MUSEUM AND INSTITUTE OF ZOOLOGY
POLISH ACADEMY OF SCIENCES

FRAGMENTA FAUNISTICA

Fragm. faun.	Warszawa, 30.12.2000	43	Supplement	131–138

11th International Congress of Myriapodology, 20–24 July 1999, Białowieża, Poland
PROGRESS IN STUDIES ON MYRIAPODA AND ONYCHOPHORA

Harald HAUSER

Heterodactyly in the genus *Craspedosoma* (Diplopoda, Chordeumatida): an observation error

Abstract: Heterodactyly means that the processes of podosternites of the genus *Craspedosoma* LEACH, 1815, have very different lengths. Gonopod morphological examinations of a large series of *C. rawlinsii* LEACH, 1815 from the whole area of the distribution did not reveal any differences regarding the length of the podosternite processes. Analysis of the spatial structure of the podosternite produce projections which look like brachy-, meso- and macrodactylous form was carried out. It is apparent that part of the described morphological variability, as well as a number of the described taxa, are caused by misjudgements regarding the spatial structure of the podosternite. The history and the effects of heterodactyly are discussed.

Key words: Diplopoda, *Craspedosoma*, gonopod morphology, taxonomy

Author's address: Staatliches Museum für Naturkunde Görlitz, PF 300 154, 02806 Görlitz, GERMANY

INTRODUCTION

The number of described species, subspecies and varieties in the genus *Craspedosoma* is immense. Verhoeff, e.g., described 11 subspecies and 100 varieties of *C. alemannicum* VERHOEFF, 1910 (SCHUBART 1963). Many of these were seperated by differences which are based on characteristics of the posterior gonopods, the so-called podosternite. The podosternite is shaped somewhat like a crown with six spikes on an oval base. There are three anterior and three posterior processes/spikes, constituting two lateral pairs and a median pair (Fig. 1). Heterodactyly (VERHOEFF 1915 a, 1916, 1917, 1939) means that the processes of the podosternites may have very different lengths (brachy-, meso-, macrodactylous), not only within one species but also within the same population.

HAUSER H. 2000. Heterodactyly in the genus *Craspedosoma* (Diplopoda, Chordeumatida): an observation error. In: WYTWER J. & GOLOVATCH S. (eds), Progress in Studies on Myriapoda and Onychophora, Warszawa XIV+396 pp. Fragm. faun. 43 (Suppl.): 131–138.

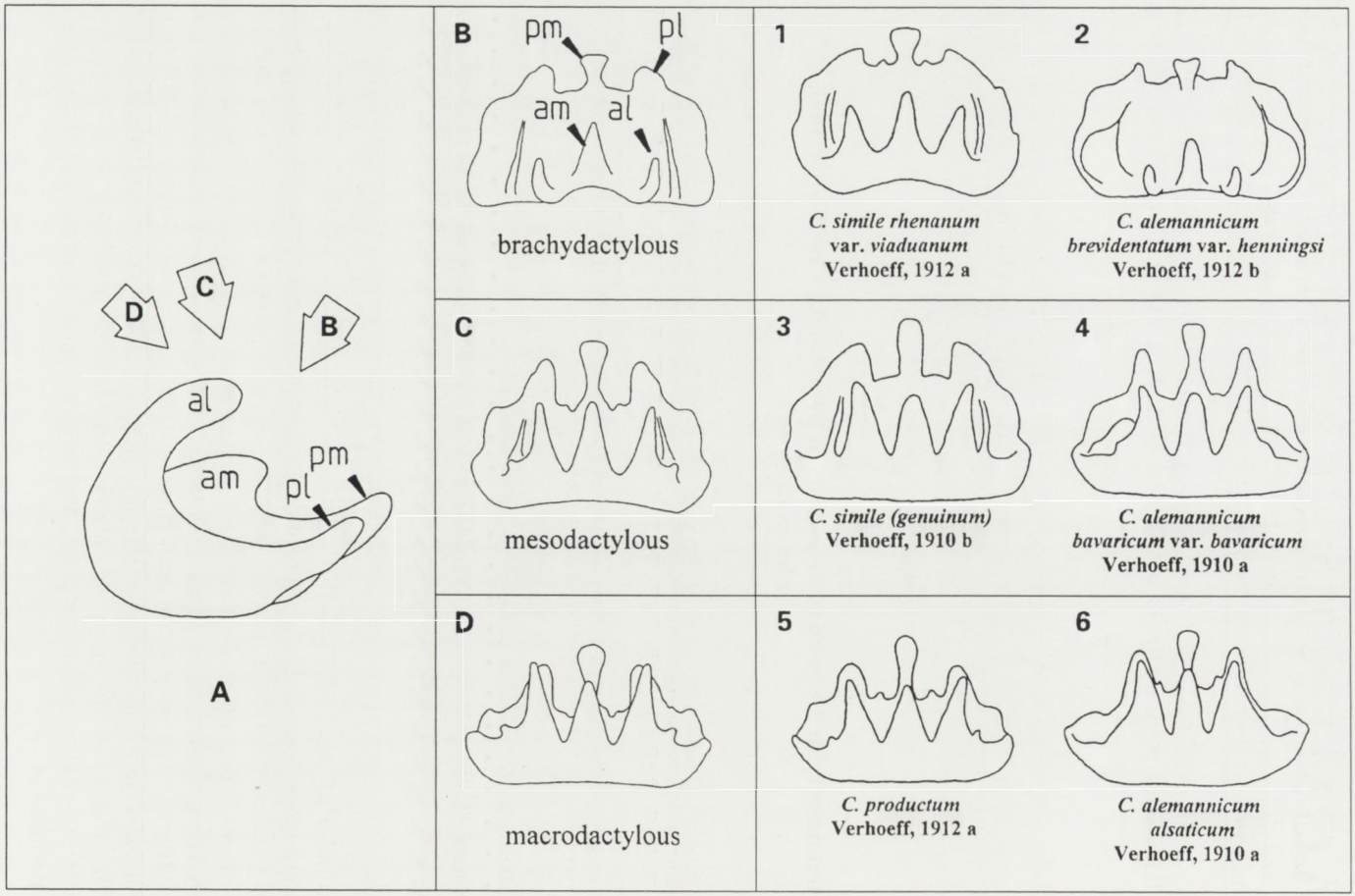

Fig. 1. A–D: Different perspectives of a podosternite of *C. rawlinsii*. al: anterior lateral process, am: anterior mesal process, pl: posterior lateral process, pm: posterior mesal process. 1–6: Drawings of heterodactylous *Craspedosoma* taxa redrawn from VERHOEFF (1910 a: 4, 6; 1910 b: 3; 1912 a: 1, 5; 1912 b: 2).

The lengths of the podosternite processes are an important characteristic in the complicated determination keys, which Verhoeff has set up for the genus *Craspedosoma*. Most of the *Craspedosoma* taxa described by Verhoeff are based on this characteristic. How did Verhoeff determine the lengths of the podosternite processes? This question has to be answered in order to solve the problems related to the taxonomy of the genus *Craspedosoma*.

MATERIAL AND METHODS

The podosternites were dissected and put in glycerine gelatine for microscopic investigations without using a cover glass. Glycerine gelatine has the advantage that the gonopods can be placed and fixed in a required position. It can be liquified by heating (melting point 35°C) in order to alter the position of the object. This procedure can be repeated as often as desired.

A podosternite is a complex spatial structure. Drawn from different perspectives it is seen as producing differently shaped images. Therefore, it is necessary to look at it from various sides in order to understand its shape.

In perspective A (Fig. 1), the longitudinal axis of the oval base of the podosternite is perpendicular to the drawing plane. In perspective B, the plane of the oval basis is parallel to the drawing plane. In perspectives C and D, the podosternite is turned by steps on the longitudinal axis. Projections created in this way were analysed and compared with published drawings, in particular those of Verhoeff.

600 podosternites from the whole area of the distribution of the *C. rawlinsii*-complex were examined by this method of polyperspective projection. For example, three series of *Craspedosoma rawlinsii rawlinsii* LEACH, 1815 (sensu SPELDA 1991), from Freiburg (SW Germany), Göteborg (S Sweden) and Bialowieża (E Poland) were compared (Fig. 2).

Finally type material of *Craspedosoma germanicum suevicum* var. *extremum* VERHOEFF, 1939 and *C. alemannicum brevidentatum* var. *abbreviatissimum* VERHOEFF, 1916 was examined (Zoologische Staatssammlung München).

RESULTS

Different perspectives of the same podosternite can produce projections that look like brachy-, meso- and macrodactylous forms. This result suggests that heterodactyly is not a natural phenomenon but an error of observation.

The following aspects support this statement:

1. A study of 600 specimens from the whole area of the distribution did not confirm the extreme polymorphism of podosternites of *Craspedosoma* described by VERHOEFF (1912 a, 1916, 1917, 1939). Using a standardised perspective, the samples showed no differences in podosternites beyond the expected local and geographical variability (Fig. 2).

Fig. 2: *C. rawlinsii*. Lateral perspectives of podosternites. Examples of variability in the lengths of the podosternite processes. al, am, pl, pm: see Fig. 1. SW Germany: Kaiserstuhl W Freiburg i.Br.; S Sweden: Björlanda W Göteborg; E Poland: Bialowieża National Park.

2. When turning a podosternite step by step, projections are produced which can be associated with illustrations of the description of brachy-, meso- and macrodactylous *Craspedosoma* taxa as published by Verhoeff (Fig. 1).

3. The lateral projection of the podosternite shows a correlation with the perspective for some characteristics used by Verhoeff, for example, the length of the anterior lateral processes in comparison with the anterior mesal process. Fig. 1 shows three frontal perspectives which may result from the production of a permanent mount. In comparison with the front central process the different perspectives make the front lateral processes appear shorter (B), equally long (C) or longer (D).

4. The original permanent mount used by Verhoeff for the description of *Craspedosoma germanicum suevicum* var. *extremum* VERHOEFF, 1939 was opened and re-examined. Brachydactylous projections could be produced (Fig. 3) using the podosternite which Verhoeff described as extremely macrodactylous. It does not differ from other podosternites when applying the well standardised lateral perspective.

Verhoeff did not standardise the perspective when making his morphological studies. He determined the lengths of the podosternite processes by using the front perspective although they can only be accurately estimated by means of the lateral view of the podosternite. Only the perspective of the lateral view can reliably be standardised.

DISCUSSION

Knowledge of the fact that heterodactyly is based on an observation error is the key to the understanding of Verhoeff´s voluminous and complicated *Craspedosoma* literature. About 90% of the *Craspedosoma* taxa described by Verhoeff are based on heterodactyly. These taxa again, form the basis for interpretations by Verhoeff in respect of zoogeography, ecology and evolution.

How can the importance of the length of the podosternite processes for Verhoeff´s *Craspedosoma* taxonomy be demonstrated? It is the position of this characteristic in his determination keys. The length of the podosternite processes is regularly used as a separating characteristic at early positions within the keys. Couplets containing this character lead to false determinations, namely to nonexistent taxa. Fig. 4 shows the dichotmous outline of a determination key of VERHOEFF (1916). Out of 89 nominal taxa only eight can be defined by characters other than lengths of podosternite processes. Thus, 91% of the "taxa" can be straightforwardly discarded. A detailed presentation of the taxonomic consequences will be published elsewhere.

When dividing Germany into zoogeographic regions, Verhoeff used *Craspedosoma* taxa to define endemic forms (VERHOEFF 1915 b, 1916, 1917). For the Alemannic region ("alemannischer Gau", VERHOEFF 1915 b) he enumerated 16 endemic species and subspecies, among them 7 *Craspedosoma* taxa, and he named 4 *Craspedosoma* subspecies out of 5 endemic taxa for the Danube region ("Donaukreis"). All these species and subspecies are heterodactyl phantoms.

Verhoeff recognised morphological-ecological races ("heteroklimatisches Verhalten", VERHOEFF 1914, 1915 a, 1917) when considering the distribution of the heterodac-

tylous forms. According to his studies, brachydactylous forms are favoured by a cooler climate, macrodactylous forms by a warmer climate and mesodactylous forms hold an intermediate position regarding the climate

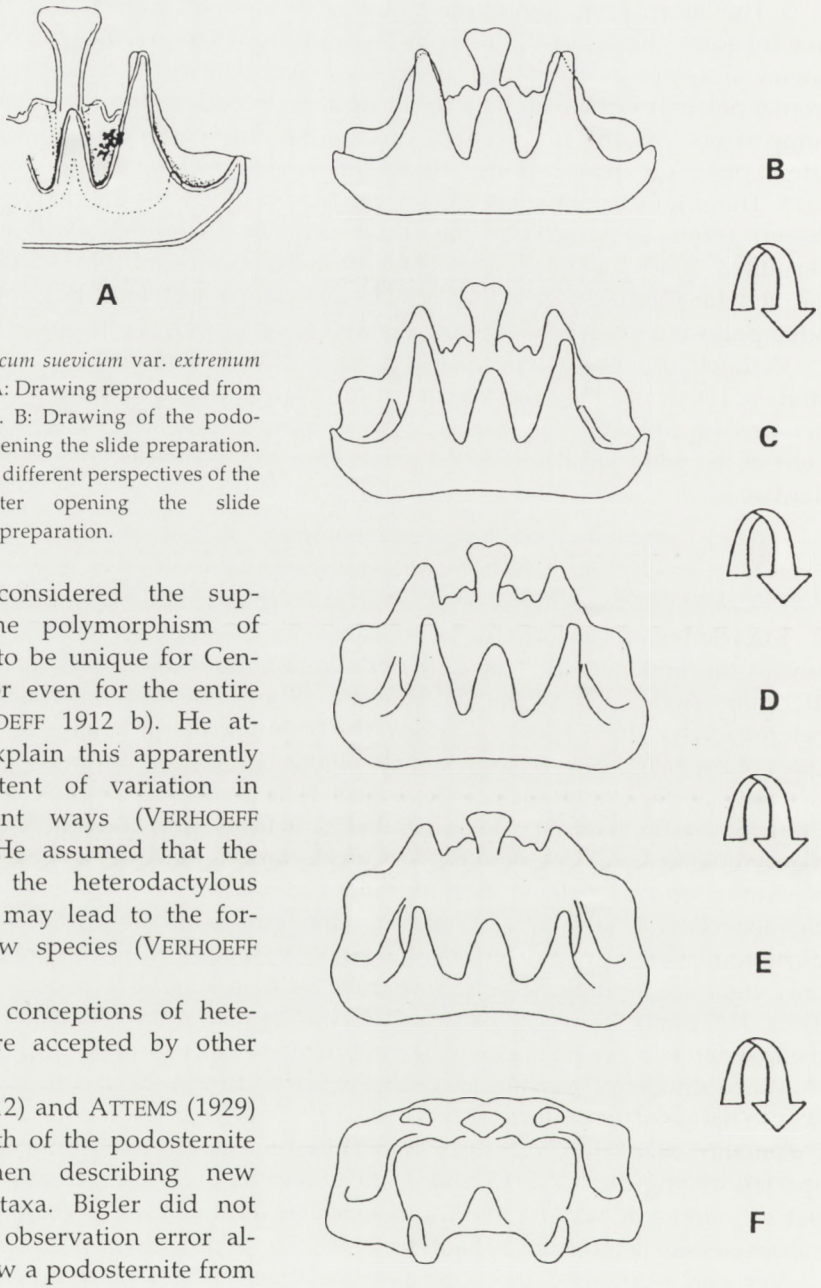

Fig. 3: *C. germanicum suevicum* var. *extremum* VERHOEFF 1939. A: Drawing reproduced from VERHOEFF (1939). B: Drawing of the podosternite before opening the slide preparation. C–F: Drawings of different perspectives of the podosternite after opening the slide preparation.

Verhoeff considered the supposed extreme polymorphism of *Craspedosoma* to be unique for Central Europe or even for the entire world (VERHOEFF 1912 b). He attempted to explain this apparently enormous extent of variation in many different ways (VERHOEFF 1915, 1939). He assumed that the variation of the heterodactylous podosternites may lead to the formation of new species (VERHOEFF 1914, 1916).

Verhoeff´s conceptions of heterodactyly were accepted by other authors.

BIGLER (1912) and ATTEMS (1929) used the length of the podosternite processes when describing new *Craspedosoma* taxa. Bigler did not recognise the observation error although he drew a podosternite from two different perspectives.

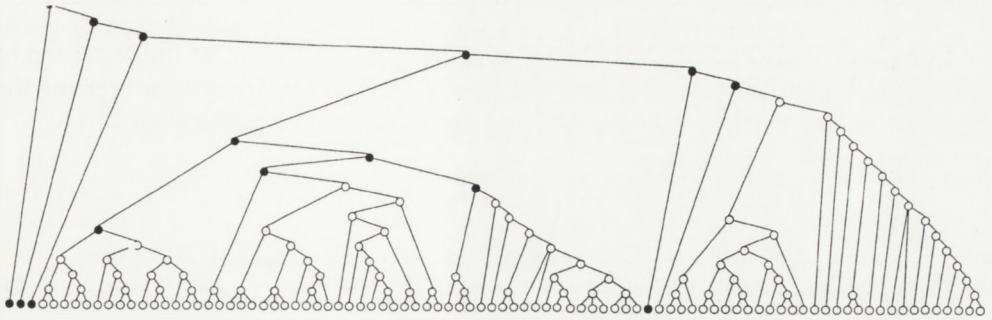

Fig. 4: Dichotomous outline of a determination key (VERHOEFF 1916) for the genus *Craspedosoma*. Black points: part of the key, not based on heterodactyl characteristics. White points: part of the key, based on heterodactyl characteristics.

In faunistic studies, BIGLER (1913) and LOHMANDER (1925) associated the inspected *Craspedosoma* specimens with variations of Verhoeff´s system and interpreted the findings concerning zoogeography. ATTEMS (1929), SCHUBART (1934), BROLEMANN (1935), DEMANGE (1981) and TADLER (1989) adopted parts of Verhoeff´s determination keys and drawings, thus using heterodactylous taxa. Brolemann and Schubart partly repeated the geographic-climatic interpretations of heterodactyly. In this connection, Brolemann proclaimed evidence of an enviromental effect regarding the morphology of Diplopoda. DUNGER & VOIGTLÄNDER (1990) considered the possibility that the heterodactylous morpho-ecological races may offer an explanation for the pioneer behaviour of *C. rawlinsii* regarding studies of millipede succession. This question can clearly be answered: with regard to the genus *Craspedosoma* there do not exist any ecological races which are determinable by means of podosternite morphology.

Extreme variability or local polymorphism regarding *Craspedosoma* have never been confirmed by studies of authors since Verhoeff, Attems and Bigler. RICHTER (1967), TADLER (1989), DUNGER & VOIGTLÄNDER (1990) and SPELDA (1991) investigated extensive series. None of these authors makes any comment in respect of remarkable differences regarding the lengths of podosternite processes. On the contrary, Richter as well as Dunger & Voigtländer accentuated the uniformity of the compared podosternites. They classified all examined specimens as uniformally macrodactylous. Verhoeff is the only author who has described brachydactylous forms. The restudy of Verhoeff´s type material (for example *C. alemannicum brevidentatum* var. *abbreviatissimum* VERHOEFF, 1916) shows that brachydactylous podosternites are occasional, and extreme, projections which result from the production of permanent mounts without the use of standardisation of perspective.

The most astonishing aspect of the result of this study is its simplicity! Obviously, the complex spatial structure of millipede gonopods is underestimated and until now, by no means, methodically solved. A description of gonopods should expressly include a spatial analysis of the structures and the standardisation of the perspectives used in order to avoid false conclusions. An explicit prerequisite for a valid description should be that the used characteristics are independent of perspective.

ACKNOWLEDGMENTS

I am grateful to Dr. Göran Andersson and Dr. Jolanta Wytwer for the provision of *Craspedosoma* material from Sweden and Poland, and to Dr. Hubert Fechter for the provision of type material from the Zoologische Staatssammlung München.

REFERENCES

ATTEMS C. 1929. Die Myriapodenfauna von Albanien und Jugoslavien. Zool. Jahrb. Syst. 56: 269–356.

BIGLER W. 1912. *Xylophageuma zschokkei* n. sp. und einige neue Craspedosomiden. Zool. Anz. 39, 23/24: 693–698.

BIGLER W. 1913. Die Diplopoden von Basel und Umgebung. Rev. suisse Zool. 21: 675–793.

BRÖLEMANN H. W. 1935. Myriapodes Diplopodes. In: Fauna de France 29. Lechevalier, Paris, 283 pp.

DEMANGE J. M. 1981. Les Mille-Pattes. Boubeé. Paris, 288 pp..

DUNGER W., VOIGTLÄNDER K. 1990. Succession of Myriapoda in primary colonization of reclaimed land. In: MINELLI A. (ed.), Proceedings of the 7th International Congress of Myriapodology: 219–227. E. J. Brill, Leiden, 480 pp.

LOHMANDER H. 1925. Sveriges diplopoder. Göteborgs Kungl. Vetenskaps- och Vitterhets-Samhälles Handlingar, 4. Följden, 30(2): 1–115.

RICHTER H. 1967. Zur Diplopodenfauna des Osterzgebirges. Faunistisch-ökologische und morphologisch-biologische Untersuchungen in Blockhaldebiotopen. Abh. Ber. Naturkundemus. Görlitz 42, 4: 1–62.

SCHUBART O. 1934. Tausendfüßler oder Myriapoda I: Diplopoda. In: DAHL F. (ed.), Die Tierwelt Deutschlands und der angrenzenden Meeresteile. 28. Teil. Gustav Fischer, Jena, 318 pp.

SCHUBART O. 1963. Progoneata, Opisthogoneata. In: BROHMER, EHRMANN & ULMER (eds), Die Tierwelt Mitteleuropas, Bd. II, Leipzig, 51 pp.

SPELDA J. 1991. Zur Faunistik und Systematik der Tausendfüssler (Myriapoda) Südwestdeutschlands. Jahresb. Ges. Natur. Württemberg 146: 211–232.

TADLER A. 1989. Funktionsanatomie der Kopulationsorgane und Paarungsverhalten der Diplopoda-Chordeumatida *Craspedosoma transsilvanicum*, *Haploporatia eremita* und *Mastigona bosniense*. Diss. Univ. Wien, 56 pp.

VERHOEFF K. W. 1910 a. 31.–35. Aufs.: Beiträge zur Kenntnis der Glomeriden, Juliden, Ascospermophoren und Lysiopetaliden, sowie zur Fauna Siliziens. Untersuchungen über Art- und Gruppensystematik, Morphologie, nachembryonale Entwicklung, Biologie und Geographie. Nova Acta Leopoldina, Halle 92: 139–448.

VERHOEFF K. W. 1910 b. 37. Aufs.: Deutsche Craspedosomiden. Sitz.-Ber. Naturforsch. Frd. Berlin 1910: 19–62

VERHOEFF K. W. 1912 a. Zur Kenntnis deutscher und norwegischer Craspedosomen. Zool. Anz. 39: 499–511.

VERHOEFF K. W. 1912 b. Zur Kenntnis deutscher Craspedosomen. Sitz.-Ber. Ges. Naturforsch. Frd. Berlin 1912: 67–90.

VERHOEFF K. W. 1914. Zur Kenntnis süddeutscher Craspedosomen. Zool. Anz. 44: 336–361.

VERHOEFF K. W. 1915 a. Polymorphismus bei Chilognathen und seine Abhängigkeit von äußeren Einflüssen. Zool. Anz. 45: 378–382, 385–390.

VERHOEFF K. W. 1915 b. Die Kreise des alemannischen Gaues, der helvetische Rheintaldurchbruch und zwei neue deutsche Chordeumiden. Zool. Anz. 45: 398–419.

VERHOEFF K. W. 1916. Beiträge zur Kenntnis der Gattungen *Macheiriophoron* und *Craspedosoma*. Zool. Jahrb. 39: 273–416.

VERHOEFF K. W. 1917. Zur Kenntnis der Zoogeographie Deutschlands zugleich über Diplopoden, namentlich Mitteldeutschlands und für die biologische Beurteilung der Eiszeiten. Nova Acta Leopoldina, Halle 103, 1: 1–156.

VERHOEFF K. W. 1939. Über Craspedosomen aus Baden und die Variationen des *Craspedosoma germanicum* Verh. Entstehung des Polymorphismus. Zool. Anz. 128: 257–270.