to two-dimensions; the viscid spiral becomes a temporary one.

Step VII demonstrates that the typical orb-web is not the end of the development. There are reductions to be observed on both sides and here also we find convergences. They depend on the spiders giving up the hub as their place of residence. Parts of the orb are reduced, and one radius functions as a trap-line. The animals stay on the margin, thus again coming in contact with the environment. *Zygiella* and many other representatives of Araneidae live in hiding-places which could be called "tertiary" retreats, if we allow the evolution of orb-weaving behavior. *Hyptiotes* does not need a retreat; the spider is so excellently adapted to twigs of spruces that it is scarcely visible.

These two separate phylogenetical ways, leading from primitive webs to the highly developed orb-webs of cribellate and ecribellate spiders — as they have been outlined above — have only hypothetical character, and they have to be considered with the same restrictions as any other phylogenetical construction which is not based on palaeontological data but only on recent material and facts. Though our knowledge is not yet sufficient, these ideas may contribute to the discussion about evolution of spiders.

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