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Autor: Kraus, Otto

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Female spider genitalia, systematics and phylogeny (Arachnida: Araneae) – from Menge to Wiehle

Otto Kraus

ABSTRACT

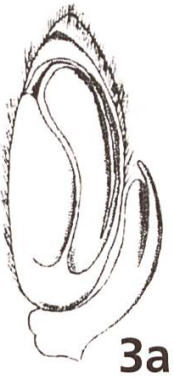
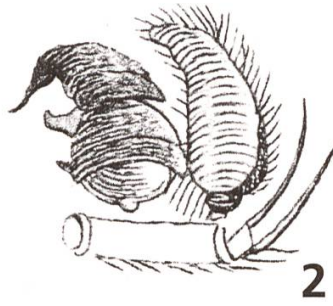
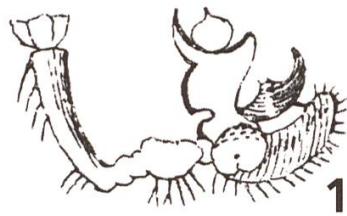
Contrib. Nat. Hist. 12: 781–793.

Up to our present times, many taxonomists have continued to illustrate female genitalia as seen from the outside, i.e., the epigynum. In this way, translucent internal structures of the vulva may be disregarded or only alluded to. This method seems to be adequate for the purposes in basic alpha taxonomy. However, as long as 140 years ago, Menge studied the internal details much more carefully. This more precise approach was broadly used and introduced by Wiehle from 1931 onwards. Only a minority of workers, Thaler included, followed him by accepting this promising, but more laborious method. From Menge onwards almost all these arachnologists were trained zoologists.

Keywords: Araneida, taxonomy, phylogeny, female genitalia, methods of study, history.

Introduction

Male and female spider genitalia were already figured by Clerck in his "Aranei Suecici" (1757 [for nomenclatural purposes deemed to have been published on January 1, 1758]). When diagnosing spider species, he incidentally used differences in structure as an extra detail. Later authors followed him in principle, insofar as they illustrated male pedipalps and female epigynes, but Menge (1808–1880) was the first worker who considered and carefully illustrated previously neglected internal structures of the female genitalia, as seen for example in his monograph "Preussische Spinnen" (1866–1879). The purpose of the present overview is to present an insight into later developments. Menge's views remained almost ignored. A century later, however, they finally culminated in Wiehle's approach (e.g. 1961, 1967a, b); he tried



Figs. 1–2. Illustrations of male palps by Clerck (1757), x 1.5; – 1: *Nerie-ne montana* (CLERCK, 1758), expanded [pl. 3, tab. 1, fig. 2]; – 2: *Larinioides sclopetarius* (CLERCK, 1758) [pl. 2, tab. 3, fig. 2].

Figs. 3–4. Illustrations of genitalia by L. Koch (in Koch & Keyserling 1871–1890), x 1.5. – 3: *Clubiona cambridgei* L. KOCH, 1873; a) palp, b) epigynum [pl. 33, fig. 4a, 5a]; – 4: *Badumna longinqua* (L. KOCH, 1867) [sub *Clubiona silvana* L. KOCH, 1872, pl. 26, fig. 1a].

to understand different structures from a functional point of view, including co-adaptation of male and female genital organs. Nonetheless, the principles introduced by Wiehle were successfully applied by only a minority of later authors, one of them was Thaler.

Early approaches

Considering the optical facilities available in Linné's time, the illustrations of male palpi reproduced in Clerck's pre-Linnéan work "Aranei Suecici" are remarkably detailed (Figs. 1–2). They are comparable to those of other early workers, such as Martyn ("Aranei or a Natural History of Spiders", 1793). On the other hand, Lister ("Naturgeschichte der Spinnen", 1778) did not feature any genital organs. Considerable heterogeneity continued during the first half of the 19th century. Many classical authors, such as (with isolated exceptions) Walckenaer ("Tableau des Aranéides", 1805; "Histoire naturelle des Aranéides", 1806) and also C.L. Koch, in the 16 volumes of "Die Arachniden" (1836–1848), did not illustrate genital organs at all. In his "Monographie der Spinnen" (1821–1836), Hahn included just one single illustration of a palp of a mygalomorph spider.

The number of known species was low in these early days. Coloured illustrations showing the habitus of whole animals, frequently accompanied by a second illustration showing the natural size or the position of the eyes, were

deemed sufficient to allow the recognition of the different species. This may also be true for purely verbal descriptions.

Nonetheless, it is difficult to understand why this disregard of the diagnostically most important genital structures was continued by a minority of later authors, some of them well-known. Examples are various papers even by Simon (1868) and also authors such as Staveley (1868), Thorell (1875) and, finally, Strand from 1900 onwards.

Traditional practice

In the second half of the 19th century, most authors presented acceptable or even good illustrations of male spider palps. Some workers continued to ignore female genitalia completely; see e.g. Blackwall (1861–1864), Hentz (1875 ["The spiders of the United States"]), Vinson (1863 ["Aranéides des îles de la Réunion..."]). Most araneologists did, however, also include drawings of the epigynes. Examples are the famous classical works by Bösenberg (1901–1903 ["Die Spinnen Deutschlands"]), Bösenberg & Strand (1906 ["Japanische Spinnen"]), Chyzer & Kulczyński (1891–1897 ["Araneae Hungariae"]), Keyserling (1880–1893 ["Die Spinnen Amerikas"]), and L. Koch & Keyserling (1871–1890 ["Die Arachniden Australiens"]) (Figs. 3–4). Epigynes were almost universally illustrated by presenting external details visible on the ventral surface in front of the epigastric furrow. Occasionally internal underlying structures such as spermathecae were more or less diffusely indicated. In most cases, this kind of presentation of diagnostic features was and still is adequate for the purposes of alpha taxonomy. This is exemplified by the fact that Roewer (1928 ["Araneae", in "Die Tierwelt Mitteleuropas"]) simply copied most of the illustrative materials for his identification manual from Chyzer & Kulczyński's monograph of Hungarian spiders (1891–1897); for decades, Roewer's keys proved quite reliable for identification purposes.

Up to our own times, this style of illustrating spider genitalia, and specifically of highlighting differences in female structures, has remained unchanged. Drawings have occasionally been replaced by SEM pictures, but there have been few efforts to interpret structural features, including functional aspects.

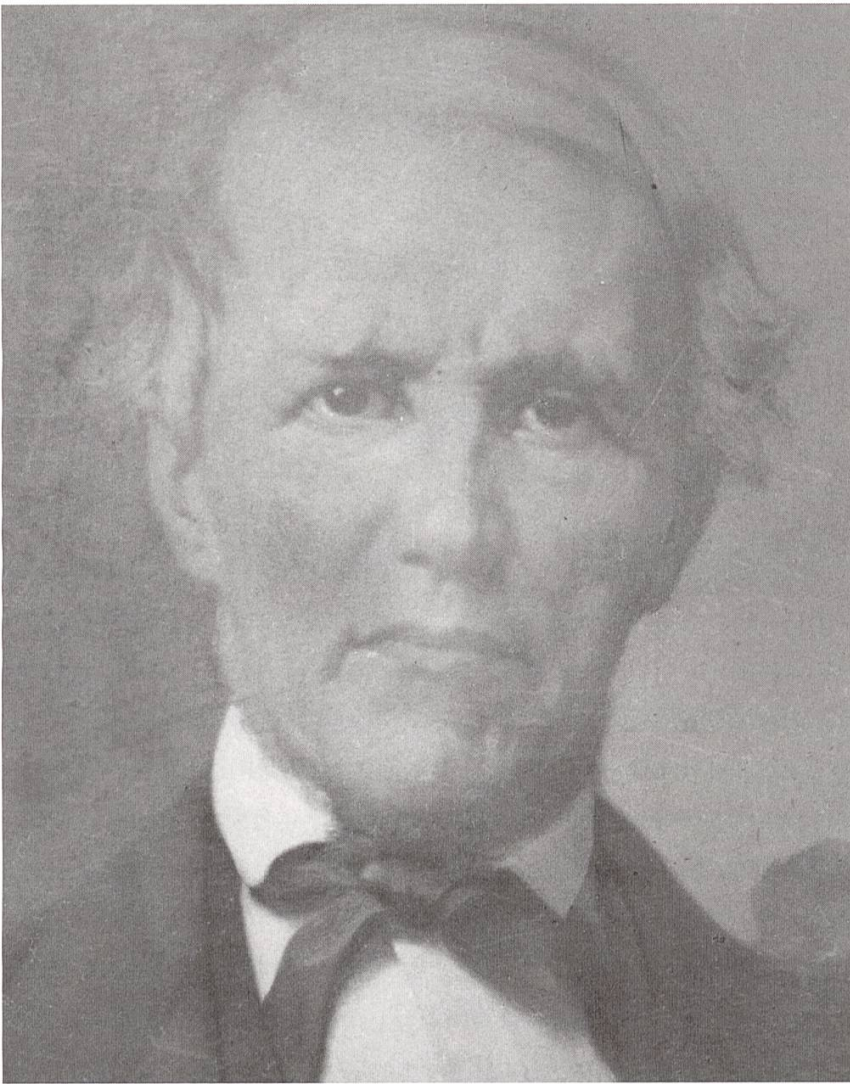


Fig. 5.
Anton Menge
(1808–1880).

Understanding structure and function

First attempts

As already indicated, the first araneologist to include details of spider genitalia and try to understand their function from a biological point of view was Menge (Fig. 5). He was far ahead of his time. This is especially documented in his monograph "Preussische Spinnen" (1866–1879). He presents detailed information on spiders' habits and especially on external and also internal anatomical details. The academic level at which this information is presented indicates that Menge was a trained zoologist. As a student at the university of Bonn from 1828 to 1832, he also studied physics and chemistry, and he continued his academic education in Berlin until 1833. He was 28 years old when he was called to the position of a professor at the Petrischule in Danzig (1836). For decades he played an important role as secretary of the "Naturforschende Gesellschaft Danzig".

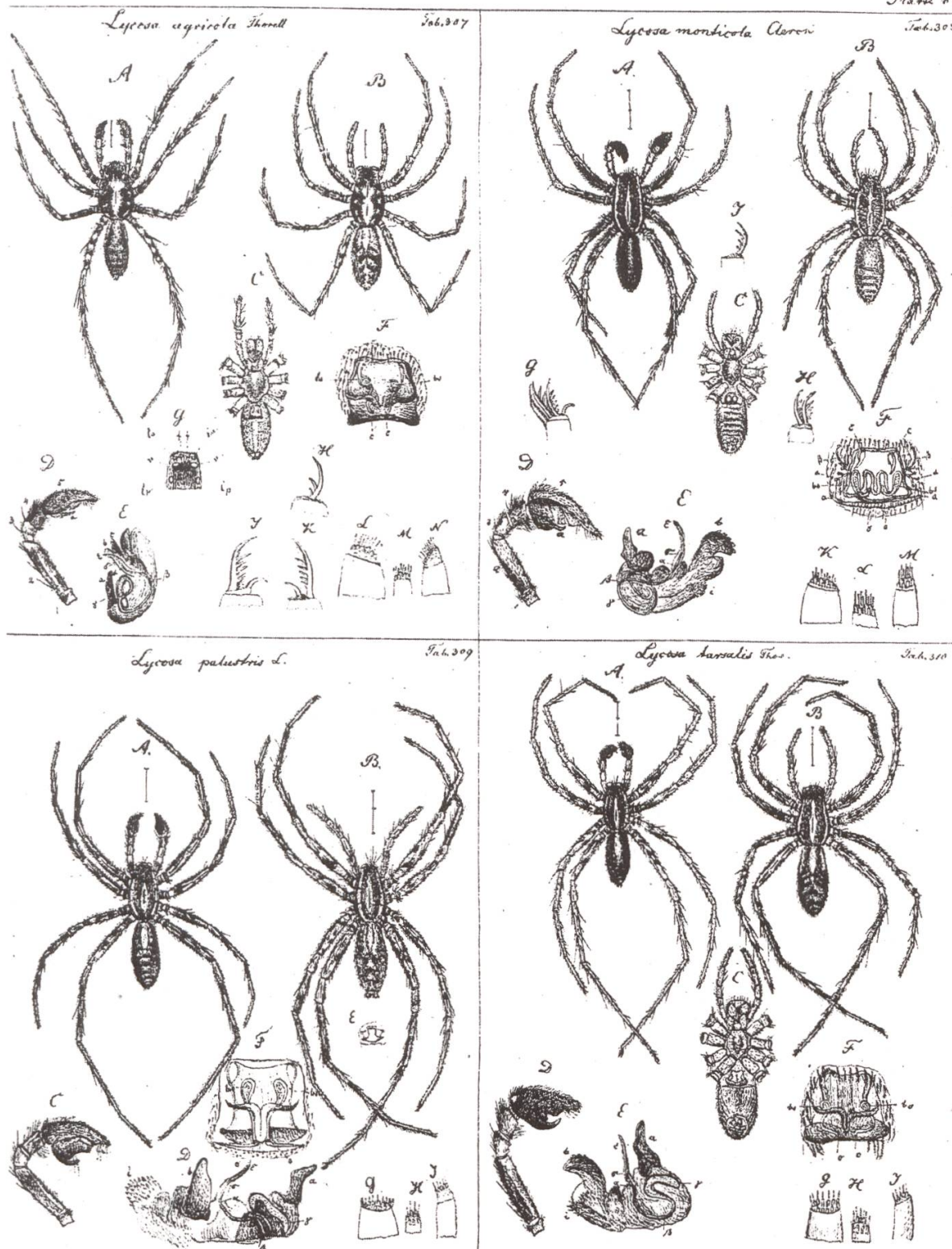
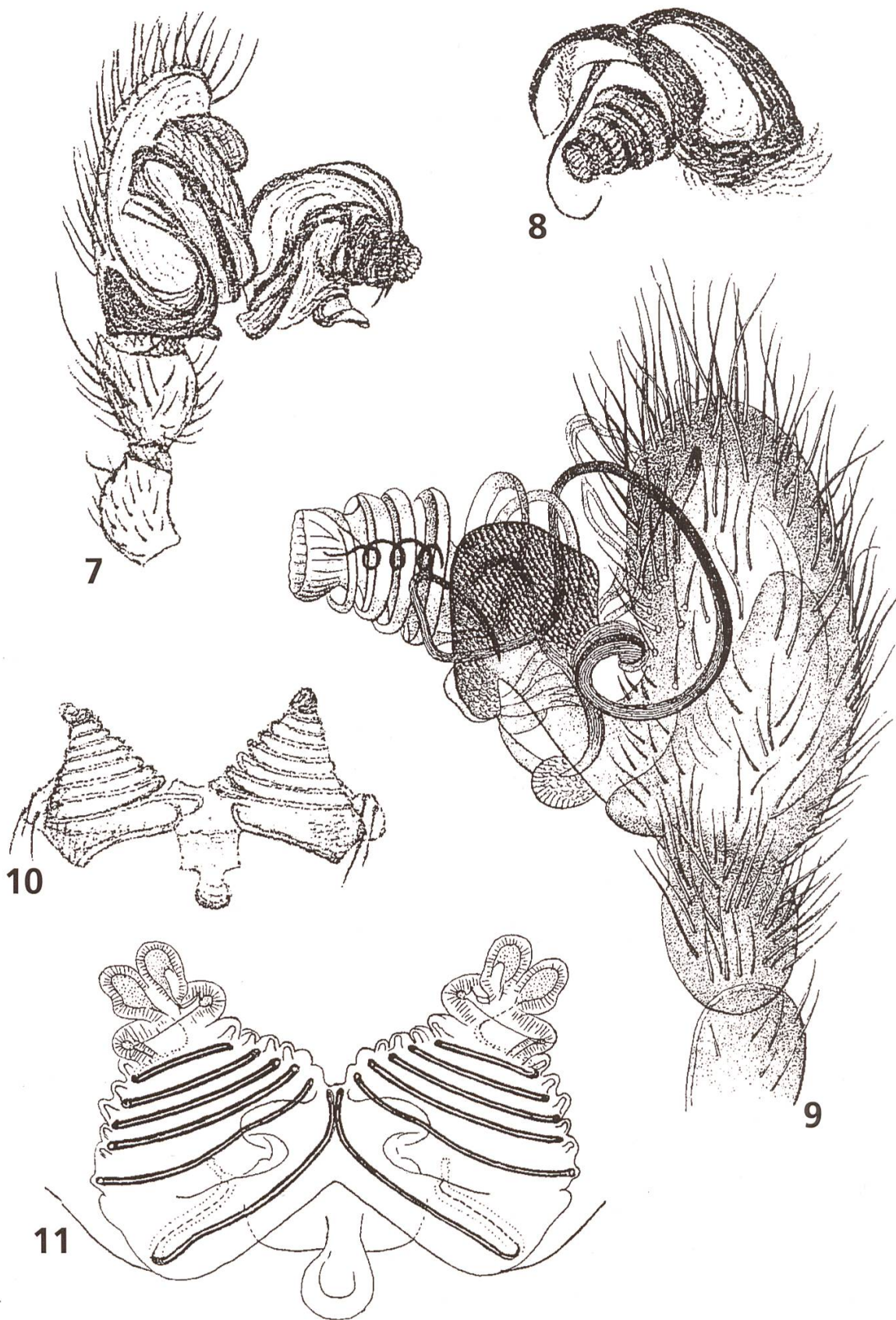


Fig. 6. Example of Menge's illustrations (x 0.94): his "Platte, 88, Tab. 307–310". – Clockwise: *Par-dosa agricola* (THORELL, 1856); *P. montana* (CLERCK, 1758); *P. palustris* (LINNÉ, 1758); *P. paludicola* (CLERCK, 1758).

Unfortunately, the illustrations in his "Preussische Spinnen" were repro-duced as photolithographic prints of hardly more than minute size (Fig. 6). Despite this disadvantage (apparently due to the need to keep printing costs low) it is obvious how carefully pedipalps and, especially, female genitalia were studied and figured. Drawings of epigynes simultaneously included remark-

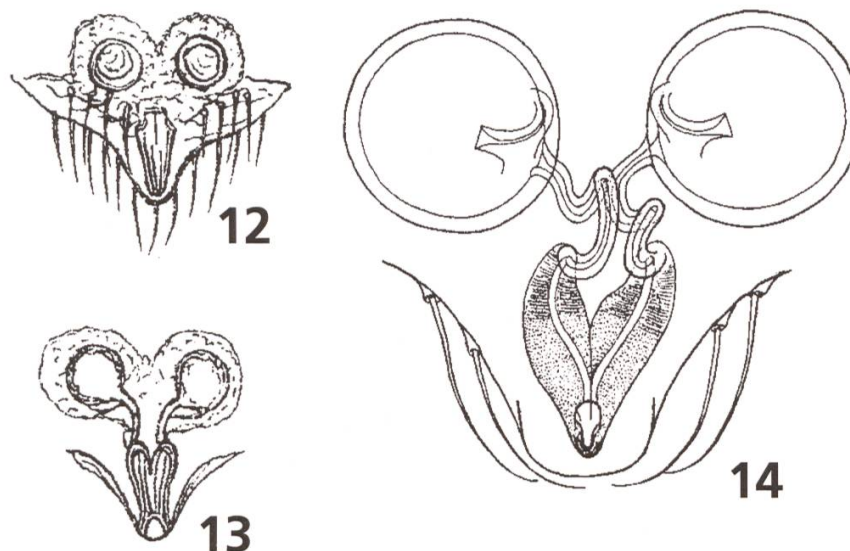


Figs. 7–11. Comparison: Illustrations of palpi and epigynes/vulvae of *Linyphia triangularis* (CLERCK, 1758) by Menge (1866) [sub *L. macrognatha* MENGE, 1866], Lebert (1878), and Wiehle (1956). – 7–8: Palp and terminal part of bulb (Menge, x 2); – 9: Palp (Lebert, x 1.2); – 10: Epigyne/vulva (Menge, x 2); – 11: Same (Wiehle, x 0.6).

Figs. 12–14. Comparison: Illustrations of epigynes/vulvae of *Neottiura bimaculata* (LINNÉ, 1758).

– 12–13: Menge's figures, x 2;

– 14: Wiehle's figure, x 0.7.



ably precise details of internal chitinous structures, especially introductory ducts and spermathecae (Figs. 7–8, 10). Even glands surrounding sclerotized spermathecae were seen and illustrated (Figs. 12–13). In his illustrations, it is not always possible to distinguish external surface structures from internal chitinous components. In his diagnoses and descriptions, Menge included additional comments on features of male pedipalps and also of female genitalia. Familiar terms of our days, such as "Cymbium", "Alveolus", "Spermophor" and "Embolus", were coined by Menge.

No information is available on how he studied such details technically. His illustrations indicate that Menge must have prepared slides and used a compound microscope (some authors, including F. Dahl, used micaceous leaves instead of glass slides).

Attempts to locate any parts of his collection (including any slides) or fragments of his library on spiders that might have survived, unfortunately failed. If such materials were still in existence, it may well be that they were destroyed at the end of the Second World War in 1945, including type material.

There is only one qualified contemporaneous approach: Lebert's work on "Bau und Leben der Spinnen" (1878). He carefully describes different structures of male palps and epigynes/vulvae. Aspects of terminology are discussed. Lebert coined the designation "Paracymbium", in addition to terms already introduced by Menge (see above).

His figures are excellent in quality and size. Whilst Lebert's work is considerably underillustrated, he was a pioneer in distinguishing components of the male pedipalpal bulb, including precise figures of various types in an expanded stage (Fig. 9). He mentions paired conical screw-like structures of the epigynum of *Linyphia triangularis* and refers to a corresponding component of the male bulb. This seems to be the first indication of co-adaptation in copulatory

organs of spiders. Menge (1866: 101) was also aware of such features (Figs. 7–8, 10), but he did not refer to the possibility of a lock-and-key function.

Another contemporary worker, McCook (1893: 127, fig. 127) discussed structural details of and ideas on the function of male palps and female epigynes/vulvae and presented a figure (taken from Wagner 1888) showing the complex of epigynum and introductory and fertilization ducts in an *Araneus* species.

Comstock's excellent work on the composition of male palpal organs (1910) was a milestone; however, he disregarded female counterparts completely. Järvi's studies ("Das Vaginalsystem der Sparassiden", 1912, 1914; see Jäger & Koponen 2005) included histology. But this work remained limited to a single higher taxon and was not directly intended for taxonomic purposes.

F. Dahl & M. Dahl (1927) and also M. Dahl (e.g. 1926, 1931) broadly used external and internal chitinous structures of female genitalia for taxonomic purposes, especially in their monographs in the series "Die Tierwelt Deutschlands". But both authors were primarily interested in presenting differences as such – close to some kind of a "fingerprint principle". The function of different parts of the vulvae and also aspects of co-adaptation between male palps and female epigynes/vulvae remained disregarded.

Innovation

From 1931 onwards, new ideas and thinking were introduced by Wiehle (Fig. 15) (see Kraus 1984a). The emphasis is still on accurate drawings of male palps and female epigynes in his monograph of the orb-weavers (Araneidae) (1931), and he remarks that epigynes, i.e. external female genital structures, are regarded as sufficient for identification purposes. But when appropriate, he also presented precise illustrations of vulvae (1931, figs. 132, 136). He made considerable progress in his monograph on the Theridiidae (1937). Referring to Engelhardt (1910), Wiehle expressly states (1937: 120) "Die Epigyne ist oft wenig charakteristisch, dagegen ist der Bau der Vulva klar und unterscheidet nahe verwandte Arten ganz sicher". He therefore presented separate figures of theridiid epigynes and vulvae (Fig. 14). Introductory ducts, spermathecae, fertilization ducts and other internal chitinous structures were differentiated and indicated by corresponding lettering. Wiehle was also interested in aspects of function, co-adaptation and the possibility of using genital structures for deducing phylogenetic patterns (1961, 1967a, b).

This approach was continued in succeeding papers. It culminated in Wiehle's masterpiece, his monograph of the Central European Erigonidae (1960

Fig. 15.
Hermann Wiehle
(1884–1966);
phot. O. Kraus, 1962.



[sub "Micryphantidae")] – with 1147 figures! Although he owned a stereomicroscope, Wiehle used his compound microscope almost exclusively, also when drawing.

It should be noted that Wiehle – like Menge before him – was a trained zoologist who achieved his doctor's degree under Gerhardt (1875–1950) at the university of Halle, Germany, in 1927. His thesis on "Beiträge zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden und Uloboriden" (1927) was the first milestone on the way to a better understanding of the evolution of orb-webs in both cribellate and ecribellate spiders. This background explains his rather laborious scientific approach. But this explains why many taxonomists in araneology did not follow him. They continued, and still continue, to present illustrations for purposes simply of species distinction. In certain taxonomic monographs, authors illustrate ventral and dorsal views of what they uniformly

call "epigynum"; they thoughtlessly no longer differentiate between epigynum in its conventional sense and internal vulval structures. The same practice is used in recent issues of a well-known arachnological journal.

Like Menge's original but still more elementary working style, Wiehle's approach also remained widely neglected by practising taxonomists – again for decades. Parallels between the two authors are exemplified by Figs. 10–11 and 12–14.

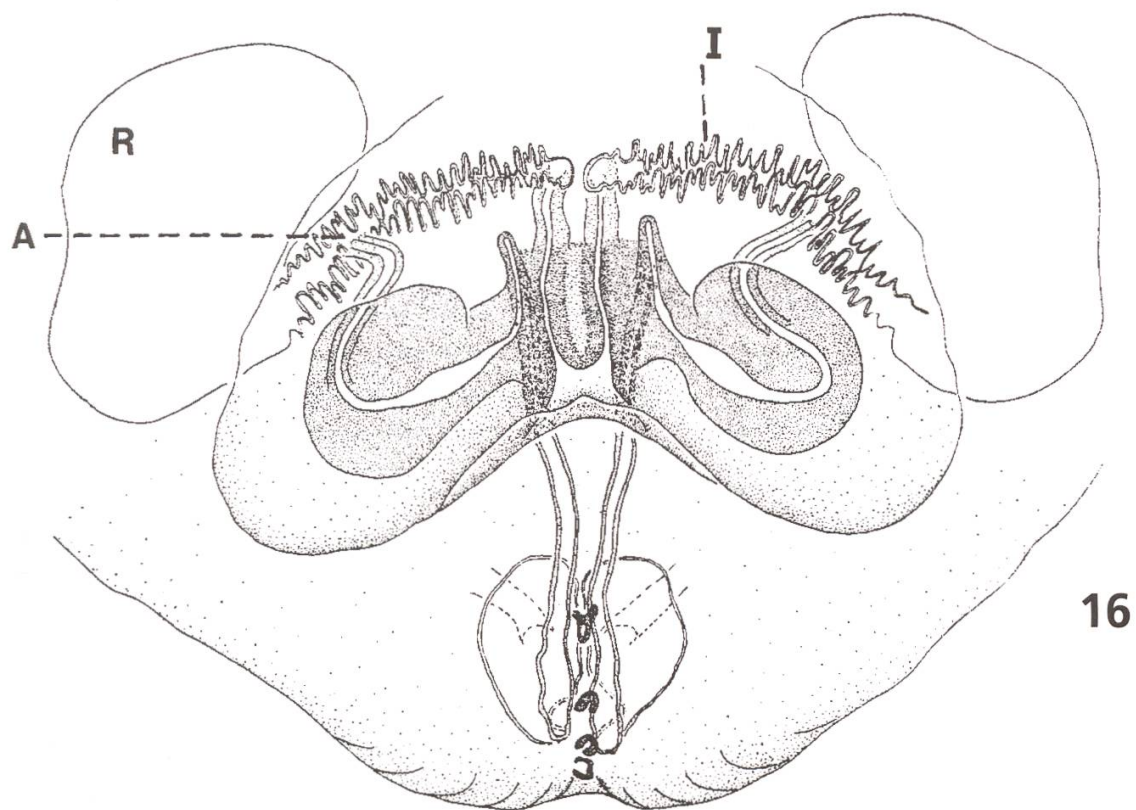
Kraus and his co-workers accepted Wiehle's approach (e.g., Baum 1972; Grimm 1985; Kraus & Baur 1974; Kraus & Kraus 1988; Loerbroks 1984). Whereas Wiehle macerated vulval structures by using KOH (occasionally even by boiling objects in diluted KOH), these workers embedded non-macerated epigynes/vulvae in Hoyer's mixture (similar to Berlese's mixture) (Kraus 1984b). This method has the advantage that components, especially of vulval structures, remain in their original position; artefacts due to dislocation are excluded. Another important aspect is that transparency is combined with a light refraction index of the mixture that is remarkably different from the corresponding index of chitin. Usage of a large rectangular cover glass (instead of a regular slide) permits access to the embedded object from both sides.

This advanced method permitted Baum (1972), for example, to discover details that had previously been overlooked (Figs. 16–17), e.g., unsclerotized receptacula (R), part 2 of introductory ducts (I), and anastomoses between introductory and fertilization ducts (A). Synapomorphies of this kind confirmed the sister group relationship of the (cribellate) Oecobiinae and the (ecribellate) Urocteinae. In other instances, such as Gnaphosidae, fine analysis of details enabled Grimm (1982) to differentiate sibling species.

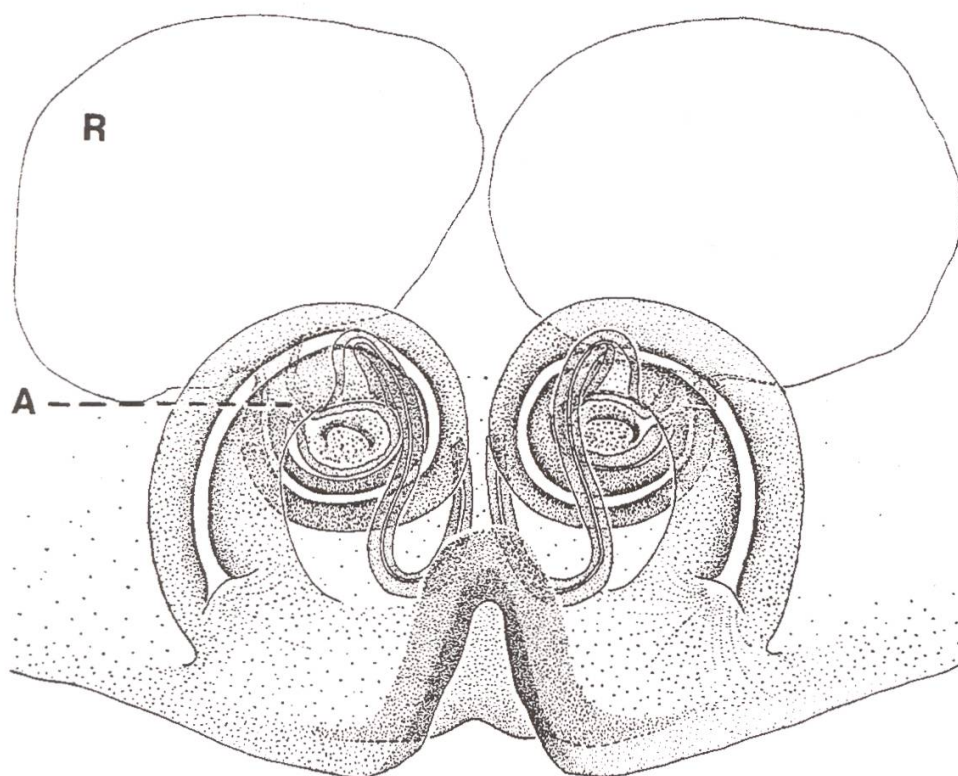
In his numerous papers, Thaler carefully followed such principles as had originally been established by Menge and considerably improved by Wiehle and others. He successfully continued this tradition. In December 2000, Thaler's contribution was awarded Wiehle's pocket-lens, still in its almost worn-out leather case – as the present author received it in 1966 (see this volume, fascicule 3, p. 1461, fig. 14).

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Figs. 16–17. Illustrations of vulvae of oecobiid spiders showing previously overlooked delicate details (Baum 1972). – 16: *Oecobius callariorum* (DUGÈS, 1836); – 17: *Uroctea compactilis* (L. KOCH, 1878).

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Address of the author:

Prof. Dr. Otto Kraus

Zoologisches Institut und Zoologisches Museum, Universität Hamburg

Martin-Luther-King-Platz 3

D–20146 Hamburg, Germany

E-mail: otto.kraus@zoologie.uni-hamburg.de

