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## *Paradiphascon manningi* gen. n. sp. n., a New Water-Bear from South Africa, with the erecting of a new subfamily Diphasconinae (Tardigrada)

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**Abstract:** *Paradiphascon manningi* gen. n. sp. n., a new semiterrestrial eutardigrade from South Africa (Cape Province) is described. The new taxon is related to the *Diphascon* lineage (the family Hypsibiidae Pilato, 1969). Several characters, some examined with SEM, indicate its ancestral status among hypsibiids with annulated pharyngeal tube. A new subfamily Diphasconinae is proposed to accommodate the genera *Paradiphascon* gen. n., *Diphascon* Plate, 1889 and *Hebesuncus* Pilato, 1987. The systematic position of *Hebesuncus* is unclear and its placement in Diphasconinae subfam. n. is tentative. Phylogenetic relationships within the family Hypsibiidae are discussed.

**Keywords:** Tardigrada, *Paradiphascon manningi* gen. n. sp. n., South Africa, Diphasconinae subfam. n., taxonomy, phylogeny

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### Introduction

Past twenty years have brought radical changes in the systematics of eutardigrades that started with a new classification proposed by Pilato (1969a, 1969b). Since then, numerous descriptions of new forms (eg. Pilato 1971, 1982b, 1987b, Christenberry & Higgins 1979, Kristensen 1982a, 1982b, Pilato & Beasley 1987) and some other contributions (Pilato 1975, 1982a, 1987a, 1989, Schuster et al. 1980, Bertolani 1981, Maucci 1981, Greven 1982, Bertolani & Kristensen 1987) considerably improved the system and enhanced our knowledge about taxonomy and evolutionary trends within the Eutardigrada.

When studying South African tardigrades, I have encountered a peculiar form representing both a new species and new genus. Some aspects of its morphology throw new light on systematic arrangement within the family Hypsibiidae Pilato, 1969. In this paper I describe the form, discuss its systematic status and propose a new subfamily to accommodate the new genus and related taxa.

### Materials and Methods

The field sample of moss and soil was collected into a paper envelope. Tardigrades and their eggs were extracted by the method described by Dastych (1985). The specimens were mounted on microslides either in chloral gum (Faure's or Swan's medium), polyvinyl-lactophenol or glycerol and sealed with a varnish. Light microscope examinations, drawings and micrographs were carried out using phase and interference contrast.

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Specimens selected for SEM observations were transferred from water into hot Bouin's medium, dehydrated in graded ethanols, critical-point-dried, arranged on double sticky tape and coated with gold. Micrographs were made using the scanning electron microscope CamScan S4.

Abbreviations used in illustrations (Figs. 1–26) are as follow: cb= cuticular bar, da= dorsoanterior apophyse on mouth tube, dam=dorsoposterior apodeme on mouth tube, f= furca, g= granules on cuticular sculpture, las= lamella-like structures around the mouth opening, ls= lobe-like structures on head segment, lu= lunula, pa= pharyngeal apophyses, pn- pharyngeal needle, pt= pharyngeal tube, su= stylet support, t= dorsal thickenings on mouth tube, va= ventroanterior apophyse on mouth tube.

## Description of New Taxa

### *Paradiphascon* gen. n.

Diagnosis: Semiterrestrial eutardigrades belonging to the family Hypsibiidae Pilato, 1969. Head segment provided with three flat lobes in its frontal ("facial") part, i. e. a median and two lateral. Upper parts of lateral lobes shaped like a pair of roundish and flattened dome-tipped structures. Mouth opening surrounded by a flat ring of wrinkled cuticle, instead of the usual six peribuccal lobes. Buccopharyngeal apparatus of *Diphascon*-type, with a ring of lamella-like structures around upper edge of mouth cavity. Mouth tube without strengthening bar and terminated in its posterior part with a strikingly large and striated posteriodorsal apodeme (= "drop-like" structure: Pilato, 1987a). Pharyngeal tube relatively wide, conspicuously short and annulated. Claw system of *Hypsibius*-type, with formula "2121". The smooth and ovoid eggs are deposited into the shedded cuticle.

Type Species: *Paradiphascon manningi* sp. n.

Etymology: *Para* (= near, Gr.); *Diphascon* (etymology unclear). The latter term was coined by Plate (1989) for tardigrades with elongated pharyngeal tube.

Remarks: The *Diphascon*-type of buccopharyngeal apparatus and hypsibioid claw system place the new genus within the family Hypsibiidae and close to the genus *Diphascon* Plate, 1889. Recently the latter taxon has been split into four genera, i. e. *Hebesuncus*, *Diphascon*, *Mesocrista* and *Platicrista* (see Pilato 1987). Subsequently, within the genus *Diphascon* two subgenera were proposed based on presence (the subgenus *Diphascon*) or absence (the subgenus *Adropion*) of posteriodorsal apodeme on the mouth tube (= "drop-like" structure: op. cit.). Pilato placed *Mesocrista*, *Platicrista* and *Itaquascon* Barros, 1939 within the subfamily Itaquasconinae as sharing common origin and excluded from the subfamily the genera *Diphascon* and *Hebesuncus*, thus leaving their phylogenetic status open.

*Paradiphascon* gen. n. can be distinguished from the four genera by unique three lobes on the head segment, by a ring of lamella-like structures around its mouth opening, and by the following combination of other characters.

In the new genus the anterior apophyses of mouth tube are shaped as "semilunular hooks", similarly as in *Diphascon* and *Hebesuncus* (however, with some modification), and they are differently formed ("ridge-like": op. cit.) in *Mesocrista* and *Platicrista*. Within the eutardigrades, only the subgenus *Diphascon* and *Paradiphascon* gen. n. are equipped with a posteriodorsal apodeme on the mouth tube. The apodeme is, however, uniquely striated, strikingly large, and differently shaped in the new genus compared to that in *Diphascon*. The new genus shares a short pharyngeal tube with all the discussed taxa, with the exception of the genus *Diphascon* in which the tube is distinctly longer. However, the tube is decidedly thinner, shorter and indistinctly annulated in *Hebesuncus* compared to *Paradiphascon* gen. n. The presence of pharyngeal apophyses is common to the last two taxa (and *Diphascon*). Contrarily, in *Mesocrista* and

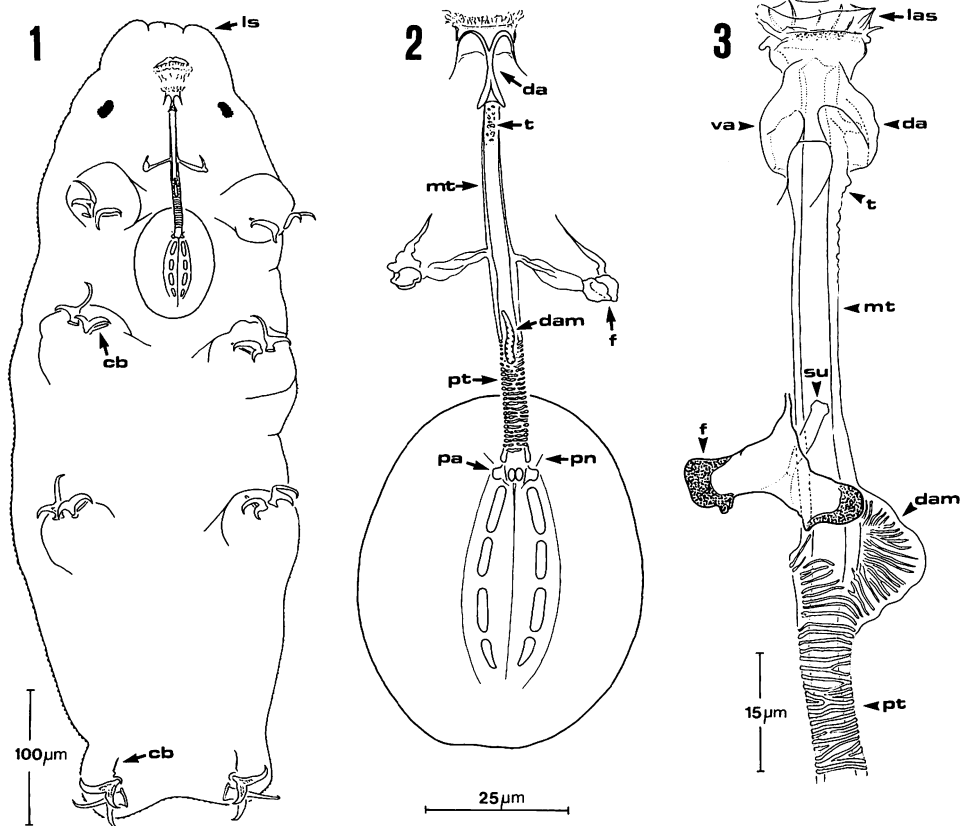
*Platicrista* the pharyngeal tube is relatively wider and without similar structures.

*Paradiphascon manningi* sp. n.

**Diagnosis:** As for genus. A large dumpy paradiphasconid with double-formed cuticular granulation, buccopharyngeal apparatus and eyes large. Pharynx with three macroplacoids (their size formula: I>III>II) and a conspicuously large microplacoid. Claws with lunules. Internal claws of I to IV pairs of legs with cuticular bars at their bases.

**Description:** The body is dumpy, with short legs (Figs. 1, 7) and is white. Dark-green material in the hindgut suggests that the species may be phytophagous or algivorous. The length of the body ranges from 218 to 770  $\mu\text{m}$  (holotype: 580  $\mu\text{m}$ ).

The eye spots are strikingly large (Figs. 1, 13), being up to 19  $\mu\text{m}$  in diameter and are composed of numerous black or dark-brown granules. The cuticle is thick. The cuticular sculpture covering the body is peculiarly formed, i.e. it is composed of minute polygonal plates with a tiny granula protruding from the middle of each plate (Figs. 8, 25). It is rare that there are two granules on each polygon or that the granules are elongated or are even lacking. The sculpture is



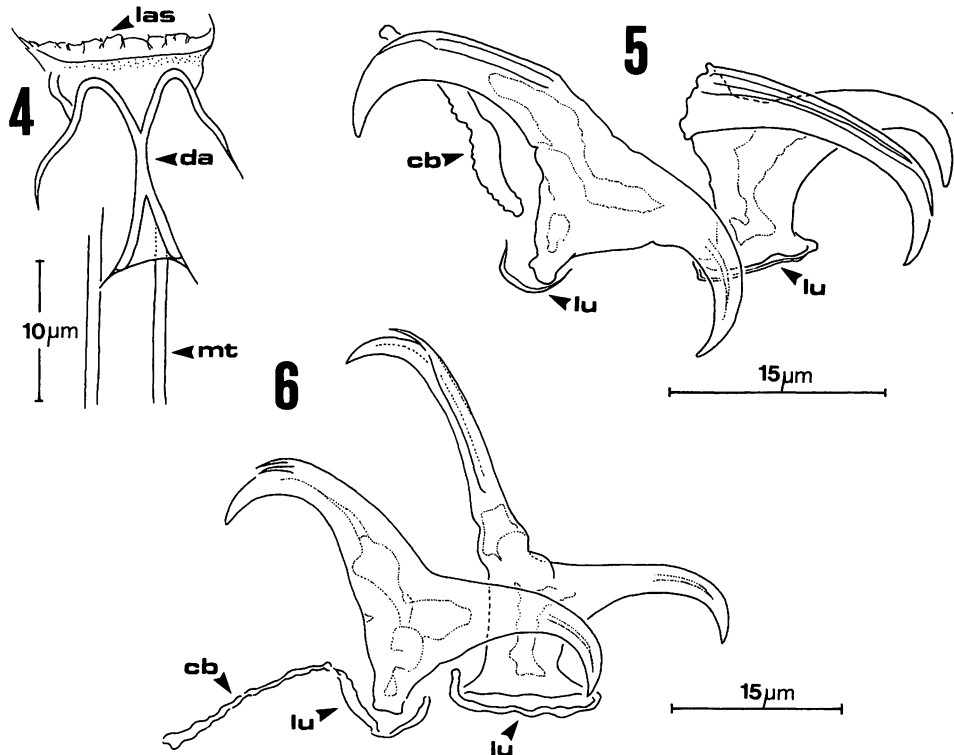
Figs. 1–3. *Paradiphascon manningi* gen. n. sp. n.: 1: whole animal in ventral view; 2: buccopharyngeal apparatus; 3: mouth- and pharyngeal tube, lateral view (all abbreviations explained in “Materials and Methods”).

well developed on dorsal and lateral parts of the body. The plates are tiny on the legs. In ventral areas the cuticle is smooth. The plates are up to 4.5  $\mu\text{m}$  in diameter; their usual diameter being about 2–3  $\mu\text{m}$ . Cribrate areas in cuticle occur, pores are absent.

The head segment above the mouth opening has three distinctly separated and well-defined, flat lobe-like structures. There are two lateral lobes and a medial one between them (Figs. 1, 7, 9–11, 13–14). They are clearly visible under the scanning electron microscope, but are less discernible using light microscopy. The median lobe is divided into two smaller and elongated parts by a more or less pronounced vertical furrow (Figs. 1, 9). The upper part of each lateral lobe is rounded and protruded more than the rest of the lobe and thus forms a distinct but flattened dome-tipped structure (Figs. 9, 10).

The mouth opening is large, subterminal and is surrounded by a flat ring composed of wrinkled cuticle (Figs. 9, 12). The ring is poorly defined in its lower ventral part. The external edge of the upper part of the ring protrudes slightly and forms some kind of "upper lip". This "lip" is usually divided into two smaller and poorly defined lobes (crests). No peribuccal lobes (6) characteristic for Hypsibiidae have been observed.

The buccopharyngeal apparatus is large (Figs. 1, 2, 15–17). The mouth opening leads to a spacious subcavity which has a membranous and wrinkled cuticular wall and itself terminates as a wide and shallow mouth cavity (Figs. 2–4, 12). The anterior edge of the mouth cavity is surrounded by a ring composed of wrinkled, thin, short and hardly discernible lamella-like structures



Figs. 4–6. *Paradiphascon manningi* gen. n. sp. n.: 4: mouth cavity in dorsal view; 5: claws of II pair of legs; 6: claws of IV pair of legs.

(Figs. 3, 4, 21, 22). Apical parts of the structures are usually slightly down turned. Their location in relation to the mouth cavity is similar in some degree to that found in *Adorybiotus coronifer* (Richters, 1903), excellently illustrated by Maucci (1986: Figs. 112b, 154). There are about 10–14 such rudimentary lamellae which are best seen only in some polyvinyl-lactophenol or Swan's preparations. The inside wall of the anterior part of the mouth cavity in larger specimens is covered with tiny granules, about 0.3  $\mu\text{m}$  in diameter (Figs. 3, 4). The mouth cavity is hidden within the head segment.

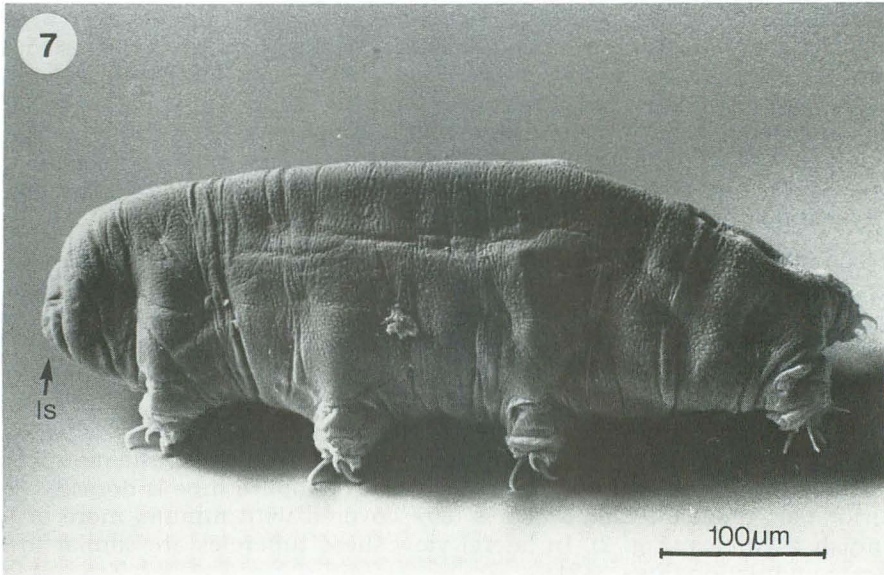
The stylets are relatively long, robust and with "typically" formed furca (Figs. 2, 3). The mouth tube is long, well sclerotized and moderately wide. Dorsal and ventral anterior apophyses on the mouth tube (for insertion of the stylet protractors) are almost symmetrical and hook-shaped, when seen in ventral view (Fig. 3). Posterior processes of the apophyses are relatively wide and form a kind of small triangular thin plate on dorsum and ventrum, and have strongly sclerotized lateral edges (Fig. 4). The stylet sheaths are median sized, their caudal processes are short. The processes on the dorsal side of the mouth tube are slightly longer than those on the ventral. The mouth tube is dorsally in its anterior part more thickened and is here covered with minute, more or less roundish tubercles (Fig. 2). In lateral view these tubercles are similar to the delicate undulation (Figs. 3, 21).

The mouth tube is terminated posteriorly with a large dorsal apodeme for insertion of the stylet retractors (= "drop-shaped" structure). The apodeme is peculiarly shaped, in that it forms a large, thin and long crest-like process covered laterally with striae which are unique as they do not appear elsewhere (Figs. 2, 3, 17, 18). The very dorsal edge of the process is smooth and is posteriorly the widest. Posteroventral edge of the mouth tube protrudes slightly (Figs. 3, 18).

The pharyngeal tube is annulated, short and relatively wide. The structure of the annulation is of the same type as that on the posteriodorsal apodeme (Fig. 3). The junction between mouth- and pharyngeal tube is not distinctly defined, the latter beginning more or less at about the middle of the length of the apodeme (Figs. 3, 18). The annulation is rather irregular and forms a kind of pseudo-spiral. The pharyngeal tube is terminated with moderately sized pharyngeal apophyses (Figs. 2, 19). Between pharyngeal apophyses and the posterior edge of the tube there are inserted thin anteriolaterally directed rods (Fig. 2), termed here "pharyngeal needles".

The ovoid pharynx is large, with three macroplacoids and a large microplacoid (Figs. 2, 15–17). The first macroplacoid is the longest, the second the shortest. The microplacoid is elongated and comma-shaped. The distance between 1st and 2nd macroplacoid is slightly shorter than that between the 2nd and 3rd. This is particularly clearly defined in juveniles or embryos (Fig. 26).

The claws increase slightly somewhat in size posteriorly and most resemble the *Hypsibius*-type. However, they are rather weakly differentiated and in several aspects are even more similar to those of the genus *Isohypsibius* Thulin, 1928 or *Doryphoribius* Pilato, 1969. The external and internal claws I to IV are provided with lunules and their primary branches have small, thin accessory spines. The external claws have wide bases and relatively large but thin lunules (Figs. 5, 6). The lunules of internal claws are distinctly smaller. All lunules are smooth. Both branches of the internal claw and the secondary branch of the external claws are relatively thick (Figs. 5, 6, 23, 24). Primary branches of the external claws are thinner, with their bases lightly sclerotized. The bases form a flexible, light-refracting unit (Fig. 6). The claws have a characteristic sculpture



Figs. 7–8. *Paradiphascon manningi* gen. n. sp. n.: 7: whole animal in lateral view; 8: cuticular surface.

internally which is similar to that of *Doryphoribius macrodon* Binda et al., 1980 or *D. citrinus* (Maucci, 1972).

At the base of internal claw I to III occurs a cuticular bar, which is elongated, usually slightly “S”-shaped and has irregularly sculptured edges (Fig. 5). The bars are directed anteromedially. A pair of bars is also developed on legs IV, a feature unique to the Eutardigrada. These bars are elongate, more or less straight and, to some degree, a prolongation of the lunules of the internal claw of leg IV (Fig. 6). The bars are about half as thin as those on legs I–III. Due to the “twisted” position of legs IV compared to legs I–III, the bars on legs IV are directed anteriorly (Fig. 1).

Measurements of 28 specimens (those of the holotype are given in parentheses): Length of buccopharyngeal apparatus 85–188 (154)  $\mu\text{m}$ . Length of mouth tube 40–72 (62)  $\mu\text{m}$ , width 3–7 (6)  $\mu\text{m}$  (external diameter measured at the stylet’s support). Posterior dorsal apodeme 9–17 (12)  $\mu\text{m}$  in length, in its posterior part 1.5–3.0 (2)  $\mu\text{m}$  wide and 4–8 (6)  $\mu\text{m}$  high. Pharynx 41–94  $\mu\text{m}$  long and 24–88

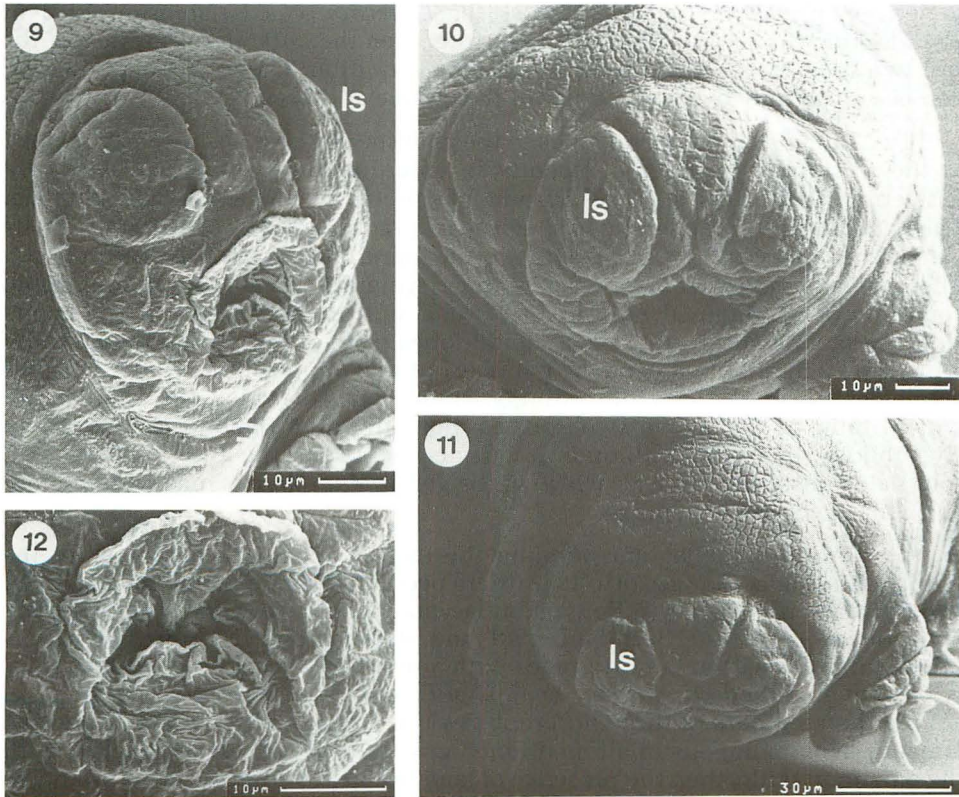
$\mu\text{m}$  wide ( $70 \times 58$ ). Length of macroplacoids: I = 6–13 (11), II = 3–9 (8), III = 4–10 (9)  $\mu\text{m}$ ; their width 2–3 (3)  $\mu\text{m}$ . The microplacoid is 2–8 (7)  $\mu\text{m}$  long. Length of external claw IV: 18–44 (37)  $\mu\text{m}$ , its main branch 13–28 (24)  $\mu\text{m}$  long. The length ratio (in %) between pharyngeal and buccopharyngeal tube is 33.3–40.1 ( $\bar{x}$  = 37.2,  $n$  = 19). The length ratio (in %) between the whole mouth tube and its unit up to the stylet supports (the so-called "pt index": Pilato 1985) is 67.0–82.0 ( $\bar{x}$  = 71.9,  $n$  = 25).

The large eggs are smooth, usually ovoid, white and 103–148  $\mu\text{m}$  long. They are deposited into shed cuticles, 3–9 eggs in each exuvium. The embryos have fully developed buccopharyngeal apparatus and claws (Fig. 26). The mode of reproduction is unknown, external sexual dimorphism not having been observed. Only three females with several oocytes were found.

Type Locality: Beine's Kloof Pass (19°7' E: 33°34' S), District of Wellington, Cape Province, South Africa. On mosses and in sandstone-derived soil of the Fynbos plant-association, at a height of 600 m above sea-level. Found on 7 August 1988, coll. J. Manning (45 specimens, 10 exuviae with eggs).

Type Repositories: Holotype, 16 paratypes and several exuviae have been deposited in the collection of the Zoologisches Museum, Hamburg (A 15/92). Three paratypes are housed in the National Museum of Natural History (Washington: USNM 235553), two paratypes are in the collection of the Natal Museum (Pietermaritzburg, South Africa: NM 495). The rest of the paratypes are in the author's own collection.

Etymology: The new species is named in honour of Dr. John Manning (Claremont, South Africa) who collected this interesting taxon.



Figs. 9–12. *Paradiphascon manningi* gen. n. sp. n.: 9: head segment, latero-frontal view; 10 and 11: head segment, frontal view; 12: mouth opening.

Remarks: Several unique characters of *Paradiphascon manningi* sp. n. readily separate this form from other tardigrades in the family Hypsibiidae with annulated pharyngeal tube. Such features include the double-formed cuticular granulation, dome-shaped lateral lobes on the head segment, lamella-like structures surrounding mouth opening, striated and large postero-dorsal apodeme on the mouth tube, short and wide pharyngeal tube, cuticular bars at the bases of internal claws IV and absence of (six) peribuccal lobes around the mouth opening. A question arises whether the above characters are primitive or derived conditions. Unfortunately the answer could not be univocal since our knowledge of the polarities in the eutardigrade character transformations is insufficient.

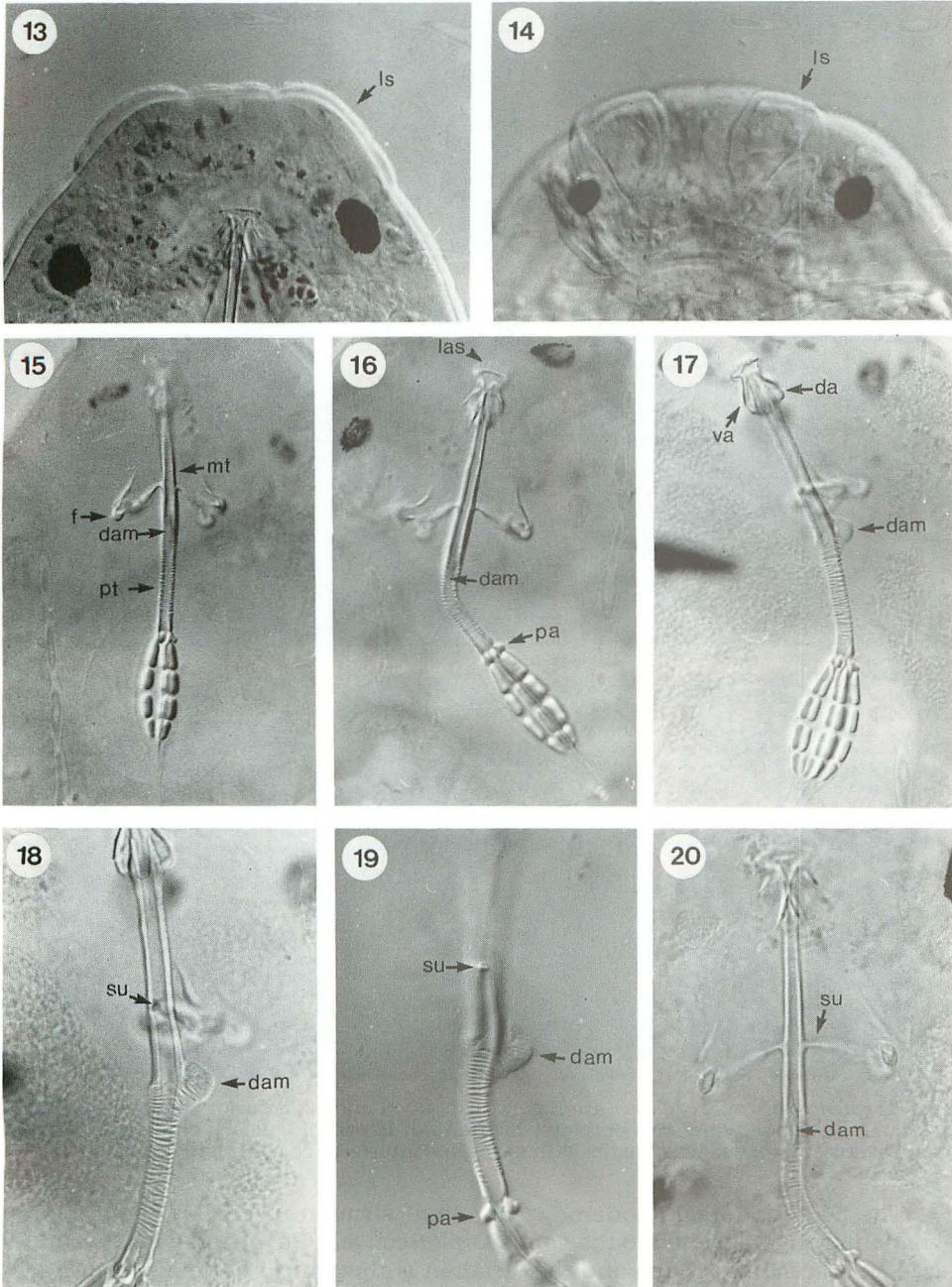
The peculiar double-formed cuticular sculpture of the new species is strikingly similar to that in *Pseudodiphascon bindae* Christenberry & Higgins, 1979, a remote relative from the family Macrobiotidae and from an insufficiently described genus (Christenberry & Higgins 1979: Fig. 7 and this paper, Fig. 8). Generally, more complex cuticle is known in Heterotardigrada than in Eutardigrada (Greven 1982). Recently, however, a plesiomorphic condition reported only in heterotardigrades, i. e. presence of pillars (rods) in the cuticle has been also observed in two eutardigrade species of the genus *Macrobiotus* Schultze, 1834 (the family Macrobiotidae: op. cit., Kristensen 1982). Hence, it is possible that "granules" located medially within tiny polygons on the cuticle in *P. manningi* sp. n. and *Pseudobiotus bindae* are homologous with the cuticular pillars. Such a homology seems to be particularly likely when one considers the very similar superficial pattern (granulation) present in the cuticle of some heterotardigrade genera, e. g. *Echiniscus* Schultze, 1840, *Testechiniscus* Kristensen, 1982 or *Pseudechiniscus* Thulin, 1911. If this is true, then the cuticular sculpture of the last two species represents a plesiomorphic condition. That question, however, can be solved only by TEM studies of the cuticle of those taxa.

Two dome-shaped lateral lobes in the new species bear a great resemblance to the structures discovered recently in eutardigrade *Halobiotus crispae* by Kristensen (1982: Figs. 9, 10, 28–30) and interpreted by him as cephalic papillae. The papillae are characteristic for heterotardigrades and they are directly innervated from deutocerebrum as it has been found also in *H. crispae* (op. cit.). These sense organs, whose presence in eutardigrades is also a plesiomorphic condition, were retained only in *H. crispae*, out of five species of the genus *Halobiotus* Kristensen, 1982. The lateral lobes of *P. manningi* sp. n. probably represent such modified cephalic papillae but that supposition requires further cytological investigation. Interestingly, among eutardigrades, the papillae are known only in the above two species, both of which belong to the family Hypsibiidae. In the Macrobiotidae, considered ancient, the anterio-lateral sensory fields described by Walz (1979) in the genus *Macrobiotus* may be homologous with the cephalic papillae.

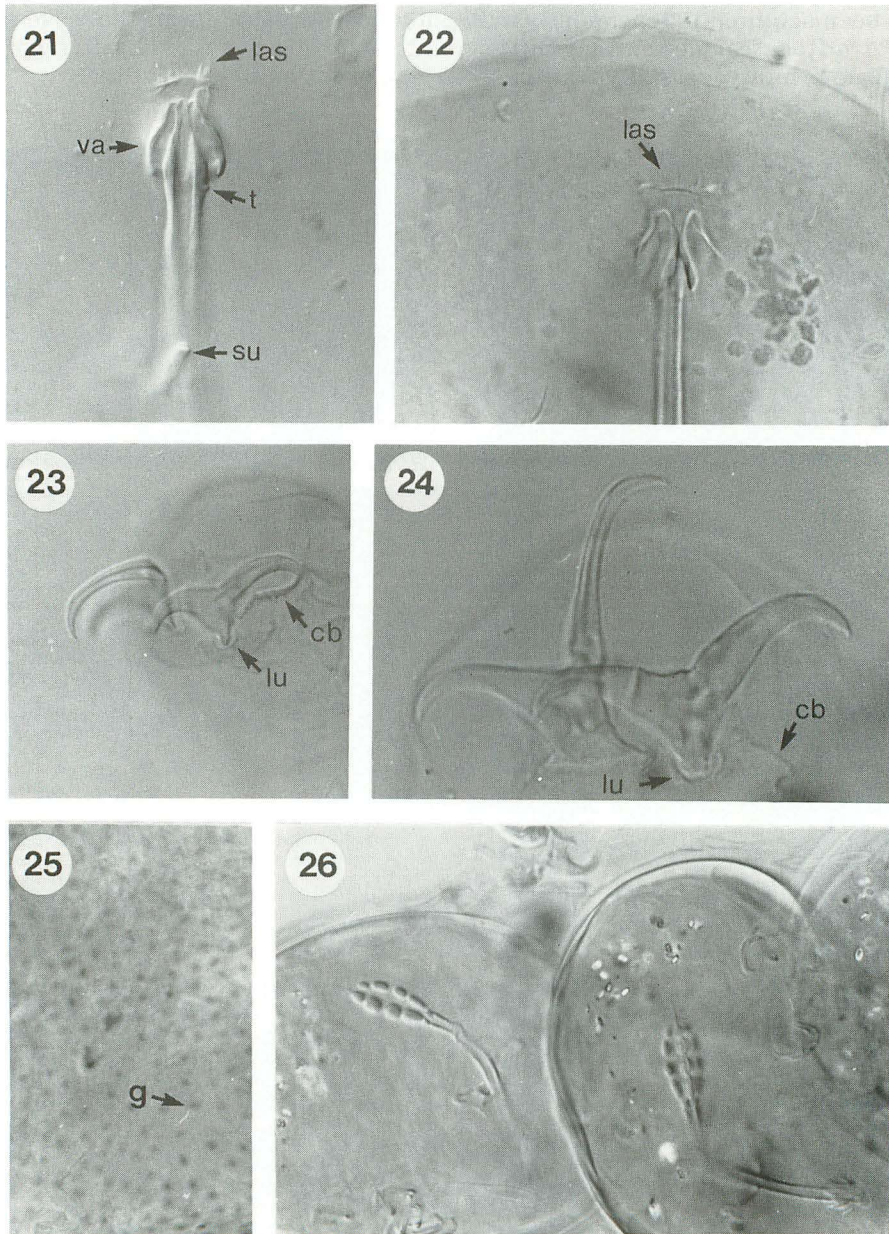
The buccal lamellae surrounding the mouth opening are present in the family Milnesiidae Ramazzotti, 1962 (there peculiarly shaped), in the majority of genera of Macrobiotidae, in Eohypsibiidae, and only in two genera of the family Hypsibiidae (*Thulinia* Bertolani, 1981 and *Pseudobiotus* Nelson, 1980). It is interesting that within eutardigrades with annulated buccal tube the character is present in *Pseudodiphascon*, *Eohypsibius* and *Paradiphascon* gen. n., i. e. among the members of three different phyletic lineages. If one recognized the lamellae as homologous in all mentioned groups, a hypothesis consistent with the parsimony rule, then the presence of lamellae in *P. manningi* sp. n. would be a plesiomorphic condition. In the new species these structures are strongly reduced (vestigial) compared to those in other taxa. However, if this character



has been acquired independently in hypothetical ancestral forms that gave rise to *Paradiphascon* gen. n. and *Diphascon*, then its absence for the latter would indicate primitiveness of *Paradiphascon* gen. n. within the lineage.



Figs. 13–20. *Paradiphascon manningi* gen. n. sp. n.: 13 and 14: the lobe-like structures on the head, dorsal and ventral view, respectively; 15–17: buccopharyngeal apparatus; 15 and 16: dorsal view, 17: lateral view; 18 and 20: mouth and pharyngeal tube, 18: lateral view, 20: dorsal view; 19: pharyngeal tube (interference contrast).



Figs. 21–26. *Paradiphascon manningi* gen. n. sp. n.: 21 and 22: anterior part of mouth tube in lateral and dorsal view, respectively; 23: claws of II pair of legs; 24: claws of IV pair of legs; 25: cuticular surface; 26: eggs with embryos (interference contrast).

The posteriodorsal apodeme (“drop-like” structure) seems to be a unique synapomorphy restricted to the genus *Diphascon* and *Paradiphascon* gen. n. Its large size, crest-like shape and the striation is thought to be retained in *Paradiphascon* gen. n. and represents plesiomorphy. Conversely, a smaller, roundish and smooth apodeme such as in the subgenus *Diphascon* is recognized here as an apomorphic condition. Complete reduction of this apodeme type found in the related subgenus *Adopion* is believed to be the most derived transforma-

tion of that character state. An intermediate taxon between these subgenera, characterized by advanced reduction of the apodeme, is *Diphascon higginsi* Binda, 1971, as may also be *D. puniceum* (Jennings, 1976) and *D. sanae* Dastych et al., 1990. The unique shape of the structure in the two last-named species (Dastych 1984, Dastych et al. 1990) indicates a status separate from the main *Diphascon* lineage. Probably both these taxa deserve a separate subgeneric rank. Thus, *Paradiphascon* gen. n. could be the taxon most similar to a hypothetical common ancestor of today's *Diphascon*. One can postulate that such an ancestral stock was provided with a short and wide pharyngeal tube and a large, striated posteriodorsal apodeme. The short annulated pharyngeal tube is believed to be a plesiomorphy compared to the elongated and derived tube present in *Diphascon*.

The peculiar cuticular bars observed on legs IV in *P. manningi* sp. n. has been found in tardigrades only once, i. e. in *Isohypsibius schaudini* (Richters, 1909) (Heciak 1976: identification uncertain). However, due to lack of access to the above material, the true character of that structure must remain unknown. The phylogenetic value of the bars IV in the new species is also problematical. If the bars are homologous with those on the first three pairs of legs, then that pattern might be considered as a plesiomorphy. Conversely, the lack of such bars and their presence only on legs I to III may represent an apomorphic condition. The above characteristics found in some species of *Diphascon* and *Isohypsibius* have also been noted in some other genera of the Eutardigrada. However, the question of homology must remain an open one. The bars IV may be also considered as an evolutionary novelty and then, an autapomorphy for the new species. The latter suggestion is thought to be less probable.

Only recently peribuccal structures have been considered as those bearing phylogenetic information (Schuster et al. 1980). However, their value is variously interpreted (Pilato 1982). Broadly speaking, not much is known about this matter as yet. One of such character, the presence of six peribuccal lobes around the mouth opening, seems to be widely distributed within the family Hypsibiidae, in that the lobes were observed at least in six genera, including *Diphascon* (Schuster et al. 1980). However, after the recent splitting of that taxon into four genera (Pilato 1987), the presence or lack of the structures within those new taxa should be confirmed again. Origin of the peribuccal lobes is not well documented, but they may be homologous with peribuccal sense organs (lobes) of which the ultrastructure has recently been described in *Halobiotus crispae* by Kristensen (1982). Whether the ring of wrinkled cuticle surrounding the mouth opening in *P. manningi* sp. n. represents such highly modified (specialized?) structure or if the ring arose independently, remains open. The problem could be cleared through TEM studies.

The large, dark pigmented eyes in the new species are believed to be a plesiomorphy and within the Hypsibiidae with annulated buccal tube that character is retained by *Hebesuncus* and partly by *Diphascon*. It is however suppressed in *Mesocrista*, *Platicrista* and *Itaquascon*. Another character, i. e. the presence of lunules in *P. manningi* sp. n. may be also a plesiomorphy, if it is postulated that the structure in Macrobotidae, Eohypsibiidae and Hypsibiidae are homologous. The shape of claws in the new species is more similar to that in the genus *Doryphoribius* or *Isohypsibius*. The opinion here is that this is another indication of primitiveness of *P. manningi* sp. n. within the discussed group of taxa. In brief, numerous and supposedly primitive characters of *P. manningi* sp. n. point to an ancestral status of the species within the Hypsibiidae which have an annulated buccal tube.

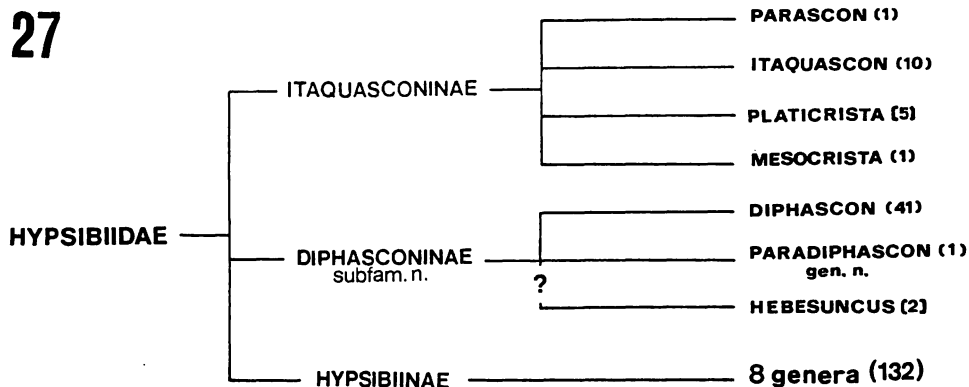
## The new subfamily Diphasconinae and notes on phylogenetic relationships within this taxon

The family Hypsibiidae, to which *Paradiphascon* gen. n. belongs, is composed of two subfamilies, i. e. Hypsibiinae and Itaquasconinae. According to an old diagnosis of Itaquasconinae (see Pilato 1969a, 1969b), the new genus should be included in that taxon. However, recent re-definition of the subfamily (Pilato 1987) excludes from the Itaquasconinae such genera as *Diphascon* and *Hebesuncus* and, consequently, *Paradiphascon* gen. n. also. Pilato (op. cit.) left the systematic position of these genera open. Bertolani (1988) refers to both these subfamilies, but places the genus *Diphascon* still within the Itaquasconinae.

The authorship of the name "Itaquasconidae", lowered by Pilato (1969a, 1969b) to subfamiliar rank needs some explanation. The term "Itaquasconidae" as a family name was used for the first time by Rudescu (1964) to include the then monospecific genus *Itaquascon*. Surprisingly, Rudescu referred it to "Fam. Itaquasconidae Bartoš 1962" and he cited as a reference "1963 Bartoš Fauna Č.S.R." (op. cit., p. 385). This citation is an obvious mistake, since no such reference could be found in the literature. Moreover, this authorship is contradicted by ambiguous information in the Bartoš' (1967) monograph. Bartoš (op. cit.) refers in the paper to the family both as "Itaquasconidae Rudescu, 1964" and also "Itaquasconidae Bartoš in Rudescu 1964" (op. cit., p. 31 and 176, respectively). In his later paper, Bartoš (1971) recorded the family name without any author.

This nomenclatorial ambiguity is partly reflected in the systematic arrangement of eutardigrades proposed by Pilato (1969a), in that he created a new family, Hypsibiidae, and divided it into two subfamilies, viz. Hypsibiinae and Itaquasconinae. The latter name evidently has the familial category introduced by Rudescu (1964) and down graded by Pilato to subfamily rank. Thus, the authorship of the category falls to Rudescu. Surprisingly, Pilato refers to the taxon as "Itaquasconinae Barros 1962" (op. cit., p. 186) and cites the author incorrectly when following Rudescu (1964). Barros never created any suprageneric category but described only the genus *Itaquascon* (see Barros 1939). Afterwards Pilato substituted the name of an already by him defined subfamily "Itaquasconinae" (op. cit., p. 186) through "Diphasconinae" in his scheme on the next page of the same paper (op. cit., p. 187), providing no explanation for the change. One can suppose that it is another mistake, since he maintains in his parallel paper on that subject (1969b, p. 842) only the correct "Itaquasconinae". Recent tardigrade monographs by Ramazzotti & Maucci (1983) and Maucci (1986) retain the family Hypsibiidae but indicate nothing about its division into two subfamilies. They present information about the mentioned arrangement, but with the incorrect name "Diphasconinae" for the "Itaquasconinae".

Due to exclusion of *Diphascon* and *Hebesuncus* from the subfamily Itaquasconinae by Pilato (1987), a decision which is here accepted, there is a need to create a category which would comprise the above two genera and the new genus *Paradiphascon*. As such a taxon a new subfamily Diphasconinae is proposed here. It should include *Diphascon* and *Paradiphascon* gen. n. and, with lesser certainty, the genus *Hebesuncus*. The name, Diphasconinae subfam. n. is derived from its type genus and has been once (mistakenly) used by Pilato (1969a: see above). Thus, the Hypsibiidae is comprised now of three subfamilies, i. e. Hypsibiinae Pilato, 1969 (8 genera: *Doryphoribius* Pilato, 1969, *Isohypsibius* Thulin, 1928, *Pseudobiotus* Nelson, 1980, *Thulinia* Bertolani, 1981, *Hypsibius* Ehrenberg, 1848, *Microhypsibius* Thulin, 1928, *Halobiotus* Kristensen, 1882, *Ramazzottius* Binda & Pilato, 1986), Diphasconinae subfam. n. (3 gen-



Figs. 27. Possible relationships within the family Hypsibiidae Pilato, 1969 (numbers in parentheses refer to the number of known species).

era: *Diphascoson* Plate, 1889, *Paradiphascoson* gen. n., *Hebesuncus* Pilato, 1987) and Itaquasconinae Rudescu 1964 sensu Pilato 1987 (4 genera: *Mesocrista* Pilato, 1987, *Platicrista* Pilato, 1987, *Itaquascon* Barros, 1939 and *Parascon* Pilato & Binda, 1987). Probable phylogenetic relationships within the Hypsibiidae are shown in Fig. 27. The genus *Parascon* is closely related to *Itaquascon* (see Pilato 1987b), but is characterized by a "simple" (not annulated) pharyngeal tube which may be interpreted as a character reversal.

Class: **Eutardigrada** Marcus, 1927  
 Order: **Parachela** Schuster et al. 1980  
 Family: **Hypsibiidae** Pilato, 1969  
 Diphascosoninae subfam. n.

Diagnosis: Eutardigrades with buccopharyngeal apparatus of *Diphascoson*-type and anterior apophyses shaped as "blunt"- or "semilunular" hooks (see Pilato 1987). Posteriorodorsal apodeme ("drop-like" structure) present or absent, pharyngeal apophyses present. Asymmetrical claws of Hypsibiidae-type. Eggs either deposited into shedded cuticle and smooth or layed freely and with ornamented shells.

Type Genus: *Diphascoson* Plate, 1889

Composition: *Diphascoson* Plate, 1889, *Paradiphascoson* gen. n. and, tentatively (?), *Hebesuncus* Pilato, 1987.

The genus *Hebesuncus* deserves some attention. The taxon comprises two species with peculiar bipolar-mountain distribution, i. e. *H. conjugens* (Thulin, 1911) and *H. schusteri* (Dastych, 1984). The former species is known from the Arctic and some high mountains in the Northern and Southern Hemisphere, although its records in the Andes (Mihelčić 1971/1972) and New Zealand (Horning et al. 1978) should be confirmed. No eggs have been found by the above authors. The egg ornamentation is a key character differentiating both taxa. However, *H. schusteri* has been recorded only from the Antarctic. The genus differs from the *Diphascoson-Paradiphascoson* gen. n. lineage in its unique asymmetry of the anterior apophyses on the mouth tube (Pilato 1987) and very short, thin pharyngeal tube with relatively poorly developed annulation. Also peculiar for *Hebesuncus* are freely deposited, ornamented eggs. In the Hypsibiidae, the latter character is known only in *Hypsibius antarcticus* (Richters, 1904) and with lesser certainty, for *H. conifer* Mihelčić, 1938. If such a mode of eggs deposition and ornamentation of their shells are homologous with those occurring in the

Macrobiotidae and Eohypsibiidae, then the character in *Hebesuncus* represents a plesiomorphic condition. Based on the above mentioned differences it can even be assumed that *Hebesuncus* belongs to a separate phyletic line and has more in common with ancestral stock which gave rise to the genus *Hypsibius*, than with the assemblage *Diphascon-Paradiphascon* gen. n. If this is true, such a separate status of *Hebesuncus* should be reflected in an additional new suprageneric category (subfamily?) within the Hypsibiidae. As a consequence, one would then suppose that the annulation of the pharyngeal tube in eutardigrades has arisen independently at least three times, i. e. twice within the Hypsibiidae and once in the Macrobiotidae (in *Pseudodiphascon*).

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## Zusammenfassung

Ein neues Bärtierchen, *Paradiphascon manningi* gen. n. sp. n. wird aus einer Moosprobe aus Südafrika (The Cape) beschrieben. Das neue Taxon ist mit der Gattung *Diphascon* verwandt. Einige seiner Merkmale zeigen seinen ursprünglichen Status innerhalb der Hypsibiidae mit spiralförmiger Schlundröhre. Die neue Subfamilie Diphasconinae wird vorgeschlagen für die Gattungen *Paradiphascon* gen. n., *Diphascon* und *Hebesuncus*. Die systematische Stellung der Gattung *Hebesuncus* ist unklar, darum ist ihr Platz in der neuen Subfamilie zur Zeit provisorisch. Die phylogenetischen Verhältnisse in der Familie Hypsibiidae werden besprochen.

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