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The Taxonomic and Nomenclatorial Status of the Milliped Generic Names *Parafontaria* Verhoeff, *Cyphonaria* Verhoeff, and *Japonaria* Attems

(Polydesmida, Xystodesmidae)

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Abstract

The correct name for the dominant Japanese genus of xystodesmid millipeds is shown to be *Parafontaria* Verhoeff, 1936, instead of *Japonaria* Attems, 1938 (*Japonaria* Verhoeff, 1936, was invalidly proposed without a designated type species). Anatomically the species of *Parafontaria* are different from all other xystodesmids in the modification of the second pair of legs of the female sex, as well as the form of the cyphopods which are located at the end of an enlarged membraneous sack. The new subfamily Parafontariinae is proposed for the reception of this one genus. *Fontaria tonominea* Attems, 1899, is redescribed from the female holotype and shown to be a species of *Parafontaria*. *P. kuhlbatzi* (Verhoeff, 1936) is confirmed as a junior synonym of *P. laminata* (Attems), and *P. armigera* (Verhoeff, 1936) considered to be at best a subspecies of *laminata*. The new name *P. laminata monticola* is proposed to replace *Fontaria (Parafontaria) kuhlbatzi montana* Verhoeff, 1941, preoccupied by *Fontaria montana* Bollman, 1887. *Polydesmus (Fontaria) dönitzi* Karsch, 1880, is resurrected as a valid species, with *Fontaria coarctata* Pocock, 1895, and *F. attemsi* Verhoeff, 1936, considered to be junior synonyms. The cyphopod structure of *Cyphonaria scabra* Verhoeff is illustrated from the type material, and the opinion expressed that this genus is probably a junior synonym of *Xystodesmus*.

1. Introduction

Knowledge of the Japanese diplopod fauna has advanced in a somewhat irregular pattern, with the initial foundations having been laid down by ATTEMs in 1909 and subsequently VERHOEFF in a large number of papers appearing between 1910 and 1941. VERHOEFF's work was a model for the studies of local authors, including TAKAKUWA, SHINOHARA, and MIYOSI, who were active from about 1934 to the recent past. A great number of new taxa were published by all these authors, but so far very little effort has been made by anyone to gather up some of the loose ends that have proliferated during this period of descriptive taxonomy.

During studies of the large Holarctic family Xystodesmidae during the past two decades, my attention has been repeatedly engaged by the genus *Japonaria*, a dominant and conspicuous element in the polydesmoid fauna of Japan. From time to time various type specimens have been examined in European collections, and considerable thought has been devoted to the status of the genus, both as regards its homogeneity and its position relative to other xystodesmid taxa. But the priority of other interests prevented any serious attempt to resolve any of the problems. Now, however, with the preparation of a classification of the Diplopoda of the world, the necessity of facing the *Japonaria* situation has become mandatory, and I set forth here some of the more significant conclusions reached during a recent survey.

The majority of the research summarized here was conducted at the Zoologische Staatssammlung München, during the summer of 1964, and I express here my best thanks to Dr. Egon Popp, at that time in charge of the myriapod collections of that museum.

2. The status of the names *Parafontaria* and *Japonaria*

The name *Japonaria* was first published as a subgenus of *Fontaria* (Verhoeff, 1936), to include Japanese xystodesmids thought to differ from the North American species of a nominate subgenus in lacking sternal spines. VERHOEFF derived his information on this point from a statement in ATTEMS' 1931 paper on "Leptodesmiden"; neither author was aware that numerous Nearctic species of "*Fontaria*" also lacked all traces of sternal spines. *Japonaria* originally included the named species *Fontaria coarctata* Pocock and the two new species *attemsi* and *falcifera*. None of the three was indicated in any way as type of the subgenus, and according to the provisions of Article 13, paragraph (b) of the International Rules of Zoological Nomenclature, such generic names have no standing in nomenclature. Moreover, no type was designated until 1938, when ATTEMS selected *falcifera* for this purpose. The name was therefore validated at that time, with ATTEMS becoming the author.

Parafontaria was also published in 1936, as a subgenus of *Fontaria*, but was monotypic with the single new species *F. (P.) armigera* Verhoeff. This name was, therefore, validly proposed.

In his big monograph on polydesmoids in Lief. 69 of *Das Tierreich* (1938) ATTEMS raised *Japonaria* to generic rank, with *Parafontaria* included as a subgenus. Like many other taxonomists of an earlier generation, neither ATTEMS nor VERHOEFF ever adhered closely to the International Rules, and so ATTEMS in 1938 saw no reason why *Japonaria*, published in June, 1936, should not be the name senior to *Parafontaria*, which appeared in September of that year.

Because of the great authority that attached to ATTEMS' works, his treatment of *Japonaria* was immediately accepted as correct by all subsequent workers, including the present author. Eventually the characters upon which VERHOEFF set aside *armigera* as type of a separate subgenus came to be questioned, however, and *Parafontaria* has generally been considered as more or less a strict synonym of *Japonaria*.

Regardless of the amount of logic which individual systematists can or cannot attach to the adoption of Article 13(b) of the Rules, it was publicized years before

its effective date, and has not been challenged in the decades following 1929. I personally feel that application of this regulation is unnecessarily severe in disqualifying the work of competent taxonomists, yet because of its universal acceptance I see no course other than its application to Verhoeffian names without prejudice.

As a result, if the two names under discussion are regarded as synonyms, *Parafontaria* Verhoeff, 1936, has priority over *Japonaria* Attems, 1938, and must be resurrected as the valid name for this group of species.

3. On the systematic position of the genus *Parafontaria* Verhoeff

As implied by its name, *Parafontaria* was originally considered to be a relative of the North American genus *Fontaria*, hence in terms of modern concepts, referable to the family Xystodesmidae. This group is now best developed in North America, but is represented also in east Asia and the Mediterranean region. Within the polydesmoid suborder Chelodesmidea, the Xystodesmidae is distinguished by a number of anatomical details, such as the unmodified condition of the 7th antennomere, separation of the gonopod cannula from the distal edge of the coxa, presence of prefemoral spines on the legs of most species, and relatively broad, compact, body form.

In the majority of its features, *Parafontaria* agrees fairly closely with the normal xystodesmid condition, although the male genitalia are unusually large. Further, although the socket of the cannula is separated from the distal edge of the gonopod coxa, there is only a very thin and fragile "bridge" (Fig. 1, B) making the separation, suggesting perhaps a primitive condition for this character. Lateral condyle (Fig. 1, C) unusually large and prominent for a xystodesmid.

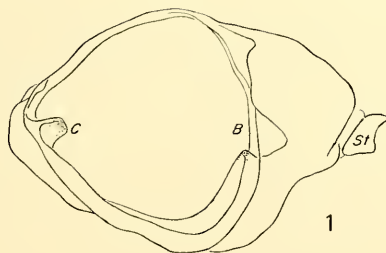


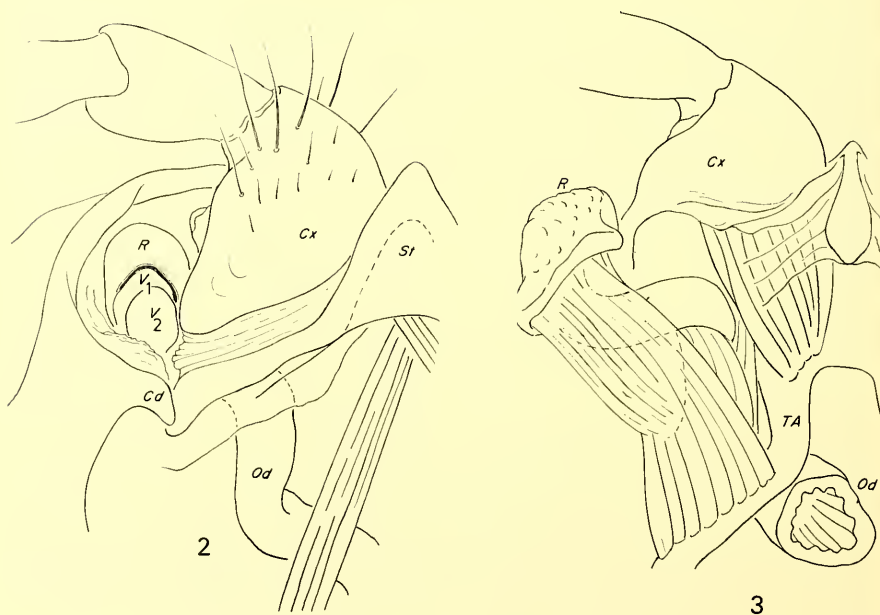
Figure 1: *Parafontaria spiraligera* (Verhoeff), coxa of right gonopod, distal aspect, telopodite removed. St, sternum; B, "bridge" setting off socket of cannula; C, lateral coxal condyle. Drawn from syntype.

On the other hand, the anatomy of the second pair of legs and adjoining reproductive structures of the female sex is so singular and disjunct, that nothing comparable is known within the entire order Polydesmida. Since the Verhoeff Collection at München contained female specimens of species of *Parafontaria*, I was able

to investigate this matter at least in its major features. It seems highly likely that the form of the second sternum of females not only sets this genus apart systematically, it also may provide a good means of distinguishing between species.

To show the normal condition for xystodesmids, I illustrate here the second sternum of *Apheloria trimaculata* (Wood), a common species in northeastern United States. Figure 2 shows the sternum in anterior view, with adjacent parts of the pleurotergum and cyphopod included. The sternum (St) is triangular medially, but the lateral extensions are slender, and articulate against a prominent condyle (Cd) from the pleurotergum. The cyphopod is located in a membranous invagination posterior to the condyle, and is usually visible when in the retracted condition. As in most xystodesmids, the cyphopod consists of a relatively large subhemispherical basal plate or receptacle (R), containing two opposed valves (V_1 , V_2). Seen in aboral (posterior) aspect (Fig. 3), with most of the connective tissue and muscle removed, the receptacle is entered from behind by the distal end of the oviduct (Od), which courses mediodorsal, crossing in front of the tracheal apodeme (TA), and thence posterior paralleling the esophagus.

In contrast, the corresponding regions in *Parafontaria* differ remarkably both in shape of the sternum and coxa of the second legs, and in the characters of the



Figures 2, 3: *Apheloria trimaculata* (Wood), sternal complex of second pair of legs of female. 2: sternum and base of left leg, oral aspect, with part of pleurotergum shown at left. 3: the same region after removal from pleurotergum, aboral aspect, with cyphopod displaced laterad. Cd, pleurotergal-sternal condyle; Cx, coxa; Od, oviduct; R, cyphopod-displaced laterad. St, sternum; TA, tracheal apodeme; V_1 , V_2 , inner and outer valves of cyphopod.

cyphopods, which are placed at the end of enormously enlarged membranous vesicles traversed by the oviduct.

The sternum (Fig. 4 & 6, St) is nearly transverse, as wide laterally as at middle, and the anterior surface of the lateral ends is strongly convex. No tracheal apodemes were observed, but the original dissections were not made with a view toward anatomical studies, and details may have been overlooked. The musculature of the legpair and sternum requires to be studied carefully from fresh material of *Parafontaria*.

The coxae, so far as known, are broadened laterally and very short, and differ strongly in appearance in the two species examined. On the posterior side they tend to be closely applied to the sternum, and in one species are partly fused with it (Fig. 7).

Taking the foregoing characteristics of *Parafontaria* into account, it is clear that they warrant setting this genus apart in some formal category. In my opinion, a conservative evaluation would emphasize the general overall xystodesmid facies of these species, but oppose *Parafontaria* to all other members of the family:

Parafontariinae, new subfamily

With the single genus *Parafontaria* (syn. *Japonaria* Attems, 1938), and defined on the basis of the modifications of the female anterior sternum as discussed in the preceeding paragraphs.

The remaining genera of xystodesmids, having normally constructed 2nd sterna in the female sex, comprise an anatomical unity of rank equal to the Parafontariinae:

Xystodesminae, new status

(Nomen translatum herein, ex family Xystodesmidae Cook, 1895)

Approximately 50 genera comprise this large group, the great majority of them endemic in North America. A tentative classification into tribes is at present being prepared for publication.

4. Notes on the status and identity of several species of *Parafontaria*

During the course of literature survey and the examination of material, some information bearing on the taxonomic status of several species was obtained, and the opportunity is here taken to present these data for the benefit of other persons who may have the occasion to work with this genus.

Parafontaria tonominea (Attems), comb. nov. (Figs. 4—5)

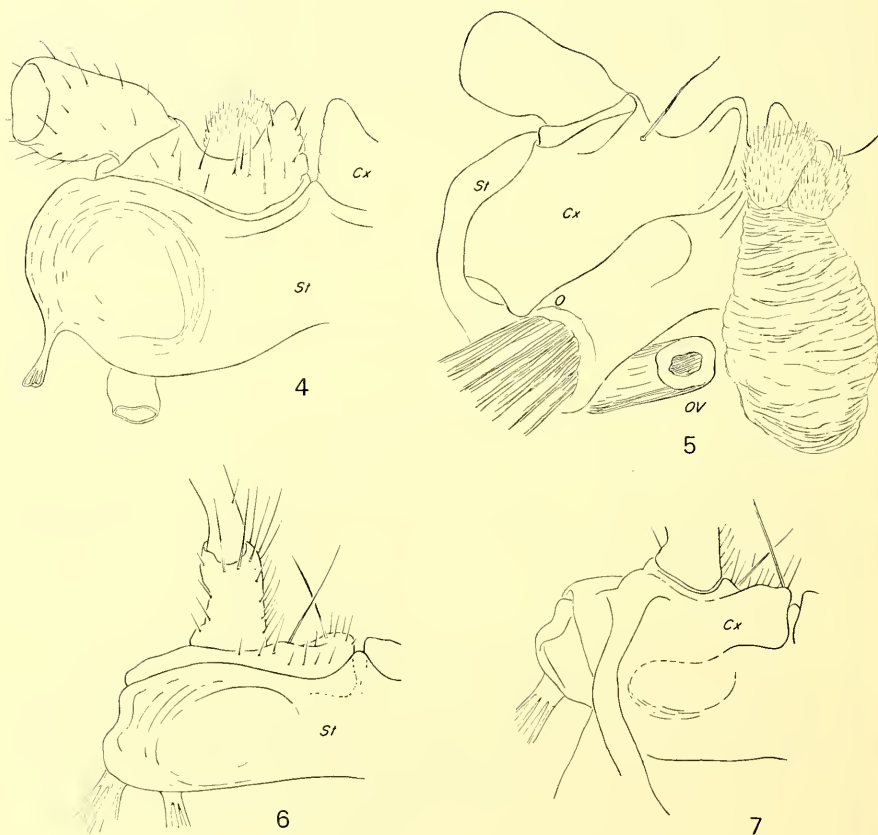
Fontaria tonominea Attems, 1899, Denks. Akad. Wiss. Wien, vol. 68, p. 260, pl. XIII, fig. 310. ♀ holotype, Zool. Mus. Hamburg, from "Tonomine. Yamato, Centraljapan."
Apheloria tonominea: Attems, 1938, Das Tierreich, lief. 69, p. 171.

Through the kindness of Frl. Dr. G. Rack I was able to study the female holotype of this long-enigmatic species. In general external form of the body there is an

obvious concordance with other species of *Parafontaria*, and this affinity is reflected also in the female genital structure.

In comparison with that of *P. laminata* (Figs. 6 and 7), the 2nd sternum of the female is much more expanded laterally and convex toward the lateral ends. The coxae are shorter than those of *laminata*, not extending lateral to end of sternum, and are prominently produced distally at their median ends.

On the aboral side (Fig. 5), the coxa is reasonably distinct from the sternum except laterally, where it is overlapped somewhat by a caudally recurved lobe of the latter. A very large bundle of retractor muscle (tracheodorsal?) extends dorso-lateral from each side of the sternum. The remarkable membraneous basal sac



Figures 4—7: sternal complex of two species of *Parafontaria*. 4: left side of sternum and base of left leg, *P. tonominea* (Attems), from holotype. 5: the same structure, aboral aspect, showing the enlarged and modified distal region of the oviduct characteristic of this genus. 6: left side of sternum and base of left second leg, *P. laminata* (Attems), oral aspect. 7: the same structure, aboral aspect, cyphopod and oviduct removed, from syntype of *Fontaria kuhlgatzii* Verhoeff. Cx, coxa; OV, oviduct; St, sternum.

preceding the sclerotized cyphopod parts is shown on the left side in Fig. 5. The oviduct enters this structure near its base and apparently continues through it at least part-way to the cyphopod sclerites. Unfortunately, this dissection was made prior to awareness of the unusual conditions, and most of the muscle attachments were dislodged.

Parafontaria laminata (Attems), comb. nov. (Figs. 6—7)

Fontaria coarctata laminata Attems, 1909, Ark. Zool., vol. 5, no. 3, p. 29, pl. 1, figs. 14, 15.

Syntypes (Naturh. Mus. Wien, Mus. Comp. Zool., and perhaps elsewhere), from "Mangaesi" (Ausflug auf den Fusi-yama), south central Honshu, Japan.

Fontaria (*Parafontaria*) *Kuhlgatzii* Verhoeff, 1937, Zool. Anz., vol. 117, p. 318, figs. 1, 2.

Type material (gonopod preparations and some female specimens) Zool. Staatssammlung München, from "Japan, Unajuki".

Japonaria (*Japonaria*) *laminata*: Attems, 1938, Tierreich, Lief. 69, p. 177 (with *kuhlgatzii* as synonym).

Japonaria laminata: Takakuwa, 1942, Annotat. Zool. Japonenses, vol. 21, p. 42 (confirms Attems' synonymy of *kuhlgatzii* with *laminata*).

Fontaria (*Parafontaria*) *kuhlgatzii* + *laminata*: Verhoeff, 1941, Zool. Anz., vol. 136, p. 67.

Comparison of Figures 6 and 7, made from a female syntype of *kuhlgatzii* at München, with the comparable drawings for *P. tonominea*, reveals impressive difference of a magnitude unusual for congeneric female millipeds. The sternal convexities here are much less developed, and the coxa of the 2nd legs is entirely different in shape, extending lateral to end of sternum, and not produced distally at the median end as in *tonominea*. Seen in posterior aspect, the proximal edge of the coxa is partly fused with the sternum (as shown by the dashed line).

The form of the cyphopod and the enlarged vesica upon which it is connected, however, is generally similar to that shown for *tonominea*. It may be identified as a problem of the greatest interest, to learn more of the anatomy and physiology of the female genitalia in this genus, and the matter is recommended to any Japanese naturalist having the necessary fresh material and opportunity for study.

Contrary to the opinion of VERHOEFF in his 1941 paper, I find no reason for separation of *kuhlgatzii* from *laminata* as a separate species. The sole justification which he advanced was the lesser degree of curvature of the telopodite in the former, a difference which I think was illusory only, being produced by pressure of the cover glass of the preparation. In 1960 I was able to examine VERHOEFF's type preparation and prepare drawings which were compared with type material of *laminata* in the Attems collection at Wien. No appreciable structural differences could be verified.

Parafontaria laminata armigera (Verhoeff)

Fontaria (*Parafontaria*) *armigera* Verhoeff, 1936, Zool. Anz., vol. 115, p. 301, figs. 4—6.

Syntypes (Zool. Staatssammlung München) from Suwa, near Tokyo, Japan.

Japonaria (*Parafontaria*) *armigera*: Attems, 1938, Das Tierreich, Lief. 69, p. 179.

Japonaria laminata armigera: Takakuwa, 1942, Annot. Zool. Japon. vol. 21, p. 42.

After reviewing the pertinent type material at München and Wien, I can concur entirely with the opinion expressed by TAKAKUWA, that *armigera* can only be regarded as a subspecies of *laminata* at best.

Parafontaria laminata monticola, nom. nov.

Fontaria (*Parafontaria*) *kublgatzi montana* Verhoeff, 1941, Zool. Anz., vol. 136, p. 67, 68, figs. 5, 6. Syntypes (Zoll. Staatssammlung München) from Mt. Ontake, (Ontake-san), 35.53 N, 137.29 E, Honshu, Japan; R. Yosii leg. 12 Oct. 1938. Preoccupied by *Fontaria montana* Bollmann, 1887, Proc. U. S. Nat. Mus., vol. 10, p. 622.

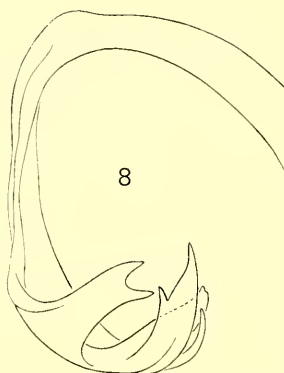


Figure 8: *Parafontaria doenitzi* (Karsch), distal half of telopodite of right gonopod, lateral aspect. Drawn from holotype.

Parafontaria doenitzi (Karsch), comb. n. (Fig. 8)

Polydesmus (*Fontaria*) *Dönitzi* Karsch, 1880, Zeitschr. Naturw., ser. 3, vol. 5, p. 848.

Holotype ♂, Zool. Mus. Berlin No. 810, from "Japan".

Fontaria coarctata Pocock, 1895, Ann. & Mag. Nat. Hist., ser. 6, vol. 15, p. 361, pl. 11, fig. 11 Holotype ♂, Brit. Mus. (Nat. Hist.), from "Japan". New synonymy!

Fontaria (*Japonaria*) *attemsi* Verhoeff, 1936, Trans. Sapporo Nat. Hist. Soc., vol. 14, p. 159, pl. 3, figs. 9, 10. Syntype ♂, Zool. Staatssammlung München, from Nikko, Tochigi Pref., Honshu, Japan. New synonymy!

Japonaria attemsi: Attems, 1938, Das Tierreich, Lief. 69, p. 178, fig. 197.

Japonaria attemsi: Takakuwa, 1942, Annot. zool. Japon. vol. 21, p. 41, fig. 4.

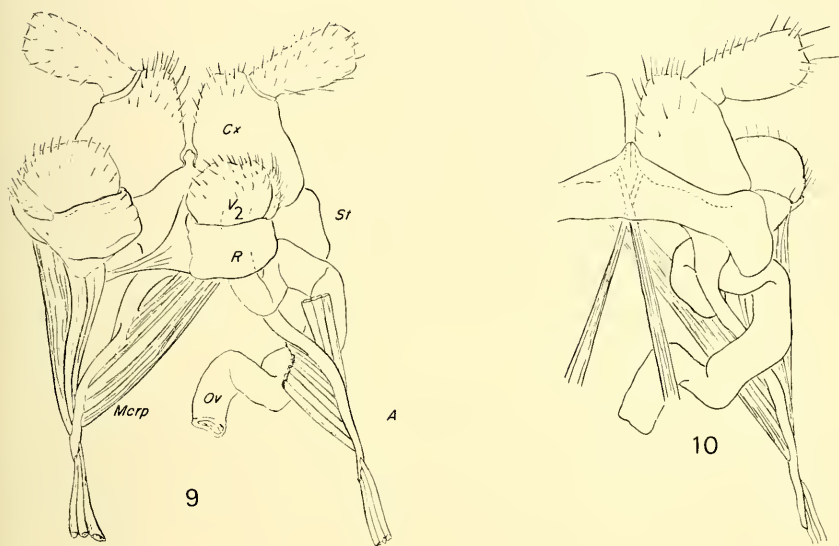
Examination of the dried holotype at Berlin in 1964 showed that *doenitzi* is without much doubt a senior synonym for both *coarctata* and *attemsi*, as a comparison of the gonopod drawing given here (Fig. 8) will show.

5. On the status of the genus *Cyphonaria* Verhoeff

Originally proposed as a subgenus of *Fontaria* (Verhoeff, 1936), the name *Cyphonaria* was monobasic with the single new species *scabra*, and distinguished from the two subgenera *Japonaria* and *Parafontaria* chiefly in having transverse rows of small tubercles on the metaterga. VERHOEFF suspected that *scabra* (known only from a single female) was really not related to the two subgenera mentioned, but, curiously enough, did not recognize any similarity with the species described in the same 1936 paper as *Takakuwaia furculigera*.

I have been able to restudy the holotype of *scabra* at München, and give here two drawings of the second sternum (Figs. 9, 10) which show very clearly the typical xystodesmid structure.

As I showed some years ago (1956) *Takakuwaia* is a junior synonym of *Xystodesmus* Cook, 1895. Now I believe that several species described in *Rhysodesmus* by Japanese authors, such as *ikaoensis* and *tuberculatus* Takakuwa, are congeneric with *Xystodesmus martensi* (Peters). All of these are small species with seriate dorsal tubercles, and I very strongly suspect that *scabra* is congeneric with them. If so, *Cyphonaria* will become a junior synonym of *Xystodesmus*. The eventual collection of topotypic males (from „Urawa, bei Tokyo“) will finally settle this point.



Figures 9, 10: Sternum and bases of second pair of legs, *Cyphonaria scabra* Verhoeff. 9: posterior (aboral) aspect, some of the musculature shown, right cyphopod deflected laterad. 10: the same structure, oral aspect. Drawn from holotype. Cx, coxa; Mcrp, posterior coxal retractormuscle of second leg; Ov, oviduct; R, receptacle of cyphopod; St, sternum; TA, tracheal apodeme; TA, tracheal apodeme; V₂, inner valve of cyphopod.

6. Literature

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