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"Peripatus" — an Approach towards a Modern Monograph

by

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Abstract: What is a modern monograph? The problem is tackled on the basis of a discussion of the complicated taxonomy of Onychophora. At first glance the phylum presents a very uniform phenotype, which led to the popular taxonomic use of the generic name *"Peripatus"* for all representatives of the group.

The first description of an onychophoran, as an "aberrant mollusc", was published in 1826 by GUILDING: To date, about 100 species have been described, and Australian colleagues (BRISCOE & TAIT, in prep.), using allozyme electrophoretic techniques, have discovered large numbers of genetically isolated populations of as yet undescribed Peripatopsidae.

The taxonomic history is reviewed in brief. Following the principles of SIMPSON, MAYR, HENNIG and others, selected taxonomic characters are discussed and evaluated. Questions arise such as: how can the pioneer classification (sensu SEDGWICK, POCOCK, and BOUVIER) be improved? New approaches towards a modern monographic account are considered, including the use of SEM and TEM and biochemical methods. The study of ecology and geographical distribution give additional clues to onychophoran taxonomy.

> "Taxonomy is a combination of science and art. Its application to classification involves human contrivance and ingenuity. There is a leeway for personal taste, even foibles, but there are also canons that help to make classifications better, more meaningful, more useful to others" (SIMPSON 1961).

1. Introduction:

"Peripatus" — the most famous representative of the Onychophora ranks high among the "Living Fossils" and the "Missing Links", and inspires both the evolutionary biologist and the layman. Few invertebrates are as anxiously hunted for but as rarely encountered as are the Onychophora. But if a zoologist is fortunate enough to obtain a few specimens the attempt to put the right name on his precious finding will turn out to be a most frustrating experience. One reason for this is that the taxonomic literature is defective and incomplete.

Some years ago the only available source was BOUVIERs impressive, but longwinded French monograph (1905, 1907), after which came a torrent of polyglot and scattered papers of highly different standards (e.g. BRUES 1935, ARNETT 1961, FROEHLICH 1968). A first attempt towards a modern taxonomic revision of the Neotropical Peripatidae was successfully undertaken by PECK (1975) at generic level. A decade later RUHBERG (1985) published a revision of the taxonomy, ecology, chorology and of phylogenetic aspects of the Peripatopsidae. But this approach towards a comprehensive monograph of the Southern Hemisphere family left gaps and unanswered questions. Some reasons for its shortcomings were a lack of field experience and the imperfectly preserved museum materials used.

In order to improve onychophoran taxonomy, and to arrive at a well grounded biospecies-concept the authoress has tried to obtain additional data from histology, ultrastructure, histochemistry,

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physiology and from other sources, in cooperation with specialists. These investigations were mainly based on personal cultures of Onychophora.

The future will show whether the gaps in RUHBERGs revisionary approach on the Peripatopsidae can be filled. At the moment there is a good chance, since most promising new peripatopsid material is available from Australia, including sexual head organs which are new to science (RUHBERG et al. 1988, TAIT & BRISCOE 1990). Above all, a thorough revision of the remaining family, the Peripatidae, on species level, is urgently needed (RUHBERG, in prep.). However, this is an even larger family than the Peripatopsidae, comprising 2/3 of all recognized onychophoran species.

The present account seeks to clarify the situation in onychophoran taxonomy and to point out some of the main problems. The results will hopefully lead to stability and uniformity in future discussions of the systematics of this archaic group of animals.

2. *"Peripatus"* — an Approach towards a Modern Monograph:

The topic under discussion imposes ad hoc two questions. First: Why do people refer to *"Peripatus"* in quotation marks instead of "The Onychophora", and second : what is a monograph, especially a modern one? Both questions will be considered carefully. This means that some aspects of onychophoran taxonomic history should be recalled, and, based on this, a possible improvement of preliminary classifications will be discussed. New approaches towards achieving a modern monographic account will be presented, namely the use of SEM and TEM in onychophoran systematics, and biochemical methods. A third question is: what are the recent problems in onychophoran systematics, and why is taxonomic research needed so urgently?

2.1. The current Situation:

The most serious problem with this group is that at least 40 % of the newer publications on various aspects of onychophoran research are based on incorrect determinations. Unfortunately, in spite of this erroneous taxonomy, far-reaching conclusions have been drawn. For example: the name *Peripatus/Peripatopsis capensis* frequently stands for all South African species, and *Peripatus/Euperipatoides leuckarti(i)* is in use for all Australian taxa, regardless of their mode of reproduction (oviparous, ovoviviparous or viviparous). However, the main concern is with the genus name *Peripatus,* wich is thoughtlessly used as a synonym for the entire phylum. Hence a basis claim is that proper species identification is the main prerequisite for sound discussions of onychophoran research.

2.2. A Monographic Account — classical and modern:

Taxonomy is the backbone of all biological sciences (MAYR 1965). The path leading from taxonomy towards a thorough classification is perfectly described in SIMPSONs "Principles of Animal Taxonomy" (1961) and in MAYRs "Principles of Systematic Zoology" (1969). According to both authors there are three different stages of "maturation" in classification: In α-taxonomy species are described, in β-taxonomy their relationships are worked out, and in γ-taxonomy evolutionary aspects are considered.

2.2.1. A classical Monograph:

A classical monograph is a complete systematic treatment which includes all levels from α to γ taxonomy. It involves a full treatment of all taxa and demands a profound knowlege of the comparative anatomy, the biology and the geographical distribution of the group under consideration. For the evolutionist such a monographic account is the most rewarding type of taxonomic publica-

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tion (MAYR 1969). An important question in its approach is always: what is ancestral (= plesiomorphic), and what is derived (= apomorphic) ? (HENNIG 1950).

2.2.2. A modern Monograph:

A modern monograph is even more comprehensive than its classical ancestor. It comprises, in addition, ultrastructural and molecular data; the latter investigations requiring large numbers of living animals of both sexes and all ages, from all ecotypes, and in a range of physiological states, to permit the establishment of baseline variabilities (MESIBOV, in litt.).

3. History of Onychophoran Taxonomy:

The first describtion of an onychophoran as an "aberrant mollusc" was published in 1826 by Reverend L. GUILDING, a shortened version of which is given here:

GUILDING (1826), Mollusca Caribbaeana:

Subregnum Mollusca, Classis Polypoda GUILD., Genus *Peripatus*

Character Genericus: Corpus molle .. contractile .. corrugatum. — Tentacula duo longa .. os subtus .. labiis papillosis .. Anus posticus .. Orificium generationis (?) distinctum, posticum, infra. — Ambulacra utrinque 33, paribus alternis extenduntur. Ungues ...

Peripatus juliformis: P. atro-fuscus, annulosè flavido maculatus .. corpore toto spinuloso-papilloso; lineâ dorsali atrâ. - Long. corp. 3 un. Lat. 3 lin. — habitat in sylvis antiquis Sti. Vincentii saepe retrogradus. — Atteritus liquorum glutinosum ob ore respuit. — Inter plantas .. ad radices montis .. unicum exemplum attonitus fort detexi.

Its is clearly evident that GUILDING had already confused the characters of lower and higher categories: there is no sharp distinction between specific and generic criteria. Thus, unfortunately, the very first description of an onychophoran already laid the cornerstone for later taxonomic confusion in this group.

During the following decades new specimens were found worldwide, and their anatomy was explored step by step. In 1853 GRUBE named the entire group "Onychophora", that implies "clawbearers". Since then the appendages have always played the major role in onychophoran taxonomy (Fig. 1), and counting their legs has ever since been, and is still important in attempting to put the right name on an animal.

In the second half of the 19th century the increasing number of specimens being described required a system of classification. In 1888 SEDGWICK began by defining species characters. But *Peripatus* as the only genus was still retained. POCOCK, six years later, was the first who dared to split this famous genus. His proposal distinguished 3 genera by the following characters and names (abbreviated version):

POCOCK (1894): Malacopoda or Prototracheata

A. Legs furnished with 4 spinous pads; generative aperture situated between legs of penultimate pair. Neotropical region and possibly Sumatra .... *Peripatus* GUILDING

B. Legs furnished with only 3 spinous pads: generative aperture behind penultimate pair of legs.

  A_1. Generative aperture between the legs of the last pair and well in advance of the anus. Australia and New Zealand .... *Peripatoides* n. gen.

  B_1. Generative aperture behind the last pair of fully developed legs and close to the anus at the hinder end of the body. South Africa .... *Peripatopsis* n. gen.

POCOCKs first approach towards a classification within this group was one of the best, and is still valid.

The latter part of the 19th century turned out to be the "Golden Age" of Onychophorology. New taxa were described from four continents. But, unfortunately, the result was a morass of scattered and multilingual papers of highly different standards. This formed the cradle for a heterogen-

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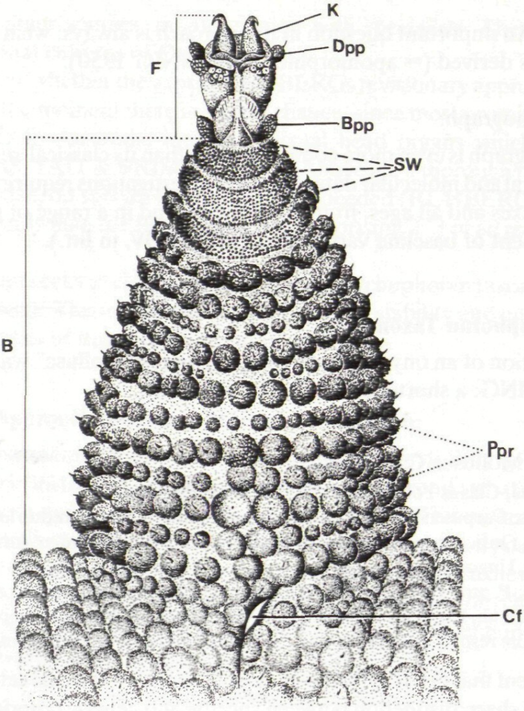

Fig. 1: *Peripatopsis capensis* GRUBE, 1866: Leg; ventral view. Modified after BALFOUR. – **B** limb, Bpp basal papilla, **Cf** coxal groove, **Dpp** distal papilla, **F** Foot, **K** claw, **Ppr** rings of papillae, **SW** spinous pads. x 30.

ous taxonomy, lacking any standardization. Modern onychophoran systematics still suffers from these "teething troubles".

The first family name Peripatidae was introduced by EVANS in 1901, who also erected 4 subfamilies in which he placed 7 genera.

EVANS (1901): Class Onychophora
Family Peripatidae
- Sub-Family Peripatinae
  - Genus 1. *Eoperipatus* (gen. nov.)
  - Genus 2. *Peripatus* (GUILDING)
  - Genus 3. *Mesoperipatus* (gen. nov.)
- Sub-Family Peripatoidinae
  - Genus 4. *Peripatoides* (POCOCK)
  - Genus 5. *Opisthopatus* (PURCELL)
- Sub-Family Peripatopsinae
  - Genus 6. *Peripatopsis* (POCOCK)
- Sub-Family Paraperipatinae
  - Genus 7. *Paraperipatus* (WILLEY)

But most honour is due to BOUVIER who wrote the first, and so far the only, complete monograph on the phylum onychophora. In two volumes (1905, 1907) he summarized meticulously all available biological information. He synonymized, and also added new taxa. His monograph comprises 50 species, included in 7 genera and 2 families, the distribution of which is shown in Fig. 2. But even BOUVIERs famous monograph does not provide a definitive taxonomy for the Onychophora. His books make difficult reading and, unfortunately, contain several serious typographical

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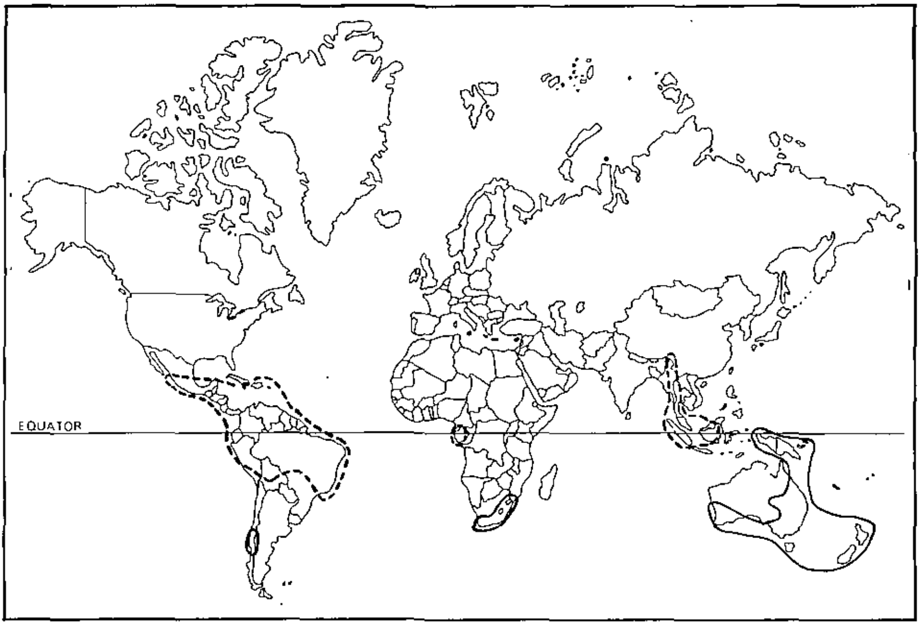

Fig. 2: Current distribution of the Onychophora. — Peripatidae (broken line) and Peripatopsidae (continuous line). Modified after WALKER. Mercator projection.

errors as far as synonymy is concerned: for example the name *Ooperipatus* (Australian oviparous genus) is in many places confused with the name *Eoperipatus* which was given by EVANS (1901) to a totally distinct genus (viviparous form from Malaysia); *Ooperipatus insignis* is on one plate called *Eoperipatus insignis*, in another place *Eoperipatus leuckarti*, whereas SAENGERs original type *Peripatoides leuckarti* is designated *Ooperipatus leuckarti* (BOUVIER 1905: 17). DENDY (1906: 177) critized BOUVIER sharply: "BOUVIER appears .. to be .. undecided as to the nomenclature of the Australian forms ... Judging from these inconsistencies I venture to hope that the author has not yet irrevocable made on his mind to adopt up erroneous nomenclature, and that he may still be willing to reconsider the question in the systematic portion of his monograph".

4. Difficulties in Onychophoran Taxonomy:

Why is onychophoran taxonomy so complicated? Some of the reasons are outlined below. Onychophora are: rare and elusive, inconvenient to collect, hard to culture. Museum material is normally old and poor, type material is often lost or mislabelled. Tracing the literature is frustrating. There is no taxonomic standardization. Within the group there is remarkably low morphological diversity, reproductive biology is still little understood. The distinguishing characters are distributed in a harpharzard pattern among the different taxa (SEDGWICK 1908).

The lack of complex and stable specific characters has perhaps been the most problematic aspect in this group, and has caused considerable taxonomic difficulties. And, of course, museum material, even at its best, will only answer a "Morphospecies-concept". Onychophora are obviously not like *Drosophila*, which could be bred pairwise in a bottle to answer a "Biospecies-concept". It is thus clearly evident that all taxonomic criteria used need careful character-weighting and evaluation sensu HENNIG (1950).

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4.1. An Attempt to overcome these Difficulties:

In 1975 RUHBERG took up the study of Onychophora. Her goal was to write a thorough monographic account covering the systematics, the ecology, behaviour, chorology and phylogenetic aspects of this archaic group of animals. In order to establish a well-founded biological species concept the authoress tried to obtain additional data from histology, ultastructure, histochemistry, physiology and other sources. As a result, a classification of one of the two existing families was published (RUHBERG 1985). In her thesis RUHBERG has attempted to lay a cornerstone for character evalution in onychophoran systematics; all morphological criteria available are discussed there (: 32 - 74).

5. Morphological Criteria in Onychophoran Taxonomy:

Among the main morphological criteria are: number of legs (within certain limits, see discussions in READ 1985, RUHBERG 1985), structural attributes of the foot (Fig. 1) such as the number of spinous pads, the position of the nephropore on the 4th and 5th pair of legs and the number, and arrangement of the foot papillae. In addition there are: the structure and distribution of the dorsal skin papillae (Fig. 3 a - d) and the male crural tubercles (Fig. 4).

RUHBERG (1985) is convinced that the latter characters rank with the best morphological criteria in onychophoran systematics, but only in the hands of an experienced taxonomist. The number of crural tubercles reaches its maximum in *Peripatus sedgwicki* which has 10 pairs (Fig. 5.). In addition there is considerable anatomical variation among female Peripatopsidae (RUHBERG 1985). By contrast the internal structure of the Neotropical Peripatidae of the same sex seems to be rather uniform (READ 1985, 1988).

These were some of the characters used in traditional descriptions, and the question now arises as to how this old classification scheme can be improved. What are the "New Characters" that help to make taxonomy of Onychophora better? New approaches towards a modern monographic account are therefore considered. These are the application of SEM and TEM and a biochemical method.

6. New Systematic Characters:

According to TYLER (1979), Electron Microscopy is especially useful in the systematics of organisms for which only a few good morphometric characters have so far been known before. But Electron Microscopy is by no means accepted as a valid tool in taxonomy. Its application requires, like the traditional morphology, careful evalution of the ultrastructural characters under consideration. Most helpful is in this case the "Homology Theorem" defined by RIEGER & TYLER (1979).

Ultrastructural research was introduced into onychophoran systematics in 1965 by LAVALLARD, and later used by other research groups (including STORCH & RUHBERG 1976 - 1990). Based on their results a few selected characters are shown here that might lead to an improvement in onychophoran systematics and phylogenetical assessment. These characters are: the dermal papillae (SEM-investigations), the male head organs (SEM), heart muscle cells (TEM) and spermatozoon structure (TEM).

6.1. The Application of SEM:

6.1.1. The Application of SEM. Dermal Papillae:

The onychophoran integument is adorned with rows of papillae. The structure and arrangement of these on the dorsal body surface was already recognized by BOUVIER (1905, 1907) as an important specific character. In his monograph he presented painstaking light microscopical illus-

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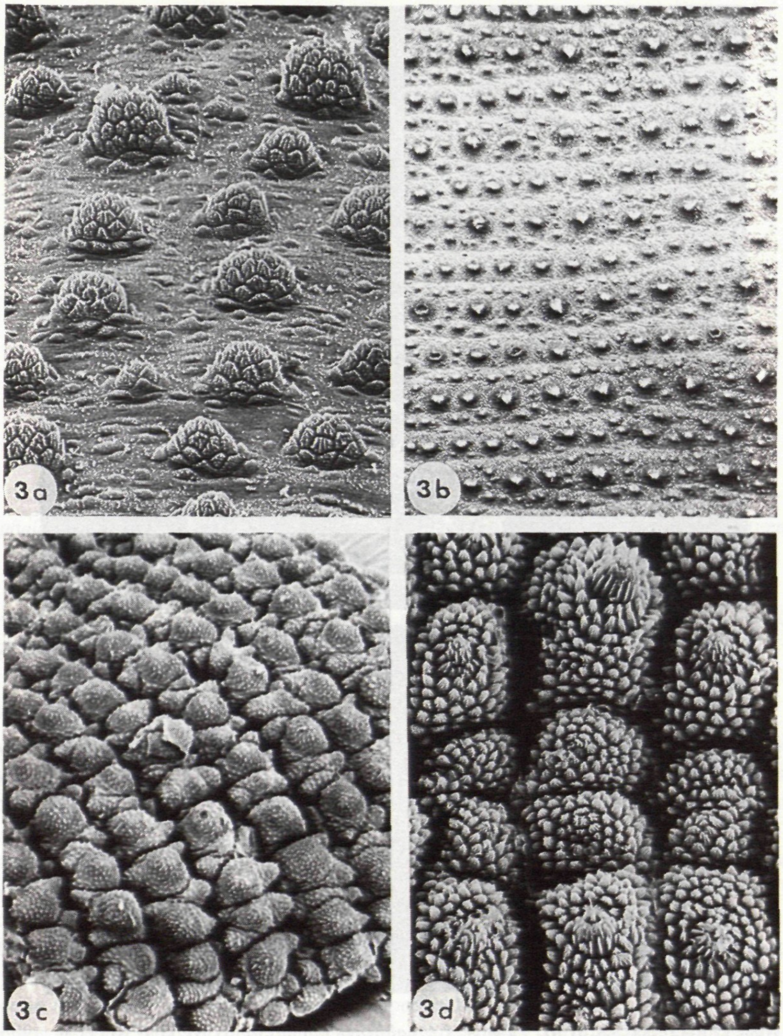

Fig. 3: Structure and distribution of the dorsal skin papillae. SEM. 3 a - c: Peripatopsidae, 3 d: Peripatidae. - 3a: *Opisthopatus roseus* LAWRENCE, 1947, x 108. 3b: *Paraperipatus papuensis* (SEDGWICK, 1909), x 50. 3c: *Peripatoides indigo* RUHBERG, 1985, x 50. 3d: spec. indet., x 108.

trations on 10 plates (1905: pl. 4 - 13). But the importance of these taxonomic characters is extremely difficult to assess from a standard light microscope. Thus, as suggested by PECK (1975), SEM was applied to the systematics of the Neotropical Peripatidae by READ (1985, 1988), and to that of the Peripatopsidae by RUHBERG (1985). SEM-methods for Onychophora are outlined in detail by WALKER (1986).

The SEM-technique gave splendid results in both families. It revealed the full detail of the most complex onychophoran body surface (Fig. 3, 6 - 11). The dorsal skin papillae are of two kinds: large and small. The larger ones are tipped with a seta, which implies a sensory function. They are

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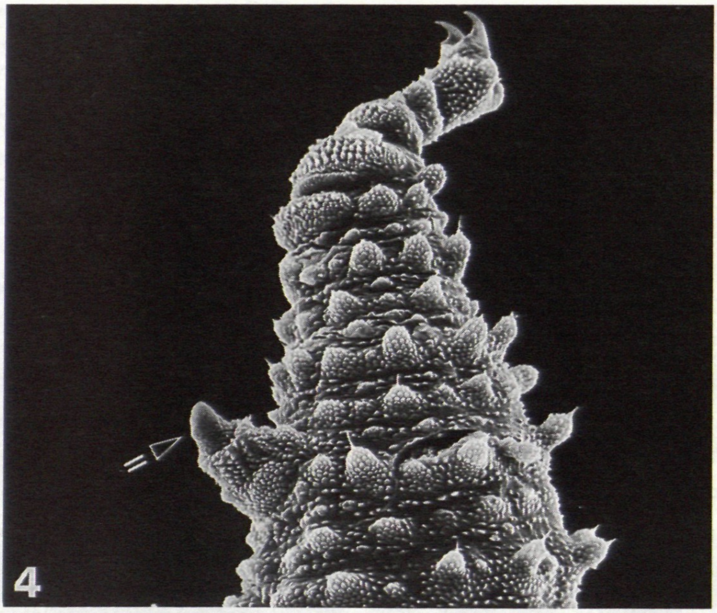

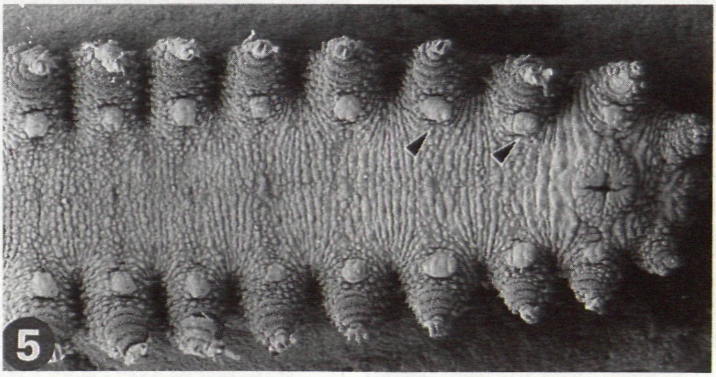

Figs 4 - 5: Male crural tubercles. SEM. – Fig. 4: *Cephalofovea tomahmontis* RUHBERG et al., 1988: First leg; lateral view. Crural papilla (arrow head) x 80. – Fig. 5: *Peripatus sedgwicki* BOUVIER, 1899: Posterior end of male body, ventral view. Distinct crural papillae (arrow heads). Genital pore between penultimate pair of legs. x 50.

called main or primary papillae. The smaller ones, called accessory or secondary papillae, lack the apical sensory bristle. In all species examined a clear distinction between primary and secondary papillae can be seen. Both types of papillae are covered with scales (Fig. 6). Their shape is highly characteristic (Fig. 3 a - d).

In the Southern Continent family Peripatosidae all dermal papillae are one-tiered. In contrast the Neotropical Peripatidae can be separated at first glance by the shape of their main papillae which are two-tiered (Fig. 7, 8).

In addition, the number of scale ranks in the apical part of the peripatid primary papilla distinctly separates genera: *Epiperipatus* has 2 - 3 scale ranks in its apex, and *Peripatus* has 4 or more

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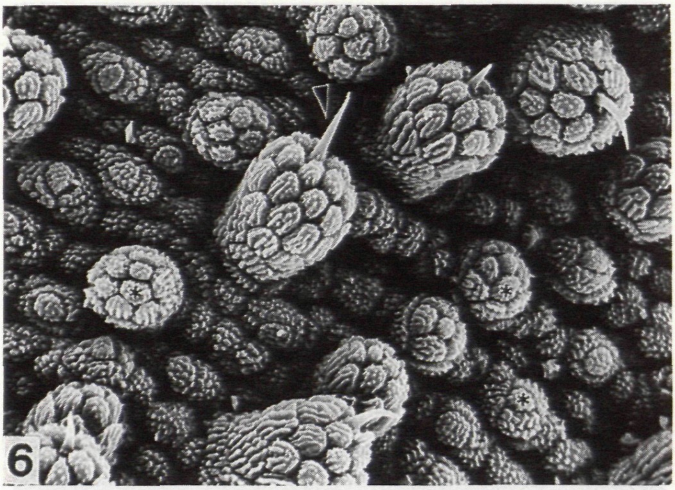

Fig. 6: *Cephalofovea tomahmontis* RUHBERG et al., 1988: dorsal skin of young male. SEM. Primary papilla (arrow head), secondary papillae (asters). x 530.

(READ 1985). The pattern and the distribution of the dorsal dermal papillae are also very characteristic (RUHBERG 1985, Figs 62 - 69).

6.1.2. The Application of SEM. Head Organs:

Recently discovered male sexual head organs (TAYLOR, in litt. 1985, RUHBERG et al. 1988, TAIT & BRISCOE 1990) are also under SEM investigation. These organs lie on the dorsal head-surface of mature males collected from Eastern Australia. In some species they are highly complex structures; varying from a cluster of modified dermal papillae to deep cavities. These pits may show different elaborate structures; e.g. sclerotized claw-like forms, spines or even stylets. Shape and size of the male head organ vary with age and stage of maturity of the animal. These organs are most prominent and exposed in the breeding season (RUHBERG et. al. 1988). It is speculated that they are used for sperm transfer. In part this assumption has been confirmed as sperm was found in two different head organs (TAIT & BRISCOE 1990). However, how copulation itself takes place in the newly discovered Australien species remains doubtful. But these peculiar head morphologies provide new and complex taxonomic characters for Onychophora (Figs 9, 10, 11).

6.1.3. The Application of SEM. Results:

In contrast to standard Light Microscopical results SEM reveals full details of the onychophoran body surface (WALKER 1986). A: The shape and arrangement ot the two types of papillae (primary and secondary) varies intraspecifically and is thus an important taxonomic feature (READ 1985, RUHBERG 1985). B: The dorsal head region in males of a few newly discovered and yet undescribed Australian species displays highly elaborate structures. These complex sexual head organs represent distinct new criteria. Moreover, they fulfil one of HENNIGs main criteria, the "Kriterium der Kompliziertheit der Merkmale" (HENNIG 1950). These new and elaborate structures are of considerable significance in phylogenetic studies. They occur in both oviparous and viviparous species. They demonstrate that male Australian Peripatopsidae have evolved most complex secondary sexual structures, at least as diverse as the reproductive strategies of their female mates (TAIT, in litt).

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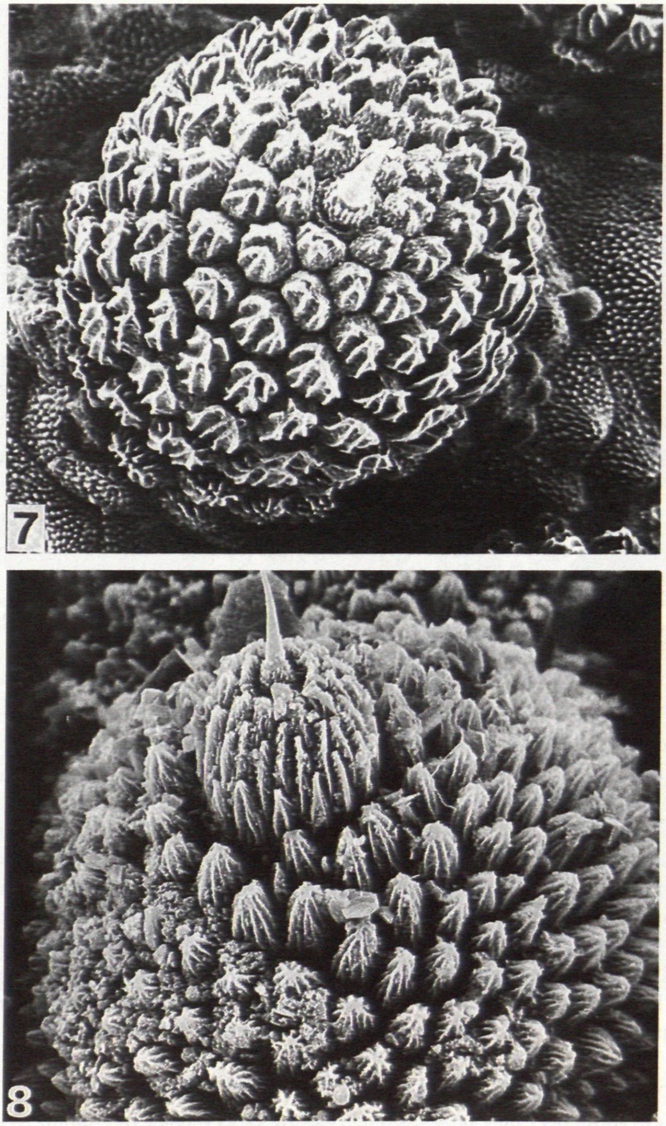

Figs 7 - 8: Characteristic shape of primary papillae in different representatives of the two onychophoran families. SEM. Fig. 7: *Opisthopatus cinctipes* PURCELL, 1899 (Peripatopsidae): primary papillae one-tiered. x 1,000. – Fig. 8: *Macroperipatus ohausi* (BOUVIER, 1900) (Peripatidae): primary papilla two-tiered. x 1,000.

Both these results show that a sound modern taxonomic revision in the Onychophora demands the use of Scanning Electron Microscopy. The application of SEM clearly gives better results than the pioneer standard Light Microscopical methods. The advantage of this technique, in contrast to TEM, is that it is not dependent on live material, and that it can be carried out even with 100-year-old museum material.

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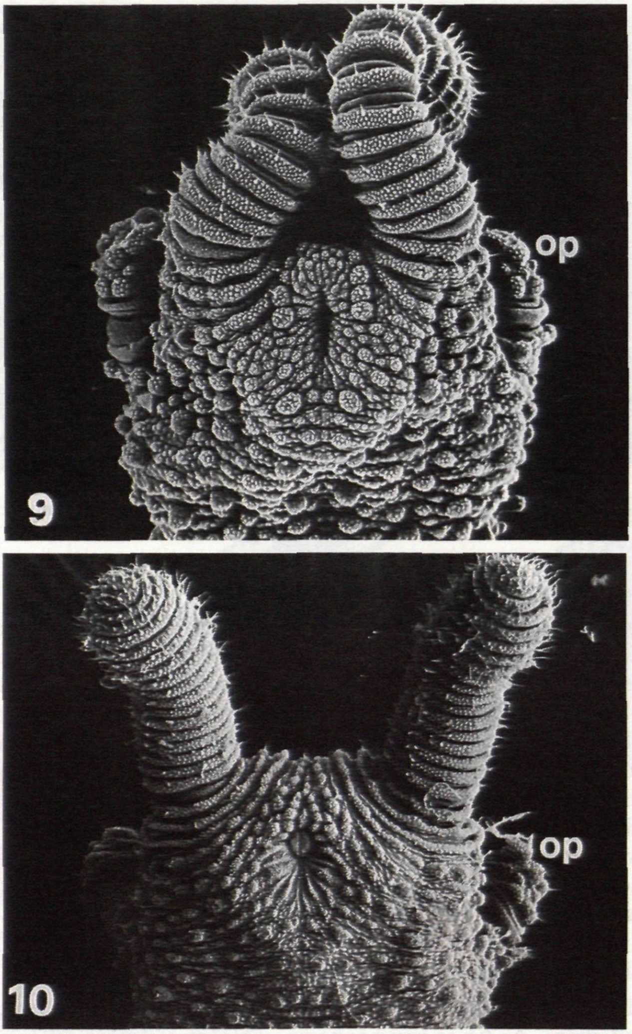

Figs 9 - 10: Male head organs in newly discovered Australian Peripatopsidae. SEM. – Fig. 9: *Cephalofovea tomahmontis* RUHBERG et al., 1988: dorsal cephalic pit in a young male. x 80. – Fig. 10: Yet undescribed species from the Tinderry Mts., NSW: dorsal head structure in a young male. x 195.

6.2. The Application of TEM:

Can Transmission Electron Microscopy be profitably applied to onychophoran systematics? Does TEM give as good taxonomic results as SEM? To answer these questions captive animals of RUHBERGs own cultures were investigated in cooperation with other scientists (e.g. STORCH & RUHBERG 1976-1990, NYLUND et al. 1988). Based on their results two examples are presented here to underline (A) taxonomic and (B) phylogenetic considerations. These examples are: A spermatozoa, and B heart muscle cells.

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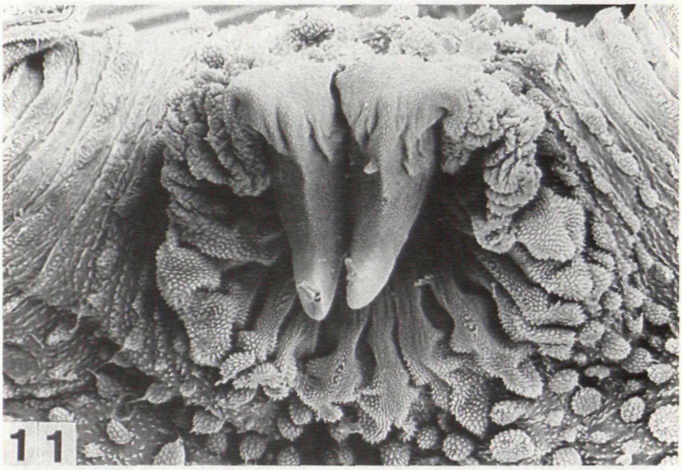

Fig. 11: Same species as in Fig. 10: dorsal head structure in a mature male with hardened hooks. x 195.

6.2.1. The Application of TEM. Spermatozoa:

The ripe onychophoran spermatozoon is approximately 200 - 300 µm long and filiform (STORCH & RUHBERG 1983). Its head is long and straight and may occupy more than 1/3 of its whole length. It is sculptured by helical folds. The middle piece is composed of a solid mitochondrial mass. The tail is long and grooved (Fig. 12). The general shape of the spermatozoon, the nucleus, midpiece and tail are obviously very similar in different onychophoran taxa, in viviparous as well as in oviparous species. Slight interspecific differences are restricted to length and diameter of the nucleus, to the number of mitochondria forming the midpiece, and to the number of peripheral microtubules in the tail (STORCH & RUHBERG 1983).

But there is one obvious character that clearly separates the two families: the helical ridges sculpturing the head of the spermatozoon seem to be much more prominent in the Peripatidae than in the Peripatopsidae (Figs 12 - 13).

6.2.2. The Application of TEM. Heart Muscle Cells:

Phylogenetic inquiries are most important on the β- and γ-level of taxonomy. TEM helps to elucidate these questions. As far as onychophoran phylogenetic systematics is concerned, NYLUND et al. recently (1988) investigated the heart ultrastructure of four species, namely two representatives of each family. The question was: which of two onychophoran families is the more ancestral? Previous opinions had differed: while PECK (1982) regarded the Peripatidae as the more advanced family, RUHBERG (1985) favoured the opposite opinion.

The results of NYLUND et al. give strong support to the latter view. Their study indicates important differences as far as the myocardial cells are concerned: In the peripatid species examined (*Epiperipatus biolleyi* (BOUVIER 1902) and *Epiperipatus* sp. from Costa Rica), the Z-material forms attachment plaques and dense bodies and the SR (= sarcoplasmic reticulum) is poorly developed and forms sub-sarcolemmal cisternae. The mitochondria are found more or less evenly dispersed in the myocardial cells. There can be no doubt that these findings indicate a primitive condition. In the peripatopsid species examined (*Occiperipatoides gilesi* from W.-Australia, and *Peripatopsis moseleyi* from South Africa), the Z-material of the heart muscle cells is arranged in bands, and the SR is well developed, while the mitochondria are located as sub-sarcolemmal aggregations.

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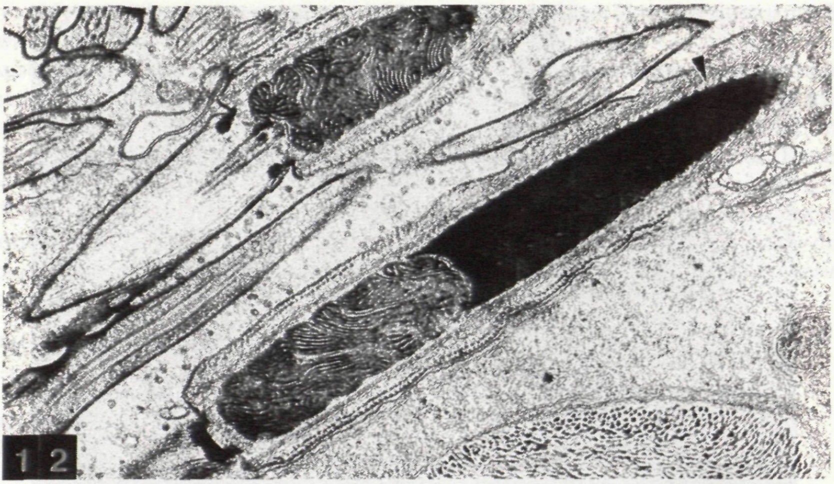

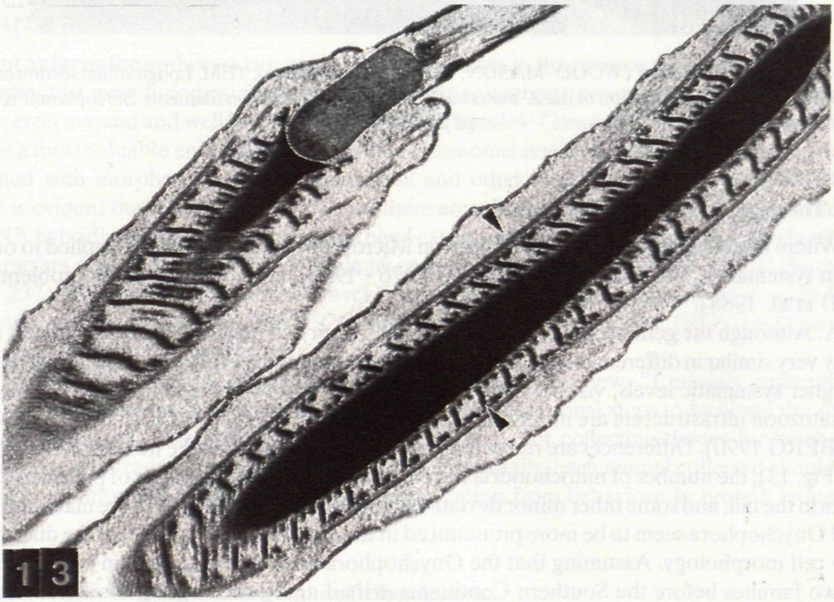

Figs 12 - 13: Spermatozoa of two representatives of the two families. TEM. – Fig. 12: *Opisthopatus cinctipes* PURCELL, 1899 (Peripatopsidae): middle piece of premature sperm cells. x 16,200. – Fig.13: *Peripatus sedgwicki* BOUVIER, 1899 (Peripatidae): Head and midpiece of advanced spermatids. x 16,200. Helical ridges (arrow heads).

Thus, the peripatopsid species show the more advanced organization (Fig. 14), and this study therefore underlines the assumption that the Peripatopsidae is the more derived family of the two (NYLUND et al. 1988).

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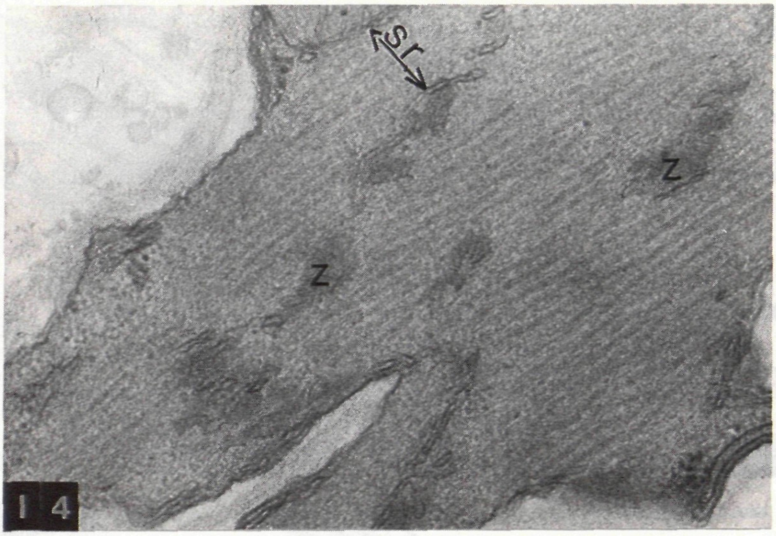

Fig. 14: *Peripatopsis moseleyi* (WOOD-MASON, 1879) (Peripatopsidae). TEM. Longitudinal section of a heart myofibre showing the organization of the Z-material (Z) and the thick and thin filaments. Sarcoplasmic reticulum (sr). x 13,500.

6.2.3. The Application of TEM. Results:

Within certain limits Transmission Electron Microscopy can be profitably applied to onychophoran systematics (STORCH & RUHBERG 1976 - 1990), and to phylogenetic problems (NYLUND et al. 1988).

A. Although the general shape of the sperm cells, their cell nucleus, midpiece and tail are obviously very similar in different onychophoran species, slight interspecific variation can be detected. On higher systematic levels, viz. between genera and the two recognized families, differences in spermatozoon ultrastructure are much more distinct (BACCETTI & DALLAI 1977, STORCH & RUHBERG 1990). Differences are restricted to length and diameter of the nucleus, to its helical ridges (Fig. 13), the number of mitochondria forming the midpiece, the number of peripheral microtubules in the tail, and some other minor deviations. Interspecific differences in the male genital system of Onychophora seem to be more pronounced in the anatomy and cytology of the ducts than in sperm cell morphology. Assuming that the Onychophora are a very old phylum which separated into two families before the Southern Continents drifted apart, their sperm ultrastructure is extremely conservative (STORCH & RUHBERG 1990).

B. Investigations of the heart muscle cells of representatives of both onychophoran families have clarified some hitherto controversial phylogenetic issues. TEM results (NYLUND et al. 1988) give strong evidence that the Peripatopsidae is the more advanced family of two. This example has shown that TEM research has significantly enriched the methods of phylogeny in a thorough monograpic approach on β- and γ-level.

6.3. Molecular Data in Onychophoran Systematics:

Molecular data focus attention upon mechanisms of evaluation at the level of gene structure and function. It is hoped that "these characters would give so-to-speak a scuba-diving-equipment to study the submerged portion of the taxonomoc iceberg" (MAYR 1965). At the moment it is per-

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haps too early to decide whether or not our high hopes will be fulfilled. However, there is much work underway in this sector as far as onychophoran research is concerned.

Australian colleagues (BRISCOE & TAIT, in prep.), tried a new approach to onychophoran systematics: that of allozyme electrophoresis. Following extensive collections throughout Australia they have till now identified 50 yet undescribed species (TAIT & BRISCOE 1990); which are considered to be genetically different from the 11 currently recognized taxa from this area. These "new species" are defined primarily on the basis of their allozyme profiles, and it is believed by BRISCOE & TAIT that a certain amount of fixed gene difference is a clear indicator for specific status in Onychophora. At least some of the novel taxa from Eastern Australia are also morphologically distinct: these possess the enigmatic head structures which have been mentioned before while considering SEM approaches (Figs 9 - 11).

Onychophora, Number of recognized species:

Reference:	Number of species
GUILDING (1826)	1
BOUVIER (1905, 1907)	50
BRUES (1923)	80
KAESTNER (1960)	70
RUHBERG (1985)	100
TAIT & BRISCOE (in prep.)	± 150

But as far as the authoress can judge the relationships in the prospective "new species" which lack distinctive morphological features are not clear enough at present, and much remains to be done to erect a sound and well founded "Biochemical Species-Concept". However, electrophoretic data are a most valuable enrichment to a modern taxonomic revision, provided they are "prudently combined with morphological, biogeographical and other biological evidence" (MESIBOV in litt.). It is evident that biochemical data (and there are many more modern promising techniques; e.g. DNA hybridization, cytochrome c) also need careful evalution. MAYR states:" Single molecular characters are, of course, as susceptible to convergence as are the morphological characters" *(1982: 237). But particularly with the Onychophora there is another danger: these so-called* "Living Fossils" are rare and elusive. The IUCN-Red Data Book (WELLS et al. 1983) lists them as vulnerable and in danger of extinction.

DESSAUER (1969: 371) gives an interesting prospective view: "Certainly, museums will begin to accumulate banks of frozen tissues and will take additional steps to facilitate the work of molecular biologists. Field men will be taught techniques for collecting tissues for biochemical studies along with traditional museum procedures. Eventually, each animal collected should serve as a source of information at many levels of organization from behaviour to protein sequence".

7. Behaviour, Ecology and Geographical Distribution:

The most important goal of a sound classification is a maximum of information content which leads to predictive value. Preserved museum material by its very nature provides insufficient and limited information only. As a consequence, considerable emphasis must be placed on biological characteristics. Such non-morphological information derives from behaviour, ecology and other sources. On the other hand "specimens cannot be understood and properly classified unless they are treated as sample of natural populations" (MAYR 1969: 51). In addition, geographical patterns *are among the most useful resources for clarifying confused taxonomic views, and are a most helpful* test of systematic hypotheses. According to MAYR (1969) the superior taxonomist is mainly interested in two main geographical characters: (1) general biogeographic patterns for evalution of higher taxa, and (2) the allopatric-sympatric relationship as criterium for conspecific and/or nonconspecific populations. MAYR states: "The reason for the great taxonomic value of geographical

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distribution is evolution and monophyly. Just as every taxon is descended from a common ancestor, so is every colonisation across a barrier effected by a founder species. In other words, there is high probability that related species in an area are descendants of a common ancestor" (1969: 140 - 141). In addition, the knowledge of behaviour and population biology leads to assessments and characters of maximum value in evaluating biological species (WILSON 1969).

Table 1: Current situation in taxonomy of onychophoran genera.

Peripatidae EVANS, 1901	
Peripatus GUILDING, 1826	14 spp., 6 ssp.
Eoperipatus EVANS, 1901	3 spp.
Mesoperipatus EVANS, 1901	1 sp.
Oroperipatus COCKERELL, 1908	19 spp.
Epiperipatus CLARK, 1913	14 spp., 2 ssp.
Macroperipatus CLARK, 1913	7 spp., 1 ssp.
Plicatoperipatus CLARK, 1913	1 sp.
Typhloperipatus KEMP, 1913	1 sp.
Heteroperipatus ZILCH, 1954	1 sp.
Speleoperipatus PECK, 1975	1 sp.
Totals	10 gen., 62 spp., 9 ssp.
Peripatopsidae BOUVIER, 1904	
Peripatoides POCOCK, 1894	3 spp.
Peripatopsis POCOCK, 1894	7 + 3 spp.
Paraperipatus WILLEY, 1898	4 + 4 spp.
Opisthopatus PURCELL, 1899	2 spp.
Ooperipatus DENDY, 1901	1 sp.
Metaperipatus CLARK, 1913	1 + 1 spp.
Austroperipatus BAEHR, 1977	1 sp.
Euperipatoides RUHBERG, 1985	1 + 1 spp.
Mantonipatus RUHBERG, 1985	1 sp.
Occiperipatoides RUHBERG, 1985	2 spp.
Ooperipatellus RUHBERG, 1985	2 + 1 spp.
Paropisthopatus RUHBERG, 1985	2 spp.
Cephalofovea RUHBERG et al., 1988	1 + 1 spp.
Tasmanipatus RUHBERG et al., 1991	2 spp.
Totals	14 gen., 29 + 11 spp.

8. Conclusions:

A modern monographic revision must be a comprehensive treatise including all classical attributes sensu SIMPSON, MAYR and HENNING, and additional data derived from modern techniques. It must always aim to elucidate phylogeny. The detailed study of behaviour, ecology and geographical distribution will give additional important clues for taxonomy. All characters are principally of equal value if carefully evaluated.

It remains to be seen whether the key to sound onychophoran systematics is to be found either in chemotaxonomy, or in genetics, or other sources. But it should always be kept in mind that Onychophora are listed as "vulnerable" and in danger of extinction, and thus need protection (WELLS et al. 1983). Above all there is still great need of basic α-taxonomy in this archaic group of animals.

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