3932
NH

Morphological and Phylogenetical Studies in the Isopoda (Crustacea).
Part 1: The Pleon Trunk in the Phreatoicidea

By Friedhelm Erhard, Stuttgart

With 19 figures

Summary

The skeleton and musculature of the pleon trunk as well as further anatomical characters in the australian species *Metaphreatoicus australis* (Chilton, 1891) (Phreatoicidea) are described. As far as possible, functional interpretations on the skeletal and muscular systems are proposed. Each anatomical character, documented in *Metaphreatoicus*, is checked in further phreatoicidean species from Australia, Tasmania, India and South Africa to reconstruct groundpattern characters of the Phreatoicidea. The comparison with corresponding morphological data in the taxon Oniscidea indicates character transformations inside the Isopoda. First judgments on the polarity assessment of characters are discussed.

Zusammenfassung

Das Skelet und die Muskulatur des Pleonrumpfes sowie weitere anatomische Merkmale der australischen Art *Metaphreatoicus australis* (Chilton, 1891) (Phreatoicidea) werden dokumentiert. Soweit dies möglich ist, werden Hypothesen zur Funktion des Skelet-Muskel-Systems vorgeschlagen. Jedes der an *Metaphreatoicus* beschriebenen anatomischen Merkmale wird an weiteren Phreatoicidea-Arten aus Australien, Tasmanien, Indien und Südafrika überprüft, um Grundplan-Merkmale der Phreatoicidea zu rekonstruieren. Der Vergleich mit entsprechenden morphologischen Daten des Taxon Oniscidea weist auf Merkmalstransformationen innerhalb der Isopoda hin. Erste Einschätzungen zur Lesrichtung der Merkmale werden diskutiert.

Contents

1. Introduction

In the recent past, several studies on the phylogenetic-systematic relationships of the main groups of Isopoda have been undertaken using mainly literature data and characters of the external morphology (SCHMALFUSS 1989, WÄGELE 1989, BRUSCA & WILSON 1991). A comparison of these analyses reveals the agreement of the cited authors on the existence of a monophylum which includes the aquatic isopod groups Epicaridea, Valvifera, "Flabellifera", Anthuridea and Gnathiidea. On the other side, the systematic position of certain subordinate taxa inside this group as well as the relationships of the remaining isopod taxa Phreatoicidea, Asellota, Microcerberidea, Calabozoidea and Oniscidea have been the subject of controversy. Therefore, further reliable data are needed as a basis for a stable classification of the taxon Isopoda.

As a contribution towards a reliable phylogenetic system, new comparative investigations on the internal anatomy are planned to disclose further characters which might be useful to clarify the inconsistancies in reconstructing the phylogenetic relationships. In this connection it is referred to recent studies on the pleon in terrestrial isopods (ERHARD 1995a, b, 1996, 1997, in press). The results of these investigations have been used to propose a hypothesis on the phylogenetic relationships between the main groups of terrestrial isopods and to reconstruct some oniscidean groundpattern characters. Within the new project, this data base shall be used to compare the pleonal anatomy in different isopod suborders.

The first part of this larger study, submitted in the present publication, is the description of the pleon trunk in the taxon Phreatoicidea and the reconstruction of groundpattern characters of the group as well as the comparison with the situation

in terrestrial isopods. Further parts will follow. For the time being, the research program includes furthermore the description of the pleopod anatomy in the Phreatoicidea, the reconstruction of the pleonal anatomy in basal representatives of the Asellota and an analysis of the phylogenetic-systematic relationships between the three taxa Phreatoicidea, Asellota and Oniscidea.

2. Material, methods and abbreviations

2.1. Material

Phreatoicidea:
  Metaphreatoicus australis (Chilton, 1891), Australia, New South Wales, Mt. Kosciusko (SMNS 14016, 14048)
  Colubotelson joyneri searlei Nicholls, 1944[1]), Australia, E-Victoria, Mt. Baw Baw (SMNS 14019)
  Onchotelson brevicaudatus (Smith, 1909), Tasmania, Great Lake, southern bank (SMNS 14047)
  Mesacanthotelson tasmaniae (Thomson, 1894), Tasmania, Great Lake, southern bank (SMNS 14047)
  Paramphisopus palustris (Glauert, 1924), Australia, Western Australia, Lake Monger (SMNS 14119; ex AM P44487)
  Phreatoicopsis terricola Spencer & Hall, 1896, Australia, Victoria, The Grampians (SMNS 14118; ex NMV J44869)
  Nichollsia kashiensis Chopra & Tiwari, 1950, India, Banaras (SMNS 12149)
  Mesamphisopus capensis Barnard, 1914, South Africa, Southern Cape, Zonder End Mountains (SMNS 15517; ex SAM A6052).

Oniscidea:
  Ligia oceanica (Linnaeus, 1767), W-France, Brittany, Roscoff
  Tylos ponticus, Grebnitzky, 1874, Greece, island of Crete, E Sitia and island of Astipalea, Maltesana (SMNS 1242, 1549)
  Mesoniscus alpicola (Heller, 1858), S-Germany, Bavaria, 6 km W Berchtesgaden
  Titanethes albus Schiödte, 1849, Slovenia, 30 km S Ljubljana, Videm-Popeć, water cave (SMNS 5080, 5253)
  Actaecia bipleura Lewis & Green, 1994, Tasmania, W Tamar River, W Greens Beach
  Oniscus asellus Linnaeus, 1758, S-Germany, Baden-Württemberg, Tübingen
Valvifera:
  Saduria entomon (Linnaeus, 1758), Finland, Tvärminne (SMNS 4205)
"Flabellifera":
  Anilocra frontalis Milne-Edwards, 1840, W-France, Brittany, Roscoff.

The systematics of the phreatoicidean species treated within the paper at hand chiefly refers to the major taxonomic revision of the group published by NICHOLLS (1943, 1944). However, the phylogenetic relationships within the suborder Phreatoicidea have received little treatment in the past and the systematics of the phreatoicidean taxa should be revised using phylogenetic-systematic methods.

As an example of questionable systematics, the genera *Metaphreatoicus* and *Colubotelson* are separated solely on the presence of 6 or 4 spines respectively on the pleotelsonic projection. KNOTT (1971: 138), therefore, questioned this character, whose expression depends on the stage in growth of the individual, to be a good feature to distinguish genera.

---

[1]) NICHOLLS (1944: 110) described this subspecies on material from Mt. Baw Baw, E-Victoria, Australia. The specimens investigated here also were collected on Mt. Baw Baw. Following NICHOLLS description of *C. joyneri searlei* there are slight differences to the specimens studied in the present investigation. Therefore, the determination of the specimens has to be considered with care.

4   STUTTGARTER BEITRÄGE ZUR NATURKUNDE   Ser. A, Nr. 581

2.2. Methods

Skeleton and musculature of the pleon were reconstructed by manual micropreparation of fuchsine-stained specimens under the stereomicroscope and by the use of histological serial sections examined under the light microscope. The thickness of the histological sections was 7 µm, they were stained in haematoxylin-eosin and azan. The skeleton was also investigated after maceration in diethylenetriamine (KRAUTER 1980) and staining in chlorazol-black (CANNON 1937).

The morphological data on the isopodan pleon and further body regions are interpreted, if possible at all at the present state of knowledge, strictly according to the method of phylogenetic systematics proposed by HENNIG (1966).

2.3. Abbreviations

A	Point of articulation
AM	Australian Museum, Sydney, Australia
As	Anus
aPrAp	Anterior apophysis of the pleopod protopodite
Att	Point of muscular attachment
Con	Connective of the ventral nerve cord
Cox	Coxopodite
dLM	Dorsal longitudinal musculature
En	Pleopod endopodite
EnDa II	Mediodistal article of male pleopod endopodite II (appendix masculina)
Ep	Pleopod epipodite
Ex	Pleopod exopodite
Gp	Genital papilla
InMb	Intersegmental membrane
IoPep	Insertion opening of pereiopod
IoPp	Insertion opening of pleopod
IoU	Insertion opening of uropod
lUAp	Lateral apophysis of uropod
M	Muscle
mdApPt	Mediodorsal apophysis of pleotelson tergite
mdApV	Mediodorsal apophysis of pleon tergite V
Mm	Muscles
mUAp	Medial apophysis of uropod
NMV	National Museum of Victoria, Australia
PeDAp	Dorsal apophysis of pereion tergite
PeGl	Pereional ganglion of ventral nerve cord
Pep	Pereiopod
PepBs	Pereiopod basipodite
PepLoc	Extrinsic pereiopod locomotor
PeSt	Pereion sternite
PeT	Pereion tergite
PlDAp	Dorsal apophysis of pleon tergite
PlEm	Pleon epimere
PlGl	Pleonal ganglion of ventral nerve cord
PlS	Pleon segment
PlSt	Pleon sternite
PlT	Pleon tergite
Pr	Pleopod protopodite
pPrAp	Posterior apophysis of pleopod protopodite
Pt	Pleotelson
PtAx	Pleotelsonic apex
PtDAp	Dorsal apophysis of pleotelson tergite
PtScl	Ventrocranial pleotelsonic sclerite
PtSt	Pleotelson sternite
PtT	Pleotelson tergite

SAM	South African Museum Cape Town, South Africa
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
StPr	Sternal processus
Tend	Tendon of connecting tissue
U	Uropod
ULoc	Extrinsic uropod locomotor
UEn	Uropod endopodite
UEx	Uropod exopodite
UPr	Uropod protopodite
Vas	Vas deferens
vLM	Ventral longitudinal musculature
vLMcl	Ventral longitudinal muscle cord of the central layer.

In the figures numerous abbreviations are completed by roman numbers which apply to correspondent pereion or pleon segments.

3. Previous investigations and terminology

In the past little attention has been paid to the pleonal skeleton and musculature system of the Peracarida and other malacostracan taxa. Apart from recent morphological studies on the oniscidean main groups (ERHARD 1995a, 1996, 1997, in press), detailed pleonal investigations on further isopod suborders do not exist. A description of the trunk musculature of some oniscideans were presented by GRUNER (1953) whereas the oniscid male genitalia were investigated in detail by LEGRAND (1946). Further less informative literature data concerning oniscidean pleon anatomy are listed by ERHARD (1995a: 3).

An extensive monograph on the anatomy and biology of the subterranean *Nichollsia kashiensis* (Phreatoicidea) has been presented by GUPTA (1989). The study includes also a brief chapter on the muscular system which permits some morphological comparisons with further phreatoicidean species. Unfortunately, the results on the pleonal musculature are not very detailed.

TAIT (1917) gives few information on *Glyptonotus* (Valvifera), MAERCKS (1930) and WILSON (1987, 1991) describe genitalia of asellotans and other isopod taxa and WÄGELE (1981, 1994) informs about the uropodal musculature of several specimens of Isopoda, Euphausiacea and Decapoda.

Limited informations on the trunk musculature of several Peracarida groups are given by CLAUS (1887) on *Apseudes* (Tanaidacea), WRZESNIOWSKI (1879) on *Goplana* (Amphipoda) and NATH (1974) on *Lepidomysis* (Mysida). Detailed descriptions on the pleon trunk musculature of Lophogastrida, Mysida, Euphausiacea, Decapoda and Anaspidacea were presented by DANIEL (1932a, b, 1933), however the complex figures make any comparison for homologization difficult. Finally, there are some more or less detailed pleonal studies on different Decapoda specimens (SCHMIDT 1915, BERKELEY 1928, COCHRAN 1935, ABRAHAMCZIK-SCANZONI 1942, PATERSON 1968) and the leptostracan *Nebalia* (CLAUS 1888).

The results of the investigation on the pleonal skeleton and musculature of *Metaphreatoicus australis* will be compared here with literature data of pleonal studies on the main groups of the Oniscidea carried out by ERHARD (1995a, b, 1996, 1997, in press). Therefore, the consecutive numbering of the muscles refers to the nomenclature used in the above cited publications. Additional muscles of *Metaphreatoicus australis* or further aquatic isopods, not yet numbered in the Oniscidea, are indicated by new numbers.

For the purpose of consistency, the terms of skeletal structures, their abbreviations and their spellings were adopted from ERHARD (1995a, 1996, 1997).

4. Skeleton and musculature of the pleon trunk

The morphological study within the paper at hand extends to the skeleton and musculature of the pleon segments I–V and the pleotelson in *Metaphreatoicus australis.* A second publication will deal with the skeleton and muscle-system of the pleopods I–III as well as structure and locomotors of the uropods in the same species.

After the description of an anatomical complex in *Metaphreatoicus australis,* characters are discussed by comparisons with further peracaridan taxa, and attempts are made to reconstruct at least some groundpattern characters of the Phreatoicidea.

The results were gathered chiefly from male specimens. It is emphasized if females were considered.

4.1. Skeleton

4.1.1. Exoskeleton (figs. 1–3)

4.1.1.1. *Metaphreatoicus australis*

The pleon of *Metaphreatoicus australis* consists of five movable segments, each bearing a pair of biramous appendages, and the terminal pleotelson with styliform uropods. The body is of subcylindrical nature. However, the pleon tergites have a strong downward development, increasing from the first to the fifth segment, to give the body an amphipod-like appearance. The pleon epimera together with the pleon sterna are forming a chamber for the pleopods which is terminally closed by the voluminous pleotelson. Furthermore, an expansion of the basipodites of the three posterior pereiopods contributes to continue the chamber forewards. Both, epimera and pereiopod basipodites V–VII are armed with marginal setae.

The pleotelson appears to be bent downwards, consequently the anus is located ventrally, not terminally as for example in *Phreatoicopsis terricola, Nichollsia kashiensis* or in most oniscidean species. On the sides of the pleotelson of *Metaphreatoicus* the laterally compressed uropods insert at the lateroanterior region which is partly covered by the epimera of the fourth and fifth pleon segments (fig. 1). The fifth pleon segment is distinctly longer than the others.

Terminal at the pleotelson, there is a projection (apex, PtAx) armed with strong spines and flanked by two smaller processus.

At the ventral wall of the body, the short and paired male genital papillae are inserted medially on the coxopodites of the pereiopods VII (fig. 2).

In *Metaphreatoicus australis* posteriorly directed sternal processus are only represented by short sternal protrusions of the pereion sternite VII and the pleon sternites I and II (cf. fig. 3).

The pleon segments I–V each have a pair of pleopods consisting of proto-, exo- and endopodites. The pleopod protopodites III–V additionally have a lateral epipodite and the pleopod exopodites II–V are separated into two lobes (fig. 2). At the second male pleopod, a basal part of the endopodite bears a lateral leaflike and a medial rodlike article. The latter serves as a gonopod and is commonly called appendix masculina.

The lateral pleotelson region behind the uropod insertion appears to be divided by a transversal suture. It may indicate the fusion line between the sixth pleon segment and the telson (fig. 1).
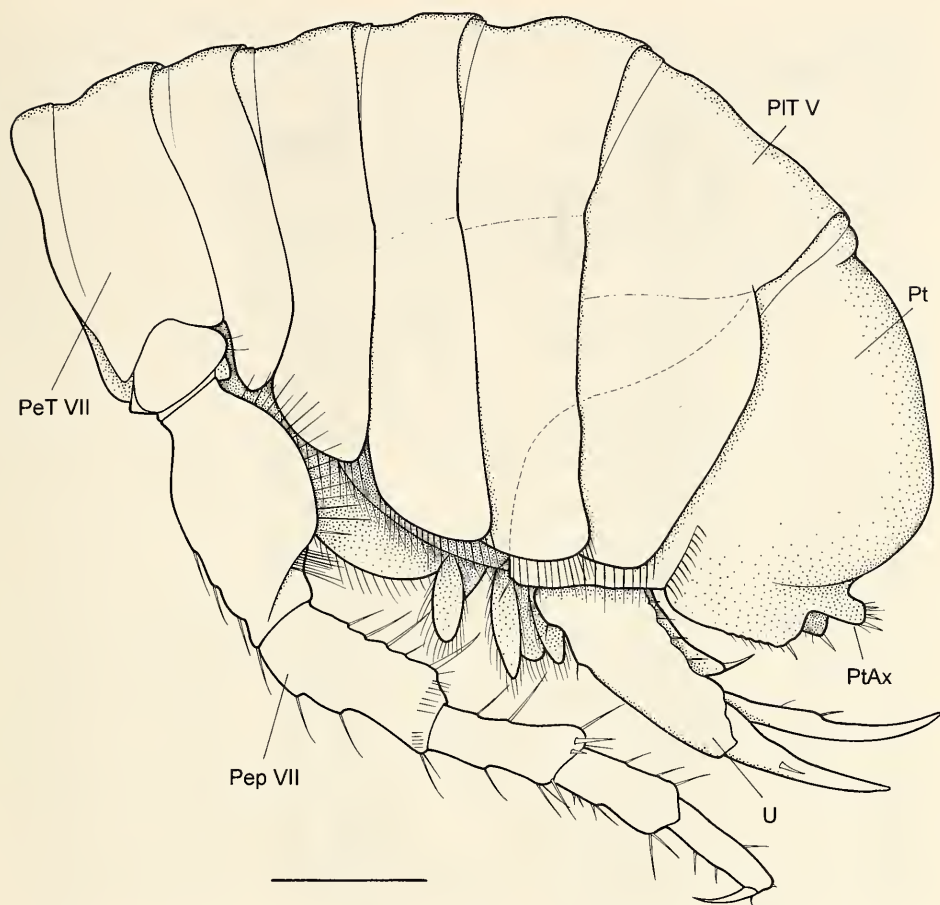
Fig. 1.   *Metaphreatoicus australis*, ♂, pleon and pereionite VII in lateral view. – Scale: 1 mm.

4.1.1.2. Comparison

– Pleon segments I–V

In *Metaphreatoicus* the pleon segments I–V are not fused and are freely movable. This character state is present in the groundpatterns of most isopod suborders and the peracaridan groups Tanaidacea, Mictacea, Spelaeogriphacea, Cumacea, Amphipoda and "Mysidacea". The character has to be considered as plesiomorphy of the taxon Phreatoicidea in respect to the isopodan groundpattern (cf. WÄGELE 1989: 235).

– Epimera of pleon segments I–V

The epimera of the pleon segments I–V are extended ventrally in *Metaphreatoicus australis*. Together with the lateroventral parts of the pleotelson, the uropod protopodites and the pleon ventrum the pleonal epimera are forming a chamber for the pleopods.
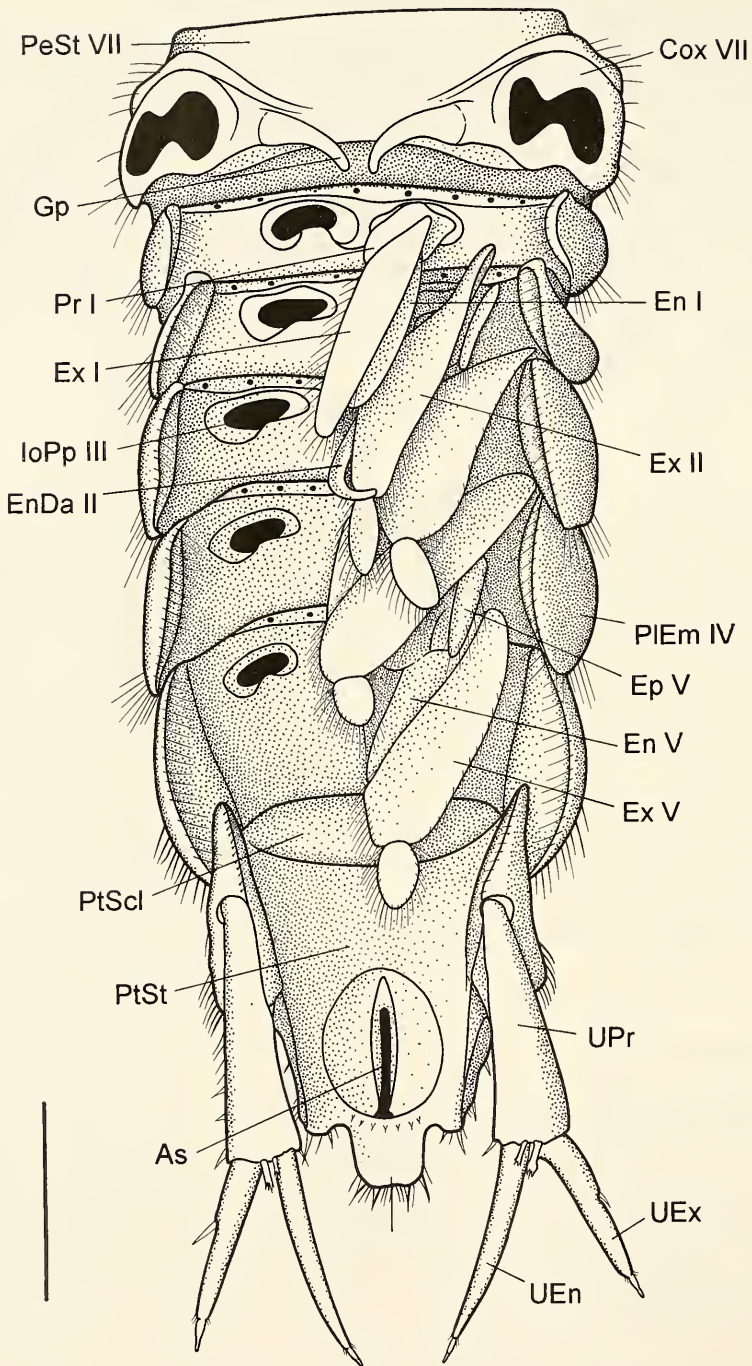
Fig. 2.   *Metaphreatoicus australis*, ♂, pleon and pereionite VII in ventral view. Pleopods of the right body side and pereiopods VII except for coxopodites removed. – Scale: 1 mm.

NICHOLLS (1943: 18) has pointed out, that phreatoicidean "forms in which this condition is well developed are those capable of swimming strongly, and there can be little doubt that this deepening of the channal in which the pleopods sweep makes these appendages more effective as natatory organs". Possibly, the manner of locomotion of the surface living phreatoicideans requires a natatory chamber to enhance the effect of the sweeping stroke of the pleopods. However, it also may be possible, that inside this channel a respiratory stream could be built up (WÄGELE 1989: 54), or the chamber gives protection to the pleopods against injury.

The described morphological character occurs in all surface dwelling species of the Phreatoicidea. Among them, *Onchotelson brevicaudatus* has developed the chamber in a perfect manner because the ventrolateral parts of the pleon as well as the uropods nearly are closing the channel at the midventral region, and thus only leaving an anterior and a posterior opening. Furthermore, it is obvious that the posterior opening is covered by the long pleotelsonic projection. Possibly, the above mentioned anatomical features are representing parts of one functional character complex of surface living phreatoicideans which we do not understand until now.

However, several subterranean phreatoicideans have short pleonal epimera scarcely covering the base of the pleopods (e.g. *Nichollsia kashiensis*). The phylogeny of the stygobiontic species has not yet been elucidated, but it appears that most of the subterranean groups represent separate invasions of the underground and that they have been derived from surface fresh water inhabiting ancestors (KNOTT 1986, WÄGELE 1990). Following this, a reduction of the ventrally extended pleonal epimera must have happened several times during evolution of stygobiontic species. Therefore, the above mentioned pleon shape caused by the ventrally extended pleonal epimera might be considered as a groundpattern character of the taxon Phreatoicidea (cf. WÄGELE 1989: 232). Since no other peracaridan taxon with the exception of the Amphipoda is showing a comparable character state, it seems to be an autapomorphy of the Phreatoicidea (cf. WÄGELE 1989: 232).

This assessment might be true, as long as the probability of a closer phylogenetic relationship between Isopoda and Amphipoda cannot be confirmed. SIEWING (1951, 1960), WATLING (1981) and DAHL (1992) argue clearly against the hypothesis of a close phyletic relation between both groups. Also WÄGELE (1989: 6) explains the superficial similarity of the external pleonal morphology in Phreatoicidea and Amphipoda by convergent evolution of characters. On the other hand, the attempt by SCHRAM (1986) to resurrect the taxon "Edriophthalma" to receive Amphipoda and Isopoda is not based on new relevant arguments.

– Pleon segment V

Most isopod taxa have subequal pleon segments, and this might be the plesiomorphous character state in the peracaridan outgroups. According to BRUSCA & WILSON (1991) and WILSON & PONDER (1992) an enlarged pleonite V occurs within the Peracarida in all species of the Phreatoicidea, the flabelliferan families Limnoriidae and Lynseiidae and the Anthuridea (in taxa where the pleonites are distinctly separate). In further isopod groups an enlarged pleonite V may occur, but not as a frequent or defining trait. At the present time, there are no further characters supporting a close relationship of the Phreatoicidea with one of the above

mentioned isopod taxa (cf. WÄGELE 1989, BRUSCA & WILSON 1991). Therefore, it may be possible that the character state has been evolved independently in the Phreatoicidea.

However, the species of the genus *Tainisopus* Wilson & Ponder, 1992 also have an enlarged pleonite V. Up to now it is unsolved, which isopod taxon would be the sistergroup of *Tainisopus* (cf. WILSON & PONDER 1992). The enlarged pleonite V could be a presumed synapomorphy of the Phreatoicidea and *Tainisopus*. But WILSON & PONDER (1992) list other characters indicating probable relationships of *Tainisopus* with the Asellota or with all "higher" isopods.

On account of these clues, this character represents at the moment a weak argument to substantiate the monophyly of the Phreatoicidea exclusive of *Tainisopus*.

– Male genital papillae

Within the Isopoda only the Phreatoicidea and the extraordinary genus *Tainisopus* have lateral penes arising directly from the coxopodites of the pereiopods VII. The genital papillae of *Tainisopus fontinalis*, however, articulate to triangular medial extensions of the seventh coxopodites which extend more medially than the coxopodites of any phreatoicidean species do (cf. WILSON & PONDER 1992).

Nevertheless, the situation of *Tainisopus* resembles also to the penial forms in Asellota, especially those of the "primitive" genus *Vermectias*. On account of the similar arrangement of the penes of *Tainisopus* and *Vermectias* WILSON & PONDER (1992) are expecting a possible synapomorphy of *Tainisopus* and the Asellota. The penes in *Vermectias* arise as cuticular outgrowths from proximal sclerites immediately medial to the functional coxopodites of the pereiopods VII (JUST & POORE 1992). JUST & POORE explain the medial migration of the genital papillae during evolution of most asellotans and all "higher" isopods by a medial extension of the above mentioned proximal sclerite along the posterior margin of the pereion sternum VII. An immediate connection between penes and pereiopod coxopodites VII without bridging by a proximal sclerite is extant inside the Isopoda only in the Phreatoicidea and, following WILSON & PONDER (1992), in *Tainisopus*.

JUST & POORE (1992), WILSON (1994) and WILSON & WÄGELE (1994) report that species of *Angeliera* and *Microcharon* (Microparasellidae) retain also the primitive isopodan condition of the male genital papillae attached directly to the coxae. However, WILSON (1994) and WILSON & WÄGELE (1994) concede that the "coxal position of the penes might be a reversion owing to the repositioning of the coxae".

In all probability, the Phreatoicidea have retained the plesiomorphous character state in relation to the isopodan groundpattern (cf. WÄGELE 1989, BRUSCA & WILSON 1991, WILSON 1991). Most malacostracan outgroups (Leptostraca, Stomatopoda, Decapoda, Thermosbaenacea, "Mysidacea", Amphipoda, Spelaeogriphacea, Mictacea) are showing a comparable condition with lateral penes or gonopores situated at the thoracopod coxopodites VIII. Within the Isopoda, an inverse evolutionary development of lateral penes starting with medial genital papillae is more difficult to explain than to assume a lateral position at the coxopodites being the original situation.

– Sternal processus

Posteriorly directed median sternal processus of the pereion or pleon segments are documented for Amphipoda, Tanaidacea, Oniscidea, Anthuridea and Valvife-
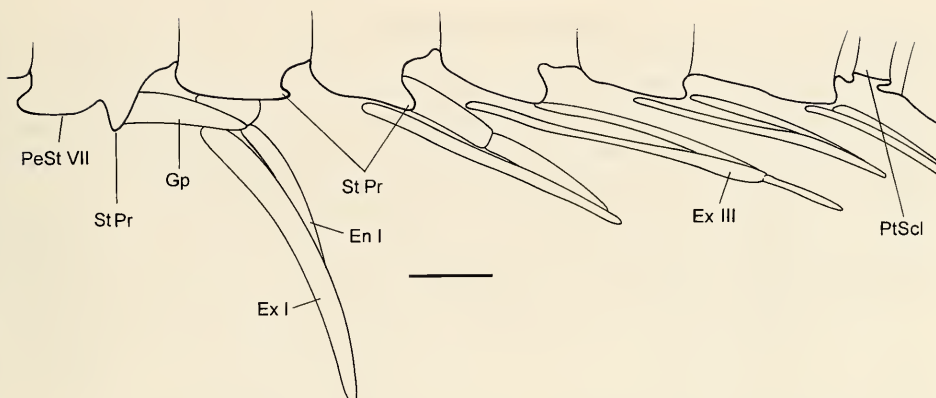
Fig. 3.   *Phreatoicopsis terricola*, ♂, median longitudinal section through the skeleton of the pleonal ventrum showing the sternal processus. – Scale: 1 mm.

ra (TAIT 1917, NICHOLLS 1943, ERHARD 1995a: 10). Median processus at different pleon segments are described by NICHOLLS (1943: 20) for phreatoicidean genera like *Eophreatoicus, Amphisopus, Mesacanthotelson* or *Phreatoicopsis*. This is confirmed by reexamination on *Phreatoicopsis terricola* where median processus are present at the pleon sternites I–V (fig. 3). Short median processus are present in *Metaphreatoicus australis, Colubotelson joyneri* and *Onchotelson brevicaudatus* on the pereion sternite VII and the pleon sternites I and II and on the pleon sternites I–V in *Mesacanthotelson tasmaniae* and *Paramphisopus palustris*. In contrast, pleonal sternal processus could not be shown in the phreatoicideans *Mesamphisopus* and *Nichollsia*. In specimens of the oniscidean genus *Ligia* long sternal processus occur medially on the caudal borders of the pleon sternites III–V (fig. 16; ERHARD 1995a: 6, fig. 8). On account of the character pattern, the presence of pleonal sternal processus probably might be a groundpattern character of the Phreatoicidea which has been reduced in some subordinate taxa.

– Apex of the pleotelson

   According to BRUSCA & WILSON (1991: 179) a dorsally curved apex of the pleotelson might be an apomorphous groundpattern character of the Phreatoicidea. However, NICHOLLS (1943: 22) pointed out that "those forms in which there is the greatest aggregation of primitive features, the telsonic projection is minute or absent". Furthermore, TIWARI (1955a, b) could not report a dorsally curved pleotelsonic projection in species of the subterranean genus *Nichollsia,* my own studies on *Nichollsia kashiensis* confirm this assessment.

   However, the surface living phreatoicideans *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus* and *Mesamphisopus,* investigated here, have all well developed pleotelsonic projections. To assess the development of such projections as an autapomorphy of a monophyletic taxon Phreatoicidea, the absence of a prolonged pleotelsonic apex (e.g. *Nichollsia, Phreatoicopsis*) has to be considered as a secondary reduction.

4.1.2. Endoskeleton (fig. 4)

4.1.2.1. *Metaphreatoicus australis*

The articulations between the trunk segments are situated laterally at the border of tergites and sternites. Therefore, the body is able to bend dorsally and ventrally chiefly by the action of the longitudinal dorsal and ventral musculature.

The anterior edges of the pleon tergites I–V have at each side nose-like apophyses serving as points of attachment for the pleopodal promotors (Mm 5 and 111–114) and further muscles (Mm 18–26a). According to ERHARD (1995a, 1996, 1997) these structures are described in the Oniscidea as "dorsal apophyses" (PlDAp), though they are situated in a more lateral than in a dorsal position in *Metaphreatoicus australis*. The serial homologous apophyses of the caudal pereion segments (PeDAp) and the pleotelson (PtDAp) are less developed in the latter species.

Each pleopod protopodite has two thin apophyses projecting dorsally into the pleon trunk. The apophysis which arises from the anterior margin of each protopodite (aPrAp) serves as point of attachment for the tergal pleopod promotor, and the posterior one (pPrAp) as point of insertion for the tergal pleopod remotor (figs. 4, 13–14).

From the anterior margin of the pleon tergite V and the pleotelson tergite a median apophysis projects forewards. That of the pleotelson (mdApPt) is much longer than the apophysis of the pleon tergite V (mdApV). Both support the longitudinal dorsal muscles of the pleon (figs. 4–6).

Between pleon sternite V and the caudal pleotelson sternite a short sclerite is inserted by transversal articular membranes (fig. 4: PtScl). The movable sclerite serves as area of attachment for the ventral longitudinal musculature (Mm 10, 12, 14, 40) and the pleotelsonic flexors (Mm 109, 110).

4.1.2.2. Comparison

– Mediodorsal apophyses of the pleotelson tergite

A mediodorsal apophysis of the pleotelson tergite could be shown in the phreatoicideans *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus, Nichollsia* as well as in the flabelliferan species *Anilocra frontalis*. In contrast, a comparable structure could not be documented in oniscidean species investigated so far (ERHARD 1995a, 1996, 1997). The pattern of character states, studied so far, probably may indicate the presence of a mediodorsal apophysis of the pleotelson tergite within the phreatoicidean groundpattern. The occurrence of mediodorsal pleotelson apophyses in further isopod taxa still has to be studied.

Unfortunately, the outgroup comparison with further peracaridan taxa based on literature data is limited. DANIEL (1932b, 1933) who described the trunk musculature in *Praunus* (Mysida), *Lophogaster* and *Gnathophausia* (Lophogastrida) did not show mediodorsal apophyses of the pleon segment VI as point of insertion of dorsal longitudinal muscles.

– Anterior apophyses of the pleopod protopodites I–V

Within the oniscidean groundpattern anterior pleopod protopodite apophyses are missing (ERHARD 1995a, 1996, 1997). The only pleopod promotor retained in the Oniscidea is M 5 within the pleonite II, all others have been completely reduced

(cf. chapt. 4.2.3.2., fig. 15). The oniscidean muscle M 5 is inserted without any apophysis on the anterior pleon sternite II. In the flabelliferan species *Anilocra frontalis* all pleopod promotors are present but the muscles are inserted directly on the protopodite front margins. However, in *Saduria entomon* (Valvifera) anterior protopodite apophyses are developed at the pleopods IV and V. The insertion of all promotors by anterior apophyses on the pleopod protopodites is developed in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson,* and *Phreatoicopsis.* In contrast, in *Paramphisopus, Mesamphisopus* and *Nichollsia* apophyses of the promotors are missing. Probably, pleopod promotor apophyses may be existent within the phreatoicidean groundpattern but only if the lack of promotor apophyses in subordinate taxa can be explained by secondary reduction.

– Ventrocranial pleotelsonic sclerite

The sclerite situated between the pleon sternite V and the caudal pleotelsonic sternite in *Metaphreatoicus australis* most likely represents the cranial part of the pleotelson. This is to state because the muscle bundles inserted there are homologa to oniscidean muscles which are inserted on the pleotelsonic front margin (e.g. M 14, M 40, cf. ERHARD 1997: fig. 86). Furthermore, it may be the sclerite derived from a ventroanterior part of a formerly free sixth pleon segment. This would prove the muscles Mm 109 and 110 to be "regular" ventrolongitudinal muscles between pleon segment VI and the telson which are flexing the telson by contraction.

In the Oniscidea a separate and movable ventrocranial sclerite of the pleotelson is missing (cf. ERHARD 1995a, 1996, 1997). In contrast, a correspondent sclerite also could be shown in *Colubotelson, Onchotelson, Mesacanthotelson, Phreatoicopsis, Paramphisopus, Mesamphisopus, Nichollsia* and in the flabelliferan species *Anilocra frontalis.* In the latter species, however, there is no intersegmental membrane between the pleon segment VI sclerite and the caudal pleotelsonic sternum.

All phreatoicidean species which have the strongly reflexed pleotelson actively use it in locomotion (e.g. *Crenoicus, Metaphreatoicus, Colubotelson, Paramphisopus*). Their body is orientated normal to the substrate (i.e. the sagittal plane forms a right angle with the plane of the bottom) and they make strong thrusts with the pleotelson onto the substrate (G. D. F. WILSON, pers. comm.). Equivalent movements have been observed also in subterranean and burrowing phreatoicideans as is reported by NICHOLLS (1943) on *Hyperoedesipus plumosus:* "... the uropods may, also, drag and kick upon the surface". GUPTA (1989: 12) describes the locomotion of burrowing *Nichollsia* (Phreatoicidea: Nichollsidae) as mostly walking but, if disturbed, can move "forward by vigorous blows of abdomen which drives the animal forward."

Mm 109 and 110 are assumed to be chiefly responsible for the above mentioned powerful thrusts of the pleotelson. To achieve that type of locomotion, a division of the pleotelsonic ventrum apparently might be favourable. It supports a higher mobility between pleon segment V and telson and a better transmission of the power of the ventral longitudinal muscles onto the caudal pleotelsonic region.

The type of moving by strong pleotelsonic thrusts probably might be an apomorphous feature of the Phreatoicidea while maintaining the ventral division between pleon segment VI and telson as well as the muscles Mm 109 and 110 rather is assumed to be a plesiomorphous than a secondarily derived character.
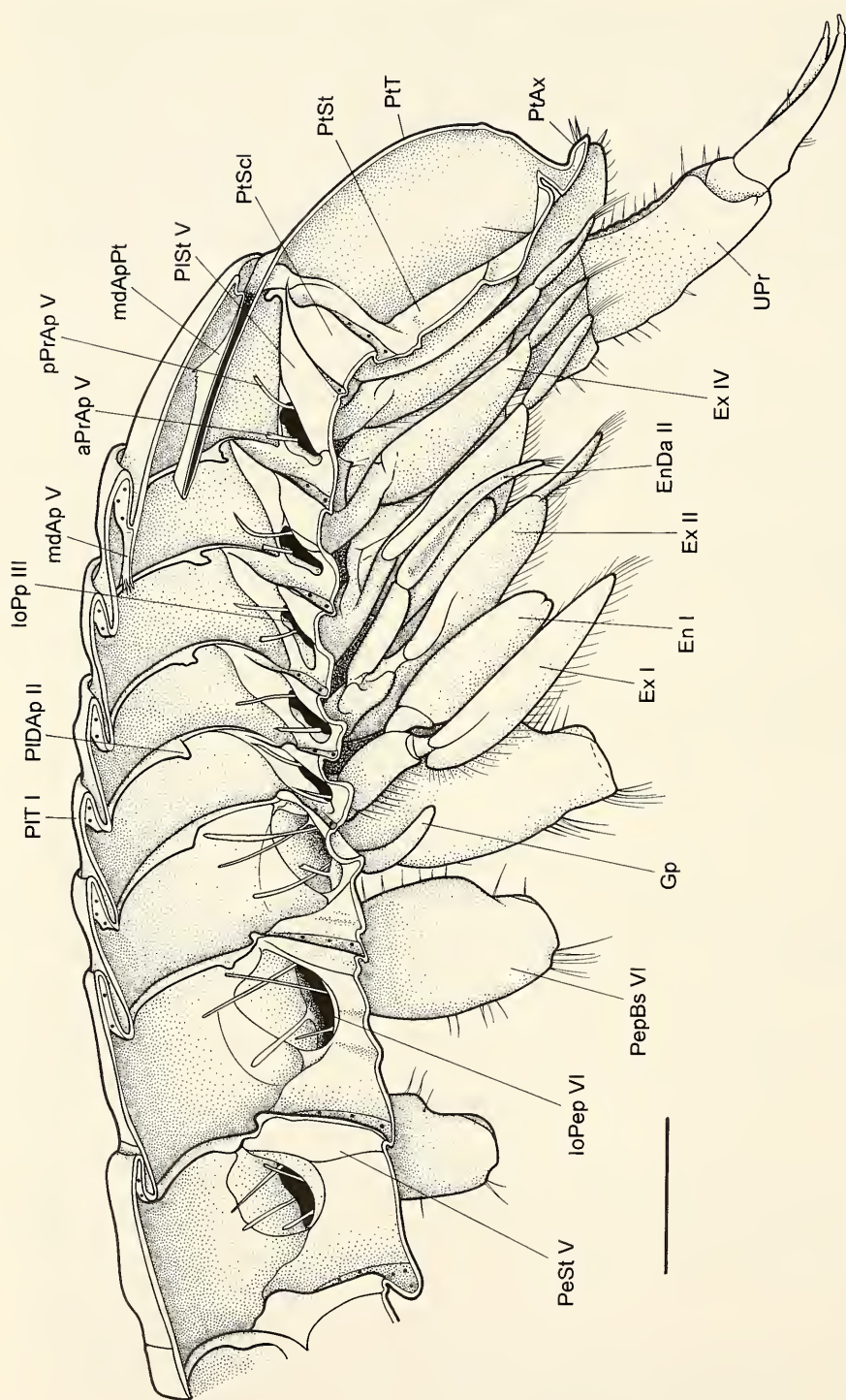
Fig. 4.　*Metaphreatoicus australis*, ♂, median longitudinal section through the skeleton of the pleon and the caudal pereion in medial view. – Scale: 1 mm.
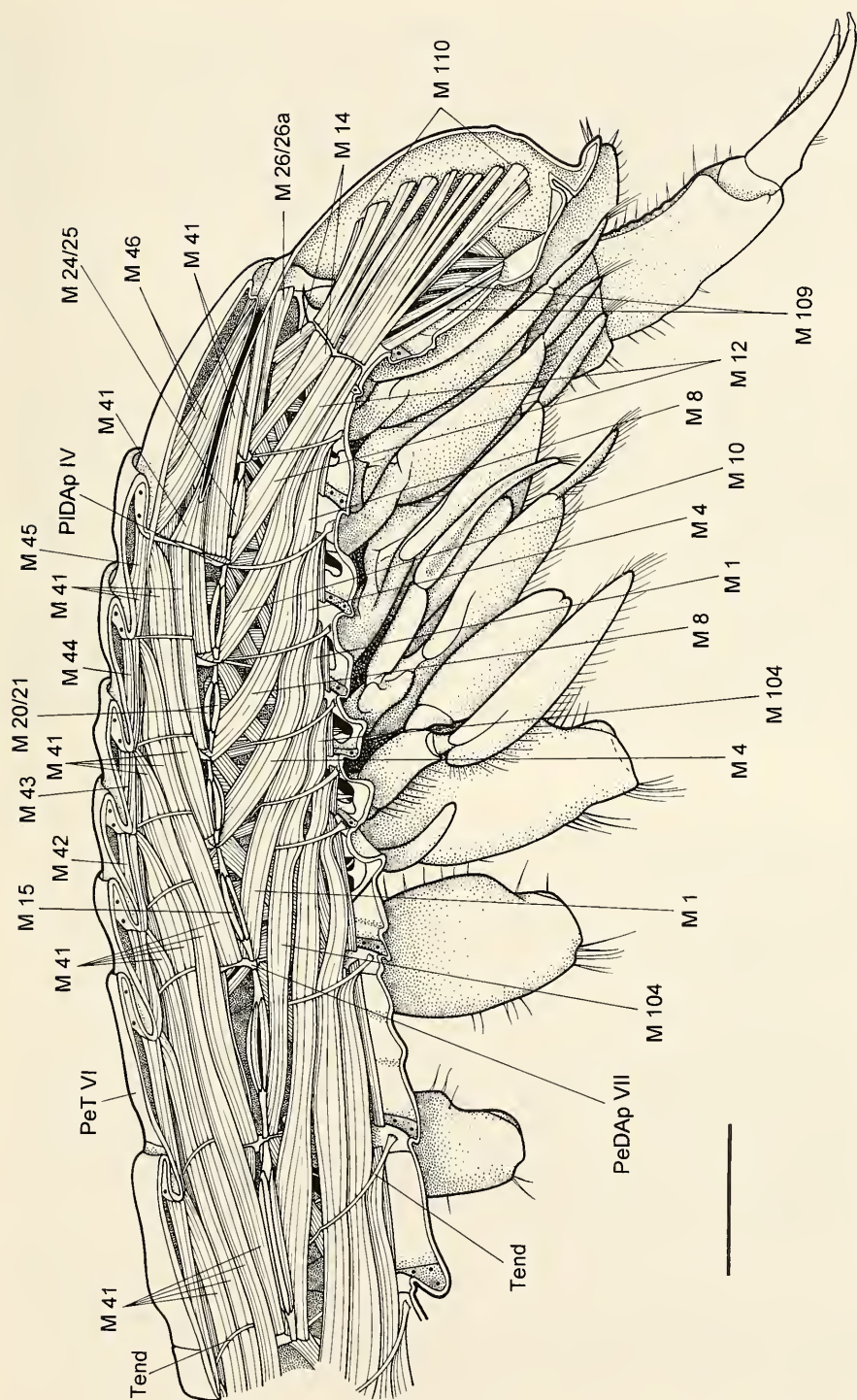
Fig. 5.   *Metaphreatoicus australis*, ♂, median longitudinal section through the pleon and the caudal pereion in medial view showing the musculature. – Scale: 1 mm.

4.2. Musculature

The pericardial septum which is also present in the pereion segments in *Metaphreatoicus australis* extends backwards within the pleon to the front margin of the pleotelson. It is attached by segmental tendons on the pleonal "dorsal apophyses" (PlDAp) and is connecting both sides of the pleon trunk as horizontal diaphragm. It separates the dorsal pericardial cavity from the ventral perivisceral sinus. In favour of clarity, the graphical documentation of the pericardial septum in *Metaphreatoicus* has been abandoned. Concerning this, it is referred to correspondent descriptions in the Oniscidea (ERHARD 1995a: 18).

4.2.1. Longitudinal musculature

In the Malacostraca the dorsal and ventral longitudinal muscles of the pleon (dLM, vLM) are differentiated into an external and an internal layer. In the case of the ventral muscle system a third central layer additionally may occur. Thus it is found to be the general plan of arrangement in groups like Leptostraca, Anaspidacea, Decapoda, Mysida, Lophogastrida and Tanaidacea (CLAUS 1887, 1888, SCHMIDT 1915, BERKELEY 1928, DANIEL 1932b, 1933, PATERSON 1968, NATH 1974). Within the Isopoda, the longitudinal muscle systems are described for *Oniscus asellus* and partly for the oniscids *Ligia oceanica, Tylos ponticus, Mesoniscus alpicola, Titanethes albus* and *Actaecia bipleura* (ERHARD 1995a, 1996, 1997).

The longitudinal muscles of *Metaphreatoicus australis* and further investigated phreatoicidean species are highly developed and are large in comparison with *Oniscus asellus*. These muscles might be involved into the powerful movements of the pleon and pleotelson which can be observed during locomotion in phreatoicidean species (see chapt. 4.1.2.2.).

4.2.1.1. Dorsal longitudinal musculature (dLM) (figs. 5–8)

4.2.1.1.1. *Metaphreatoicus australis*

On contraction, the dorsal longitudinal muscles approximates the pleon tergites and work as extensors of the pleon and the pleotelson.

4.2.1.1.1.1. External layer

Mm 42–46: Mm 42–45 each consists at one side of about five bundles per segment stretched between the front margins of neighbouring pleon tergites (figs. 5, 8). The muscle branches are located next to each other at the internal wall of the skeleton. M 46 is composed of two strong and four to six weaker muscle strands. They take their origin on the front margin of the pleon tergite V and are inserted on the median apophysis of the pleotelson tergite (fig. 4: mdApPt).

The segmental dorsal longitudinal muscles of *Metaphreatoicus australis* (Mm 42–46) have to be considered homologous to the "dorsal longitudinal muscles (d.l.m.)" of *Nichollsia kashiensis* reported by GUPTA (1989: 39), the "Musculi dorsales segmentales" of some oniscidean species described by GRUNER (1953: 154) and to Mm 42–46 of *Oniscus asellus* (ERHARD 1995a: 33).

4.2.1.1.1.2. Internal layer

M 41: The internal layer of the dLM consists of segmental as well as transgressional elements running at the inside of the external dorsal longitudinal muscles (fig. 5). The muscle system conforms to a fundamental pattern and is composed of simple units which are repeated close together within the segments of the pereion and pleon trunk. The pass of a single muscle unit from cranial to caudal is described as follows: Arising on the "dorsal apophysis" of a tergite (e.g. pleon tergite I, PlDAp), the muscle bundle passes three segmental borders and is inserted medially on the front margin of the next following tergite (pleon tergite V). Behind the first segmental border (front margin of pleon tergite II) there is no attachment whereas the front margins of the next two segments (pleon tergites III and IV) give attachment to the muscle bundle by slender tendons (figs. 5–6).

In the caudal pleon segments the basic plan of the dLM is more or less obscured by special modifications. The muscle bundle attached on the pleonal "dorsal apophysis" III passes only two instead of three segmental borders between origin and insertion, and the branch which is attached on the "dorsal apophysis" IV passes only one segmental border. The serial homologous bundle of the pleon segment V is presented only by a segmental branch. These different states of the three caudal muscle strands are caused by the fact that they are inserted altogether on the median apophysis of the pleotelson.

The dorsal longitudinal muscle system M 41 ("Musculi dorsales transgredientes" following GRUNER 1953: 154) of *Metaphreatoicus australis* has to be considered homologous to the "dorsal oblique muscles (d.o.m.)" of *Nichollsia kashiensis* described by GUPTA (1989: 40) and to M 41 of *Oniscus asellus* (ERHARD 1995a: 33).

4.2.1.1.2. Comparison

– M 46 and caudal units of M 41

The branches of M 46 in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* being situated inside the pleon segment V are strongly developed in comparison with the Oniscidea (fig. 5; ERHARD 1995a: fig. 28). An equivalent observation is reported by GUPTA (1989: 40) on the powerful dorsal longitudinal muscles within the pleon segment V in *Nichollsia kashiensis.* The author explains the strong development of these muscles by the powerful movements of the pleotelson which partly are caused by the dorsal extensors. In *Metaphreatoicus australis* and further investigated phreatoicideans the muscle strands of M 46 as well as the four caudal units of M 41 are inserted together on the median apophysis of the pleotelson tergite (figs. 4, 6: mdApPt) which is lifted up by their contraction. In the Oniscidea, the homologous muscles are inserted on the pleotelsonic front margin (ERHARD 1995a), a median pleotelsonic apophysis as point of insertion is missing (cf. chapt. 4.1.2.2.; fig. 7).
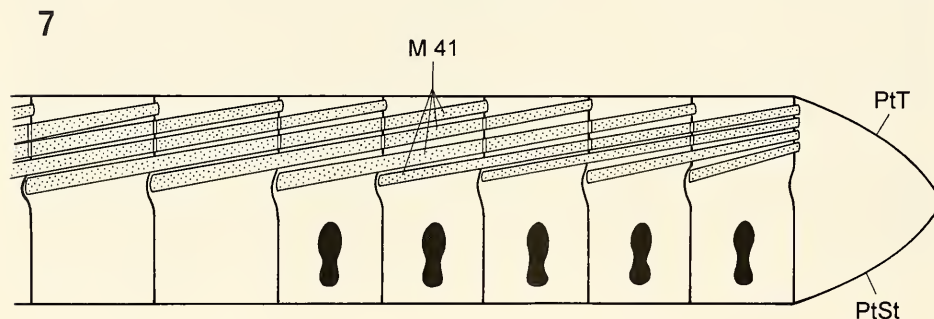
– M 41

The muscle system of M 41 in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* as well as in the terrestrial isopods *Ligia oceanica* and *Oniscus asellus* have comparable positions and comparable muscle subunits (figs. 6–7). However, the muscle bundles of

Phreatoicidea
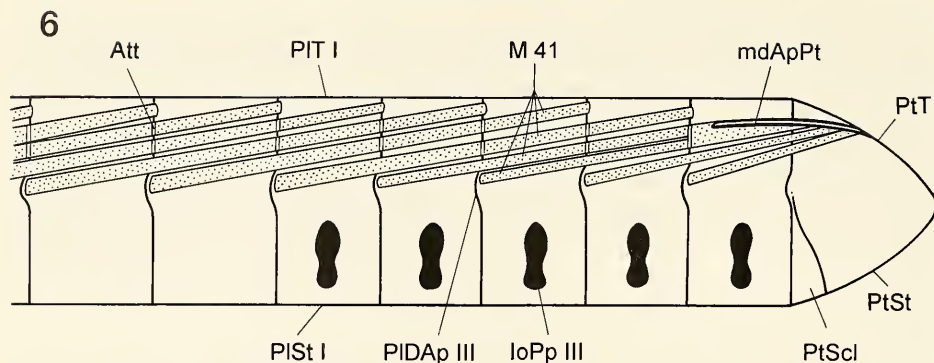
Oniscidea

Figs. 6–7.   Diagrams of the internal layer of the dorsal longitudinal musculature (M 41) within the isopodan pleon. – 6. Groundpattern Phreatoicidea; – 7. groundpattern Oniscidea.

the caudal pleon segments which are present in these phreatoicidean species and in *Ligia* obviously have been completely reduced or were integrated into the major longitudinal branch in *Oniscus asellus* (cf. ERHARD 1995a: 33). Furthermore, the individual strands of M 41 in *Oniscus* seem to be more condensed to one single branch than in the phreatoicidean species and in *Ligia*.

GUPTA (1989: 40) reported on "dorsal oblique muscles" within the pleon trunk of *Nichollsia* which have to be considered homologous to M 41 in the above mentioned phreatoicidean species. However, the author defines as point of insertion of the M 41-subunits the posteriodorsal end of a segment. In contrast, my own studies on *Nichollsia* could determine as point of attachment the front margin of the pleonal tergites as it is the situation in all isopods investigated so far *(Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus, Ligia, Oniscus).*

GUPTA (1989: 40) further describes his "dorsal oblique muscles" as covering only two segments which could be confirmed by my own observations in case of the transgressional parts. However, in *Metaphreatoicus, Colubotelson, Onchotelson,*

Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus as well as *Ligia* the homologous muscles are stretching over four segments. Therefore, *Nichollsia kashiensis* has a slightly obscured type of the internal layer of the dLM which presumably derived from the more complete version present in other phreatoicidean and oniscidean species.

Within the Peracarida, the only detailed investigations on the pleonal trunk musculature have been carried out by DANIEL (1932b, 1933). From this one may conclude that there are differences between the dorsal longitudinal muscle arrangements of *Praunus flexuosus* (Mysida), *Lophogaster typicus, Gnathophausia zoëa* (Lophogastrida) and the isopodan pattern. For example, the mysidacean species lack distinct transgressional units which, in contrast, are present in the investigated isopod species. Furthermore, the internal layer of the dorsal longitudinal muscles of the pleon in the "Mysidacea" are somewhat twisted around each other which cannot be observed within the Isopoda. Finally, the homologization of the individual muscle bundles appears to be difficult probably because of the large phyletic distance of both groups.

4.2.1.2. Ventral longitudinal musculature (vLM)

All ventral longitudinal muscles are flexors of the pleon. The ventral parts of this muscle system (Mm 34–39) approximate the pleonal sternites and thus shorten the ventral wall whereas the tergosternal subunits of Mm 1, 3, 4, 7, 8, 10, 12, 14, 105–108 additionally lift the pleonal ventrum. The vLM is differentiated into an external layer consisting of segmental subunits and a central and internal layer formed by segmental as well as transgressional elements.

4.2.1.2.1. External layer (fig. 8)

Mm 34–38: The external layer of the vLM in *Metaphreatoicus australis* consists at each body side of four (Mm 34–37) or three (M 38) bundles per pleon segment which are arranged next to each other (the serial homologa of the caudal pereion are divided into three branches). The pleonal muscles are stretched between the back margins of two successive sternites. They span over the insertion openings of the pleopods and are attached on the sclerites by tendons of connecting tissue as it is the condition in most other muscles of *Metaphreatoicus.* The muscles are located ventrally to the central and internal layer of the vLM. They have to be considered homologous to Mm 34–38 in *Oniscus asellus* (cf. ERHARD 1995a: 31) and to the "Musculi ventrales majores" described by GRUNER (1953).

M 39: The muscle which extends between the pleon sternite V and the pleotelson sternite in *Oniscus asellus* (ERHARD 1995a: 32) could not be found in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* and *Nichollsia.* This might be an apomorphous character state of the taxon Phreatoicidea.

4.2.1.2.2. Central layer (figs. 8–10)

4.2.1.2.2.1. *Metaphreatoicus australis*

Mm 3, 7, 105–108: The central layer of the vLM consists of successive subunits composed of tergosternal as well as ventral parts. The muscles take their origin on
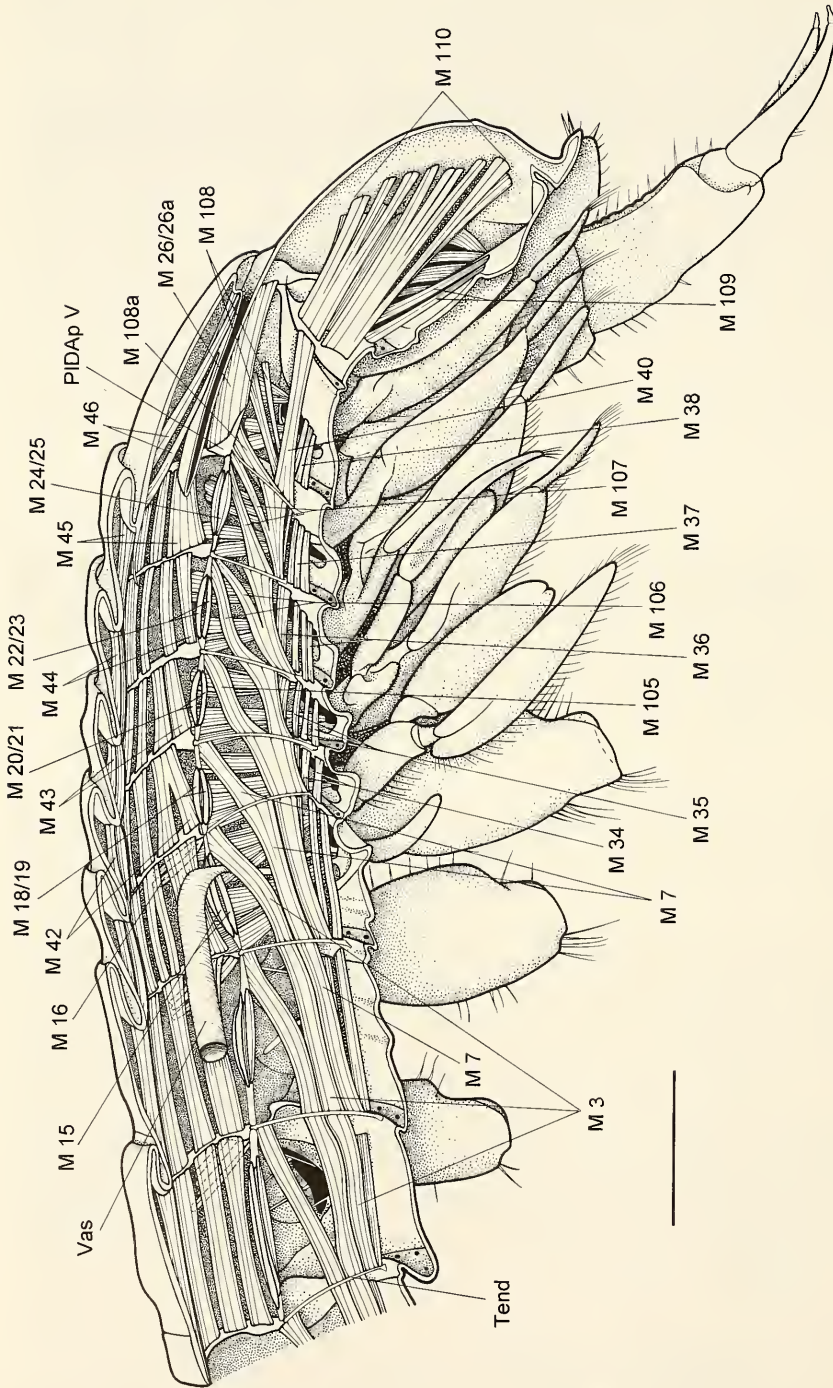
Fig. 8.   *Metaphreatoicus australis*, ♂, median longitudinal section through the pleon and the caudal pereion in medial view showing the musculature and the vas deferens. Inner layers of the dorsal and ventral longitudinal musculature and inner branches of M 46 removed. – Scale: 1 mm.

the "dorsal apophyses" of the pleonal (and pereional) tergites. The tergosternal components descend in ventrocranial direction, pass two segmental borders and are attached on the back margin of the concerning sternite by tendons of connecting tissue. They have ventral prolongations which form a ventral muscle cord passing cranially. This cord is attached also on the back margins of the sternites by slender tendons. Each subunit runs through three or two segments and passes four or three segmental borders.

The dorsoventral components of the pereional homologa in the Oniscidea have been described by GRUNER (1953) as "Musculi dorsoventrales procurrentes". Within the oniscidean groundpattern, the tergosternal units of the pleonal central layer of the vLM caudal to M 7 are completely reduced (ERHARD 1995a: 29, 1997: 20). Therefore, further serial homologa to M 3 and M 7 here documented in detail for the first time inside the isopodan pleon are indicated by the new numbers 105–108.

The above mentioned basic plan of the central layer of the vLM is slightly obscured in the different pleon segments of *Metaphreatoicus australis*. The varying types of the successive subunits are described in detail as follows:

M 3: Arises on the "dorsal apophysis" of the pleon tergite I, passes cranioventrally and is attached to a tendon which gets in touch with the pereion sternite VI and the serial homologous muscles M 7 and M 105. This dorsoventral component of M 3 consists of one bundle. The ventral prolongation is attached to the pereion sternite V and is inserted on the back margin of pereion sternite IV. At both points of attachment the prolongation of M 3 contacts two serial homologous muscles.

The same arrangement as described for M 3 applies to the serial homologous muscles of the pereion as well as the pleonal subunits M 7 and M 105 which are described briefly as follows:

M 7: Arises on the "dorsal apophysis" of pleon tergite II and is inserted on the back margin of pereion sternite V.

M 105: Arises on the "dorsal apophysis" of pleon tergite III and is inserted on the back margin of pereion sternite VI. In contrast to M 3 and M 7, the middle part of M 105 within the pleon segment I seems to be fused with the terminal part of M 106.

The dorsoventral components of the caudal muscles Mm 106–108 differ from their cranial serial homologa in being divided into two parts. Both bundles of each muscle have their origin on the same "dorsal apophysis."

M 106: Arises with two bundles on the "dorsal apophysis" of pleon tergite IV and passes cranioventrally. Within the pleon segment III the lower branch is fused with the ventral cord (prolongation of M 107). At the back margin of pleon sternite II this ventral cord is inserted. The upper branch of M 106 continues cranially to the back margin of pleon segment I where it contacts M 105. The middle part of M 105 presumably is fused with the distal part of M 106. The latter is inserted on pereion sternite VII.

The muscles M 107 and M 108 run only through two segments instead of three:

M 107: Arises with two bundles on the "dorsal apophysis" of pleon tergite V. Inside the pleon segment IV the lower branch is fused with the prolongation of M 108 and is inserted on the back margin of pleon sternite III. The upper branch of M 107 continues cranially and is inserted on the pleon sternite II.

M 108: The origin of the most caudally located subunit of the central layer should be expected on the front margin of the pleotelson. Possibly because of the enlarge-

ment of the pleon segment V, however, the points of attachment of both branches moved forward to the mid-lateral region of pleon tergite V. The tergosternal branches of M 108 run to the caudal margin of pleon segment IV and are attached there by a slender tendon. The ventral prolongation of M 108 incorporates the lower branch of the dorsoventral part of M 107 and is inserted on the back margin of pleon sternite III.

Directly behind the "dorsal apophysis" of pleon tergite V an additional muscle (M 108a) is attached which inserts on the connecting tissue of the pleonal sternite IV back margin. The muscle is strengthening the origin of the ventral cord of the central ventro-longitudinal layer within the pleon segment IV (= prolongation of M 108). Homologous muscles could be shown in *Onchotelson brevicaudatus, Mesacanthotelson tasmaniae* and *Mesamphisopus capensis.* In *Onchotelson brevicaudatus* a small correspondent muscle additionally is present at the "dorsal apophysis" IV.

M 40: In *Metaphreatoicus australis* the ventral components of the central layer of the vLM contacts the ventrocranial pleotelsonic sclerite by the flat muscle bundle M 40. It stretches between the front margin of the pleotelsonic sternite and the back margin of pleon sternite IV.

4.2.1.2.2.2. Comparison

– General condition of the central layer of the vLM

In *Metaphreatoicus Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* further serial homologous muscles to M 3 and M 7 are present within the pleon segments II–V (Mm 105–108, see fig. 9). As already mentioned above, the tergosternal branches of the pleonal central layer of the vLM in the Oniscidea are only represented by the muscles M 3 and M 7 (fig. 10; ERHARD 1995a: 29, 1997: 20). However, the ventral cord of the central layer still has been retained in *Ligia oceanica* and extends back to the pleotelson. Its individual branches, however, are condensed to a uniform strong muscle cord which is ending caudally with the subunit M 40 (fig. 10). Obviously, the condition of the pleonal central muscle layer of the vLM within the Oniscidea represents an apomorphous state in comparison with the complete phreatoicidean version.

GUPTA (1989: 41, fig. 15a) describes "lateral oblique muscles 1" (l.o.m_1) within the pleon of *Nichollsia kashiensis* which might be homologous to the subunits of the central layer in *Metaphreatoicus australis*. Following GUPTA (1989) the "l.o.m_1"-muscles "originate from the midlateral part of posterior margin and run down obliquely to the ventral margin at the anterior end of the same segment." Muscles with a pass like that only could lift a pleonal sternite to a small extent because there is no articulation axis within the same segment. On account of this, they cannot approximate neighbouring sternites to flex the pleonal ventrum.

My own observations have shown that the correspondent muscles of the central layer in *Nichollsia* have the same pass as it is the case in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* as well as all oniscidean species investigated so far (cf. ERHARD 1995a, 1996, 1997). The muscles take their origin on a "dorsal apophysis", pass two segmental borders in cranioventral direction and are inserted on the sternite back margin of the pre-preceding segment. Thus, the muscles are functioning as pleon

Phreatoicidea
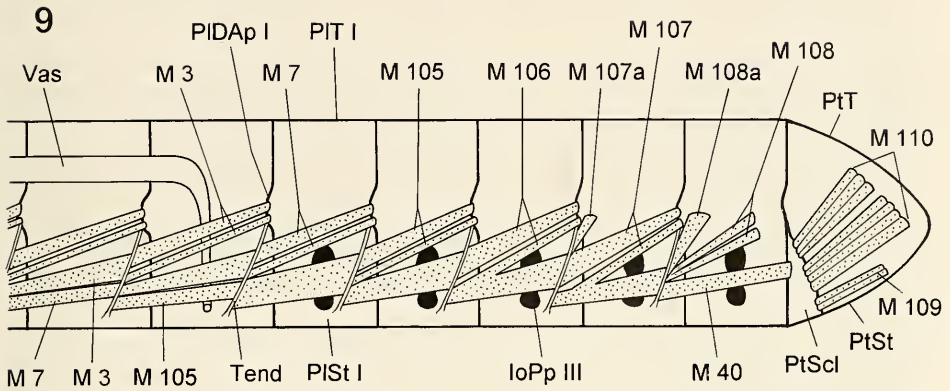
Oniscidea
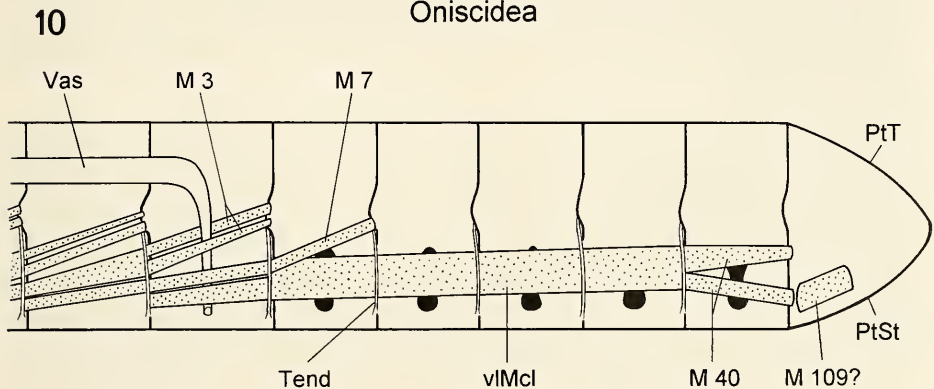
Figs. 9–10. Diagrams of the central layer of the ventral longitudinal musculature (Mm 3, 7, 105–108) and the pleotelsonic muscles Mm 109–110 within the isopodan pleon. – 9. Groundpattern Phreatoicidea; – 10. groundpattern Oniscidea.

flexors and are able to approximate neighbouring sternites by contraction. Furthermore, the muscles of the central layer of the vLM also in *Nichollsia kashiensis* have ventral prolongations forming a ventral muscle cord as it is the situation in other phreatoicidean species and the oniscidean groundpattern.

– M 108

On account of the principles of homonomy in metameric animals and corresponding to the run of its serial homologa it has to be expected that the muscle M 108 arises on the front margin of the pleotelson. However, in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* the point of insertion of M 108 is situated on the pleon tergite V instead of the pleotelson tergite front margin (fig. 8–9). This condition might represent an apomorphy of all phreatoicideans probably due to the enlargement of the pleonite V.

– Number of bundles of Mm 3, 7, 105–108

In *Metaphreatoicus australis* the tergosternal parts of Mm 106–108 each is composed of two bundles whereas the tergosternal branches of Mm 3, 7 and 105 only have one strand (fig. 8). Comparable conditions are present in *Paramphisopus palustris* and *Onchotelson brevicaudatus*, however, in these species the tergosternal part of M 105 additionally consists of two bundles. In *Colubotelson joyneri* only the tergosternal branch of M 108 is composed of two bundles, all other pleonal homologa are single strands. The same condition show *Mesamphisopus capensis* and *Nichollsia kashiensis* but the tergosternal part of M 105 additionally consists of two bundles. In *Phreatoicopsis terricola* the tergosternal units of Mm 3, 7 and 105–108 all are formed by two bundles. This is also the state in *Mesacanthotelson tasmaniae* with the exception that M 106 appears to be composed of only one branch. In *Ligia oceanica* and the oniscidean groundpattern (ERHARD 1995a: 29) the retained muscle M 3 and its serial homologa inside the pereion are composed of two bundles whereas the pleonal muscle M 7 only has one strand (fig. 10). The tergosternal parts of Mm 105–108 are completely missing in the Oniscidea. On account of the pattern of character states it has to be assumed that in the phreatoicidean groundpattern the tergosternal parts of the central layer are formed by two bundles (fig. 9).

– M 40

Within the investigated phreatoicidean species M 40 could be shown in *Metaphreatoicus*, *Colubotelson*, *Onchotelson*, *Mesacanthotelson*, *Paramphisopus*, *Phreatoicopsis*, *Mesamphisopus* and *Nichollsia* (fig. 9). A homologous muscle exists also in the terrestrial isopod *Oniscus asellus* (ERHARD 1995a: 32). There, it appears rather isolated and peculiar because all other caudal elements of the central ventro-longitudinal layer are absent. However, in *Ligia oceanica* and thus in the oniscidean groundpattern the pleonal ventral cord of the central layer is retained. M 40, which in *Ligia* is split up into two parts, forms the caudal part of it (fig. 10).

– Position of the vasa deferentia

In the oniscidean groundpattern (ERHARD 1995a: 29) as well as in the valviferan *Saduria entomon* the vas deferens of one body side passes between the two branches of M 3 (fig. 10). In *Metaphreatoicus*, *Colubotelson*, *Onchotelson*, *Mesacanthotelson*, *Paramphisopus*, *Phreatoicopsis* and *Mesamphisopus* the vas deferens runs lateral to M 3, no matter whether one (*Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Mesamphisopus*) or two (*Mesacanthotelson, Phreatoicopsis*) branches are present (fig. 9). This fact probably might be correlated with the observation reported by JUST & POORE (1992: 136). According to these authors, in isopods with medial penes the descent of the vas deferens within the pereionite VII is followed by a medial loop ventral to the vLM. In isopods with fully lateral penes the vas deferens curves in lateral direction. The first character state is present e.g. in *Aega*, *Serolis*, *Asellus*, *Pseudojanira* and many janiroid families. The latter character state occurs in the Phreatoicidea (JUST & POORE 1992).

Provided the position of the descending vas deferens to M 3 depends on the location of the genital papillae then the plesiomorphous character state in respect to the isopodan groundpattern might be that of the Phreatoicidea because the ancestral position of the isopod penes is assumed to be lateral, on the pereiopod coxopodites VII (cf. chapt. 4.1.1.2.).

4.2.1.2.3. Internal layer (figs. 5, 11–12)

4.2.1.2.3.1. *Metaphreatoicus australis*

Mm 104, 1, 4, 8, 10, 12, 14: The internal layer of the pleonal vLM is composed of tergosternal subunits whose ventral continuations, which are connected to each other, are forming a strong ventral muscle cord. The subunits have special numbers because in *Oniscus asellus, Ligia oceanica* and further oniscid species, where the muscles have been first described in detail (ERHARD 1995a: 15, 18), the tergosternal bundles of at least the caudal pleon segments are separated from the main ventral cord of the internal layer of the vLM. Therefore, the ventral continuations in *Ligia* and *Oniscus* appear as a separate layer of the vLM which has been described as Mm 32 and 33. By contrast, in *Metaphreatoicus australis* the subunits of the internal layer are arranged in a strict metameric uniformity and the tergosternal form an entity together with the ventral parts (fig. 5). Therefore, a special description of the ventral continuations as M 32 or M 33 is not necessary.

The muscles have been described superficially by GRUNER (1953) as "Musculi dorsoventrales recurrentes". To set an example for the run of the subunits, M 4 is described in detail:

M 4: Arises by a tendon of connecting tissue on the "dorsal apophysis" of pleon tergite I (figs. 4–5: PlDAp) and passes caudoventrally and medially to another tendon which gets in touch with the pleon sternite II and the muscles M 104 and M 1. At that point, M 4 integrates into the ventral part of the internal layer of the vLM. Passing caudomedially, M 4 is attached by a tendon on pleon sternite III and is connected with M 1 and M 8. M 4 is ending on the pleon sternite IV by connecting tissue which also contacts the muscles M 8 and M 10.

The cranially and caudally situated serial homologa to M 4 exactly conform to the pattern described above. Therefore, the muscles Mm 104, 1, 8 and 10 only are documented briefly:

M 104: Arises on the "dorsal apophysis" of pereion tergite VI and is inserted on pleon sternite II behind the insertion opening of pleopod II.

M 1: Arises on the "dorsal apophysis" of pereion tergite VII and is inserted on pleon sternite III.

M 8: Arises on the "dorsal apophysis" of pleon tergite II and is inserted on pleon sternite V.

M 10: Arises on the "dorsal apophysis" of pleon tergite III and is inserted on the ventrocranial pleotelsonic sclerite.

In the caudal pleon segments the general plan of the internal layer of the vLM is obscured. Because the muscles M 12 and M 14 are inserted together with M 10 on the same point (ventrocranial pleotelsonic sclerite) the muscles are shortened and some intermediate attachment points by tendons are left out:

M 12: Arising on the "dorsal apophysis" of pleon tergite IV (fig. 5: PlDAp IV) the muscle is attached by a tendon on the pleon sternite V and contacts M 10 and M 14. It is inserted together with M 10 and M 14 on the ventrocranial pleotelsonic sclerite. Like its cranial serial homologa M 12 is composed of one bundle.

M 14: Arising on the "dorsal apophysis" of pleon tergite V the muscle is inserted together with M 10 and M 12 on the ventrocranial pleotelsonic sclerite. Composed of three bundles.

4.2.1.2.3.2. Comparison

– General condition of the internal layer of the vLM

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* the internal layer of the pleonal vLM shows a strict metameric uniformity without condensation or reduction, the individual subunits are preserved in full length (figs. 5, 11). Compared with the derived situation in the Oniscidea (see below) this character state is assumed to be an ancestral condition of the internal vLM within the taxon Isopoda.

– Pass of the tergosternal parts of the internal layer

The tergosternal parts of Mm 104, 1, 4, 8, 10 and 12 in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* pass one segmental border without attachment on its way
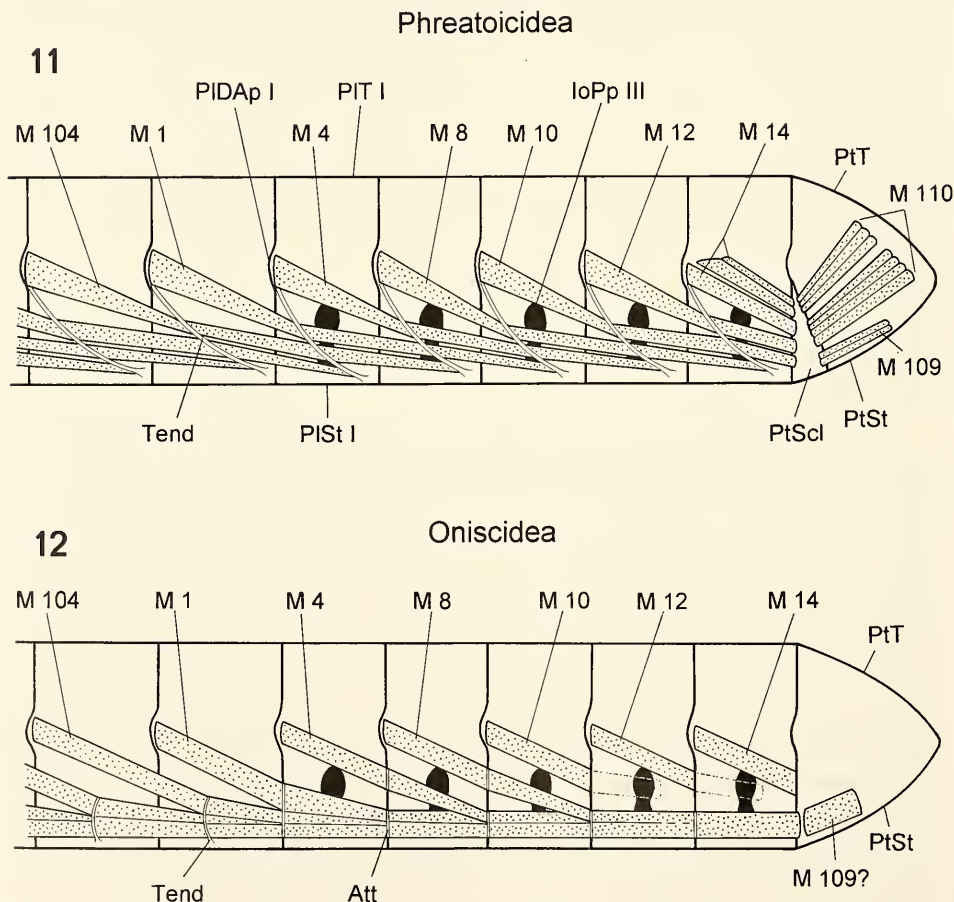
Figs. 11–12. Diagrams of the internal layer of the ventral longitudinal musculature (Mm 104, 1, 4, 8, 10, 12, 14) and the pleotelsonic muscles Mm 109–110 within the isopodan pleon. – 11. Groundpattern Phreatoicidea; – 12. groundpattern Oniscidea.

backwards and are inserted on the back margin of the next following sternite by a tendon. This is assumed to be also the situation in the phreatoicidean groundpattern. For example, M 4 arises on the "dorsal apophysis" of pleon tergite I and is inserted on the back margin of pleon sternite II.

An equivalent pattern is also present in the pereion segments of the Oniscidea, for example in *Ligia oceanica* (fig. 12)[2]. However, in the oniscidean species the tergosternal parts of the pleonal muscles M 1, 4, 8, 10, 12 do not pass one segmental border but are inserted on the next following intersegmental border by ventral apophyses. For example, M 4 arises on the "dorsal apophysis" of pleon tergite I and is inserted in the area of the segmental border between pleon sternite I and II (ERHARD 1995a, 1996, 1997). It has to be concluded that there happened an evolutionary transformation concerning the pleonal type of insertion of the correspondent musculature within a stemline of a monophyletic group which the taxon Oniscidea belongs to.

– Ventral prolongations of Mm 1, 4, 8, 10, 12

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Mesamphisopus* and *Nichollsia* the tergosternal parts of the muscles Mm 1, 4, 8, 10 and 12 are directly connected with their ventral prolongations forming a ventral muscle cord (figs. 5, 11). Within the Oniscidea direct connections between the tergosternal parts of Mm 1, 4, 8 and the ventral muscle cord of the inner layer of the vLM could be shown in several investigated species. However, the tergosternal parts of the muscles Mm 10 and 12 in all oniscidean species investigated so far are isolated from the ventral longitudinal muscle cord (fig. 12; ERHARD 1995a, 1996, 1997).

Another difference between Phreatoicidea and Oniscidea concerns the condition of the ventral part of the inner layer of the vLM: In phreatoicideans the ventral prolongations have been retained as individual branches whereas in oniscideans these branches are more or less condensed forming one uniform muscle cord (in species of the family Tylidae the correspondent ventral muscle cord has been reduced to a great extent).

The presumable plesiomorphous pattern of the internal layer of the vLM described for the Phreatoicidea is also present within the pereion segments of oniscidean species. However, inside the pleon of *Ligia oceanica, Oniscus asellus* and further investigated oniscidean species the tergosternal parts of the muscles Mm 4, 8, 10, 12 and 14 seem to be shifted laterally. Therefore, they are isolated from the main ventral cord of the internal layer (cf. ERHARD 1995a, 1996, 1997).

– M 1

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Mesamphisopus* and *Nichollsia* as well as in the oniscidean groundpattern there is no modification of M 1 in respect to its pleonal serial homologa. However, the muscle M 1 evolved to a specialized gonopod locomotor within male specimens of Mesoniscidae, Synocheta and Crinocheta (= Oniscidea: Orthogonopoda), moving the linear pleopod endopodite II (ERHARD 1997: 20).

---

[2] Earlier interpretations which include insertions on the segmental borders of the tergosternal parts of the serial homologa to Mm 1, 4, 8, 10, 12, 14 within the pereion (cf. ERHARD 1995a: fig. 24, 1996: fig. 7) are revised by the results of the present investigation.

4.2.2. Stabilizators of the pleonal "dorsal apophyses"
(figs. 5, 8)

4.2.2.1. *Metaphreatoicus australis*

4.2.2.1.1. Mm 18–26a

In *Metaphreatoicus australis* neighbouring pleonal "dorsal apophyses" (PlDAp) are braced by horizontal muscles consisting of two and in the case of M 18/19 of three branches. They are attached on the apophyses by tendons of connecting tissue (fig. 8).

Comparable muscles are present in the Oniscidea. Within the reconstructed oniscidean groundpattern of the pleon there are two muscle branches stretched between two neighbouring "dorsal apophyses" (ERHARD 1997: 24). In *Ligia oceanica,* which shows numerous plesiomorphous character states in relation to the oniscidean groundpattern, the muscle branches Mm 18–26a also are attached by tendons. However, in the Oniscidea both branches of one segment are clearly divided because the origin of the upper muscle branch is situated at a distance of the origin of the lower bundle on the "dorsal apophysis" (ERHARD 1995a: fig. 19, 1997: fig. 27). In contrast, in *Metaphreatoicus australis* the different branches of each horizontal muscle arise together by one tendon on a dorsal apophysis.

On the one hand, the horizontal muscles of *Metaphreatoicus australis* could be homologous only to the lower muscle bundles Mm 18, 20, 22, 24, 26 of the Oniscidea (cf. ERHARD 1997: fig. 27). Then, the upper oniscidean bundles (Mm 19, 21, 23, 25) could be homologous to the lower branches of the segmental dorsal longitudinal musculature (Mm 42–46).

On the other hand, the two or three branches of the horizontal muscles of *Metaphreatoicus australis* may be homologous to both, upper and lower bundles of the Oniscidea (Mm 18–26a). This hypothesis is confirmed by the fact that in the oniscidean species investigated so far (ERHARD 1995a, 1996, 1997) the bundles of the muscle pairs Mm 18/19, 20/21, 22/23, 24/25 and 26/26a always have one common point of insertion on the pleonal "dorsal apophyses" by slender tendons which is comparable to the condition of the horizontal muscle branches in *Metaphreatoicus australis.* Furthermore, with the exception of the first pleonal horizontal muscle (Mm 18/19), whose lower branch is subdivided, the caudal muscles in *Metaphreatoicus* are composed of two branches as it is the plesiomorphous situation in the Oniscidea too. Therefore, the paired oniscidean muscles Mm 18–26a with care are assumed to be homologous to the horizontal muscles in *Metaphreatoicus australis* and further phreatoicidean species.

These muscles Mm 18–26a of *Metaphreatoicus* and their tendons of insertion give attachment to the horizontal pericardial septum and additionally to transversal intersegmental tendons which descend to the sternites and ascend to the tergites.

M 18/19: A group of three bundles arising on the "dorsal apophysis" of pleon tergite I. They are inserted together on the "dorsal apophysis" of pleon tergite II.

M 20/21: Arises on the "dorsal apophysis" of pleon tergite II and is inserted on the "dorsal apophysis" of pleon tergite III. Composed of two bundles.

M 22/23: Arises on the "dorsal apophysis" of pleon tergite III and is inserted on the "dorsal apophysis" of pleon tergite IV. Composed of two bundles.

M 24/25: Arises on the "dorsal apophysis" of pleon tergite IV and is inserted on the "dorsal apophysis" of pleon tergite V. Composed of two bundles.

M 26/26a: Arises on the "dorsal apophysis" of pleon tergite V by an extended tendon of connecting tissue and is inserted on the front margin of the pleotelsonic tergite lateral to the mediodorsal apophysis. Composed of one strong and one small branch. The small bundle is situated lateral to the strong one.

4.2.2.1.2. Mm 15–17

Within the isopod pereion there are serial homologa to the pleonal muscles Mm 18–26a (cf. ERHARD 1995a, 1996, 1997). The muscle M 15 within the pereion segment VII of *Metaphreatoicus australis* is described as follows:

M 15: Arises on the "dorsal apophysis" of pereion tergite VII and is inserted on the "dorsal apophysis" of pleon tergite I. Composed of about five bundles.

In contrast to the pleonal situation, the pereional segments within the Isopoda have additional stabilizers of the "dorsal apophyses" and tergite locomotors. The muscle M 16 within the pereionite VII of *Metaphreatoicus* is described as follows:

M 16: Arises caudolaterally on the pereion tergite VII and is inserted on the "dorsal apophysis" of pleon tergite I. Composed of two bundles.

In *Metaphreatoicus australis* and *Colubotelson joyneri* the serial homologa to M 16 within the segments cranial to pereionite VII are stronger developed and consist of about four bundles. All these muscles stabilize the "dorsal apophyses" or work as segment locomotors by moving neighbouring tergites.

M 17: Not existent (see comparison: M 17).

4.2.2.2. Comparison

– Existence of M 17

An additional muscle M 17 stretches between the caudal part of the pereion tergite VII and the medial area of pleon tergite I front margin in all investigated oniscidean species (ERHARD 1995a, 1996, 1997). A comparable muscle could not be found in *Metaphreatoicus, Mesacanthotelson, Colubotelson, Onchotelson, Paramphisopus* and *Nichollsia.*

– Condition of Mm 18–26a

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Mesamphisopus* and presumably in *Nichollsia* the muscle group Mm 18/19 is composed of three bundles whereas Mm 20/21, 22/23, 24/25 and 26/26a are formed by two bundles respectively. In the oniscidean groundpattern all correspondent muscle-pairs are consisting of two branches (ERHARD 1997: 24). In the Phreatoicidea the branches of one muscle group of Mm 18–26a are attached together on the points of origin and insertion by tendons of connecting tissue. A comparable condition applies to the homologous strands in the Oniscidea with the difference that the bundles of each muscle-pair are separated at their origin (ERHARD 1995a, 1996, 1997).

– M 26/26a

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Pharamphisopus, Mesamphisopus* and *Nichollsia* the muscle M 26/26a is developed much stronger and longer in comparison to its serial homologa Mm 18/19, 20/21, 22/23 and 24/25. This condition might be a groundpattern character of the Phreatoicidea probably due to the enlargement of the pleonite V and/or the special type of locomotion by pushing off with the pleotelson. Within the oniscidean groundpattern the condition of M 26/26a is comparable to its serial homologa inside the pleonites I–IV (ERHARD 1995a, 1996, 1997).

– M 15

The oniscidean muscle M 15 always appears as single branch whereas the homologous muscle in *Metaphreatoicus* and *Onchotelson* consists of 3–5 bundles, in *Mesacanthotelson* of 2–3 bundles and in *Mesamphisopus* of two bundles.

– M 16

GUPTA (1989: 41) noticed a "lateral oblique muscle 3 (l.o.m₃)" in *Nichollsia kashiensis* which "originates from the same point of mid lateral line at the posterior end of the segment and is attached to the hypodermis infront". Considering GUPTA's fig. 15B, the muscle may correspond to M 16 which is present in *Metaphreatoicus, Onchotelson, Colubotelson, Paramphisopus* and the oniscidean species investigated so far (ERHARD 1995a, 1996, 1997). However, in all these groups M 16 and its serial homologa occur only inside the pereion whereas GUPTA (1989: 41) figures his "l.o.m₃" within the pleonite I. My own studies on *Nichollsia* could show M 16 within the pereion segment VII and serial homologa to M 16 only within the pereion segments. In *Mesacanthotelson tasmaniae* and *Mesamphisopus capensis* M 16 could not be shown.

4.2.3. Extrinsic pleopod locomotors (figs. 13–15)

4.2.3.1. *Metaphreatoicus australis*

The musculature of the typical pleon segment in *Metaphreatoicus australis* comprises dorsoventral muscles which move the pleopods forwards and backwards. These pro- and remotors arise on the tergite and pass ventromedially to the pleopod protopodites (fig. 13). Because the pleopods in terrestrial isopods usually are tipped up to the pleon ventrum, promotor and remotor has been described by ERHARD (1995a, 1996, 1997) as pleopod "depressor" and "levator".

4.2.3.1.1. Pleopod promotors (Mm 111, 5, 112–114)

M 111: Arises on the "dorsal apophysis" of the pleon tergite I front margin and is inserted on the anterior apophysis of the pleopod protopodite I. Composed of three bundles.

M 5: Arises with two branches on the "dorsal apophysis" of the pleon tergite II front margin and with one branch on the area situated caudally to the apophysis. It is inserted on the anterior apophysis of pleopod protopodite II. Homologous to M 5 within oniscidean species, where in males the muscle work as gonopod locomotor (ERHARD 1995a: 15, 30; 1996: 13).

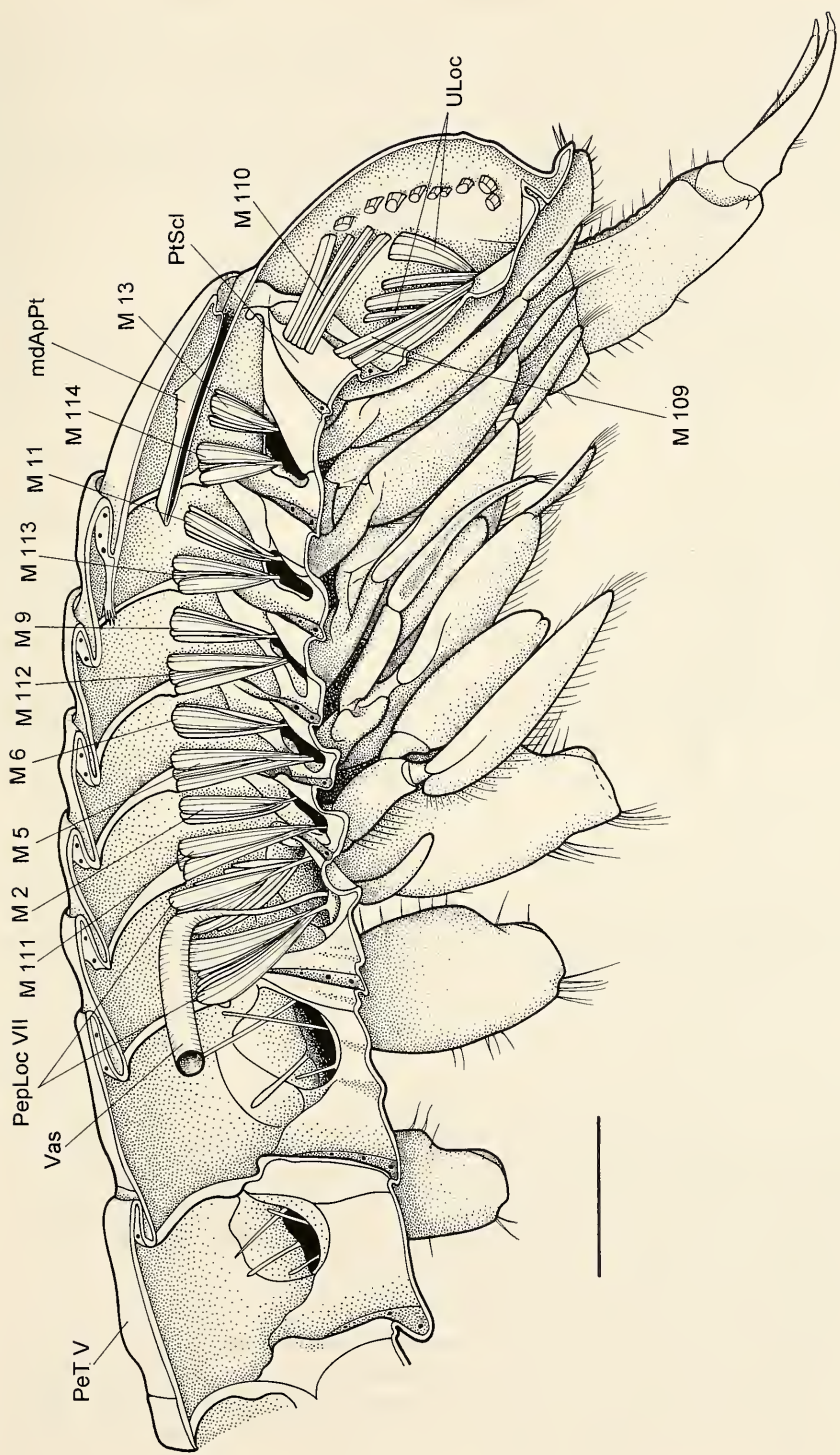**M 112:** Arises with two branches on the "dorsal apophysis" of the pleon tergite

Fig. 13. *Metapbreatoicus australis*, ♂, median longitudinal section through the pleon and the caudal pereion in medial view showing the extrinsic pleopod locomotors and the vas deferens. Dorsal and ventral longitudinal musculature and parts of M 110 removed. – Scale: 1 mm.

III front margin and with one branch on the area caudal to the apophysis. It is inserted on the anterior apophysis of pleopod protopodite III.

M 113: Arises with two branches on the "dorsal apophysis" of the pleon tergite IV front margin and with one branch on the area caudal to the apophysis. It is inserted on the anterior apophysis of pleopod protopodite IV.

M 114: Arises with two branches on the "dorsal apophysis" of the pleon tergite V front margin and with one branch on the area caudal to the apophysis. It is inserted on the anterior apophysis of pleopod protopodite V.

4.2.3.1.2. Pleopod remotors (Mm 2, 6, 9, 11, 13)

Each pleopod remotor is composed of two main bundles and about four smaller additional branches. At the area of insertion the latter are fused to two bundles. The remotors have to be considered homologous to the oniscidean muscles Mm 2, 6, 9, 11, 13 (ERHARD 1995a, 1996, 1997).

M 2: Arises caudolaterally on the pleon tergite I and is inserted on the posterior apophysis of pleopod protopodite I.

M 6: Arises caudolaterally on the pleon tergite II and is inserted on the posterior apophysis of pleopod protopodite II.

M 9: Arises caudolaterally on the pleon tergite III and is inserted on the posterior apophysis of pleopod protopodite III.

M 11: Arises caudolaterally on the pleon tergite IV and is inserted on the posterior apophysis of pleopod protopodite IV.

**M 13:** Arises caudolaterally on the pleon tergite V and is inserted on the posterior apophysis of pleopod protopodite V.

4.2.3.2. Comparison

– Occurrence and insertion of the pleopod promotors

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* as well as in the valviferan *Saduria entomon* and the flabelliferan species *Anilocra frontalis* the pleopods I–V each have one extrinsic tergosternal promotor (fig. 14). This condition represents a character of the malacostracan and isopodan groundpatterns (ERHARD 1995a: 29). In the oniscidean species investigated so far only the extrinsic promotor M 5 of the pleopod II has been retained, those of the other pleopods have been completely reduced (fig. 15). The muscle M 5 in the terrestrial isopods chiefly work as locomotor of the male pleopod endopodite II which serves as a gonopod. The muscle is not inserted on the pleopod protopodite II as it is the condition in phreatoicideans but on the pleon sternite II. In females M 5 often is reduced or completely missing (ERHARD 1995a, 1996, 1997). The oniscidean character state might represent an apomorphous feature in respect to the isopodan groundpattern.

– Composition of the pleopod promotor M 5

In *Metaphreatoicus, Colubotelson, Paramphisopus, Mesamphisopus* and *Nichollsia* M 5 as well as Mm 111–114 are composed of 3 bundles. The homologous muscles in *Onchotelson brevicaudatus* are formed by 5 branches, in *Mesacanthotelson tasmaniae* by 2 bundles. Within the Oniscidea M 5 consists of 1 or 2 bundles (ERHARD 1995a, 1996, 1997).
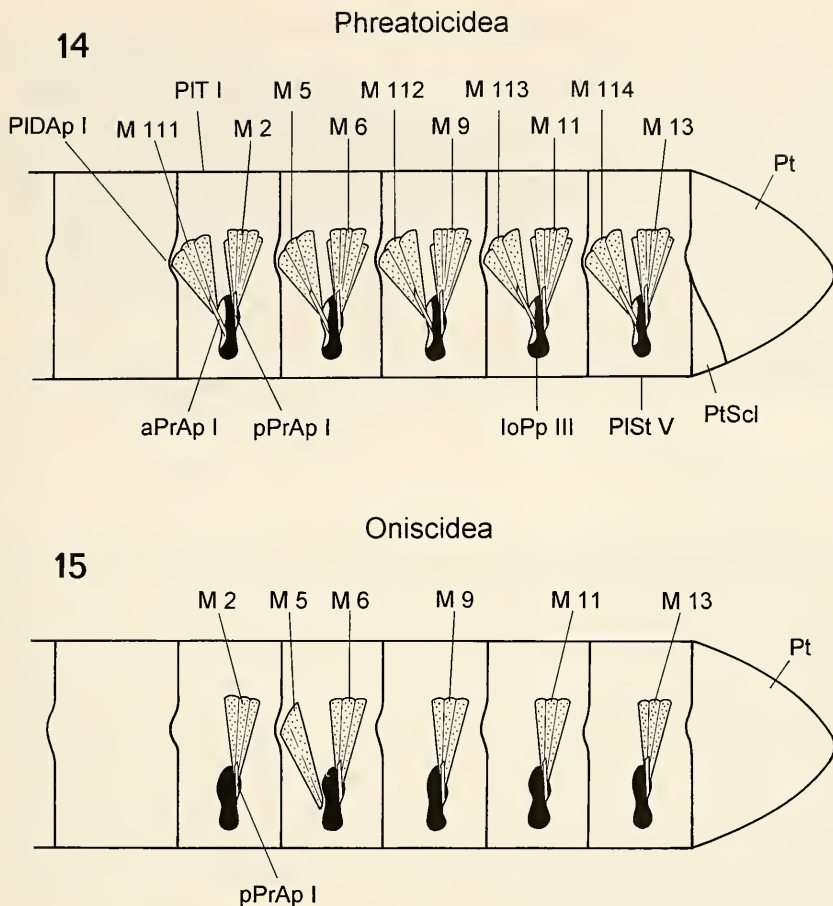
Figs. 14–15. Diagrams of the extrinsic pleopod locomotors within the isopodan pleon. – 14. Groundpattern Phreatoicidea; – 15. groundpattern Oniscidea.

– Composition of the pleopod remotors Mm 2, 6, 9, 11, 13

The muscles Mm 2, 6, 9, 11, 13 in *Metaphreatoicus australis, Colubotelson joyneri* and *Paramphisopus palustris* consist of two strong and about four weak bundles. In *Onchotelson brevicaudatus* the muscles are composed by 3 strong and about 4 weak bundles. In *Mesacanthotelson tasmaniae* each remotor consists of numerous equal branches forming one unit. *Mesamphisopus capensis* and *Nichollsia kashiensis* have pleopod remotors with about 4 bundles. Within the oniscidean groundpattern the homologous muscles are composed by three branches. In subordinate groups of the terrestrial isopods the number of branches may be further diminished (ERHARD 1997: 23).

4.2.4. Pleotelsonic musculature (figs. 8–10, 13, 16)

4.2.4.1. *Metaphreatoicus australis*

Within the caudal region of the phreatoicidean pleotelson the presence of numerous muscle bundles is conspicuous (figs. 8–9). They belong to the pleotelsonic muscles M 109 and M 110 working as prolongation of the vLM. The muscles flex the caudal part of the pleotelson by contraction.

M 109: Arises medially on the ventrocranial pleotelsonic sclerite, passes caudally and is inserted on an internal ridge (suture) of the sternite of the caudal pleotelsonic part. The muscle is composed of two small bundles.

M 110: Arises on the ventrocranial pleotelsonic sclerite and is inserted on the caudal wall of the pleotelsonic tergite. The strong muscle is composed of about 13 bundles.

4.2.4.2. Comparison

– Pass of M 110

On account of its sternotergal pass in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus* and *Mesamphisopus* it is questionable whether M 110 derived from longitudinal musculature. However, in the burrowing *Phreatoicopsis terricola* the enlargement of the fifth pleon segment is not very conspicuous and the pleotelson seems to be not so strongly bent downwards as for example in *Metaphreatoicus australis.* In coherence with that, the anus is situated in a more terminal position instead of a ventral subterminal one. The muscle M 110 in *Phreatoicopsis* appears like the terminal part of a ventral longitudinal muscle cord inserted on the lateral sternite as well as on the lower area at the lateral tergite of the caudal pleotelsonic part. In account of this, it might be possible that the sternotergal pass of M 110 in *Phreatoicopsis* and other phreatoicideans derived from ventral longitudinal muscles.

WÄGELE (1994: 94) figures the muscle "M III" of *Mesamphisopus capensis* which has an equivalent appearance as M 110 in *Metaphreatoicus, Onchotelson, Mesacanthotelson, Paramphisopus* and *Colubotelson.* However, WÄGELE (1994: 93) described his "M III" as dorsal pleotelson muscle and his figure 6A indicates the muscle arises dorsally on the intersegmental area of pleon segment V and pleotelson. A redetermination of the origin of M 110 ("M III") in *Mesamphisopus capensis,* however, confirms its ventral attachment on the ventrocranial pleotelsonic sclerite as is the condition of the homologous muscles in further investigated phreatoicideans.

GUPTA (1989: 42, fig. 15D) describes an "anterior levator muscle (a.lev.m.)" of *Nichollsia kashiensis* which could be identified by my own preparations as the homologon to M 110 of *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus.* The sternotergal muscle might be involved in the strong flexions of the pleotelson which is reported by GUPTA (1989: 12) as type of locomotion in *Nichollsia.* Elsewhere, GUPTA (1989: 44) pointed out that "the telson and inner rami (of the uropods) work as defensive organ" in *Nichollsia kashiensis.* This observations give evidence for the retention of the phreatoicidean-specific pleotelsonic type of locomotion and musculature in at least one subterranian representative of the Phreatoicidea.
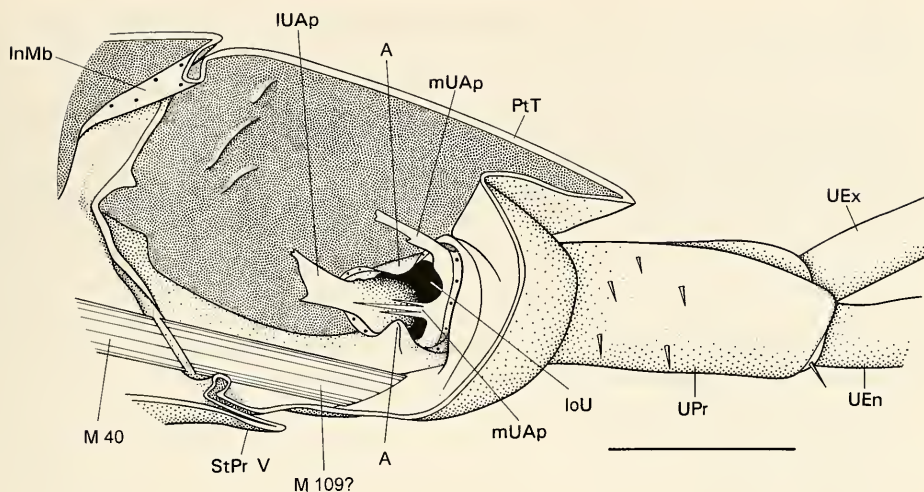
Fig. 16.   *Ligia oceanica,* ♂, median longitudinal section through the pleotelson in medial
view showing the pleotelsonic flexor M 109? – Scale: 1 mm.

– Existence of M 109 and M 110

The muscles M 109 and 110 could be shown in *Metaphreatoicus, Colubotelson,
Onchotelson, Mesacanthotelson, Phreatoicopsis, Paramphisopus, Mesamphisopus*
and *Nichollsia.* Their typical appearance in phreatoicideans might be coherent
with the division of the pleotelsonic sternum into the short ventrocranial sclerite
(pleon sternum VI?) and the long caudal part (telsonic sternum?) as well as with
the high mobility of the pleotelson during locomotion (cf. chapt. 4.1.2.2.).
In the mysid *Praunus* as well as in the lophogastrideans *Lophogaster* and *Gnatho-
phausia* two-divided flexors of the telsonic tail lobe are present (DANIEL 1932b,
1933). It might be possible that they are homologous to Mm 109 and 110 of the
phreatoicids or to parts of them. As already mentioned above (chapt. 4.1.2.2.), the
ventral division of the pleotelson in phreatoicideans might be a retention of an an-
cestral condition as well as the existence of Mm 109 and 110.
Neither of these muscles could be shown within the terrestrial isopod *Oniscus
asellus* (ERHARD 1995a: fig. 26). However, in the basal oniscid *Ligia oceanica* there
is a flat fan-shaped muscle which arises on the front margin of the pleotelsonic
sternite, representing a caudal prolongation of the vLM (figs. 10, 16: M 109?). It
passes caudally and is inserted on the middle part of the pleotelsonic sternite. The
occurrence of this muscle which probably represents a homologon to the phrea-
toicidean muscles M 109 or M 110 also might be interpreted as a retention of a
primitive state. However, a phreatoicidean-like movable sclerite of the cranial
pleotelsonic sternum could not be shown in *Ligia oceanica.*

5. Other anatomical features

5.1. Ventral nerve cord (figs. 17–18)

In species of the taxon Phreatoicidea the pleonal ganglia of the ventral nerve cord are positioned in a strict metameric pattern (fig. 17): Each pleon segment bears one pair of ganglia as it is the ancestral status within the Articulata groundpattern. However, the pleonite V has incorporated the ganglia of the pleon segment VI which fused with the telson. Consequently, ganglia of the ventral nerve cord are missing inside the pleotelson which is innervated by the pleonal ganglia VI situated inside the pleonite V. This condition could be shown in *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Mesamphisopus* and *Nichollsia* and might be a groundpattern character of the taxon Phreatoicidea.
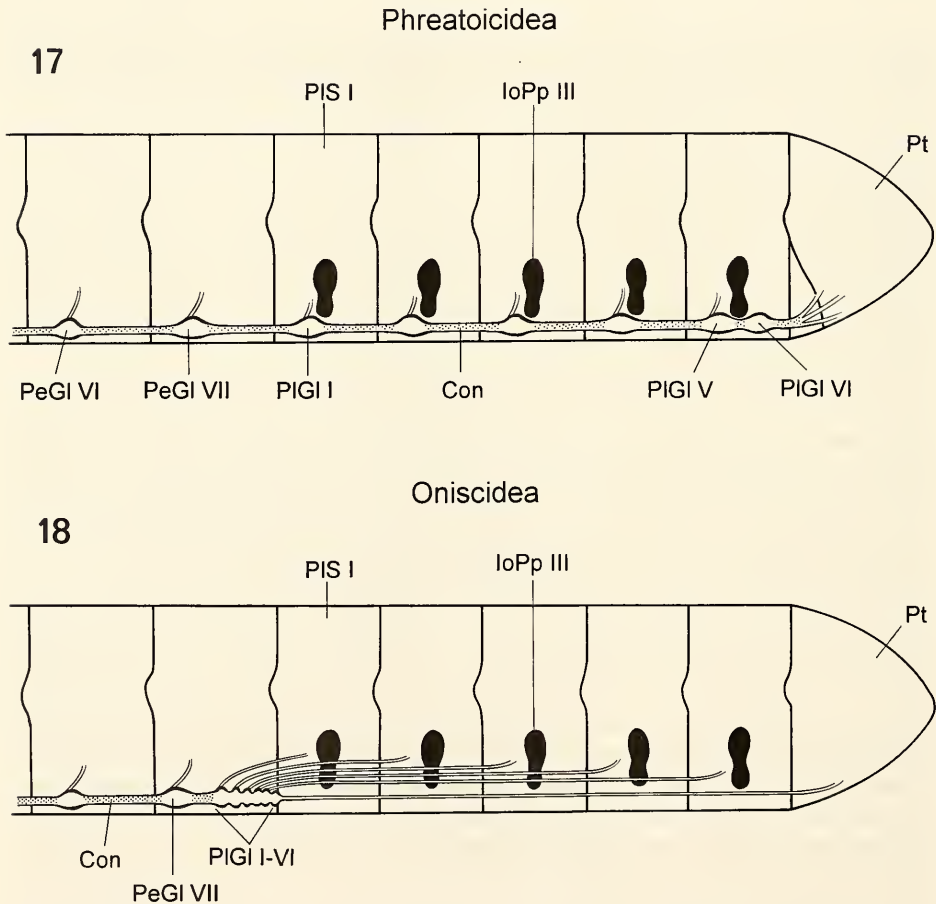
Figs. 17–18. Diagrams showing the position of the ganglia of the ventral nerve cord within the isopodan pleon. – 17. Groundpattern Phreatoicidea; – 18. groundpattern Oniscidea.

In the Oniscidea the ancestral state is rather obscured (fig. 18). All six pairs of pleonal ganglia have been shifted into the pereionite VII and are situated close behind the pereional ganglia VII. The ganglia of the pleon are more or less condensed, inervating the pleonites by long slender nerves. In *Ligia* the pairs of pleonal ganglia still can be observed as isolated structures whereas in *Tylos,* and representatives of the Synocheta and Crinocheta only an uniform ganglia mass is present (cf. VANDEL 1943: 106). The comparison between Oniscidea and Phreatoicidea reveals the oniscidean character state to be apomorphous.

5.2. Testicular follicles (fig. 19)

Within the Isopoda the number of testicular follicles per body side usually are three or less, in the Phreatoicidea, however, it appears to be higher (WÄGELE 1989: 56, fig. 28). According to TIWARI (1962) and GUPTA (1989) *Nichollsia kashiensis* normally has 6 follicles but the number can vary from 2 to 9. Following BARNARD (1927), in *Mesamphisopus capensis* occur 8–10 follicles, my own manual preparations of *Mesamphisopus capensis* yielded the number of 5–6 testicular lobes per bodyside whereas in *Metaphreatoicus australis* 5–7 (fig. 19) and in *Onchotelson brevicaudatus* 8 follicles could be determined. Only in *Colubotelson joyneri* with 3 testicular lobes per side the number appears comparatively low.

The question whether the high number of testicular follicles in phreatoicidean species represents a plesiomorphy in relation to the isopodan groundpattern or was caused by secondary increase was already discussed by WÄGELE (1989: 56). Ontogenetic investigations could answer the question.
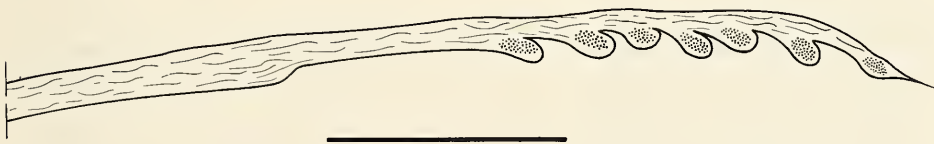

Fig. 19.   *Metaphreatoicus australis,* ♂, distal part of the testis with testicular follicles. – Scale: 1 mm.

6. Conclusions

Within the phreatoicidean and isopodan groundpatterns the pleon segments I–V and the pleotelson are not fused and are freely movable (chapt. 4.1.1.2.).

An apomorphous groundpattern character of the Phreatoicidea might be the strong downward development of the pleonal epimera. Together with the lateroventral parts of the pleotelson, the uropod protopodites and the pleon ventrum, the pleonal epimera are forming a chamber in which the pleopods are located (chapt. 4.1.1.2.).

A groundpattern character of the Phreatoicidea represents the enlargement of the pleon segment V. In connection with the polarity assessment it has to be taken into consideration that the character state occurs also in the incertae sedis group *Tainisopus* as well as in further isopod taxa like the Anthuridea (chapt. 4.1.1.2.).

Within the phreatoicidean and isopodan groundpatterns the male genital papillae are inserted in all probability medially on the pereiopod coxopodites VII (chapt. 4.1.1.2.).

The presence of pleonal sternal processus might represent a groundpattern character of the Phreatoicidea and probably of the taxon Isopoda (chapt. 4.1.1.2.).

A dorsally curved apex of the pleotelson might be an apomorphous groundpattern character of the Phreatoicidea but only in case the absence of a prolonged pleotelsonic apex (e.g. *Nichollsia, Phreatoicopsis*) is caused by secondary reduction (chapt. 4.1.1.2.).

"Dorsal apophyses" at the anterior edges of the pleon and pereion tergites serving as point of attachment for the limb promotors and further muscles are present in all investigated phreatoicideans and oniscideans as well as in specimens of the taxa *Saduria* (Valvifera) and *Anilocra* (Cymothoidae) (chapt. 4.1.2.2.).

A mediodorsal apophysis of the pleotelson tergite serving as point of attachment for the dorsal longitudinal muscles Mm 41 and 46 has to be considered as a phreatoicidean groundpattern character. A comparable structure does not exist in the oniscidean species investigated so far. The oniscidean muscles Mm 41 and 46 insert directly on the pleotelsonic front margin (chapt. 4.1.2.2. and 4.2.1.1.2.).

The presence of anterior and posterior apophyses at the pleopod protopodites has to be considered as a common character state in Phreatoicidea whereas in Oniscidea only posterior pleopod apophyses are developed (chapt. 4.1.2.2.).

The division of the pleotelsonic sternum into a cranial sternite which might be the ventral rest of a formerly freely movable pleonite VI and a caudal telsonic sternite is interpreted as a plesiomorphy which is retained within the taxon Phreatoicidea (chapt. 4.1.2.2.).

In phreatoicidean species the pleotelson extensors M 46 and the caudal parts of M 41 are strongly developed in comparison with the homologous oniscidean muscles. Probably, this has to do with the powerful movements executed by the phreatoicidean pleotelson (chapt. 4.2.1.1.2.).

The muscle M 39 of the external layer of the ventral longitudinal musculature, which extends between the pleon sternite V and the pleotelson sternite in the oniscidean species, could not be shown in the Phreatoicidea. This might be an apomorphous character state of the latter group (chapt. 4.2.1.2.1.).

The complete phreatoicidean type of the central muscle layer of the vLM inside the pleon represents an ancestral state within the taxon Isopoda. Reductions and condensations of subunits as they occur in the Oniscidea have to be considered as apomorphous features (chapt. 4.2.1.2.2.2.).

The point of insertion of the ventral longitudinal muscle M 108 is shifted cranially from the pleotelsonic front margin into the pleonite V in phreatoicids. The question whether only the phreatoicidean or already the isopodan groundpattern contains this apomorphy has to be examined by future in- and outgroup comparisons (chapt. 4.2.1.2.2.2.).

In the oniscidean groundpattern as well as in valviferan species the vas deferens of one body side passes between the two branches of the ventral longitudinal muscle M 3. In phreatoicids the vas deferens runs lateral to M 3. If there exists a correlation between the run of the vas deferens and the position of the genital papilla, the phreatoicidean condition might represent the plesiomorphous state. However, further anatomical comparisons are necessary to clear these points (chapt. 4.2.1.2.2.2.).

In the Phreatoicidea the internal layer of the pleonal vLM shows a strict metameric uniformity without condensation or reduction. This character state is assumed to be a plesiomorphous condition within the taxon Isopoda. Within the Oniscidea anatomical transformations of the internal layer are present. They concern the type of insertion of the tergosternal muscle-units, the prolongations of the caudal subunits and the condensation of the ventral muscle cord (chapt. 4.2.1.2.3.2.).

In the phreatoicidean species the horizontal muscle M 26/26a is developed much stronger and longer in comparison to its serial homologa and to the homologous oniscidean muscle. This condition might be an apomorphous character state in respect to the isopodan groundpattern (chapt. 4.2.2.2.).

The oniscidean horizontal muscle M 15 always appears as single branch whereas the homologous muscle in the Phreatoicidea is composed of two or more bundles (chapt. 4.2.2.2.).

Within the isopodan and phreatoicidean groundpatterns the pleopods I–V each have one extrinsic tergosternal promotor and one remotor. The oniscideans have retained only one promotor M 5 of the pleopod II, the extrinsic promotors of the other pleopods have been completely reduced. The oniscidean M 5 is not inserted on the pleopod protopodite II as it is the plesiomorphous condition retained in the phreatoicideans but on the pleon sternite II. The oniscidean character state might represent an apomorphous feature in respect to the isopodan groundpattern (chapt. 4.2.3.2.).

The retention of the telsonic flexors Mm 109 and 110 has to be considered a plesiomorphy within the phreatoicidean groundpattern. However, the character polarity assessment of the tergosternal run of the phreatoicidean muscle M 110 has to be analyzed by further anatomical studies (chapt. 4.2.4.2.).

In phreatoicidean species the pleonal ganglia of the ventral nerve cord are positioned in a strict metameric pattern. In the Oniscidea all six pairs of pleonal ganglia have been shifted into the pereionite VII which might be an apomorphous character state in respect to the isopodan groundpattern (chapt. 5.1.).

Within the Isopoda the number of testicular follicles per body side usually are three or less. In the Phreatoicidea, however, high numbers of follicles appears to be a common feature (chapt. 5.2.).

It is to summarize, that the phreatoicidean pleon shows some characters of plesiomorphous state which have an apomorphous condition in the Oniscidea. These characters concern the position of the genital papillae and, probably, the pass of the vasa deferentia in relation to the central layer of the ventral longitudinal musculature, the retention of a free pleon sternite VI, the ancestral condition of the pleonal longitudinal musculature, the extrinsic pleopod locomotors and their type of insertion as well as the ventral nerve cord.

On the other hand, the analysis of the phreatoicidean pleon reaveals some conditions which might be apomorphous in comparison with the Oniscidea. These characters concern the strong downward development of the pleonal epimera (1), the enlargement of the pleon segment V, probably the dorsally curved apex of the pleotelson (2), the strong development of the pleotelsonic muscles Mm 26/26a, 41 and 46 and the lack of the ventral longitudinal muscle M 39. At the present state of knowledge only the pleonal characters 1 and 2 could be determined as autapomorphies of the taxon Phreatoicidea which might substantiate the monophyly of the group. The

presence of the other presumptive apomorphous characters in further isopod groups has to be tested by future anatomical studies.

In case of several characters of the phreatoicidean pleon the polarity still has to be determined by in- and outgroup comparison which, probably, will be done by further investigations within the scope of future parts of the publication series at hand. These pleonal characters concern the presence of the mediodorsal apophysis of the pleotelson tergite, the development of anterior apophyses at the pleopod protopodites, the point of insertion of the ventral longitudinal muscle M 108, the existence of M 17, the tergosternal pass of the pleotelsonic flexor M 110 as well as the number of testes follicles.

There are some conspicuous features within the phreatoicidean pleotelson which might belong to a functional character complex. In the Phreatoicidea the high mobility of the pleotelson (pleotelsonic thrusts, see chapt. 4.1.2.2.) and its functional importance maybe for locomotion or protection strategies against predation appears to be important. On this score the strong development of the tergosternal telson flexor M 110 and correlated with that, the voluminous development of the pleotelson itself has to be considered. Further characters are the powerful condition of the pleotelson extensors Mm 26/26a, 41 and 46 and probably the occurrence of the mediodorsal pleotelsonic apophysis as well as the enlargement of the pleonite V for sheltering the mass of powerful musculature and, connected therewith, the transfer of the point of origin of M 108. Also the strong development of the pleon flexors Mm 10, 12 and 14 should be taken into consideration as well as the retention of the freely movable pleon sternite VI as abutment for the pleotelsonic muscles. On the other hand, the strong downward development of the pleonal epimera forming a chamber for the pleopods and the development of a dorsally curved apex of the pleotelsonic tergite might represent parts of another functional complex of surface living phreatoicideans which we do not understand until now (cf. chapt. 4.1.1.2.).

Presumably, some of the above mentioned individual characters might differ only gradually from their states present in the isopodan groundpattern but the pleotelsonic condition as a whole and its extraordinary type of locomotion, possibly, has to be considered an apomorphous character complex of the taxon Phreatoicidea.

7. Acknowledgments

8. References

ABRAHAMCZIK-SCANZONI, H. (1942): Beiträge zur Kenntnis der Muskulatur und des Innenskeletts der Krabben. – Zool. Jb. (Abt. Anat.) 67: 293–380; Jena.

BARNARD, K. H. (1927): A study of the freshwater isopodan and amphipodan Crustacea of South Africa. – Trans. R. Soc. S. Afr. 14: 139–215; Cape Town.

BERKELEY, A. A. (1928): The musculature of Pandalus danae, Stimpson. – Trans. R. Can. Inst. 16: 181–231; Toronto.

BRUSCA, R. C. & WILSON, G. D. F. (1991): A phylogenetic analysis of the Isopoda with some classificatory recommendations. – Mem. Queensld Mus. **31**: 143–204; Brisbane.

CANNON, H. G. (1937): A new biological stain for general purposes. – Nature **139**: 549; London.

CLAUS, C. (1887): Ueber *Apseudes latreillii* Edw. und die Tanaiden. II. – Arb. zool. Inst. Univ. Wien **7**: 139–220; Vienna.

– (1888): Ueber den Organismus der Nebaliden und die systematische Stellung der Leptostraken. – Arb. zool. Inst. Univ. Wien **8**: 1–148; Vienna.

COCHRAN, D. M. (1935): The skeletal musculature of the blue crab, *Callinectes sapidus* Rathbun. – Smithson. misc. Collns **92**: 1–76; Washington.

DAHL, E. (1992): Aspects of malacostracan evolution. – Acta Zool. **73**: 339–346; Stockholm.

DANIEL, R. J. (1932a): The abdominal muscular systems of *Paranaspides lacustris* (Smith). – Proc. Trans. Liverpool biol. Soc. **46**: 26–45; Liverpool.

– (1932b): Comparative study of the abdominal musculature in Malacostraca. Part II. – Proc. Trans. Liverpool biol. Soc. **46**: 46–107; Liverpool.

– (1933): Comparative study of the abdominal musculature in Malacostraca. Part III. – Proc. Trans. Liverpool biol. Soc. **47**: 71–133; Liverpool.

ERHARD, F. (1995a): Vergleichend- und funktionell-anatomische Untersuchungen am Pleon der Oniscidea (Crustacea, Isopoda). Zugleich ein Beitrag zur phylogenetischen Systematik der Landasseln. – Zoologica **145**: 1–114; Stuttgart.

– (1995b): Untersuchungen am Skelet-Muskel-System des Landassel-Pleon (Isopoda, Oniscidea). Ein Beitrag zur phylogenetisch-systematischen Stellung der Familie Mesoniscidae. – Verh. dt. zool. Ges. **88.1**: 144; Stuttgart, Jena & New York.

– (1996): Das pleonale Skelet-Muskel-System und die phylogenetisch-systematische Stellung der Familie Mesoniscidae (Isopoda: Oniscidea). – Stuttgarter Beitr. Naturk. (A) **538**: 1–40; Stuttgart.

– (1997): Das pleonale Skelet-Muskel-System von *Titanethes albus* (Synocheta) und weiterer Taxa der Oniscidea (Isopoda), mit Schlußfolgerungen zur Phylogenie der Landasseln. – Stuttgarter Beitr. Naturk. (A) **550**: 1–70; Stuttgart.

– (In press): Phylogenetic relationships within the Oniscidea (Crustacea, Isopoda). – Isr. J. Zool. **44**; Jerusalem.

GRUNER, H.-E. (1953): Der Rollmechanismus bei kugelnden Landisopoden und Diplopoden. – Mitt. zool. Mus. Berl. **29**: 148–179: Berlin.

GUPTA, L. P. (1989): Monograph on *Nichollsia kashiensis* Chopra & Tiwari 1950 (Crustacea: Isopoda: Phreatoicoidea: Nichollsidae). – Mem. zool. Surv. India **17**: 1–160; Calcutta.

HENNIG, W. (1966): Phylogenetic systematics. – 263 pp.; Urbana, Chicago & London (Univ. Illinois Press).

JUST, J. & POORE, G. C. B. (1992): Vermectiadidae, a new primitive asellote isopod family with important phylogenetic implications. – J. crust. Biol. **12**: 125–144; Lawrence.

KRAUTER, D. (1980): Ein rasch arbeitendes, schonendes Mazerationsmittel für Chitinpräparate: Diäthylentriamin. – Mikrokosmos **69**: 395–397; Stuttgart.

KNOTT, B. (1971): Studies on some tasmanian phreatoicids. – B. Sc. Thesis Univ. Tasmania, Hobart (unpubl.): 1–146; Hobart.

– (1986): Isopoda: Phreatoicidea. – *In:* BOTOSANEANU, L. (ed.): Stygofauna mundi: 486–492; Leiden (Brill & Backhuys).

LEGRAND, J.-J. (1946): Les coaptations sexuelles des Oniscoidea. – Bull. biol. Fr. Belg. **80**: 241–388; Paris.

MAERCKS, H. H. (1930): Sexualbiologische Studien an *Asellus aquaticus* L. – Zool. Jb. (Abt. Physiol.) **48**: 399–508; Jena.

NATH, C. N. (1974): Studies on the abdominal musculature of the subterranean mysid, *Lepidomysis longipes* (Pillai and Mariamma). – Int. J. Speleol. **6**: 173–180; Weinheim.

NICHOLLS, G. E. (1943): The Phreatoicoidea (Part I) – The Amphisopidae. – Pap. Proc. R. Soc. Tasm. **1942**: 1–145; Hobart.

– (1944): The Phreatoicoidea (Part II) – The Phreatoicidae. – Pap. Proc. R. Soc. Tasm. **1943**: 1–157; Hobart.

PATERSON, N. F. (1968): The anatomy of the Cape Rock Lobster, *Jasus lalandii* (H. Milne Edwards). – Ann. S. Afr. Mus. **51**: 1–232; Cape Town.

SCHMALFUSS, H. (1989): Phylogenetics in Oniscidea. – Monitore zool. ital. (N.S.), Monogr. **4**: 3–27; Florence.

SCHMIDT, W. (1915): Die Muskulatur von *Astacus fluviatilis* (*Potamobius astacus* L.). – Z. wiss. Zool. **113**: 165–251; Leipzig.

SCHRAM, F. R. (1986): Crustacea. – 606 pp.; New York (Oxford Univ. Press).

SIEWING, R. (1951): Besteht eine engere Verwandtschaft zwischen Isopoden und Amphipoden? – Zool. Anz. **147**: 166–180; Leipzig.

— (1960): Neuere Ergebnisse der Verwandtschaftsforschung bei den Crustaceen. – Wiss. Z. Univ. Rostock (math.-nat. Reihe) **9**: 343–358; Rostock.

TAIT, J. (1917): Experiments and observations on Crustacea. Part IV. Some structural features pertaining to *Glyptonotus*. – Proc. R. Soc. Edinb. **37**: 246–303; Edinburgh.

TIWARI, K. K. (1955a): Nichollsidae, a new family of Phreatoicoidea (Crustacea: Isopoda). – Rec. Indian Mus. **53**: 293–295; Calcutta.

— (1955b): Another new species of *Nichollsia* (Crustacea: Isopoda: Phreatoicoidea). – Rec. Indian Mus. **53**: 379–381; Calcutta.

— (1962): A note on the testes in *Nichollsia kashiense* Chopra & Tiwari (Isopoda, Phreatoicoidea, Nichollsiidae).– Crustaceana **3**: 247–248; Leiden.

VANDEL, A. (1943): Essai sur l'origine, l'évolution et la classification des Oniscoidea (isopodes terrestres). – Bull. biol. Fr. Belg. (Suppl.) **30**: 1–136; Paris.

WÄGELE, J.-W. (1981): Zur Phylogenie der Anthuridea (Crustacea, Isopoda). Mit Beiträgen zur Lebensweise, Morphologie, Anatomie und Taxonomie. – Zoologica **132**: 1–127; Stuttgart.

— (1989): Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. – Zoologica **140**: 1–262; Stuttgart.

— (1990): Aspects of the evolution and biogeography of stygobiontic Isopoda (Crustacea: Peracarida). – Bijdr. Dierk. **60**: 145–150; Leiden.

— (1994): Review of methodological problems of 'Computer cladistics' exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). – Z. zool. Syst. Evolut.-Forsch. **32**: 81–107; Hamburg & Berlin.

WATLING, L. (1981): An alternative phylogeny of peracarid crustaceans. – J. crust. Biol. **1**: 201–210; Lawrence.

WILSON, G. D. F. (1987): The road to the Janiroidea: Comparative morphology and evolution of the asellote isopod crustaceans. – Z. zool. Syst. Evolut.-Forsch. **25**: 257–280; Hamburg & Berlin.

— (1991): Functional morphology and evolution of isopod genitalia. – *In:* BAUER, R.T. & MARTIN, J. W. (ed.): Crustacean sexual biology: 228–245; New York (Columbia Univ. Press).

— (1994): A phylogenetic analysis of the isopod family Janiridae (Crustacea). – Invertebr. Taxon. **8**: 749–766; Melbourne.

WILSON, G. D. F. & PONDER W. F. (1992): Extraordinary new subterranean isopods (Peracarida: Crustacea) from the Kimberley Region, Western Australia. – Rec. Aust. Mus. **44**: 279–298; Sydney.

WILSON, G. D. F. & WÄGELE, J.-W. (1994): Review of the family Janiridae (Crustacea: Isopoda: Asellota). – Invertebr. Taxon. **8**: 683–747; Melbourne.

WRZESNIOWSKI, A. (1879): Vorläufige Mittheilungen über einige Amphipoden. – Zool. Anz. **2**: 447–450; Leipzig.

Author's address:

Dr. FRIEDHELM ERHARD, Staatliches Museum für Naturkunde (Museum am Löwentor), Rosenstein 1, D-70191 Stuttgart.
e-mail: h.f.erhard@t-online.de.