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Proceedings of the 13th International Congress of Myriapodology

**Bergen, Norway
25th – 29th July 2005**

NORWEGIAN JOURNAL OF ENTOMOLOGY

Proceedings of the 13th International Congress of Myriapodology
Bergen, Norway

Bjarne Meidell, Lars Ove Hansen & Lauritz Sømme
Editors

Bergen, Norway
25th-29th July 2005

BERGEN MUSEUM
UNIVERSITY OF BERGEN

The 13th International Congress of Myriapodology, University of Bergen, Norway 26th - 29th July 2005

Bjarne Meidell

In 1968, in Paris, at the very first international congress of myriapodology, the Centre Internationale de Myriapodologie (CIM) was established. The center's address was and still is, at the Museum Nationale d'Histoire Naturelle in Paris. Since then, the myriapodologists affiliated to the Paris Museum has served this field of zoology towards scientists all over the world. The activities of CIM, which materializes each year in form of a bulletin, gives an overview on the scientific research being done on Myriapoda as well as Onychophora, both ongoing projects as well as an extensive list of published papers by its members. The bulletin also includes an updated list of members with any information needed for contact. It also provides a forum for planning future congresses of myriapodology.

This volume of the Norwegian Journal of Entomology is dedicated to this non-entomological assembly of terrestrial arthropods, the Myriapoda. These animals have been given relatively little attention in the Nordic countries, seldom more than one active scientist in each country at any time. For those who wants a broader introductions to these fascinating animals the second volume of the Nationalnyckeln til Sveriges flora och fauna, cowering all Nordic species, is recommended. (www.nationalnyckeln.se).

As decided in 1999 in Bialowieza, Poland, at the 11th International Congress of Myriapodology, and later (2002) confirmed in Mtunzini, KwaZulu-Natal, South Africa, at the 12th congress, the 13th International Congress of Myriapodology was arranged at the University of Bergen, Norway 24th to 29th July 2005.

Fiftyfour scientists from all continents took part in the congress (see separate list). The program started, according to tradition, with a reception at Sunday evening (the day of arrival), followed by two days of scientific sessions, a whole day excursion, two more days of scientific sessions and a farewell dinner at Friday night.

The reception was held in the Museum of Natural History and on the menu were Norwegian food specialities. The reception was sponsored by the University of Bergen.

The scientific sessions (lectures as well as poster sessions), including coffee breaks and lunches were held in the Jura Building of the university. Twentysix lectures were given and 29 posters presented, se lists below. The topics covered a broad specter of myriapod research, as well as on onychophorans. Ulf Scheller showed a film on the behavior of symphylans and pauropods. Half of the lectures and 12 of the posters are in this volume presented as full papers or as short communications.

One evening several participants gathered in the museum for a discussion on segmentation and body rings, especially of diplopods. This discussion is summarized by Wolfgang Dohle at the end of this volume.

Seventy four persons took part in the excursion Norway in a nutshell on Wednesday. As a bonus, we got a guided tour in the near 750 years old church at Voss.

The formal assembly of CIM took place at the last session on Friday. This section was in the hands of CIM's general secretary Jean-Jacques Geoffroy from the Paris museum. The next congress (2008) is planned for Görlitz, Germany, and the one thereafter (2011) is planned for Australia.

The host for this congress was The Natural History

Collections of Bergen Museum/University of Bergen, former Museum of Zoology.

The organizers, Per Djursvoll and Bjarne Meidell, would like to express their thanks to all those who contributed to make this congress a success, local helpers in alphabetic order: Tom Alvestad, Gudrun Bakkerud, Ingrid Herø, Lita Greve Jensen, Petter Jordan, Christian Meidell, Jan Erik Soltveit, Inger-Karin Steen-Hansen, Magnus Vabø, and Jan Erik Vold, Endre Willassen.

Also thanks to those who contributed as chair men (listed under lectures below) and to those who made the referees on the scientific contributions in this congress volume.

Special thanks to the editor of The Norwegian Journal of Entomology, Professor emeritus Lauritz Sømme and his co-editor Lars Ove Hansen, for their efforts of making this congress volume possible.

End of July is always a risky period concerning our famous Bergen weather. Those participants that left Bergen disappointed, missing the rain, are welcome back, anytime! (The summer of 2006 has been extremely hot and dry!)
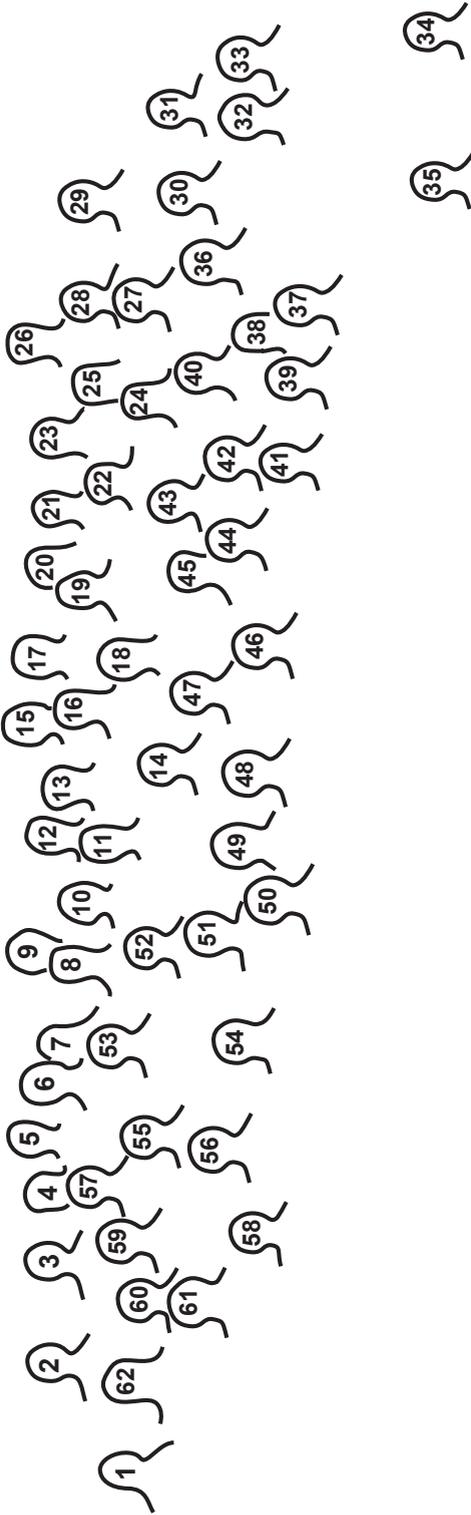
1. Gudrun W. Bakkerud
2. Chagas-Junior, Amazonas
3. Dumjahn, Petra
4. Sammler, Svenja
5. Dányi, László
6. Tuf, Ivan H.
7. Roggenbuck, Helma
8. Hilken, Gero
9. Damen, Wim
10. Dohle, Winolde
11. Koch, Markus
12. Edgecombe, Greg
13. Lewis, John
14. David, Jean-Francois
15. Dohle, Wolfgang
16. Enghoff, Henrik
17. Mueller, Carsten H. G.

18. Korsós, Zoltán
19. Andersson, Göran
20. Stagl, Verena
21. Rosenberg, Jörg
22. Kime, Desmond
23. Rosenberg, Barbara
24. Schileyko, Arkady
25. Hamer, Michelle
26. Jeekel, Casimir A.W.
27. Simaiakis, Stylianos
28. Slotow, Rob
29. Jeekel, Jeanne
30. Robson, Elaine
31. Stoev, Pavel
32. Lindner, Norman
33. Lindner, Beate
34. Lindner, jr.

35. Lindner, jr.
36. Tait, Noel
37. Chen, Chao-Chun
38. Read, Helen
39. Lin, Yi-Hui
40. Short, Megan
42. Chang, Li-Li
42. Mayer, Ina
43. Stutchbury, Robyn
44. Mayer, Georg
45. Chao, Jui-Lung
46. Hsu, Ming-Hung
47. Scheller, Ulf
48. Geoffroy, Jean-Jacques
49. Nguyen Duy-Jaquemin, Monique
50. Meidell, Bjarne

51. Shelly, Rowland
52. Akkari, Nesrine
53. Xylander, Willi
54. Shelley, Lourdes O.
55. Chang, Hsueh-Wen
56. Tajovsky, Karel
57. Pilz, Christian
58. Voigtländer, Karin
59. Wesener, Thomas
60. Prunescu, Paula
61. Prunescu, Carol-Constantin
62. Ruhberg, Hilke

PARTICIPANTS

Participants sorted by country.

Accompanying persons marked with an asterisk (*)

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Short, Megan
Stutchbury, Robyn
Tait, Noel

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*Stagl, Josepha
Stagl, Verena

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Stoev, Pavel

Czech Republic
*Tajovska, Eva
Tajovsky, Karel
Tuf, Ivan H.

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David, Jean-Francois
*David, Laurent
*David, Paul
Geoffroy, Jean-Jacques
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Nguyen Duy-Jacquemin, Monique

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Damen, Wim

*Dohle, Winolde
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Dumjahn, Petra
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Mayer, Georg
*Mayer, Ina
Mueller, Carsten H. G.
Pilz, Christian
Roggenbuck, Helma
Rosenberg, Jörg
*Rosenberg, Barbara
Ruhberg, Hilke
Sammler, Svenja
Voigtländer, Karin
Wesener, Thomas
Xylander, Willi

Greece
Simaiakis, Stylianos

Hungary
Dányi, László
Korsós, Zoltán

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*Jeekel, Jeanne

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Lewis, John
*Lewis, Sheila
Read, Helen
Robson, Elaine

USA
*Shelley, Lourdes O.
Shelly, Rowland

LECTURES GIVEN

Those marked with an asterisk (*) are published in the present issue. Those with two (**) are published as short communications.

MONDAY 25ᵀᴴ JULY 2005

FORMAL OPENING: Kjell Bernstrøm, University of Bergen.

CHAIRMAN BJARNE MEIDELL

Henrik Enghoff: Millipedes, taxonomy, museums, Europe, the World, the future KEYNOTE.

J.-J. Geoffroy: The cave-dwelling millipedes (Diplopoda) from China and South-East Asia, recent data, further perspectives and hot-spots of biodiversity.

Noel Tait & Robyn Stutchbury: Twenty years of Australian Onychophora (1985 – 2005).

CHAIRMAN ZOLTAN KORSOS

***Megan Short & Cuong Huynh**: In the footsteps of Filippo Silvestri: Rediscovering *Phryssonotus novaehollandiae* (Silvestri, 1923), (Diplopoda, Polyxenida, Synexenidae).

***Verena Stagl**: Robert Latzel – his life work and importance for Myriapodology.

***Monique Nguyen Duy-Jaquemin**: *Condexenus*, a new genus of the millipede family Synxenidae (Diplopoda, Polyxenida) from Namibia.

Hilke Ruhberg: The zoologist in Fridtjof Nansen INVITED LECTURE.

TUESDAY 26ᵀᴴ JULY 2005

CHAIRMAN WOLFGANG DOHLE

***Ralf Janssen, Nikola-Michael Prpic, & Wim G.M. Damen**: Decoupling of dorsal and ventral segmentation in the diplopod *Glomeris marginata* KEYNOTE.

***Steffen Harzsch, Carsten H. G. Müller & Roland R. Melzer**: Developmental mechanisms in the lateral eyes of centipedes and chilognath millipedes and their significance for the evolution of the arthropod visual system.

Georg Mayer, Thomas Bartolomeus & Hilke Ruhberg: Mesoderm differentiation in the Onychophora and its bearing on the Articulata hypothesis.

***Willi E. R. Xylander & Lutz Nevermann**: Haemocytes in Myriapoda – Types, structure and function.

Ulf Scheller: Soil microarthropods (Film)

***Stylianos Simaiakis & Moysis Mylonas**: Recent knowledge on the centipede fauna (Chilopoda) of south Aegean archipelago (Greece, Eastern Mediterranean).

THURSDAY 28ᵀᴴ JULY 2005

CHAIRMAN ROB SLOTOW

***Michelle Hamer, Robert Slotow & Saskie Lovell**: Savanna millipedes and conservation planning: can surrogates predict millipede diversity and distribution patterns? KEYNOTE.

***Göran Andersson**: Habitat preferences and seasonal distribution of developmental stadia in *Lamyctes emarginatus* (Newport, 1844) (*L. fulvicornis* Meinert, 1868) and comparisons with some *Lithobius* species (Chilopoda, Lithobiomorpha).

Karel Tajovský: Millipede and centipede assemblages of meadow habitats under different management practices.

*Ivan H. Tuf, Eva Jeřábková & Pavel Dedek: Diurnal epigeic activity of centipedes and millipedes (Chilopoda & Diplopoda).

CHAIRMAN JEAN-JACQUES GEOFFROY

*Dányi László: Faunistic research on the chilopods of Hungarian lower mountains.

Thomas Wesener: New discovered giant-pill millipede species endemic to the eastern littoral forest of Madagascar highly threatened.

Norman Lindner presened: Jörg Spelda, Markus Unsöld, Christian Pilz & Roland R. Melzer: From types to nature: GBIF and fieldwork, some examples.

FRIDAY 29ᵀᴴ JULY 2005

CHAIRMAN GÖRAN ANDERSSON

Gregory D. Edgecombe & Gonzalo Giribet: Centipede phylogeny and the relationships of Scutigeromorpha KEYNOTE.

Markus Koch & Gregory D. Edgecombe: Centipede phylogeny revisited: insights derived from the peristomatic organs.

Arkady A. Schileyko: Some notes to the taxonomic standards in the Scolopendromorpha.

**Carol C. Prunescu: A new classification of the class Chilopoda: 1. Subclass Ovodispersa, 2. subclass Ovoconecta.

CHAIRMAN JOHN G. E. LEWIS

*Carsten H. G. Müller, Jörg Rosenberg & V. Benno Meyer-Rochow: Description of the fine structural organization of lateral eyes in Chilopoda and their phylogenetic significance.

Pavel Stoev: The order Scutigeromorpha (Arthropoda: Chilopoda) in the world: a review of present systematics, with a complete checklist of hitherto described species.

John G.E. Lewis (& Sandro Minelli): The GBIF world catalogue of centipedes.

POSTERS PRESENTED

Those marked with an asterisk (*) are published in the present issue. Those with two (**) are published as short communications.

Nesrine Akkari & Saïd Nouira: Biodiversity of Myriapoda in Tunisia.

Amazonas Chagas-Júnior: The analysis of morphological characters in the taxonomy of the Scolopocryptopinae (Chilopoda, Scolopendromorpha, Scolopocryptopidae).

*Jui-Lung Chao & Hsueh-Wen Chang: Variation of the poison duct in Scolopendromorph centipedes (Chilopoda) from Taiwan.

*Chao-Chun Chen & Hsueh-Wen Chang: The millipede tribe Sulciferini, with special reference to the fauna of Taiwan (Diplopoda: Polydesmida: Paradoxosomatidae)

J.-F. David, J.-J. Geoffroy & M.-L. Célérier: Photoperiodic regulation of the life cycle in millipedes.

Petra Dumjahn & Hilke Ruhberg: A reinvestigation of *Mesoperipatus tholloni* (Bouvier, 1898) – Does this taxon represent a connecting link between the Caribbean and the Indomalayic Peripatidae?

*Andrés García Ruiz: Effects of the accidental poured of cadmium on the communities of centipedes.

Andrés García Ruiz: Biometrical study of *Scolopendra cingulata* Laterille, 1829 (Myriapoda, Chilopoda).

Tarombera Mwabvu, Michelle Hamer and Robert Slotow: The millipede genus *Bicoxidens* (Diplopoda, Spirostreptida): taxonomic problems and distribution.

**Gero Hilken & Jörg Rosenberg: First ultrastructural investigation of a salivary gland in Chilopoda: Maxilla I-gland of *Scutigera coleoptrata.*

*Gero Hilken, Christian Wirkner & Jörg Rosenberg: On the aortic diverticles of *Scutigera coleoptrata* (Chilopoda, Notostigmophora): Structure and function.

Markus Koch and Gregory D. Edgecombe: Centipede phylogeny revisited: insights derived from the peristomatic organs.

Zoltán Korsós: The millipede fauna (Diplopoda) of Hungary: a zoogeographical account.

Georg Mayer & Markus Koch: Evidence for the onychophoran antennae being modified legs.

**Carsten H. G. Müller, Jörg Rosenberg & Gero Hilken: On the fine structure of epidermal glands in Chilopoda: structure and phylogenetic aspects.

Christian Pilz: Morphometric analysis of the species pairs *Lithobius mutabilis / L. glacialis* and *L. piceus / L. tricuspis* (Chilopoda: Lithobiomorpha).

*C-C. Prunescu & Paula Prunescu: Rudimentary malpighian tubules in the order Craterostigmomorpha.

Helma Roggenbuck & Cornelia Warneke-Cremer: GBIF - Digital documentation of selected invertebrate types. Collections «Invertebrates I and II» of the Zoological Museum Hamburg (ZMH).

**Gero Hilken, Jörg Rosenberg & Carsten H. G. Müller: Ultrastructural organization of the anal organs in the so-called ano-genital capsule of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha).

Jörg Rosenberg & Gero Hilken: Ultrastructural organization of the poison gland of *Lithobius forficatus* (Chilopoda, Lithobiomorpha).

*Alfred Ernst, Jörg Rosenberg & Gero Hilken: Structure and distribution of antennal sensillae in *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha).

*Svenja Sammler, Karin Voigtländer, Henrik Enghoff, Peter Stoev & Carsten H. G. Müller: New studies on myriapods (Chilopoda, Diplopoda) from Ibiza.

*Antoni Serra, Eduardo Mateos & Carme Miquel: A soil population of *Glomeris marginata* (Villers, 1789) in a Mediterranean forest (Diplopoda, Glomerida).

Cuong Huynh & Megan Short: A preliminary study of Polyxenid millipedes (Diplopoda: Polyxenida: Polyxenidae) in Southeastern Australia.

Jörg Spelda: The Global Myriapod Information System (GloMyrIS) of GBIF-Germany - an Aid for Scientific Research.

Karel Tajovský & Klára Voženílková: Colonisation of two different post-mining chronosequences by millipedes and centipedes.

*Karin Voigtländer & Birgit Balkenhol: Studies on millipede assemblages (Myriapoda, Diplopoda) as influenced by habitat qualities of afforested mine sites.

Thomas Wesener: The giant-pill millipedes of Madagascar (Diplopoda: Sphaerotheriida: Sphaerotheriidae).

On the structure and function of the aortic diverticles in *Scutigera coleoptrata* (Chilopoda, Scutigeromorpha)

Gero Hilken, Christian S. Wirkner & Jörg Rosenberg

Hilken, G., Wirkner, C.S, & Rosenberg, J. 2006. On the structure and function of the aortic diverticles in *Scutigera coleoptrata* (Chilopoda, Scutigeromorpha). Norw. J. Entomol. 53, 107-112.

In the present study, we investigate the aortic diverticles in *Scutigera coleoptrata* by light and electron microscopy. Computer aided 3D reconstruction provides insight into the position and structure of these organs. The main head artery is the anterior cephalic aorta which branches off the anterior end of the heart in the first trunk segment. At the level of the mandibles, ventrally an unpaired short vessel emanates from the aorta. It splits and widens to paired, sac-like structure termed aortic diverticles. Regularly, these blind sacs are located above the foregut; however, their position can be shifted laterally. The wall of the blind sacs is formed by a thick, irregularly shaped myocardium. We therefore suggest that the diverticles function as accessory pumping hearts which support the flow of blood into the head. It is likely that they compensate the lack of tracheae in the heads of notostigmophoran centipedes by helping to maintain haemolymph pressure within the numerous but small head arteries. We furthermore investigated, whether these organs act as pure accessory pumping structures or if other functions prevail (e.g. as haematopoietic organs).

Key words: Dorsal heart, pump hearts, heart muscle, Chilopoda, centipedes.

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INTRODUCTION

First comparative anatomical studies on the circulatory system in Chilopoda were carried out by Newport (1843), Herbst (1891), Duboscq (1898), and Fahlander (1938). Recently, the circulatory system in Chilopoda was investigated under aspects of comparative and functional morphology and phylogeny (Wirkner & Pass 2000, 2002). The most complex vascular system can be found in the notostigmophoran centipedes as it shows some morphological adaptations with regard to the functional coupling of circulatory and respiratory tasks (Wirkner & Pass 2000, 2002). Data on the ultrastructure of circulatory organs in Chilopoda are scarce to date. Only the ultrastructure of the hearts of *Strigamia maritima* (Økland 1984), *Lithobius forficatus* (Økland et al. 1982), and *Scutigera coleoptrata* (Wirkner & Pass 2002) were investigated. The latter authors also superficially studied the ultrastructure of the aortic diverticles.

In all Chilopoda, the dorsal vessel (i.e. the heart and anterior aorta) and the ventral vessel (i.e. the supraneural vessel) are connected by the

maxilliped arch which is located in the first trunk segment. Anteriorly, the heart leads into the anterior aorta which is considerably smaller in diameter. Only in Scutigeromorpha, a short tube emanates ventrally from the aorta at the level of the mandibles and splits into paired diverticles. The diverticles were first described by Herbst (1891) as a pumping apparatus ("Pumpapparat"). Fahlander (1938) named these structures as accessory hearts ("akzessorische Herzen"), whereas Wirkner & Pass (2000, 2002) termed them aortic diverticles and conclude that they must be effective as accessory pumping structures.

The organization of the aortic diverticles is yet unclear. Therefore, we investigated the diverticles of *Scutigera coleoptrata* by 3D reconstruction and electron microscopical methods. We furthermore investigated, whether these organs act as pure accessory pumping structures or if other functions prevail (e.g. as haematopoietic organs).

MATERIAL AND METHODS

Specimens of *Scutigera coleoptrata* (Linné, 1758) were collected around Banyuls-sur-Mer, France.

Light microscopy
Dissected, Bouin fixed heads of the animals were dehydrated in ethanol and, after an intermediate step of epoxypropane, embedded in Araldit epoxy resin under vacuum. Serial semi-thin sections (1 µm) were made with a Leica Ultracut UCT ultramicrotome using diamond knives. The sections were stained with a mixture of 1% azure
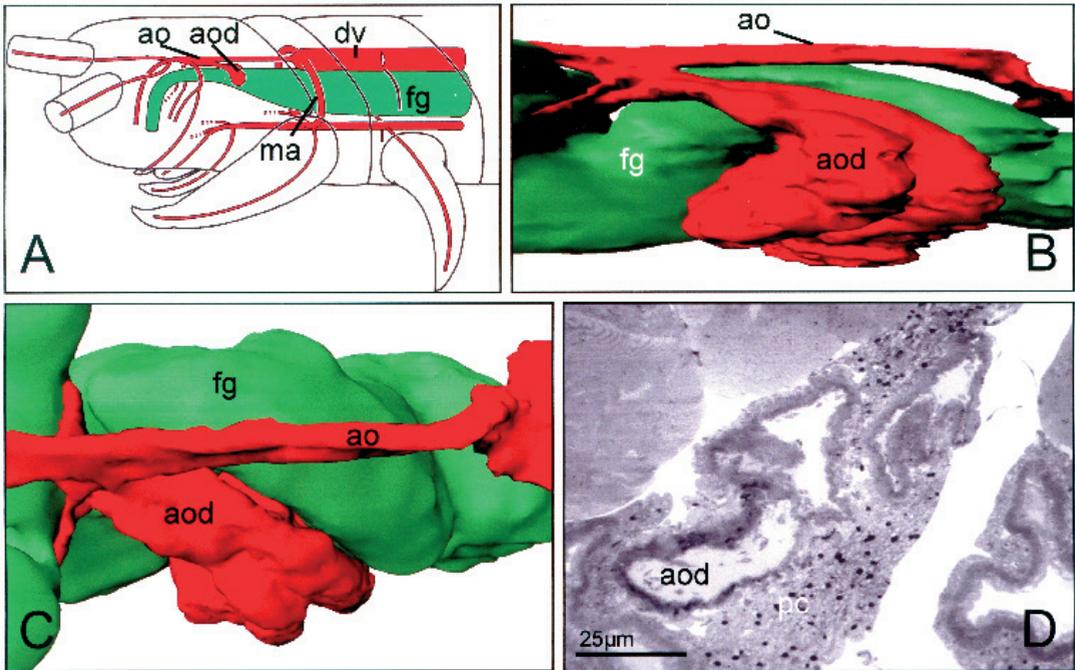
Figure 1: Aortic diverticles of *Scutigera coleoptrata*. **A:** Schematic diagram of the circulatory system and anterior trunk segments (modified after Wirkner & Pass 2000). B-C: Reconstruction of aortic diverticles using the software Imaris. In the investigated specimen, the aortic diverticles were located laterally of the foregut. **B:** Lateral view. **C:** Dorsal view. **D:** Aortic diverticle surrounded by perivascular cells and filled with numerous haemocytes, LM.

ao, cephalic aorta; aod, aortic diverticles; dv, dorsal vessel; fg, foregut; ma, maxilliped arch; LM, light microscopy, pc, perivascular cells.
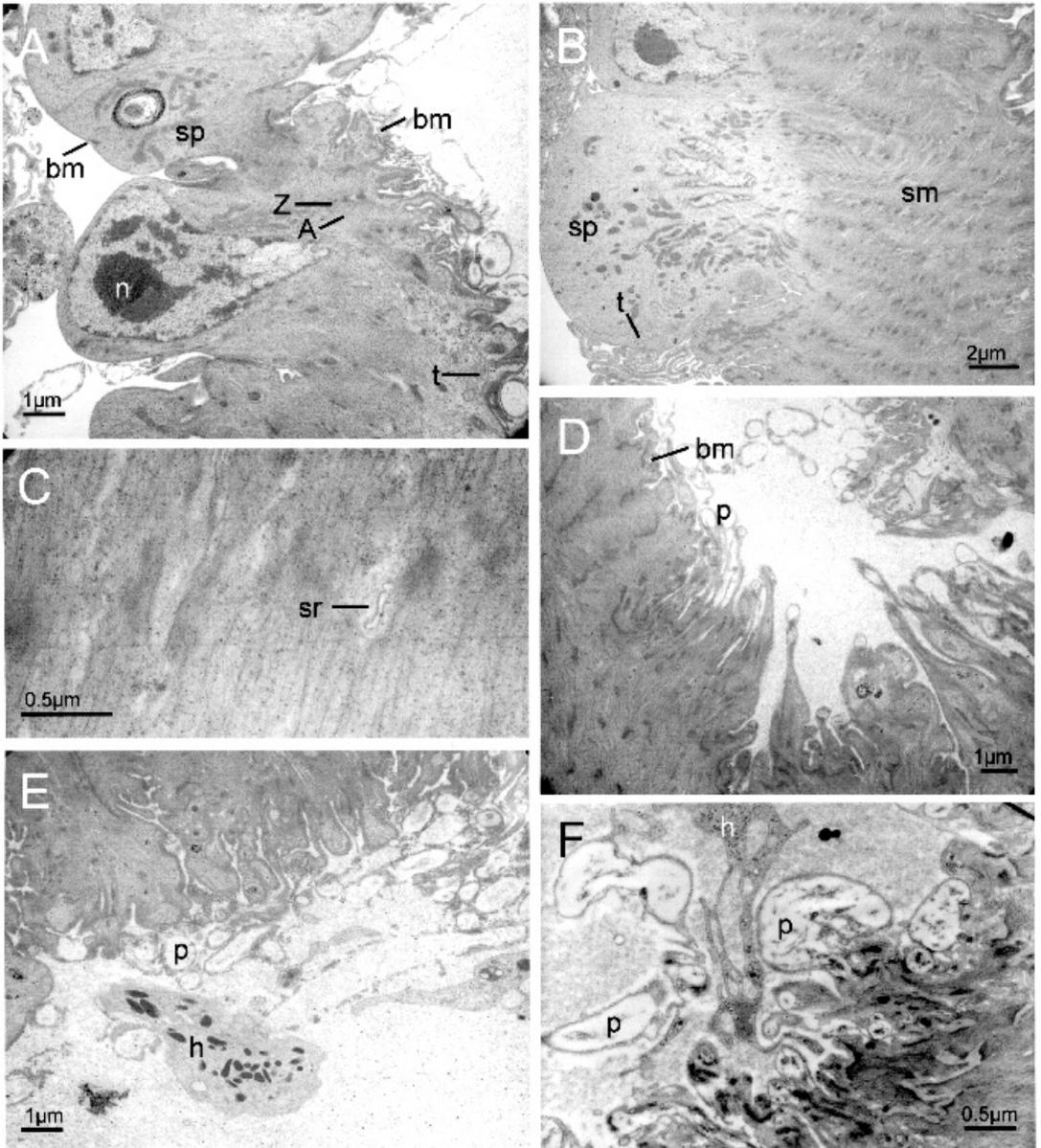
Figure 2: Aortic diverticles of *Scutigera coleoptrata* (TEM). **A:** Diverticula's wall consisting of a single-layered myocardium, covered by a thick basal lamina on the luminal and on the aluminal side. Sarcomeres show distinct Z- and A-bands. **B:** Sarcomeres located at the luminal side, organelles and nuclei are situated at the aluminal side. A transverse tubular membrane systems (T-tubules) originates from invaginations of the sarcolemma. **C:** Little developed sarcoplasmic reticulum within sarcomeres. **D:** Numerous protrusions extend into the luminal side of the aortic diverticle. **E:** The protrusions were formed by the luminal basal lamina. A haemocyte is attached to the tips of the protrusions. **F:** Protrusions, detail.
A, A-band; bm, basal lamina; h, haemocyte; n, nucleus; p, protrusion; sm, sarcomeres; sp, sarcoplasma; sr, sarcoplasmic reticulum; t, t-system; TEM, transmission electron microscopy; Z, Z-band.

II and 1% methylene blue in an aqueous 1% borax solution for approximately 5-25 s at 80-90 °C or alternatively with toluidine blue. Sections were studied using a DMSL-Leica microscope.

3D reconstructions

Semi-thin sections were digitised using a PixeLink Pl-A622C digital camera mounted on a Zeiss Axioskop. The image stacks were automatically aligned using AutoAligner 2 and manually corrected. The aligned image stack was 3D reconstructed using Imaris 4.1.3. To visualise the aortic diverticles, the structures were marked with polygons in the Surpass module implemented in Imaris. The polygons were automatically rendered and afterwards screenshots were taken of these surface renderings.

Transmission electron microscopy

For TEM investigation, heads of *Scutigera coleoptrata* were fixed in phosphate buffered (pH 7.2) paraformaldehyde (4 %), containing 15 % saturated picric acid and 0.08 % glutaraldehyde. They were postfixed with 1 % OsO_4 in the same buffer and, after alcohol dehydration, embedded in Epon. Ultrathin sections were stained with uranyl acetate and lead citrate and studied using a ZEISS EM 902 A electron microscope.

RESULTS

The head of *Scutigera coleoptrata* is densely packed with various organs (e.g. glands, foregut, central nervous system). Between these organs, the cephalic vessels are embedded. The main artery is the anterior cephalic aorta which branches off the anterior end of the heart in the first trunk segment (Figure 1A). At the level of the mandibles, ventrally an unpaired short vessel emanates from the aorta. It splits and widens to paired, sac-like structure termed aortic diverticles (Figure 1A-C). Regularly, these blind sacs are located above the foregut, however, their position
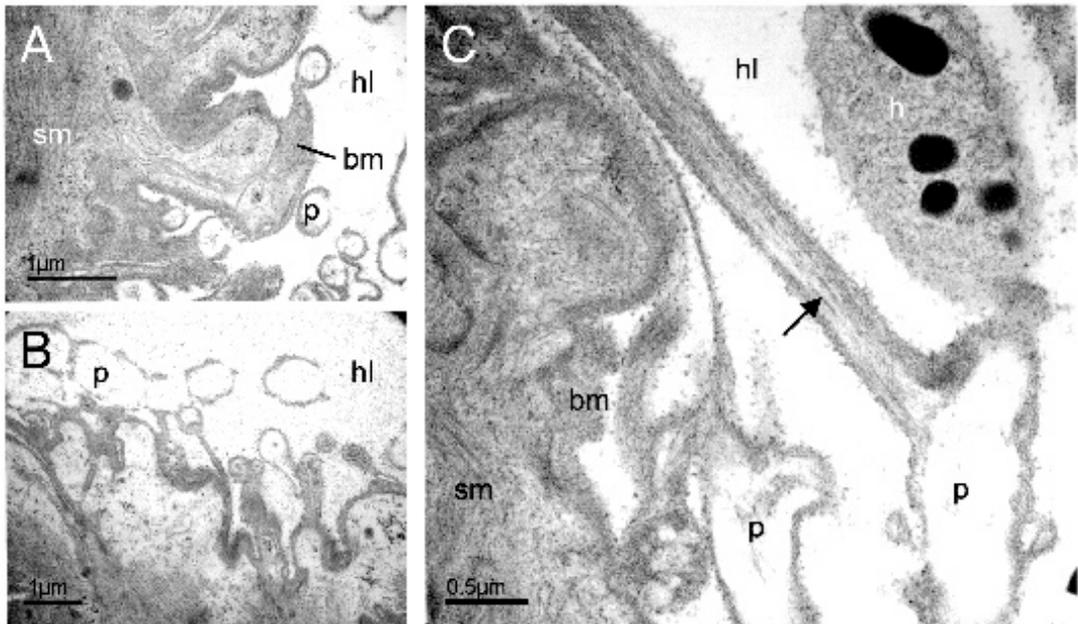
Figure 3: Luminal protrusions of the aortic diverticles of *Scutigera coleoptrata* (TEM). **A-B:** Convoluted sarcolemma with its luminal basal lamina forming sac-like protrusions. **C:** Filamentous material reaches into the protrusions (arrow). A haemocyte is attached to the tips of a protrusion.
bm, basal lamina; h, haemocyte; hl, haemolymph; p, protrusion; sm, sarcomeres; TEM, transmission electron microscopy.

can be shifted laterally (Figure 1B). They are surrounded by perivascular cells (Figure 1D), as recently described by Hilken & Rosenberg (2005).

The wall of the diverticles consists of a single-layered epithelium ("myocardium", thickness approx. 15-20 µm) that is covered on the luminal and on the aluminal side by a basal lamina (Figure 2A). The luminal basal lamina is thicker (0.3 µm) than that of the aluminal side (0.15 µm). Especially on the luminal side, the sarcolemma is increasingly convoluted (Figure 2A, D-F). The sarcomeres are polarized: The contractile material is mostly located toward the luminal side, whereas the sarcoplasma containing the huge nuclei, mitochondria, and the sarcoplasmic reticulum (SR) is located toward the aluminal side (Figure 2A-C). The myofibrils are circularly and longitudinally arranged (Figure 2A-C). The sarcomeres show distinct Z- and A-bands (Figure 2A-B). I-bands could not be detected.

A transverse tubular membrane system (T-tubules) originates from invaginations of the luminal and from the aluminal side of the sarcolemma (Figure 2A-B). Besides T-tubules, also SR-tubules could be detected (Figure 2A-C). The latter are only little developed, it penetrates the Z-bands and occurs also in the sarcoplasma (Figure 2C).

The most prominent feature of the aortic diverticles are numerous protrusions on the luminal side (Figures 2D-F, 3A-C). They look like inflated sacs and extend into the diverticula's lumen. The outer surface of these protrusions is formed by the luminal basal lamina (Figure 3A-C). However, in some cases filamentous material runs into these protrusions (Figure 3C), in other cases, they contain amorphous material (Figures 2F, 3C). Numerous haemocytes are attached to the tips of the protrusions (Figures 1D, 2E-F, 3C). Sometimes, both, haemocytes and protrusions can not clearly be separated (Figure 3C).

DISCUSSION

In Scutigeromorpha, the most peculiar and enigmatic structures of the circulatory system are the aortic diverticles. Their function and structure riddled scientists since their first description by Herbst (1891). Here, we investigated these structures for the first time ultrastructurally and three-dimensionally to a greater detail.

Aortic diverticles have been described histologically in *Scutigera coleoptrata* (Herbst 1891, Fahlander 1938, Wirkner & Pass 2002), *Thereuopoda clunifera* Wood, 1862 (Fahlander 1938), *T. longicornis* Fabricius, 1793 (Wirkner & Pass 2002) and *Thereuonema tuberculata* Wood, 1862 (Fahlander 1938). As they were exclusively found in scutigeromorph species so far, they can be hypothesised as an apomorphy for the Scutigeromorpha (see also Wirkner & Pass 2002). According to Herbst (1891), the diverticles of *S. coleoptrata* have a muscular wall and thus seem to pump the blood into the head. A similar function was concluded by Wirkner & Pass (2002). However, contrary to this, Fahlander (1938) did not find a thick muscular wall and therefore doubted their function as accessory pumps. Ultrastructurally, we can now clearly demonstrate that the aortic diverticles of *S. coleoptrata* consist of a thick and single-layered "myocardium", whose myofibrils are mostly circularly arranged. The structure of the diverticula's wall is comparable to that of the heart walls in *Lithobius forficatus* and *Strigamia maritima* (Økland et al. 1982, Økland 1984). Therefore, we can confirm the early assumption of Herbst (1891) that the aortic diverticles might function as accessory pumping organs which support the blood flow in the head.

Yet, all pumping structures need an antagonist for their function, for example the tubular hearts in arthropods are equipped with a spirally arranged myocardium which is responsible for the systole. The dorsal diaphragm, made up of connective tissue, act as antagonists and dilate the contracted heart (diastole). However, an antagonist to the strong muscle wall of the aortic diverticles of *Scutigera coleoptrata* could not be found by

now. Concluding from the variable position of the diverticles, connective tissue strands can be excluded to act as antagonists. On the other hand, the strong musculature described above can only be interpreted as an effective motor.

Nonetheless, if the diverticles act as pumps they most likely are developed due to the lack of tracheae in the head of scutigeromorphan centipedes. As they might help to maintain haemolymph pressure within the numerous but small head arteries which branch off the head aorta and supply the different organs with oxygen. In contrast, the heads of pleurostigmophoran centipedes are richly supplied with tracheae and thus the haemolymph is less involved in oxygen transport.

The double basal lamina of the myocardial wall is differently structured. On its basal side, the basal lamina is not conspicuous. But on the luminal side, the basal lamina forms protrusions that extend far into the lumen of the diverticles. Sometimes these sac-like inflations contain filamentous material. The function of these striking protrusions remains unclear. However, it is likely that they influence the haemolymph current.

On light microscopic level, the protrusions seem to be in very close contact to the haemocytes. Therefore, we checked, whether these organs act as haematopoietic organs. In spiders, prohaemocytes originate from the heart wall and are released into the lumen of the heart (Foelix 1996). However, in *Scutigera coleoptrata* we never noticed a formation of haemocytes from the muscular wall of the aortic diverticles. Haemocytes are only found in close contact with the protrusions of the luminal basal lamina. Signs of mitotic processes that give indications of haemocyte formation, have never been observed. Therefore, we may conclude with Herbst (1891) that the aortic diverticles with their thick myocardium and well ordered cardiac sarcomeres act exclusively as accessory pumping structures.

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Rudimentary supernumerary Malpighian tubules in the order Craterostigmomorpha Pocock 1902

Carol-Constantin Prunescu & Paula Prunescu

Prunescu, C.-C. & Prunescu, P. 2006. Rudimentary supernumerary Malpighian tubules in the order Craterostigmomorpha Pocock 1902. Norw. J. Entomol. 53, 113-118.

The presence of four Malpighian tubules, of which two were the normal main Malpighian tubules and the others two were rudimentary supernumerary was established by microscopic-anatomical research, on individuals of *Craterostigmus tasmanianus* collected from New Zealand and Tasmania.
All Malpighian tubules opened at the midgut–hindgut junction through the ampullar structures. The main pair of Malpighian tubules presents the lateral positions along the medium intestine and an anterior- posterior orientation. These Malpighian tubules are long and thick. They have excretory function and are present in all orders of the Class Chilopoda. Although the intestinal insertion place of the pair of supernumerary Malpighian tubules is similar with that of the main pair, there are differences which refer to the position and orientation of these rudimentary organs. In the individuals of *Craterostigmus tasmanianus* collected from New Zealand, the rudimentary supernumerary Malpighian tubules present a median-dorsal respectively median-ventral position in relation with the intestine and are both oriented parallel with the medium intestine towards the posterior zone, where is the insertion of each supernumerary tubule at the midgut-hindgut junction. In the individuals of *Craterostigmus tasmanianus* collected from Tasmania, the rudimentary Malpighian tubule with the median-dorsal position, presents a different orientation, namely from its opening through an ampulla at the level of the midgut-hindgut junction is directed caudally parallel with the posterior intestine. The other rudimentary Malpighian tubule, with median-ventral position, presents the anterior-posterior orientation parallel with the medium intestine. These rudimentary supernumerary organs are thin and short tubules which seem to be functional. The pair of the rudimentary Malpighian tubules represents a plesiomorphic character. This character might be utilised in taxonomy to establish relationships between some evolution lines and also to define new taxonomic units.

Key words: *Craterostigmus*, dorsal-ventral Malpighian tubules, New Zealand, Tasmania.

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INTRODUCTION

In a previous paper Prunescu & Prunescu (1996) presenteded the first description of supernumerary Malpighian tubules which opened at the level of the junction of the mid-gut with hind-gut, in dorsal and ventral position in *Scutigera coleoptrata* (Linné, 1758) and in median-dorsal position in *Craterostigmus tasmanianus* Pocock, 1902 originating from Tasmania.

Subsequently, following the reception of some individuals of *Craterostigmus tasmanianus* originating from New Zealand, the study was undertaken.

The results of this investigation bring new data, which could be used in the taxonomy of the *Craterostigmus* populations from Tasmania and New Zealand and for the correct disposal of the order Craterostigmomorpha in the chilopods phylogenetic tree.
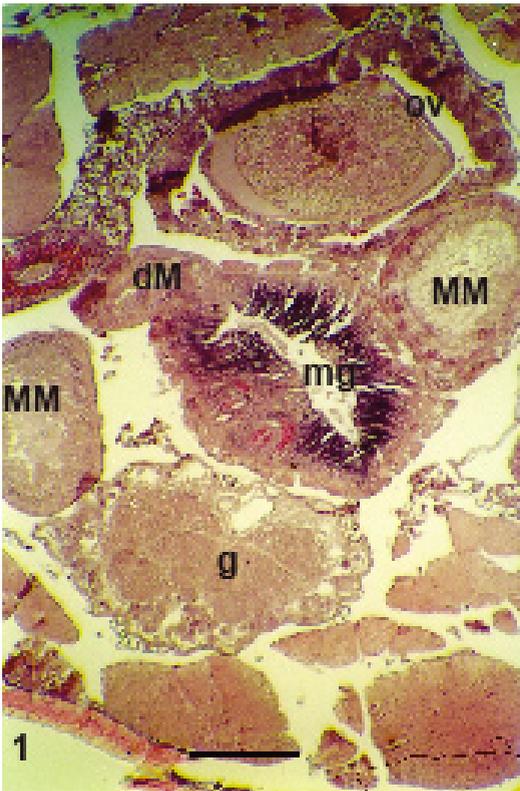
Figure 1. The opening of the dorsal Malpighian tubule (dM) in the terminal part of the mid-gut (mg) (*C. tasmanianus* from New Zealand). On the lateral sides of the intestine, note the two main Malpighian tubules (MM) in transversal section. H-E.
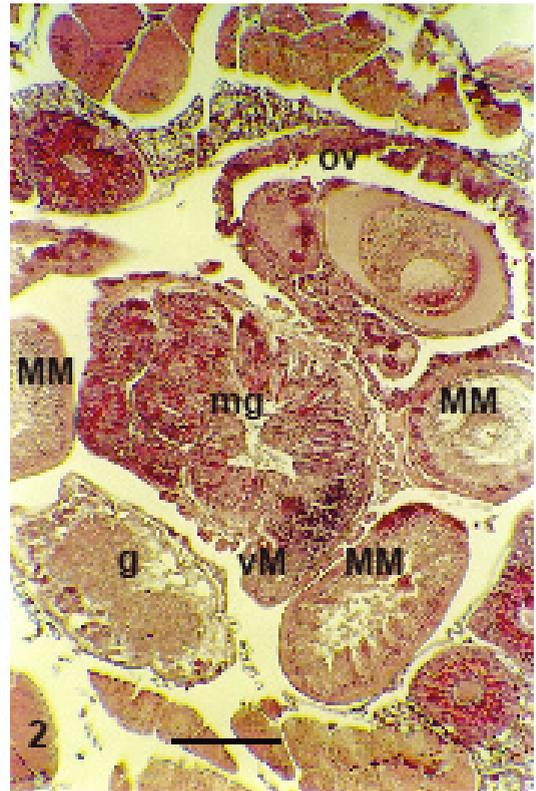
Figure 2. The opening of the ventral Malpighian tubule (vM) in the last part of the mid-gut (mg) (*C. tasmanianus* from New Zealand). H-E.

Scale bar (Figures 1-6) = 150µm.

MATERIAL AND METHODS

Several specimens of *Craterostigmus tasmanianus* originating from New Zealand, fixed in solution of glutaraldehyde, were presented by Prof. P. M. Johns. This material was gathered at Craigichurn Education Centre on 9 May 1996. The specimens of *Craterostigmus tasmanianus* from Tasmania were collected and fixed in glutaraldehyde by Dr. R. Mesibov in 1991. Two other individuals were offered by Dr. S. M. Manton in 1965. Part of this material was processed - dehydrated and embedded in paraffin - according the routine histological techniques. Serially histological sections of 5 µm were stained with hemalum-eosine (H-E). The micro-photos were realized with a camera mounted on an Amplival microscope (Zeiss-Jena).

RESULTS

from New Zealand

The openings of a dorsal Malpighian tubule (Figure 1) and of a ventral Malpighian tubule (Figure 2) were observed at the junction zone of the medium with the posterior intestine.
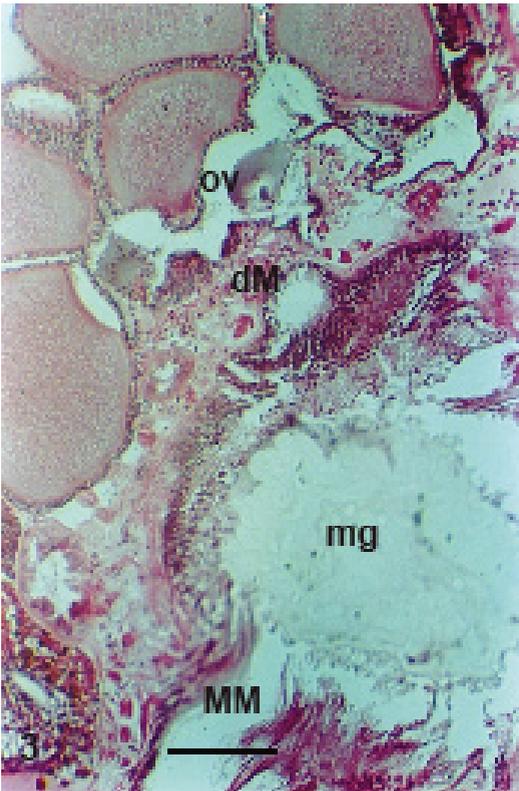
Figure 3. The dorsal Malpighian tubule (dM) opening at the mid-hind gut junction. Laterally, note the opening of one of the main Malpighian tubules (MM) (*C. tasmanianus* from Tasmania), H-E.
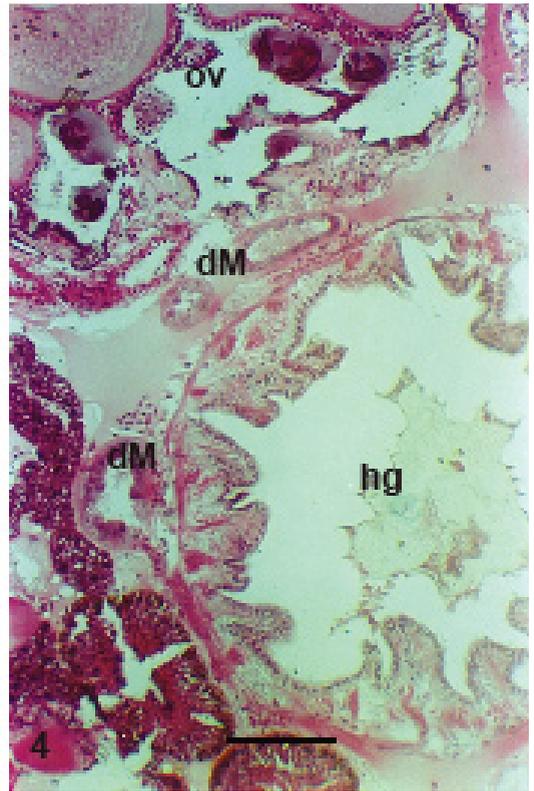
Figure 4. Note three transversal profiles through coiled dorsal Malpighian tubule (dM) at the level of the hind gut (hg), fact which demonstrates its caudal orientation (*C. tasmanianus* from Tasmania). H-E.

These tubules were supplementary to the two main Malpighian tubules, which opened on the lateral sides of the mid-gut, at the junction level. The supernumerary Malpighian tubules were of some millimeters length and very thin. The two rudimentary Malpighian tubules presented the anterior-posterior orientation (Figure 7). At the anterior distal ends they were closed in glove-finger. Their histological structure was similar to the structure of the main Malpighian tubules. At the intestinal opening, the supplementary Malpighian tubules were dilated, forming small vesicles (ampullae), by which they communicated with the intestine lumen.

from Tasmania

We repeated the study of this population using more individuals. The presence of a supplementary rudimentary Malpighian tubule with median-dorsal insertion (Figure 3) in the region of the mid-hind gut junction and the orientation towards the posterior part of the body was confirmed by the histological observations (Figure 4).

After the finding in the individuals from New Zealand of a second supplementary Malpighian tubule with median-ventral insertion, we also identified a second supplementary Malpighian
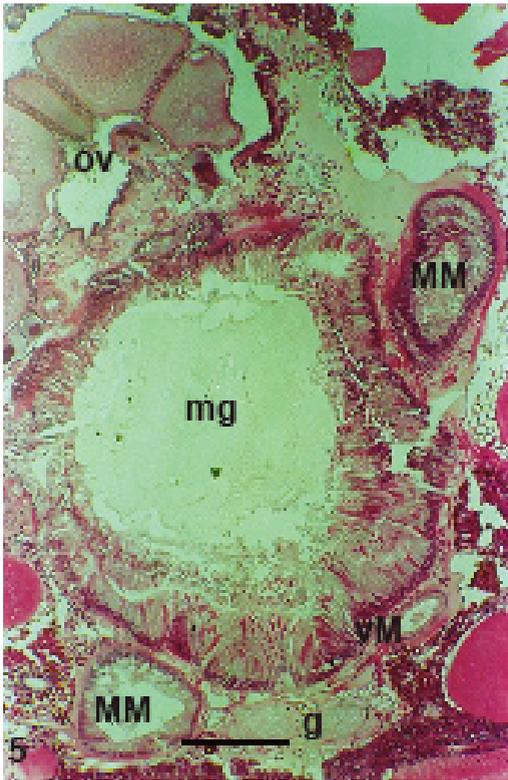
Figure 5. The ventral Malpighian tubule (vM) before its opening in the terminal part of the mid-gut (mg) (*C. tasmanianus* from Tasmania). H-E.
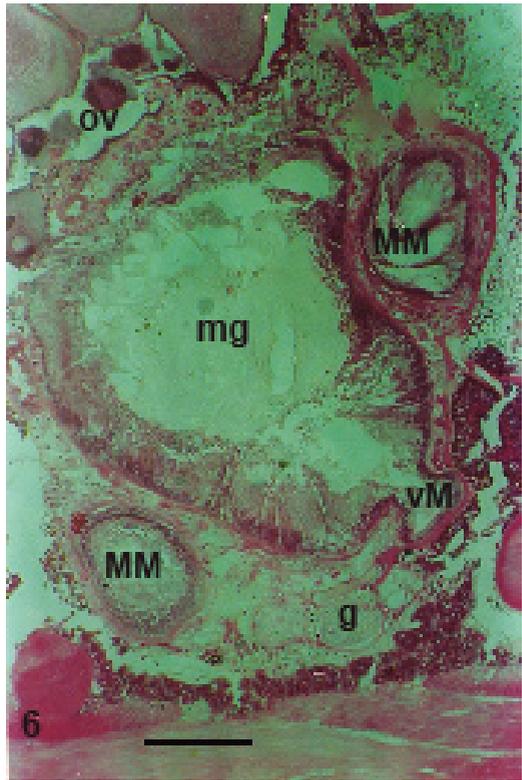
Figure 6. The opening of the ventral Malpighian tubule (vM) in the terminal part of the mid-gut (mg) (*C. tasmanianus* from Tasmania). H-E. ov: ovary; g: ventral nervous ganglion.

tubule with median-ventral insertion (Figures 5 and 6), in *Craterostigmus* exemplars from Tasmania. This rudimentary Malpighian tubule was oriented towards the anterior part of the body (Figure 8).

In both *Craterostigmus* populations, the two functional Malpighian tubules of great size, bilaterally inserted at the junction of the medium gut with the posterior gut were present (Figures 1, 2, 3, 4, 5 and 6). These two main Malpighian tubules are present in all chilopods (Lewis 1981), preserving the same opening places in the terminal segment of the medium intestine at the junction with the posterior intestine.

DISCUSSION

In a previous paper (Prunescu & Prunescu 1996) we described in *Scutigera coleoptrata,* the supernumerary Malpighian tubules presenting dorsal and ventral insertions at the terminal level of the mid-gut. We verified the existence of these supplementary Malpighian tubules in *Scutigera coleoptrata* and we confirm again their presence.

The presence of these rudimentary Malpighian tubules in the orders Scutigeromorpha and Craterostigmomorpha has phylogenetic importance because till now, these orders have not been considered as related.

The presence of the two Malpighian rudimentary tubules in the order Craterostigmomorpha and the absence of such tubules in the representatives of the order Lithobiomorpha, suggests the fact that the order Craterostigmomorpha had not derived during the evolution from chilopods of lithobiomorph type as it result from the phylogenetic tree, successively proposed by Prunescu (1965), Shinohara (1970), Dohle (1985), Shear & Bonamo (1988), Borucki (1996), Hilken (1997).

The presence of the two rudimentary super-numerary Malpighian tubules in *Scutigera coleoptrata* and in the two populations of *Craterostigmus tasmanianus* could not be explained, but only if we admit the existence of the supernumerary Malpighian tubules similarly localized in the last common ancestor of Chilopoda.

The orientation from the anterior to posterior direction (Figure 7) of the supernumerary rudimentary Malpighian tubules in the population from New Zealand is a plesiomorphic character, corresponding to the orientation of the main Malpighian tubules.

The orientation of the supernumerary dorsal Malpighian tubule of the *Craterostigmus* population from Tasmania is apomorphic, derivated, because the dorsal Malpighian tubule is posterior-anterior oriented (Figure 8). This position occurred following the modification of the anterior-posterior plesiomorphic position of the homologous dorsal tubule.

The particular orientation of the rudimentary supernumerary Malpighian tubules in the two populations of the species *Craterostigmus tasmanianus* places the New Zealand population in a group having probably the rank of new family, distinct from the family Craterostigmidae Pocock 1902.
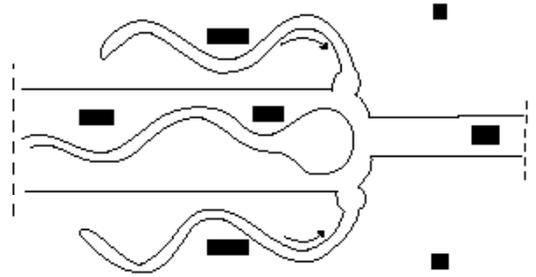
Figure 7. Schematic representation of the supernumerary Malpighian tubules insertion. *Craterostigmus tasmanianus* from New Zealand. Abbreviations: dMt = dorsal Malpighian tubule; vMt = ventral Malpighian tubule; MT=main Malpighian tubule; mg=mid-gut; hg=hind-gut; D=dorsal; V=ventral.
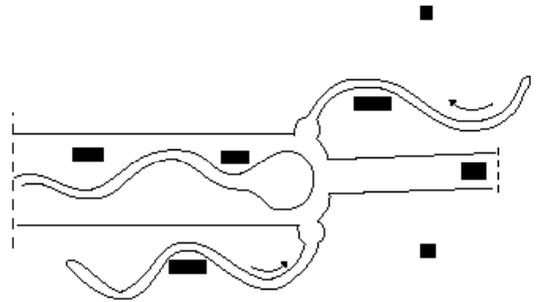
Figure 8. Schematic representation of the supernumerary Malpighian tubules insertion. *Craterostigmus tasmanianus* from Tasmania. Abbreviations see Figure 7.

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Fine structural organization of the poison gland of *Lithobius forficatus* (Chilopoda, Lithobiomorpha)

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Rosenberg, J. & Hilken, G. 2006. Fine structural organization of the poison gland of *Lithobius forficatus* (Chilopoda, Lithobiomorpha). Norw. J. Entomol. 53, 119-127.

The modification of the legs of the first trunk segment into maxillipeds with its characteristic poison claws is the most prominent autapomorphy of the Chilopoda. Our study on the organization of the poison gland of *L. forficatus* clearly shows that the glandular epithelium is composed as a compound gland organ with hundreds of epidermal gland units. The whole gland is covered by a basal lamina. All gland units surround the lumen of the common venom duct that opens on the tip of the maxilliped. Each epidermal gland unit consists of three different cell types: a secretory cell, an intermediary cell, and two canal cells. The intermediary and the canal cells form a conducting canal that opens into the venom duct. Proximally, these cells enclose a spacious extracellular reservoir, filled with the secretion of the secretory cell. The single, voluminous and pear shaped secretory cell is invaginated distally, forming an extracellular reservoir. The intermediary cell is lined by a smooth cuticular intima only in its upper part of the duct, whereas the canal cells are completely covered by a cuticle. Apically the distal canal cell forms a complex cuticular valve, which regulated the secretion flow. We can demonstrate that the glandular units of the poison gland of *L. forficatus* are similarly structured as isolated epidermal glands and compound epidermal gland organs hitherto studied in Myriapoda. Beside the composition of three different types of cells (secretory cell, intermediary cell, canal cell), the apex of the intermediary cell is covered by a smooth cuticle only in its distal part. This characteristic feature is stated as a synapomorphy of the Myriapoda.

Key words: Compound gland organ, epidermal gland, fine structure, Chilopoda, centipedes.

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INTRODUCTION

The modification of the legs of the first trunk segment into maxillipeds with its characteristic poison claws is the most prominent autapomorphy of the Chilopoda. Newport (1845) recognised first that the forcipules, which he termed 'mandibles', contain a poison gland. The venom is used to kill the prey. After his extensive comparative histological studies on the poison glands of several representatives of the Chilopoda, Mac Leod (1878) differentiates between poison glands and head glands. In many studies of the nineteenth century, the poison gland was confused with other head glands (Plateau 1878, Duboscq 1895). Additional studies on the histology of the poison gland of *L. forficatus* were accomplished by Herbst (1891), Karlinski (1883) and Sograf (1880). Duboscq (1894, 1895, 1896, 1898a,b) compared the topography of the poison gland of different representatives of Lithobiomorpha, Scolopendromorpha, and Geophilomorpha.
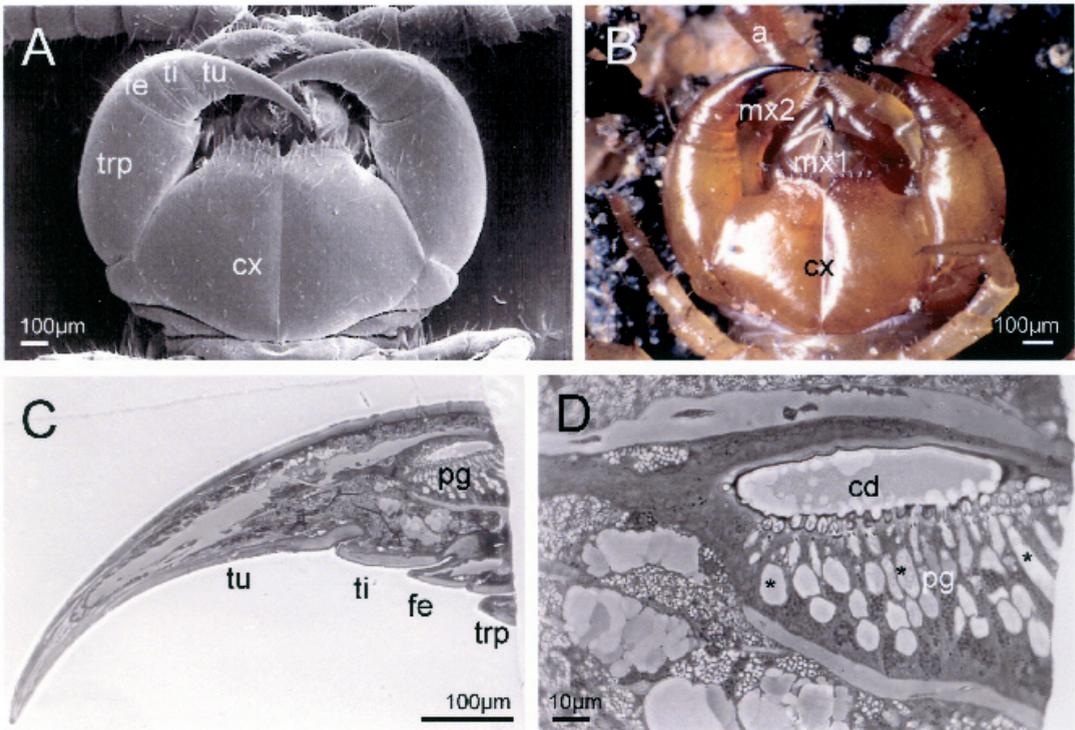
Figure 1. *Lithobius forficatus.* **A.** Ventral view of the head with the maxilliped (SEM). **B**. Ventral view of the head with the maxilliped (LM). **C**. Longitudinal section of the maxilliped with tarsungulum, tibia, and femur containing the poison gland. The common poison duct is partly seen (LM). **D.** Detail of the poison gland with wide extracellular spaces (*) surrounding the common poison duct (LM).
a, antenna; cd, common poison duct; cx, coxa of maxilliped; fe, femur; LM, light microscopy; mx1, maxilla 1; mx2 , maxilla 2; pg poison gland; SEM, scanning electron microscopy; ti, tibia; trp, trochantero-prefemur; tu tarsungulum.

According to all studies, the poison gland consists of numerous unicellular glands grouping around a common poison duct.

Hitherto ultrastructural investigations were done only on poison glands of two species of the Scolopendromorpha, *Scolopendra morsitans* (Dass & Jangi 1978) and *Ethmostigmus rubripes* (Ménez et al. 1990). According to these investigations, the poison glands mainly consists of secretory cells and basal muscle cells. The secretory cells undergo a secretion cycle. Recently, several investigations focussed on epidermal glands in Chilopoda (Müller et al. 2003, Hilken et al. 2003, Hilken et al. 2005). It becomes evident that epidermal glands could be classified into isolated epidermal glands and compound epidermal gland organs. However, the glandular units are comparably structured (Hilken et al. 2005). The aim of the present study is to reconstruct the cellular organization of the glandular units of the poison gland of *Lithobius forficatus.* Additionally, we want to clarify, whether the poison gland belongs to isolated or compound epidermal glands.

MATERIAL AND METHODS

Specimens of *Lithobius forficatus* (Linné, 1758) were collected around Cologne, Germany. Specimens were anesthetized with CO_2 , cut into

several parts and preserved as described below. For TEM investigation, heads of *L. forficatus* were fixed in a modified Karnowsky fixative, containing paraformaldehyd (2 %) and glutaraldehyd (2.5 %) in phosphate-buffered saline (PBS; pH 7.2) and postfixed in 2% OsO_4/PBS (pH 7.2). Objects were embedded in Epon 812. Semithin sections (0.5-1 μm) were stained with toluidin blue. Sections were studied using a DMSL-Leica light microscope. Ultrathin sections were stained in uranyl acetate and lead citrate and examined with a ZEISS EM 109 T transmission electron microscope. For scanning electron microscopy (SEM; CAMSCAN DV4) objects were critical point dried and sputter-coated with gold.

RESULTS

Light microscopy
In *Lithobius forficatus*, the poison gland is situated in the maxilliped. The gland extents from the tibia up to the distal part of the trochantero-prefemur (Figure 1A-D). A common poison duct passes through the poison claw and opens subterminally at the tarsungulum. In the area of the tibia, femur, and trochantero-prefemur, the common poison duct is surrounded by the huge multilayered glandular epithelium (about 40μm high) of the poison gland. The cuticle of the common duct is pierced by numerous pores (Figures 1D, 2A,B). The poison duct is formed by a single layer of undifferentiated canal cells, lined by a thick cuticle.

Ultrastructure
The glandular epithelium consists of numerous multicellular glandular units. Each of them is composed of three different cells types: a huge secretory cell, an intermediary cell, a proximal, and a distal canal cell (Figure 4). The canal cells form the conducting canal. The elongated intermediary and the proximal canal cells enclose a wide extracellular space that is filled with the secretion of the secretory cell. The entire glandular epithelium is surrounded by a basal lamina (Figure 3D,F).

Canal cells
We can distinguish two different canal cells that formed the cuticular conducting canal, a distal and a proximal canal cell (Figure 4).

Distal canal cell
The distal canal cell encloses a wide atrium that opens into the common poison duct (Figures 2A-D, 4). The atrial duct is lined by a wide cuticle (about 0.6 μm). The moderate electron-dense cytoplasm contains, beside the nucleus, only few organelles, e. g. some mitochondria and some cisternae of the ER.

Proximal canal cell
The proximal canal cell is more complex structured. In its distal part up to the intermediary cell, the cell surrounds the conducting canal filled with fine granular material. In the transition zone of the distal and the proximal canal cell, the cuticle of the proximal canal cell becomes distinctively thin (about 240 nm). The cuticle protrude deeply into the atrium and forms a nozzle-like structure that project into the atrium like a valve. In transverse sections, the nozzle-like structure looks like a four-leafed clover (Figures 2A-D). More proximally, the cuticle becomes very thin (about 200 nm) and lines the conducting canal up to the intermediary cell. In the distal part of the canal cell, a ring-shaped cuticular pad is formed (Figures 2A-B,E), noticeable even in light micrographs (Figure 1D). The apical cell membrane of the proximal canal cell is differentiated into more or less short microvilli that are embedded in an electron-lucent subcuticular layer beneath the osmiophilic cuticle (Figures 2D-E). Within the cytoplasm several mitochondria, cisternae of rough endoplasmic reticulum (rER) and some electron-lucent vesicles are seen. In its proximal part, the cell forms a small cytoplasmic leaflet that encloses together with the intermediary cell a wide extracellular space. The longish nucleus is situated in the basal part of the cell (Figures 3C,E, 4).

Intermediary cell
The small intermediary cell connects the proximal canal cell and the secretory cell. The intermediary cell surrounds the apex of the secretory cell and
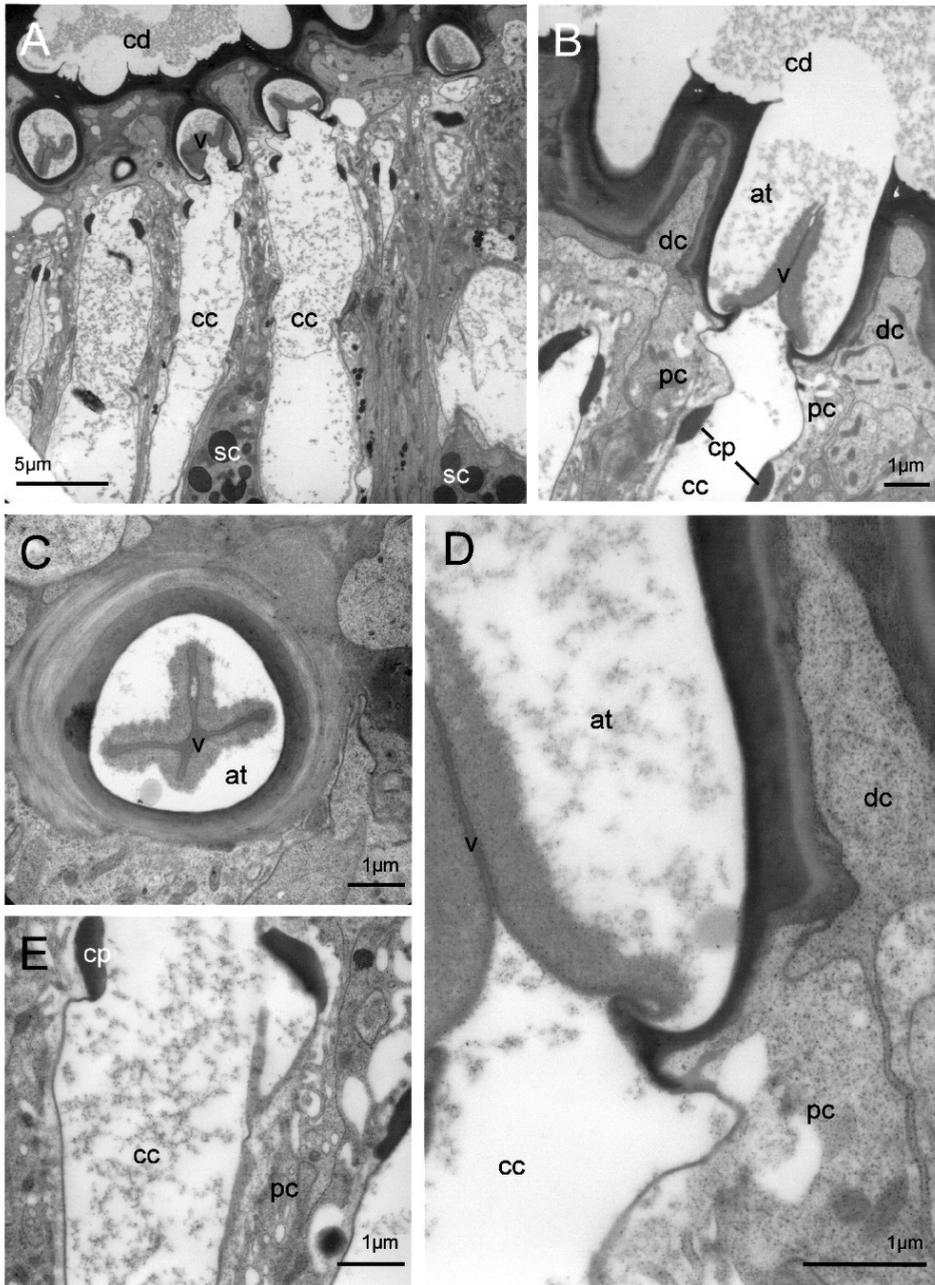
Figure 2. *Lithobius forficatus,* poison gland (TEM). **A**. Overview of the distal part of the glandular epithelium of the poison gland. **B**. The atrial duct is formed by the distal canal cell. The proximal canal cell forms a valve (nozzle-like structure) that projects into the atrium. A part of the cuticle is modified to a ring-shaped cuticular pad. **C.** Cross section of a closed valve. **D**. Most distal part of the proximal canal cell with the beginning of the valve. **E.** Distal part of the proximal canal cell with ring-shaped cuticular pad and cuticular lining of the conducting canal.

at, atrium; cc, conducting canal; cd, common poison duct; cp, cuticular pad; dc, distal canal cell; pc, proximal canal cell; sc, secretory cell; TEM, transmission electron microscopy; v, valve.

encloses a widened extracellular cavity (Figures 3A-B, 4). The cell apex is differently structured. Only in its distal part, a delicate cuticle is formed that disappeared in its proximal part (Figures 3A-B). Proximally, the intermediary cell extends to form a small cytoplasmic leaflet that encloses together with that of the proximal canal cell an extracellular space. The cytoplasm appears rather electron-lucent, it contains short cisternae of ER, some mitochondria, and several electron-dense vacuoles (0.2-0.5 μm in diameter). The longish nucleus is situated in the basal part of the cell (Figures 3E, 4).

The leaflet-like projections of the intermediary cell (0.1-0.3μm high) form a wide extracellular space filled with secretion. The thin projections of the proximal canal cell (0.2-0.3 μm high) surround the intermediary cell in this area. The apical cell membrane of the intermediary cell is not lined by a cuticle.

Secretory cell
The secretory cell is connected to the intermediary cell and overlie laterally the extracellular space (Figure 4). The secretory cell apex penetrate the envelope, formed by the leaflet-like projections of the intermediary cell and the proximal canal cell.

The single and voluminous secretory cell is pear shaped. Its narrow apex invaginates forming a widened extracellular reservoir that is lined by microvilli. (Figure 3A-B). The cell is filled by numerous osmiophilic spherical vacuoles, filled with stacked inclusions (Figure 3D,G). The vacuoles merge with the apical cell membrane. Within the cytoplasm, the vacuoles are surrounded by cisternae of rER, free ribosomes, and mitochondria (Figure 3D-E). The nucleus is located in the basal part of the cell (Figures 3D, 4).

DISCUSSION

Up to now, only the ultrastructural organization of the poison gland of different species of the Scolopendromorpha are investigated (Dass & Jangi 1978, Ménez et al. 1990). In both studies, the secretory unit is described to be unicellular, consisting of a secretory cell only. However, the present study reveals that the poison gland of *Lithobius forficatus* shows a completely different structure. Here, the poison gland is characterised as a compound epidermal gland organ, composed of hundreds of multicellular epidermal gland units. Each unit consists of three different cell types, a secretory cell, an intermediary cell, and two different canal cells. Thus, it belongs to the 4-cell gland category of epidermal glands in Chilopoda, classified by Hilken et al. (2005).

The venom secretion of the secretory cell is released by exocytosis into the extracellular reservoir, formed by the apex of the secretory cell. The secretion fluid is stored within the extracellular space, formed by the proximal projections of the intermediary and the proximal canal cell. The inner boundary of the extracellular space is formed by the intermediary cell and is not lined by a cuticle. Finally, the venom fluid is released via the conducting duct into the common poison duct. The discharge of the secretion will be controlled by special structures of the proximal canal cell, the ring-shaped sphincter pad and the nozzle-like structure that acts as a non-return valve.

We can demonstrate that the multicellular gland units of the poison gland are comparably structured as other isolated and compound epidermal gland organs in Chilopoda (Hilken et al. 2005). All these gland organs are composed of numerous gland units. Each glandular unit consists of one or two secretory cells, a single intermediary cell, and one or two canal cells. The extracellular reservoir of the secretory cell is not lined by a cuticle. The intermediary cell encloses a conducting canal. As a common feature, the cell apex of the intermediary cell is only in its most distal part covered by a distinct cuticle that continues to the cuticle of the canal cells (Hilken et al. 2005).

However, the findings of the ultrastructural organization of poison glands of Chilopoda are contradictory. But we find indications that these differences are mainly based on misinterpretations.
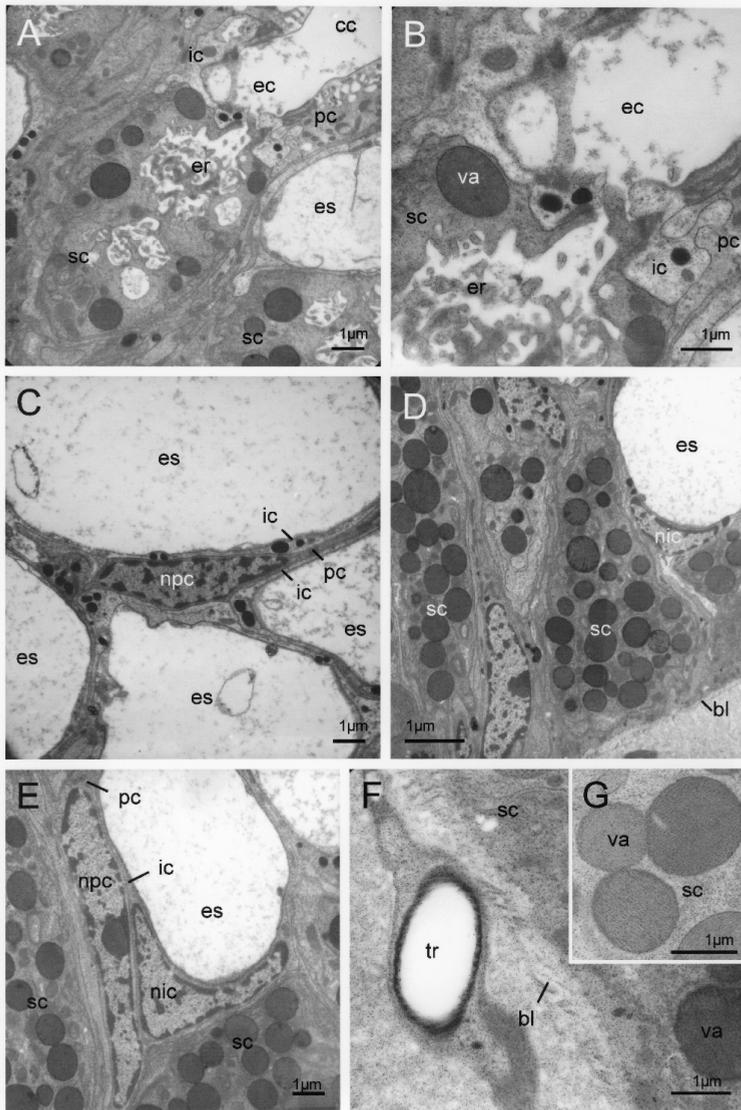
Figure 3. *Lithobius forficatus,* poison gland (TEM). **A.** The pear shaped distal part of the secretory cell is surrounded by a small intermediary cell. **B.** Higher magnification with the apex of the secretory cell and an intermediary cell. Only the distal part of the intermediary cell is lined by a faint cuticle. Microvilli of the apex of a secretory cell extend into the extracellular reservoir. **C.** Four extracellular spaces lined by cytoplasmic projection of the intermediary and the proximal canal cells. **D.** Extracellular space with adjacent nucleus of a intermediary cells, surrounded by secretory cells. **E.** Basal part of the poison gland with different secretory cells filled with vacuoles. The extracellular space is lined by a small cytoplasmic sheath of an intermediary and a proximal call cell with their nuclei. **F.** Secretory cell extends up to the common basal lamina. **G**. Secretion vacuoles of the secretory cell with stacked inclusions.

bl, basal lamina; cc, conducting canal; ec, extracellular cavity; er, extracellular reservoir; es, extracellular space; ic, intermediary cell; nic, nucleus of the intermediary cell; npc, nucleus of the proximal canal cell; pc, proximal canal cell; sc, secretory cell; TEM, transmission electron microscopy; tr, tracheole; va, vacuoles.

According to Dass & Jangi (1978), the venom glands of *Scolopendra morsitans* Linné, 1758 consists of secretory cells, hypodermal cells, muscle cells, and basal membrane cells. The secretory cells undergo different phases of secretory activity (Barth 1967, Dass & Jangi 1978). The secretory cells form at its apex a sphincter-like cuticular ring and open into an atrium by means of a nozzle-like structure that acts as a non-return valve. The secretion is of a holocrine type. New secretory cells are added by division and differentiation of hypodermal cells. The poison gland has its own contractile system to eject the secretion into the common poison duct. Muscle fibres are found either at the periphery adjacent to the basal lamina or they are arranged in radial disposition around the secretory cells and extend from the basal lamina to the cuticular lining of the conducting canal.

Within the glandular units of the poison gland of *L. forficatus*, a sphincter-like cuticular ring and a valvular structure are observed. Both structures are identically developed in *L. forficatus* and in *S. morsitans*. In the latter species, the secretory cell is described to form the cuticular ring and the valve (Dass & Jangi 1978). But here we can show that these structures are formed exclusively the proximal canal cell. So it is assumed that in *S. morsitans* the existence of a proximal canal cell was overlooked by Dass & Jangi. In addition, based on the comparably location it is most likely that the hypodermal cells are identical to the here described distal canal cells. The 'basal membrane cells' of *S. morsitans* might be confused with the basal projections of the proximal canal cell and the intermediary cell, whose nuclei are situated in the basal part of each glandular unit. The widened extracellular spaces found in *Lithobius forficatus* are misinterpreted as degenerated secretory cells by Dass & Jangi (1978).

In *Ethmostigmus rubripes* Brandt, 1840, the venom apparatus is formed by glandular cells, a 'basement membrane and septa', and three types of muscles (Ménez et al. 1990). The so-called basement membrane consists of a thin sheath of 'connective tissue'. This tissue enclose a peripheral muscle layer and encapsulates the secretory cells. The discharge of the venom secretion appeared to be by exocytosis (Ménez et al. 1990) similarly observed in *L. forficatus* in the present study. The authors denied the occurrence of a nozzle serving as a non-return valve in *E. rubripes*. However, this structure was figured in their Figure 7b, but was misinterpreted as venom granules. In this context, the existence of a proximal canal cell, forming the valve, was also overlooked. In one of their overview micrographs (Ménez et al. 1990, Figure 3d) a single secretory cell is figured, filled up with secretory vacuoles. This cell is situated beside two additional, very thin cells with their longish nuclei. Both cells surround a wide extracellular space. After the findings of the present study in *L. forficatus*, these cells correspond to the proximal cytoplasmic projections of the proximal canal cell and the intermediary cell.

In both, *S. morsitans* and *E. rubripes*, peripheral and longitudinal muscles were described, surrounding the poison gland and encapsulating the secretory cells (Dass & Jangi 1978, Ménez et al. 1990). The function of the different muscle fibres seems to expel venom from the lumen of the secretory cells into the lumen of the common poison duct. Therefore, it is astonishing that in the venom gland of *Lithobius forficatus*, muscular fibres could not be detected, neither in the periphery of the gland nor between the glandular units. This fact is difficult to explain. The mode of expelling venom out of the conducting canal in *L. forficatus* is not yet clear.

According to our state of knowledge and the above mentioned interpretations, the glandular units of the poison gland of the three investigated chilopods are multicellularly composed. Beside a secretory cell, an intermediary cell, a proximal, and a distal canal cell seems to exist also in both representatives of Scolopendromorpha. Hilken et al. (2005) recently show that the existence of a small intermediary cell has been overlooked repeatedly in previous ultrastructural investigations on epidermal glands in Chilopoda. Most epidermal glandular units of epidermal glands share the same ground pattern in Chilopoda and Diplopoda (Hilken et al. 2005).

The present study demonstrates that also poison glands of Chilopoda are composed as compound epidermal glands and that their glandular units show the same ground pattern as other epidermal glands in Myriapoda.
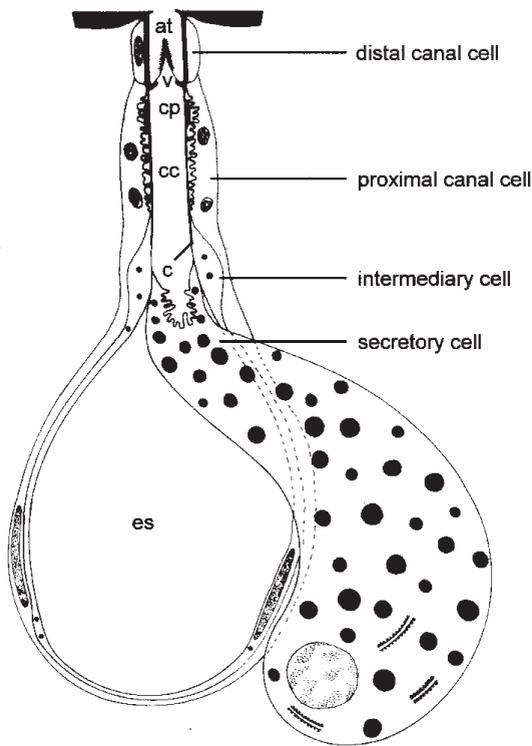
Figure 4. *Lithobius forficatus.* Schematic representation of the glandular unit of the poison gland.
at, atrium; c, cuticle; cc, conducting canal; cp, cuticular pad; es, extracellular space; v, valve.

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The XXVII Nordic-Baltic Congress of Entomology

July 29 - August 4, 2007, Uppsala, Sweden
First Announcement / Call for Papers

The world of multicellular organisms largely consists of insects, both on the species level and on the individual level. The number of entomologists is also large, but not nearly large enough considering the size of the field. For entomologists, there is always a need to meet with like-minded people, exchange experiences and partake of the latest research results.

For many years, these meetings have been organised in the form of national and international conventions and symposia, including meetings for entomologists from the five Nordic countries. From 1997 on, the Nordic meetings have welcomed participants from the Baltic countries, and we have also been fortunate to have participants from France, Germany, Great Britain, Russia, Ukraine and Poland.

The XXVII Nordic-Baltic Congress of Entomology will be held in Uppsala, Sweden, on July 29 - August 4, 2007. This meeting coincides with the 300th anniversary of the birth of Carolus Linnæus (Carl von Linné). The city in which he lived and worked as teacher, researcher and innovator was Uppsala. The Entomological Society of Uppland is honoured to be hosting this congress, and we are delighted to welcome you to Uppsala.

Regarding the programme, we welcome contributions (talks or posters) within ecology, systematics, physiology and other relevant areas. We intend to look at the preliminary applications in order to prepare a first draft of the programme. However, we already know that we will include lectures on systematics and the Linnæan walks around Uppsala, where we will make excursions for a couple of days.

We invite non-binding preliminary registrations to be submitted before May 31, 2006. In the autumn of 2006, when the fee has been set, we will need a final, binding registration. We are looking into various means of external financing, and it is our ambition to set the fee at around EUR 150 or lower. Undergraduate students will be offered special stipends to help defray the costs.

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- Member of Entomological Society
     [yes / no, if yes give name of society]
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You are heartily welcome to the congress!
The Entomological Society of Uppland

Dorso-ventral differences in gene expression in Glomeris marginata (Villers, 1789) (Myriapoda: Diplopoda)

Ralf Janssen[+#], Nikola-Michael Prpic[+] and Wim G. M. Damen

Janssen, R., Prpic, N.-M. & Damen, W. G. M. 2006. Dorso-ventral differences in gene expression in *Glomeris marginata* (Villers, 1789) (Myriapoda: Diplopoda). Norw. J. Entomol. 53, 129-137.

Some arthropods display a discrepancy in the number of ventral and dorsal metameric structures. The trunk of millipedes (Diplopoda) has more sternites and leg pairs on the ventral side than tergites on the dorsal side. As the metameric body plan is laid down during embryonic development, an analysis of genes that play a role in the formation of the segmental structures may give insights into the origin of this dorso-ventral discrepancy. We have previously analysed a number of segmentation genes in the millipede *Glomeris marginata* and were able to show that these genes display different expression patterns ventrally compared to the dorsal side. Here we summarize the data on the expression of segment polarity genes and Hox genes, and in addition show the analysis of additional genes that encode the T-box transcription factors H15-1 and H15-2. All hitherto examined *Glomeris* segmentation genes including the two *H15* genes show a remarkable difference in dorsal and ventral expression patterns. This result suggests that there must be a decoupling of dorsal and ventral segmentation processes in this millipede and provides an explanation for the discrepancy in the number of dorsal and ventral structures. This decoupling has important implications for the alignment of tergites and sternites/leg pairs in diplopods.

Keywords: Millipede, Myriapoda, *Glomeris marginata, engrailed, wingless, H15 genes, midline, hedgehog, cubitus interruptus,* diplosegmentation.

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INTRODUCTION

One of the hallmarks of the arthropods is the segmented body plan. During ontogeny the arthropod body is built from reiterated units. The subdivision of the body into segmental units therefore is most obvious during embryogenesis, but can also be clearly recognized in the adult body plan. The segmented nature of the arthropod body is obvious from reiterated structures such as e.g. the tergites that cover the dorsal side, the sternites and appendage pairs on the ventral side, and the reiterated ganglia of the central nervous system. But also other structures, such as the dorsal vessel (the heart), form from segmentally reiterated precursors. Most people are familiar with arthropod species that display a "regular" segmentation, i.e. in which there is an equal number of dorsal and ventral segmental components, and thus each dorsal tergite correlates with one sternite and one pair of limbs (where present).

However, there are exceptions that display discrepancies in the number of dorsal and ventral structures. A prominent example are the millipedes (Diplopoda). Millipedes have more sternites and leg pairs on their ventral side than tergites on their dorsal side. The name "Diplopoda" already refers to the phenomenon that they seem to have segments with two pairs of legs each; these special segments are called diplosegments. But also in other myriapod groups, e.g. the Pauropoda, the Symphyla, and in the Scutigeromorpha among the Chilopoda, there is a discrepancy between the number of tergites on the dorsal side and the number of leg pairs on the ventral side. This phenomenon of a discrepancy in the number of dorsal and ventral metameric structures is not restricted to a number of myriapod groups, but is also seen in other arthropods, like in some crustaceans (e.g. Notostraca) and some insects (e.g. larvae of the fly genus *Pericoma*).

We try to get insights into the question how these dorsal-ventral discrepancies can be explained. The example we use in our studies is the pill millipede *Glomeris marginata* (Villers, 1789) (Myriapoda, Diplopoda). The trunk of an adult *Glomeris* animal consists of twelve tergites. The first one is rather small and is also called collum, and is followed by eleven tergites (tergite II-XII), the last one (tergite XII) being a posterior shield. On the ventral side, however, there are 17 pairs of legs in females and 19 pairs of legs in males. There is thus a clear discrepancy between the number of dorsal metameric structures (twelve tergites) and the number of ventral metameric structures (17 or 19 pairs of legs) in an adult *Glomeris*. One important question is: what causes this discrepancy in numbers of dorsal and ventral metameric structures? As the arthropod body plan is laid down during embryogenesis, an analysis of the genes acting during the formation of the metameric units may provide answers to this question. Therefore, we have analysed the expression patterns of segmentation genes during the formation of the germ band in *Glomeris*. Here we summarize our previous work on segmentation genes in *Glomeris* (Janssen et al. 2004, Janssen & Damen 2006), and add new data on additional genes. In addition we provide an outlook to future work. Our data show that all segmentation genes studied so far display a remarkable difference in expression on the dorsal and ventral side in the embryo. The data support the notion that there must be a decoupling of the machinery underlying segmentation on the dorsal and the ventral side (Janssen et al. 2004).

Another intriguing and related question is in which way the dorsal and ventral metameric structures in millipedes should be aligned with each other. This is the subject of a longstanding dispute, and has led to different, contradicting assignments (for detailed discussion, see Janssen et al. 2006, Dohle 1964, Wilson 2002). The decoupling of dorsal and ventral segmentation also sheds new light onto this issue.

DEVELOPMENT OF THE DORSAL TISSUE IN *GLOMERIS*

The embryonic development of *Glomeris marginata* has been described in detail in Dohle (1964, 1974) and Janssen et al. (2004). Shortly after formation of the cumulus, a small aggregation of cells that is the first sign of the forming germ band, the embryo is divided into a so-called *regio dorsalis* and a *regio germinalis*. The *regio dorsalis* will become extra-embryonic tissue, whereas the *regio germinalis* is the presumptive anterior portion of the germ band. Within the regio germinalis the head segments as well as the first trunk segment form almost simultaneously (Janssen et al. 2004). Behind the *regio germinalis* another important structure is forming: the posterior growth zone. This growth zone generates all remaining segments via terminal addition.

It is important to note, that up until stage 3 (for staging see Dohle 1964, Janssen et al. 2004) the germ band, comprising the *regio germinalis* and the posterior growth zone, only consists of presumptive ventral tissue. It is only after the onset of stage 3 that dorsal tissue starts developing on the germ band (including the growth zone). This dorsal tissue first is located laterally to the
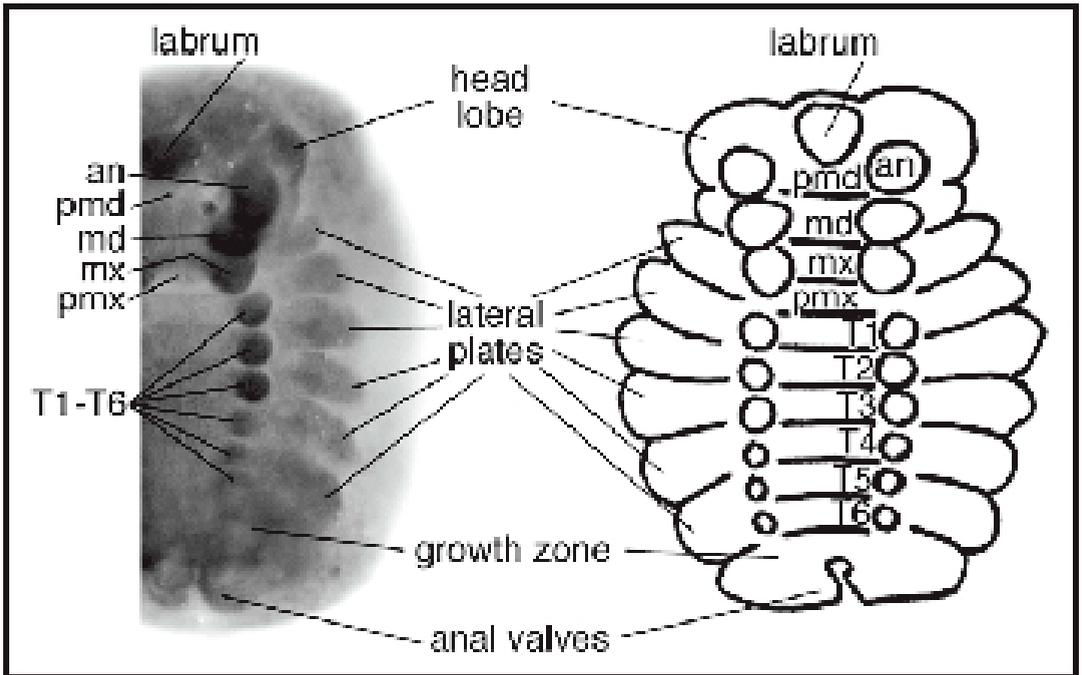
Figure 1. Explanatory figure of a *Glomeris* embryo at stage 5. The left image is a DAPI stained embryo (inverted) and the cartoon to the right explains the most important terms for morphological structures visible at stage 5. Please note that this cartoon is re-used in Figure 4 and 6. Abbreviations are: an, antenna; md, mandible; mx, maxilla; pmd, premandibular segment; pmx, postmaxillary segment; T1-T6, trunk segment 1 to 6.

ventral tissue (hence the name "lateral plates"), but steadily grows during development until the lateral plates meet on the dorsal side and fuse during dorsal closure. When studying dorsal and ventral pattern formation this heterochrony of dorsal and ventral tissue formation must be kept in mind.

EXPRESSION OF SEGMENT-POLARITY GENES

Both the ventral tissue and the dorsal tissue comprise metamerically repeated blocks. We concentrate here on the trunk region of the germ band. In the older embryo at stage 5 (when both dorsal and ventral tissue are fully developed) the ventral tissue in the trunk consists of eight metameric blocks, each of which bears a single pair of legs. The dorsal tissue consists of six

metameric blocks that are called lateral plates (Dohle 1964) (Figure 1). We have previously studied gene expression in the dorsal and ventral metameric blocks (Janssen et al. 2004). We have first focused on homologs of *Drosophila melanogaster* segment polarity genes. These genes are known from the fruit fly *Drosophila* to have an important role in segment formation (Nüsslein-Volhard & Wieschaus 1980) and thus may also play a role in the establishment of the metameric blocks that are present in the millipede *Glomeris*.

We have studied the expression of the segment polarity gene homologs *engrailed, hedgehog, wingless,* and *cubitus-interruptus* (Janssen et al. 2004). The expression of these genes is well conserved in the segments of all arthropods studied so far (Damen 2002, Hughes & Kaufman
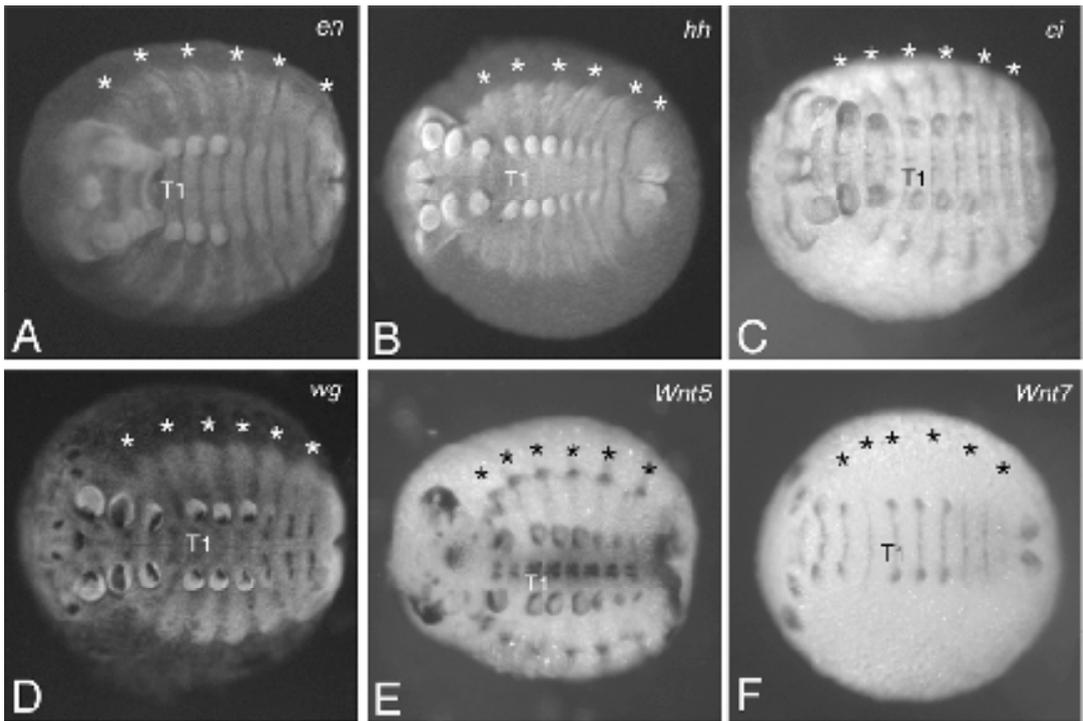
Figure 2. Expression of segment polarity genes in *Glomeris marginata* embryos. A) Expression of the *engrailed* (en) gene (dark stripes) in a DAPI counter stained embryo (bright staining). The dorsal and ventral stripes of engrailed expression are not connected. B) Expression of the *hedgehog (hh)* gene (dark stripes) in a DAPI counter stained embryo (bright staining). Similar as for *engrailed*, the dorsal and ventral stripes of *hedgehog* expression are not connected. C) Expression of the *cubitus interruptus* (ci) gene in a bright field micrograph. D) Expression of the *wingless (wg)* gene (dark stripes) in a DAPI counter stained embryo (bright staining). Ventral the *wingless* gene is expressed in segmentally reiterated stripes; dorsal there is no *wingless* expression visible. E, F) Expression of the *Wnt5* and *Wnt7* genes in a bright field micrograph. *Wnt7* is expressed in ventral segmentally reiterated stripes, however, neither *Wnt5* nor *Wnt 7* are expressed in dorsal reiterated stripes. The dorsal expression of *Wnt5* is in presumptive precursors of the dorsal vessel that develops dorsal-most of the lateral plates. The asterisks mark the dorsal metameric units. The position of the first trunk segment is marked by T1.

2002), and we thus expected to find conserved expression patterns also in *Glomeris*. In the ventral metameric blocks of *Glomeris*, all these genes were expressed as expected from their conserved expression in other species: both *engrailed* and *hedgehog* are expressed in the posterior portion of the ventral blocks, and *cubitus-interruptus* is expressed in the anterior portion of the blocks (Figure 2A-C). The *wingless* gene is expressed in a stripe of cells anteriorly adjacent to the *engrailed/hedgehog* expressing cells (Figure 2D). Surprisingly, however, the patterns in the dorsal blocks are not very similar to the ventral patterns: *engrailed and hedgehog* are expressed roughly in the middle of the dorsal blocks (Figure 2A,B), and not at their posterior end as is the case in the ventral blocks, and cubitus-interruptus is expressed in the posterior portion of the dorsal blocks (Figure 2C), contrasting with the ventral blocks where *cubitus-interruptus* is expressed in
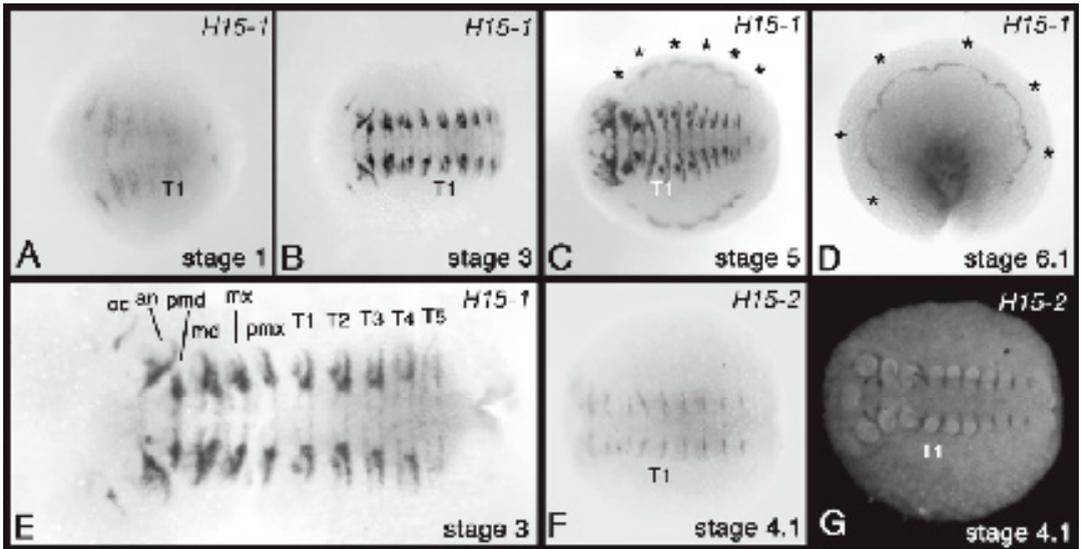
Figure 3. Expression of *H15-related* genes in *Glomeris marginata* embryos. Embryonic expression of *H15-1* (A-E) and *H15-2* (F,G). The expression of *H15-1* starts in early embryos (A); in stage 3 embryos (B and E; panel E is flat preparation of embryo in B) the *H15-1* gene is expressed in segmentally reiterated double stripes on the ventral side. The most prominent stripe of this double stripe is in the morphological indentations. At later stages only this latter stripe remains visible (e.g. the stage 5 embryo in panel C). There is no segmentally reiterated expression of *H15-1* on the dorsal side. In addition, *H15-1* is expressed in the developing appendages (see Prpic et al. 2005) and in the developing dorsal vessel (asterisks). D) Lateral view of a stage 6.1 embryo. At this stage the embryo is rolled in at its ventral side. E), flat preparation of embryo in B. F) and G), Stage 4.1 embryo. The *H15-2* gene is ventrally expressed in segmentally reiterated stripes. *H15-2* is also expressed in the appendages (Prpic et al 2005). There is no dorsal *H15-2* expression. The position of the first trunk segment is marked by T1. Abbreviations are: oc, ocular segment; an, antenna; md, mandible; mx, maxilla; pmd, premandibular segment; pmx, postmaxillary segment; T1-T6, trunk segment 1 to 6.

the anterior portion. Most surprisingly, however, we found that *wingless* is not expressed at all in the dorsal blocks (Figure 2D). This is surprising, because in *Drosophila* all these genes are integral parts of a signalling loop and the expression of these genes in the ventral blocks is consistent with this loop being conserved in *Glomeris*. The lack of *wingless* in the dorsal blocks, however, suggests that this signalling loop is not operating in the dorsal blocks.

Because this interpretation is difficult to accept, given the obvious conservation on the ventral side, we also studied other members of the gene family to which *wingless* belongs (the *Wnt* gene family).

Our rationale was that another Wnt gene might substitute for *wingless* on the dorsal side. We were able to isolate fragments for two other Wnt genes, which we denote as *Wnt5* and *Wnt7* (Janssen et al. 2004) but like wingless itself they are not expressed in the dorsal blocks (Figure 2E,F). Of course, this does not rule out the possibility that even further Wnt genes take the role of *wingless* in the signalling loop on the dorsal side.

Further work on the action of the *wingless/hedgehog* signalling loop including other members of these two pathways is needed to conclusively establish the role of *wingless* in the dorsal metameric blocks. In this context the *H15*-related
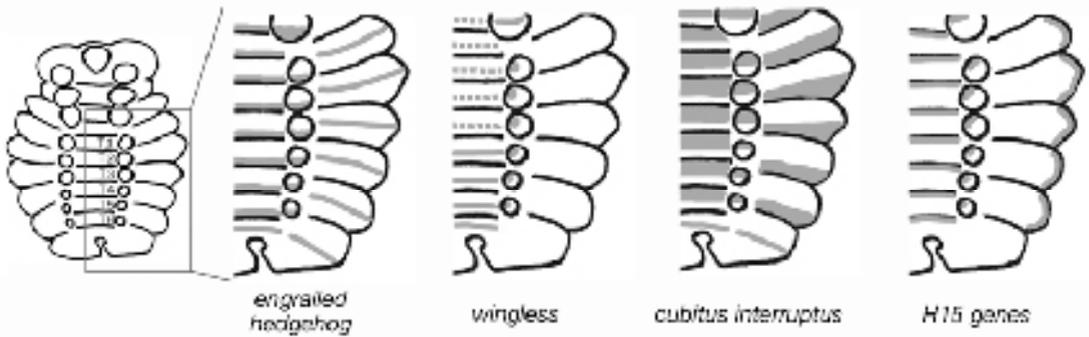
Figure 4. Schematic summary of segment polarity gene expression in *Glomeris* embryos. For an explanation of the cartoon see Figure 1. Gene expression is shown in grey.

genes are of interest. In *Drosophila* there are two genes, *H15* and *midline*, that are expressed in a segment-polarity gene like fashion (Buescher et al. 2004, Prpic et al. 2003). Both genes have been shown to be required in the *wingless/hedgehog* signalling loop to regulate the expression of *wingless* and the data also suggest that *H15* and *midline* might be activated by hedgehog (Buescher et al. 2004). Thus, both genes are components of the *wingless/hedgehog* signalling loop (see Figure 5A). We have previously identified two members of *H15*-related genes in Glomeris, which we have designated as *H15-1* and *H15-2*, but so far the expression of these genes has been studied only in detail in the appendages (Prpic et al. 2005). Here we also have analysed the expression of these genes in the developing metameric units (Figure 3). In these developing metameric units both genes are expressed in a similar fashion, except that *H15-2* is expressed at much lower levels than *H15-1*. In the ventral blocks, both *H15* genes are expressed in the morphological indentations between the blocks (Figure 3), and therefore directly posterior to the *engrailed* stripes, which is similar to the expression of *H15* and *midline* in *Drosophila* (Buescher et al. 2004) (Expression patterns summarized in Figure 4). However, both *Glomeris H15*-related genes are not expressed in the dorsal metameric blocks, thus giving further support to the idea that there is no Wingless-signalling taking place in the dorsal blocks of *Glomeris* (Figure 5A,B).

EXPRESSION OF HOX GENES

We have recently also studied homologs of genes from another layer of the *Drosophila* segmentation gene cascade: the Hox genes (Janssen & Damen 2006). The Hox genes are responsible for transferring specific identities to the segments (McGinnis & Krumlauf 1992). A certain combination of Hox gene expression determines the identity of the segment in question. If these combinations are experimentally changed, the identity of the segment is changed towards that segment that normally has the combination of Hox genes that has been generated experimentally (homeotic transformations). The expression patterns of Hox genes differ quite substantially between different arthropod groups, given the huge differences in body tagmosis and segment morphologies in arthropods. However, the anterior borders of most Hox expression patterns appear to be largely conserved in most arthropods.

We have previously shown that *Glomeris* has a full complement of ten Hox genes including a *Hox3* and a *fushi-tarazu* homolog. Most of these Hox genes are expressed in both the ventral and the dorsal metameric blocks (Janssen & Damen 2006). Surprisingly, the anterior border of the expression of the single Hox genes is not identical in dorsal and ventral blocks: the anterior borders do not align. The dorsal expression always terminates more posterior than the ventral expression (Figure 6). In most cases the difference between dorsal
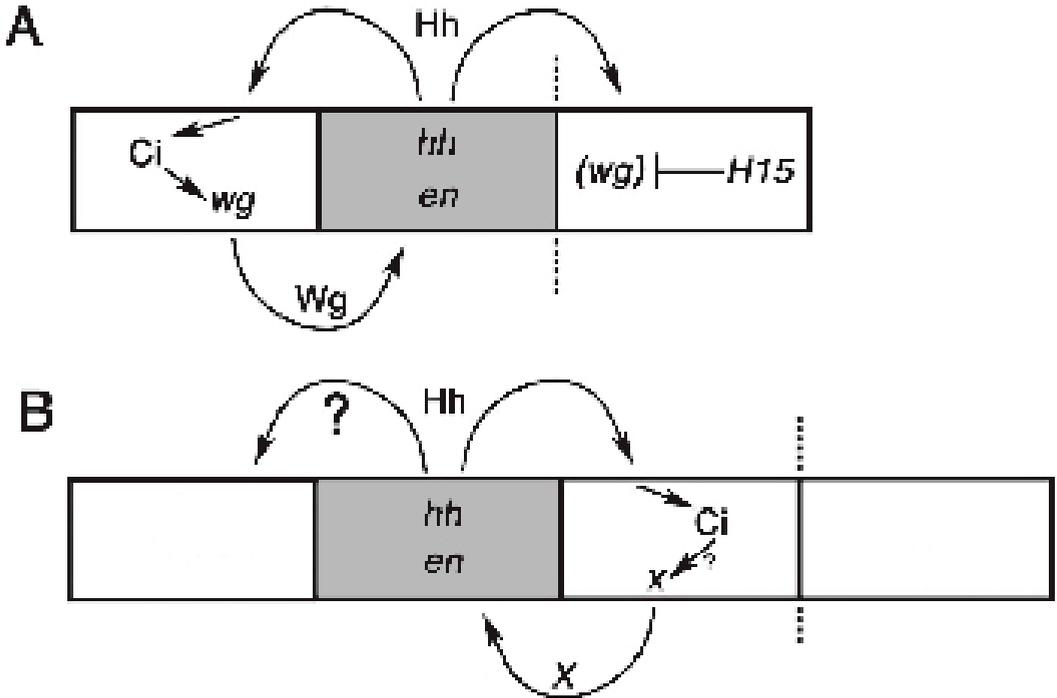
Figure 5. Schematic summary of proposed segment polarity gene interactions in *Glomeris margi-nata*. A) A regulatory loop operates during segment formation in *Drosophila*. Based on the gene expression patterns, we propose that this loop is conserved in the ventral metameric units in *Glomeris*: Cells anteriorly adjacent to the morphological segment boundary (dotted line) express *engrailed* (en) and emanate Hedgehog (Hh) protein. Hh travels to neighbouring cells: in anterior cells it activates Cubitus interruptus (Ci), which in turn leads to the segregation of Wingless (Wg) protein that signals back to the *engrailed/hedgehog* (*en/hh*) expressing cells, thus closing the regulatory loop. In posterior cells, activation of the *wingless* (*wg*) gene by Hh signalling is inhibited by *H15/midline*. B) In the dorsal epidermis, the *en/hh* expressing cells are not located next to the morphological boundary between the dorsal metameric units (dotted line). We speculate that Hh protein emanates from there to adjacent areas. In posterior cells it might activate Ci, since *ci* is expressed there. However, a signalling loop would require the segregation of a molecule analogous to Wg on the ventral side. So far no candidate for such a molecule is known (denoted by "x" (for the gene) and "X" (for the protein) in the figure). The effect of Hh on anterior cells is entirely unclear (large question mark).

and ventral expression is about one half worth of a ventral metameric block, with the exception of *fushi-tarazu*, where the difference is almost an entire ventral block. In addition, the three anterior Hox genes *labial (lab), proboscipedia (pb)* and *Hox3* are only expressed ventrally, whereas the adjacent dorsal tissue appears to develop without input from the homeotic selector genes.

DECOUPLING OF DORSAL AND VENTRAL PATTERN FORMATION DURING SEGMENTATION

The segment polarity genes in *Drosophila* are the ones that establish the orientation within the segments and also maintain the borders between the segments. They are thus very important components of the pattern formation process
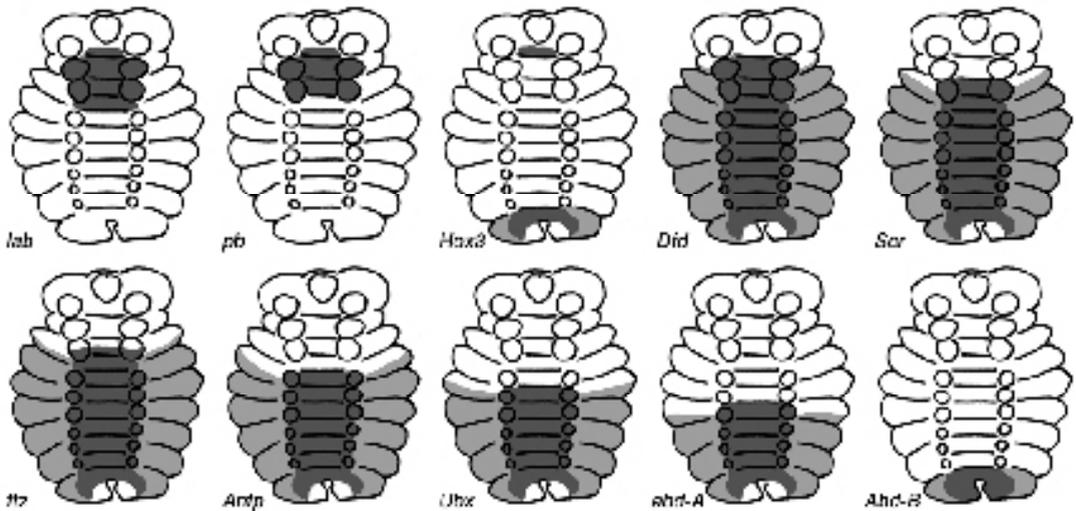
Figure 6. Schematic summary of Hox gene expression in *Glomeris*. Please note that all gene expressions are simplified; for a detailed account of spatio-temporal expression of the ten Hox genes of *Glomeris* see Janssen and Damen (2006). For an explanation of the cartoon of the stage 5 germ band of *Glomeris* see Figure 1. Dark grey denotes Hox expression in ventral tissue; light gray denotes Hox expression in dorsal tissue. Gene names are as follows: *lab, labial; pb, proboscipedia; Dfd, Deformed; Scr, Sex combs reduced; ftz, fushi tarazu; Antp, Antennapedia; Ubx, Ultrabithorax; abd-A, abdominal-A; Abd-B, Abdominal-B.*

during *Drosophila* segmentation. The data from *Glomeris* suggests that the ventral metameric blocks are established through a conserved mechanism. The dorsal blocks, however, display some significant differences in gene expression, most notably the absence of expression of factors involved in *wingless* signalling. This suggests that the dorsal metameric blocks must be established through a different mechanism. The pattern formation in dorsal and ventral blocks appears to be independent from each other. This is supported by the expression of the Hox genes: the anterior expression borders do not align in dorsal and ventral blocks. Since the Hox genes convey identity to body regions it can be speculated that the identity of dorsal and ventral blocks is determined independently.

Thus, the expression of both segment polarity genes and Hox genes unanimously suggest that the patterning processes concerned with polarity, delimitation, and identity determination

are different and independent in the dorsal and ventral metameric blocks. We conclude therefore that dorsal and ventral segmentation in *Glomeris* is decoupled.

Returning to our initial question: "what causes the discrepancy in numbers of dorsal and ventral metameric structures?", we might now give a preliminary answer: since the establishment of the dorsal metameric structures seems to be decoupled from the establishment of the ventral metameric structures, there is no necessary reason why both independent processes should produce the same number of metameric blocks. A similar decoupling of dorsal and ventral segmentation might also explain other cases of dorsal-ventral discrepancies in the arthropods, some of which have already been mentioned in the introduction.

Of course, many open questions remain. The mechanisms on the ventral side of *Glomeris* seem to be similar to the segmentation mechanisms

in other arthropods. But the dorsal mechanisms largely remain obscure. Further studies, especially with respect to Wingless-signalling will hopefully give further insight into the development of the dorsal blocks. Another issue is the ramifications the dorso-ventral decoupling has for the formation of the exoskeleton in the adult animal. In most arthropods dorsal and ventral metamerization is coordinated, leading to an exoskeleton with aligned dorsal and ventral elements. It is known that in *Glomeris* and other millipedes the dorsal exoskeletal plates (tergites) cannot be aligned easily with the exoskeletal plates on the ventral side (sternites) and, based on the dorso-ventral differences in gene expression, we have proposed elsewhere a model that correlates the different exoskeletal elements on the ventral and on the dorsal side (Janssen et al. 2006). Our model takes into account that the boundaries delimiting the tergites do neither correlate to the embryonic boundaries of the lateral plates nor to the boundaries of the ventral embryonic segments; for details we refer to Janssen et al (2006). The model provides a solution of the problem of tergite to sternite/leg pair correlation in basal milipedes with non-fused exoskeletal elements and can be extrapolated to derived species with exoskeletal rings.

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Variation of the poison duct in *Chilopoda centipedes* from Taiwan

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Chao, J. L. & Chang, H. W. 2006. Variation of the poison duct in *Chilopoda centipedes* from Taiwan. Norw. J. Entomol. 53, 139-151.

We present a new technique to observe the structure the poison ducts of the forcipules of chilopod centipedes under light microscope. We examined twenty one species in fourteen genera of chilopods from Taiwan, *Thereuopoda, Lithobius, Bothropolys, Esastigmatobius, Scolopendra, Rhysida, Otostigmus, Scolopocryptops, Cryptops, Scolioplanes, Stigmatogaster, Mecistocephalus, Prolamnonyx, and Taiwanella*. Morphology and structure of poison ducts of chilopoda are consistent in the higher taxa genera and families. Morphological characters of poison duct support a close relationship between *Scolopocryptops* and Scolopendridae, suggesting that the current separation of Cryptopidae from Scolopocryptopidae is correct. We also revised Takakuwa's description of the poison duct of *Scolopocryptops rubiginosus*, and consider *Taiwanella yanagiharai* is a valid species in the genus *Taiwanella*.

Key words: poison calyx, glycerin, transparent specimens, taxonomy.

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INTRODUCTION

The forcipules (maxillipedes) are one of the common characters of Chilopod centipedes. Each forcipule of Chilopoda comprises four articles: trochanteroprefemur, femur, tibia, and tarsungulum (Lewis et al. 2005, Figure 1). Within each forcipule is a poison duct opening to the tip of the tarsungulum and ending in a poriferous region, poison calyx, which connects to the poison glands by many short tubular canals (Figure 2). Because it is an internal structure and small in size, it is difficult to observe the poison ducts under dissecting microscope and light microscope. Therefore, the structure of the poison duct had rarely been studied and described in Chilopoda centipedes, and only few morphological figures of the forcipules with their poison ducts have been drawn (Takakuwa 1940a, b, 1941, Verhoeff 1940, Lewis 1996, 1999, 2002, Bonato et al. 2002,

Foddai et al. 2003). Takakuwa (1940b) drew and described a short poison duct in the tarsungulum of the forcipules of *Otocryptops rubiginosus* (L. Koch, 1878) (now *Scolopocryptops rubiginosus* (L. Koch, 1878)) (Figure 1c). When studying this species with new material, we found his description and figure might have some mistakes. With a new and simple method developed in our lab, we considered it was necessary to re-examine the poison ducts of Chilopoda. With the variation of the structure and length of the poison ducts in centipedes, we considered that the characters of the poison ducts may suggest some information about the relationships among members of Chilopoda.

MATERIALS AND METHODS

We examined the poison ducts of twenty one species of Chilopoda (Table 1), including one
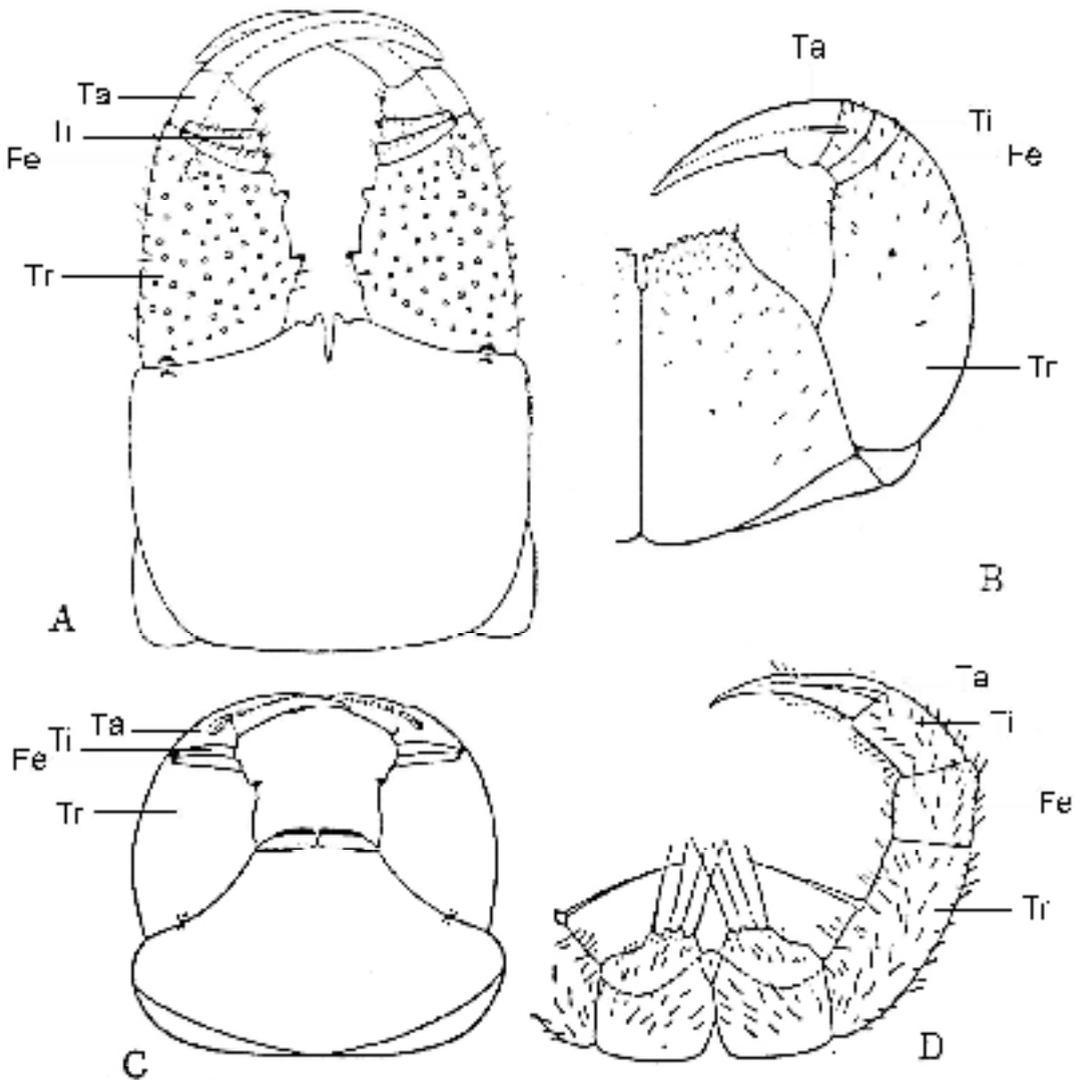
Figure 1. The forcipules of Chilopoda are composed of four parts: tarsungulum (Ta), tibia (Ti), femur (Fe), and trochanteroprefemur (Tr). A. *Mecistocephalus takakuwai*. B. *Bothropolys asperatus*. C. *Scolopocryptops rubiginosus*. D. *Thereuonema hilgendorfi*. (after Takakuwa1940).

species of Scutigeromorpha, *Thereuopoda clunifera* (Wood, 1863); four species of Lithobiomorpha, *Esastigmatobius longicornis* Takakuwa, 1936, *Lithobius ongi* Takakuwa, 1941, *Bothropolys asperatus* Koch, 1878, , and *Bothropolys richthofeni* Verhoeff, 1938; ten species of Scolopendromorpha, *Scolopendra subspinipes* Leach, 1815, *Scolopendra morsitans* Linnaeus, 1758, *Rhysida longipes longipes* (Newport, 1845), *Rhysida immarginata* (Porat, 1876), *Otostigmus scaber* Porat, 1876, *Otostigmus aculeatus* Haase, 1887, *Scolopocryptops rubiginosus* (L. Koch, 1878), *Scolopocryptops capillipedatus* (Takakuwa, 1938), *Cryptops japonicus* Takakuwa, 1934, and *Cryptops nigropictus* Takakuwa, 1936; six species of Geophilomorpha, *Taiwanella yanagiharai* Takakuwa, 1936, *Mecistocephalus smithi* Pocock, 1895, *Mecistocephalus mikado*
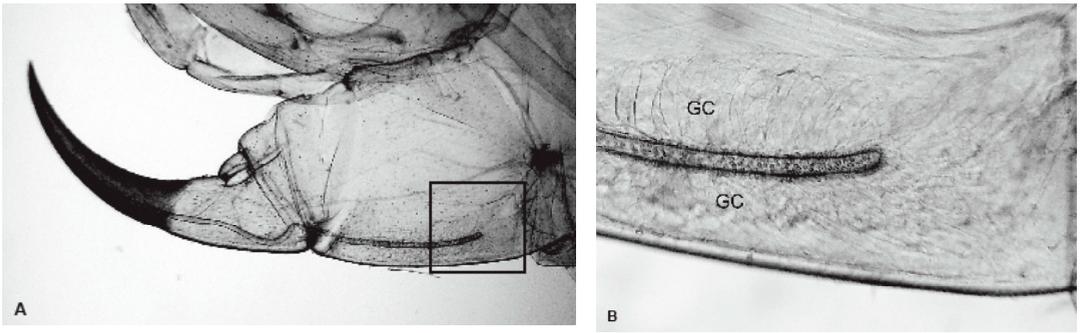
Figure 2. Micrographs of the poison calyx of *Scolopendra subspinipes*. A. The poison gland is around the poison calyx. B. The cylindrical poison calyx has numerous short tubular canals connecting the poison glandular cells (GC).
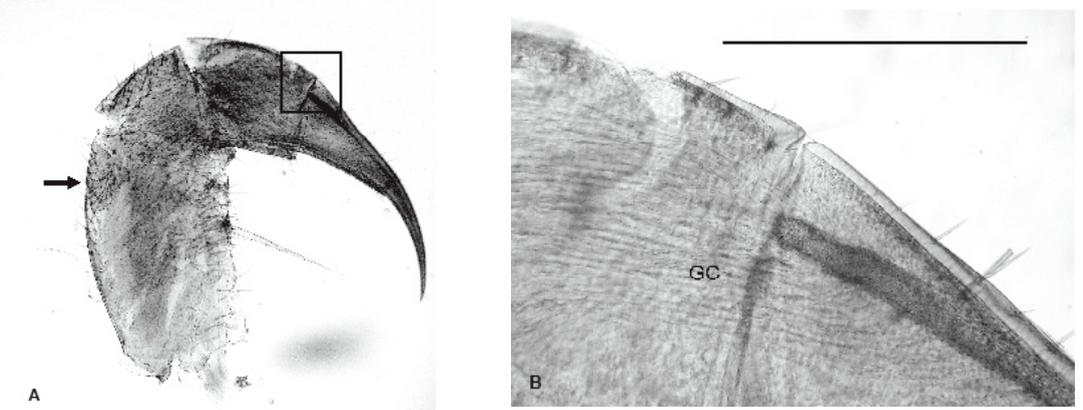
Figure 3. Micrographs of the poison duct of *Thereuopoda clunifera*. A. The cylindrical poison calyx is located at the base of the tarsungulum, but the poison gland extends across tibia and femur, reaching the anterior part of trochanteroprefemur (arrow). B. The poison gland cells (GC) are around the poison calyx. Scale is 0.4 mm.
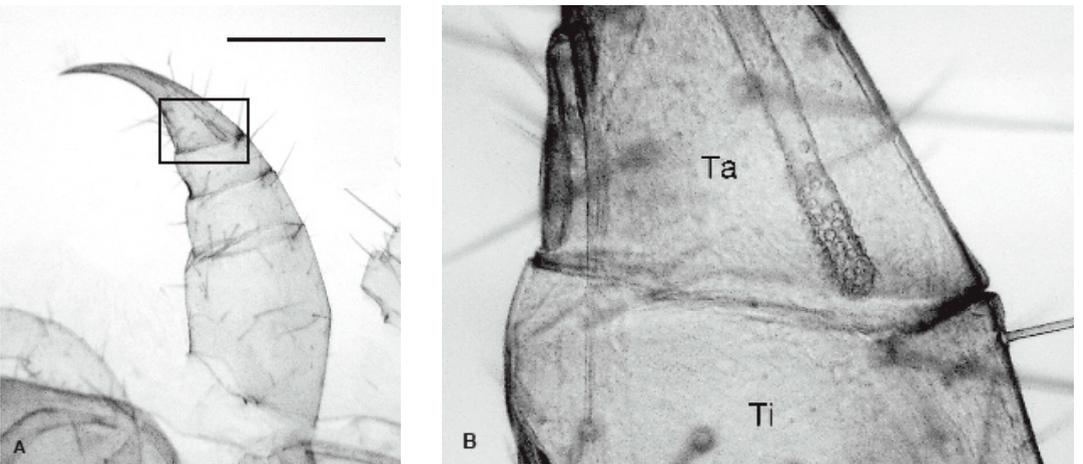
Figure 4. Micrographs of the poison duct in *Esastigmatobius longicornis*. A. The poison duct is located within tarsungulum (Ta). Scale is 0.3 mm. B. The poison calyx is cylindrical with about 100 pores.

Table 1. The situations of poison calyxes of Chilopoda. Ta: tarsungulum; Ti: tibia; Fe: femur; Tr: trochanteroprefemur; Co: coxosternum. +: Situated; -: Absent.

Species	Situation of poison calyx				
	Ta	**Ti**	**Fe**	**Tr**	**Co**
Scutigeromorpha					
Scutigeridae					
Thereuopoda clunifera (Wood, 1863)	+	-	-	-	-
Lithobiomorpha					
Henicopidae					
Esastigmatobius longicornis Takakuwa, 1936	+	-	-	-	-
Lithobiidae					
Lithobius ongi Takakuwa, 1941	+	+	-	-	-
Bothropolys asperatus Koch, 1878	+	+	-	-	-
Bothropolys richthofeni Verhoeff, 1938	+	+	-	-	-
Scolopendromorpha					
Scolopendridae					
Scolopendra subspinipes Leach, 1815	+	+	+	+	-
Scolopendra morsitans Linnaeus, 1758	+	+	+	+	-
Rhysida longipes longipes (Newport, 1845)	+	+	+	+	-
Rhysida immarginata (Porat, 1876)	+	+	+	+	-
Otostigmus scaber Porat, 1876	+	+	+	+	-
Otostigmus aculeatus Haase, 1887	+	+	+	+	-
Scolopocryptopidae					
Scolopocryptops rubiginosus (L. Koch, 1878)	+	+	+	+	-
Scolopocryptops capillipedatus (Takakuwa, 1938)	+	+	+	+	-
Cryptopidae					
Cryptops japonicus Takakuwa, 1934	-	-	-	+	-
Cryptops nigropictus Takakuwa, 1936	-	-	-	+	-
Geophilomorpha					
Mecistocephalidae: Mecistocephalinae					
Taiwanella yanagiharai Takakuwa, 1936	+	+	+	-	-
Mecistocephalus smithi Pocock, 1895	+	+	+	-	-
Mecistocephalus mikado Attems, 1928	+	+	+	-	-
Mecistocephalidae: Aruppinae					
Prolamnonyx holstii (Pocock, 1919)	+	+	+	+	+
Himantariidae					
Stigmatogaster japonica Takakuwa, 1935	-	+	-	-	-
Geophilidae					
Scolioplanes maritimus japonicus Verhoeff, 1935	-	-	+	+	-
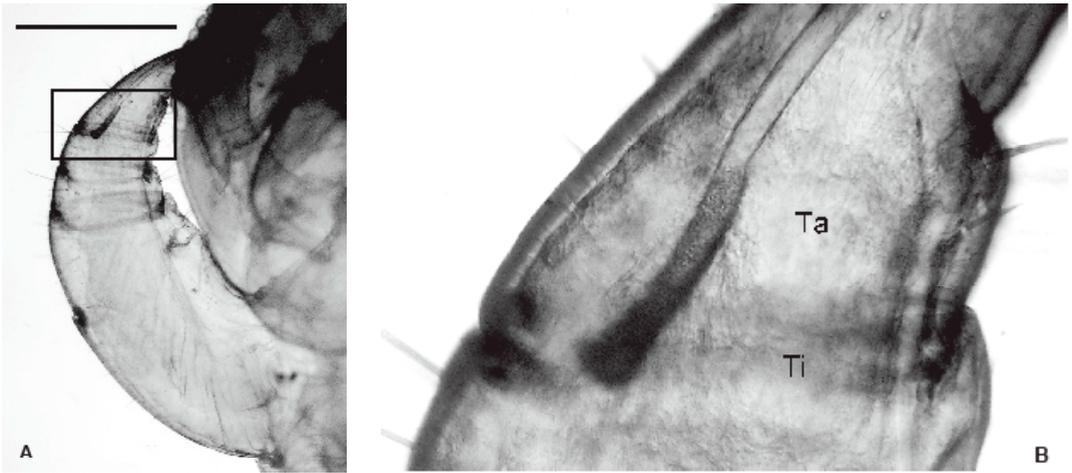
Figure 5. Micrographs of the poison duct in *Bothropolys richthofeni*. A. The poison duct reaches the tibia (Ti). Scale is 0.8 mm. B. The poison calyx is bell-shaped at bottom with numerous small pores.
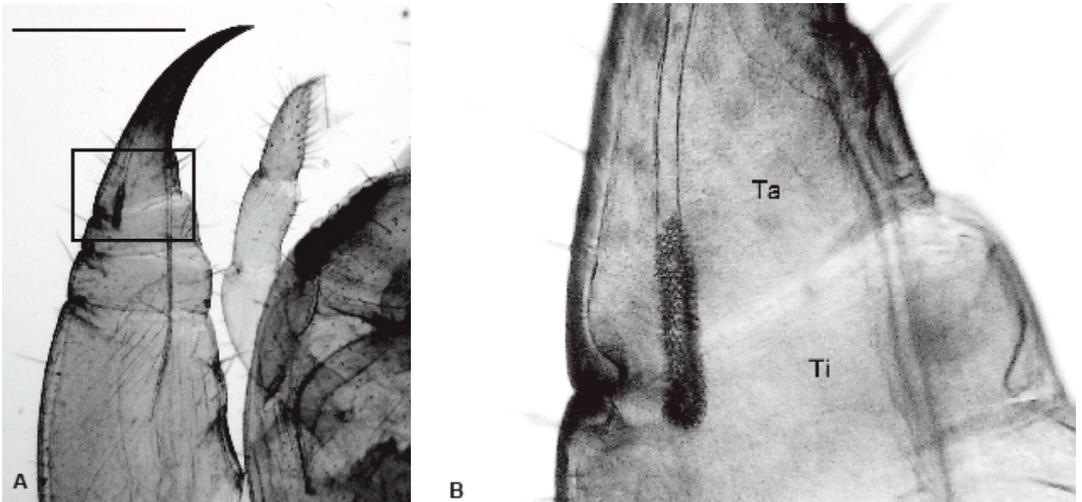
Figure 6. Micrographs of the poison duct in *Bothropolys asperatus*. A. The poison duct reaches the tibia (Ti). Scale is 0.5 mm. B. The cylindrical poison calyx is thick at base and with many small pores.

Attems, 1928, *Prolamnonyx holstii* (Pocock, 1919), *Stigmatogaster japonica* Takakuwa, 1935, and *Scolioplanes maritimus japonicus* Verhoeff, 1935. Centipedes were anaesthetized and sandwiched between two glass slides, then fixed and immersed in glycerin (99.5%) over one week. The specimens were then observed under light microscope. Long immersion in glycerin makes the specimens transparent, so that the poison ducts can be observed without dissection.

RESULTS

We found the shape and length of poison ducts varied among species. The poison duct may
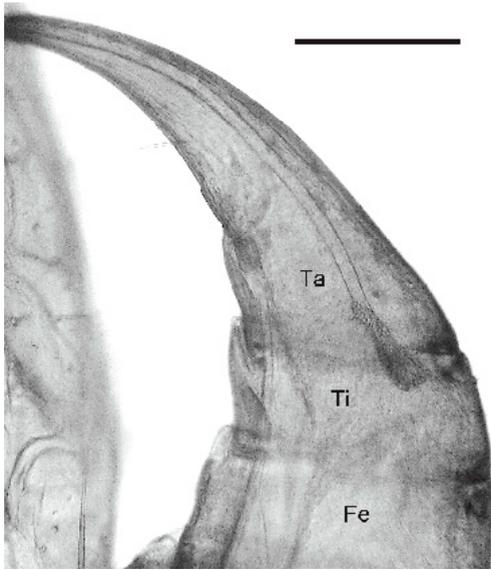
Figure 7. Micrograph of the poison duct in *Lithobius ongi*. The bended poison calyx reaches the anterior part of tibia (Ti) with about 200 small pores. Scale is 0.2 mm.
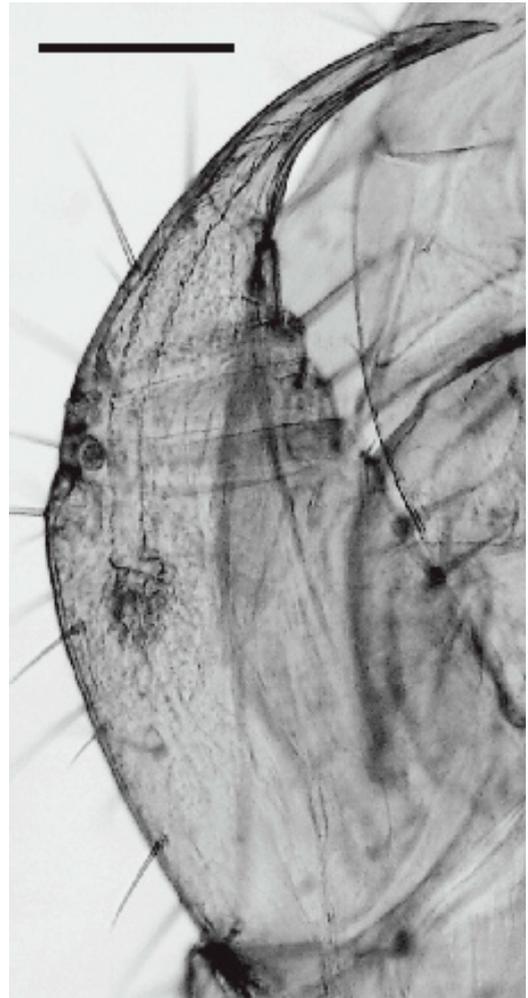
Figure 8. Micrograph of the poison duct in *Cryptops japonicus*. The anterior non-porous duct reaches trochanteroprefemur, and the poison calyx situates the anterior part of trochanteroprefemur. Scale is 0.1 mm.

reach tarsungulum, intermediate articles (tibia and femur), trochanteroprefemur or coxosternum (Table 2). The shapes of poison calyxes may be short cylindrical, long elongated cylindrical, subcordate, round or bell-bottomed.

In Scutigeromorpha, the poison duct of *Thereuopoda clunifera* is located entirely within the tarsungulum (Figure 3). The poison gland cells

distribute across tibia and femur, reaching to the anterior part of trochanteroprefemur. The poison calyx of poison duct is a short elongated cylinder with numerous small pores, and the number of pores increases towards the posterior part.

In Lithobiomorpha, the poison duct of *Esastigmatobius longicornis* is also located within the tarsungulum (Figure 4), and the poison
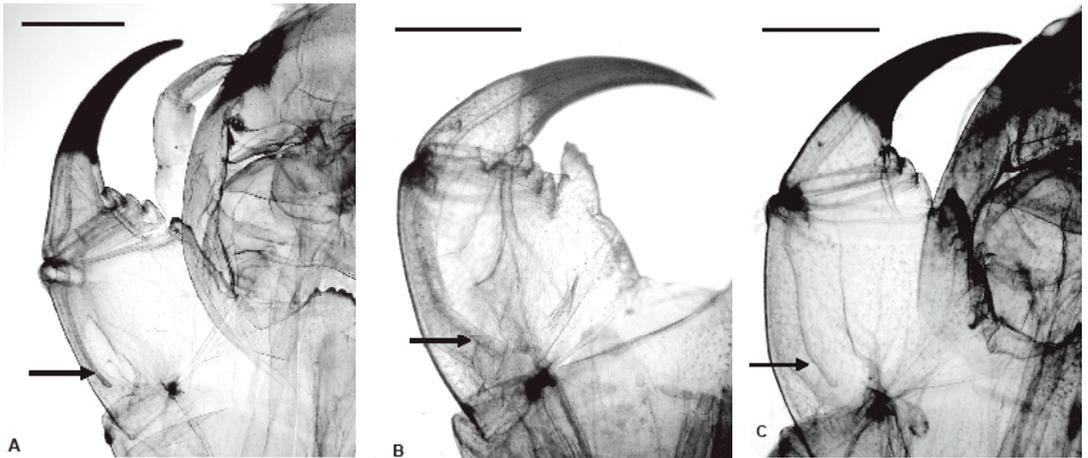
Figure 9. Micrographs of the poison ducts in Scolopendridae. A. *Scolopendra subspinipes* (scale is 1.2 mm). B. *Otostigmus aculeatus* (scale is 0.5 mm). C. *Rhysida immarginata* (scale is 0.5 mm). Their cylindrical poison calyxes (arrow), reaching the base of trochanteroprefemur, are arched with numerous pores.
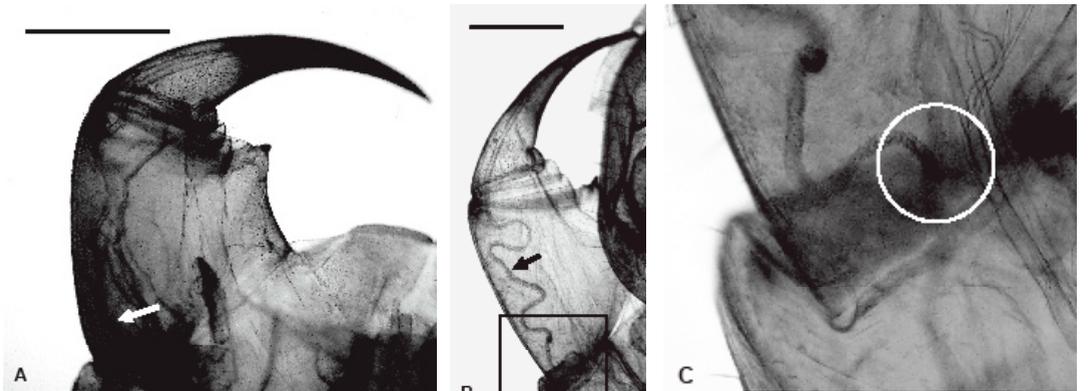
Figure 10. The poison ducts of *Scolopocryptops* are cylindrical and longest among all specimens examined, being serpentine in the trochanteroprefemur (arrow). A. *Scolopocryptops rubiginosus* (scale is 1.0 mm). B. *Scolopocryptops capillipedatus* (scale is 0.5 mm). C. The end of poison calyx reaches the edge between trochanteroprefemur and coxosternum (circle). A trachea passes the end of poison calyx ventrally. It is easily to treat the trachea as the extension of poison calyx.

calyx is a short cylinder with some pores (about 100 pores). As the poison duct also located within the tarsungulum, the poison calyx of *Bothropolys richthofeni* is cylindrical with a bell-shaped thick bottom, and with numerous small pores (over 500 pores). The poison calyx of *Bothropolys richthofeni* (Figure 5), *B. asperatus* (Figure 6) and *Lithobius ongi* (Figure 7) all run into tibia. But in *B. richthofeni*, the base is thick, while in *L.*

ongi, the calyx of is a bended and bell-bottomed cylinder with broader base.

In Scolopendromorpha, the poison duct runs into the trochanteroprefemur. The poison ducts of *Cryptops japonicus* and *C. nigropictus* are attaining to the anterior part of trochanteroprefemur, and their poison calyxes are a round mass with only some pores assembling at the
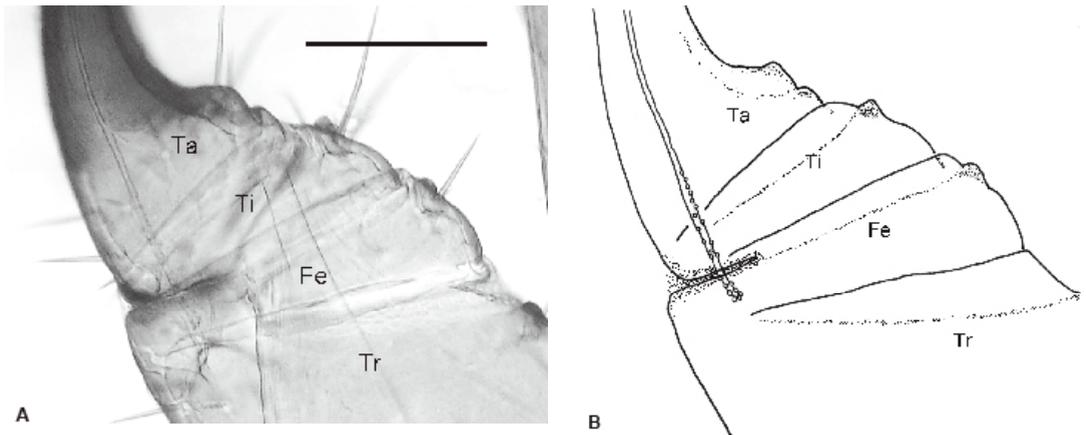
Figure 11. A. Micrograph of the poison duct in *Taiwanella yanagiharai*. Scale is 0.2 mm. B. Schematic interpretation of the cylindrical poison calyx, as it is very slender with a few and piecemeal pores, and situates from tarsungulum (Ta) to femur (Fe).
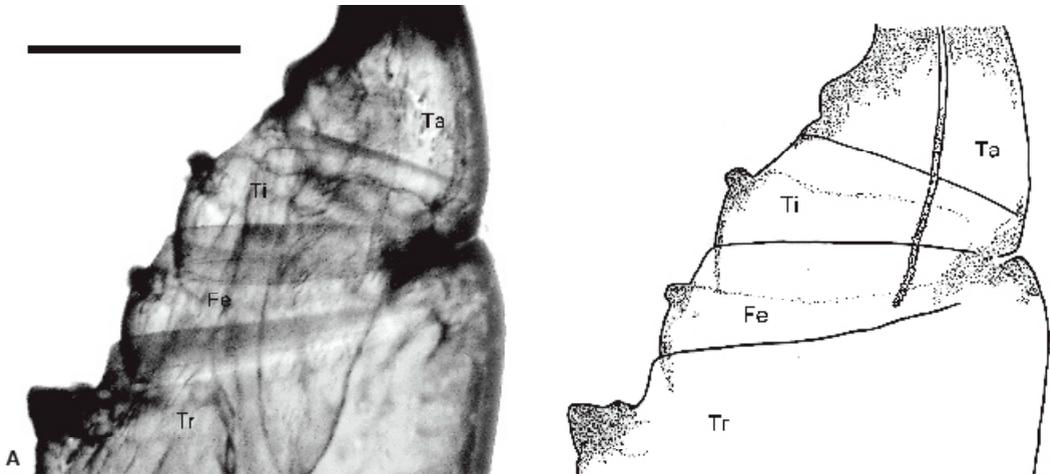
Figure 12. A. Micrograph of the poison duct in *Mecistocephalus smithi*. The poison duct reaches the femur (Fe). Scale is 0.5 mm. B. Schematic interpretation of the cylindrical poison calyx in which is a very slender cylinder.

base of poison duct (Figure 8). In *Scolopendra subspinipes, S. morsitans, Rhysida longipes, R. immarginata, Otostigmus aculeatus* and *O. scaber* the poison ducts are attaining to the base of trochanteroprefemur, and their poison calyxes are a long elongated cylinder with numerous pores (Figure 9). Nevertheless, in *Scolopocryptops rubiginosus* and *S. capillipedatus*, both the poison calyxes are a longest elongated cylinder and it is serpentine in the trochanteroprefemur (Figure 10).

This result corrected Takakuwa's description and figure about the poison duct of *S. rubiginosus*.

In Geophilomorpha, the poison duct of *Taiwanella yanagiharai* is quite thin relative to its forcipules, and reaches all the way to the femur. The poison calyx is an elongated cylinder from the base of tarsungulum to the femur, and with only a few tiny pores (Figure 11). In both *Mecistocephalus smithi* (Figure 12) and *M. mikado* (Figure 13), the
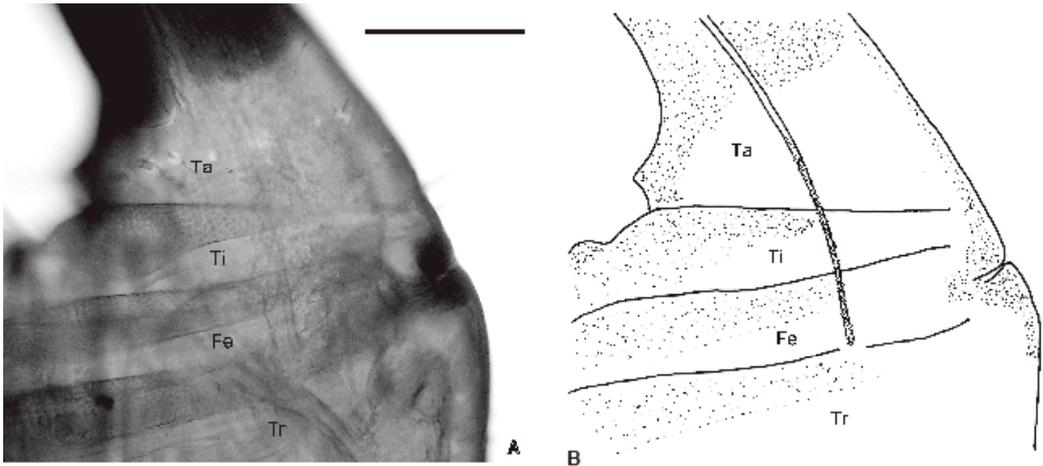
Figure 13. A. Micrograph of the poison duct in *Mecistocephalus Mikado*. The poison duct reaches the femur (Fe). Scale is 0.2 mm. B. Schematic interpretation of the poison calyx is very slenderly cylindrical.
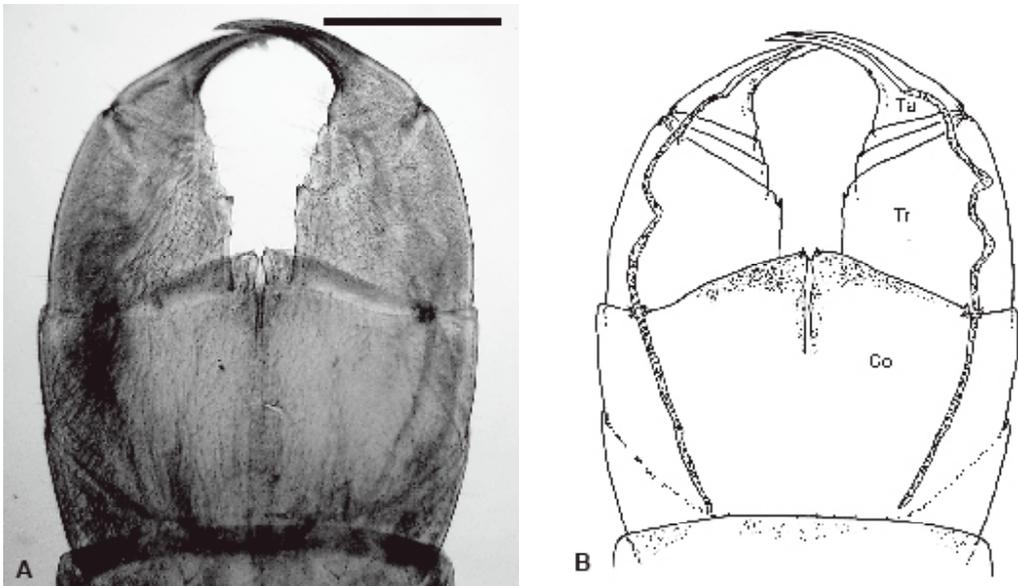
Figure 14. A. Micrograph of the poison duct in *Prolamnonyx holstii*. Scale is 1.0 mm. B. Schematic interpretation of the poison calyxes in which are longest cylindrical and from tarsungulum to the base of the coxosternum (Co) with numerous small pores.

poison ducts are very thin, and the poison calyxes also are elongated cylinders which attaining to the femur. In *Prolamnonyx holstii*, the poison calyx is an elongated cylinder, and it crosses through the trochanteroprefemur, attaining to the coxosternum (Figure 14). In *Stigmatogaster japonica*, the poison calyx is a short cylinder with many small pores, and situating into tibia (Figure 15). However, the poison calyx of *Scolioplanes maritimus japonicus* is sub-cordate type with

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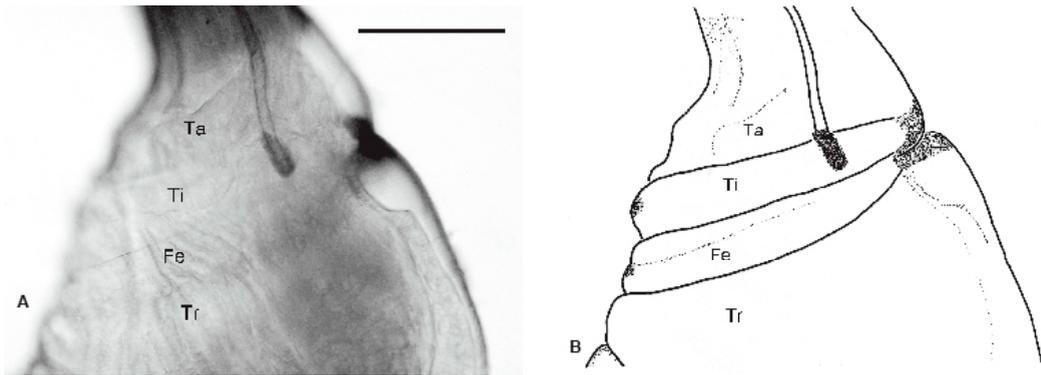
Figure 15. A. Micrograph of the poison duct in *Stigmatogaster japonica*, the short poison calyx is cylindrical with many small pores. Scale is 0.2 mm. B. Schematic interpretation of the poison calyx in which is situating into tibia (Ti).
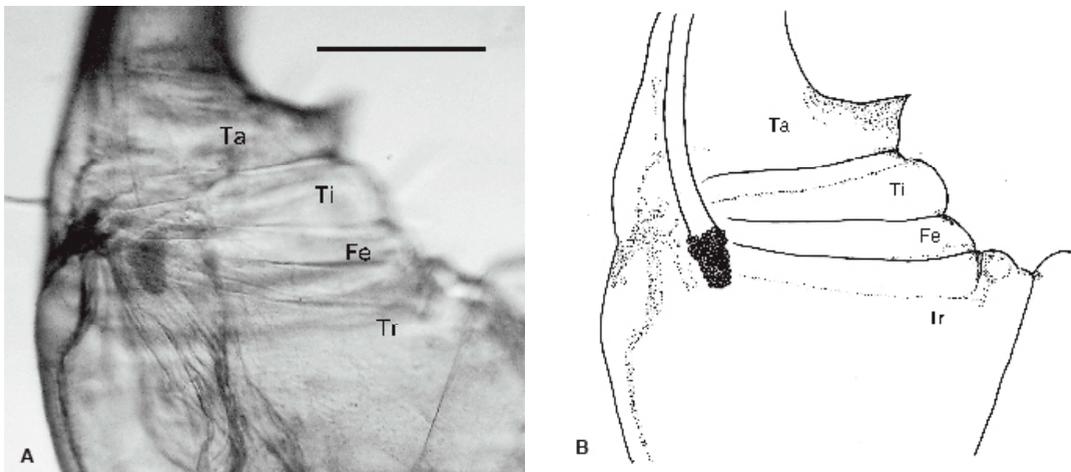
Figure 16. A. Micrograph of the poison calyx in *Scolioplanes maritimus japonicus.* The poison calyx is sub-cordate type with many small pores. Scale is 0.2 mm. B. Schematic interpretation of the poison calyx in which situates at femur (Fe) and the tip of trochanteroprefemur (Tr).

many small pores, and is situated from the femur to the tip of trochanteroprefemur (Figure 16).

DISCUSSION

The length of the poison duct of Taiwanese centipedes can be separated into four classes. The shortest ones, as the calyx of poison duct being located within the tarsungulum, are found in *Esastigmatobius and Thereuopoda*. The calyx

of *Bothropolys, Lithobius, Mecistocephalus, Scolioplanes, Stigmatogaster;* and *Taiwanella* reaches the intermediate articles (tibia and femur). In *Cryptops, Otostigmus, Rhysida, Scolopendra,* and *Scolopocryptops,* it reaches the trochanteroprefemur. The longest, being in *Prolamnonyx,* reaches the coxosternum.

The shapes of the calyx also differ among species. In Lithobiomorpha, the calyx of *Bothropolys* and *Lithobius*, both of family Lithobiidae, being
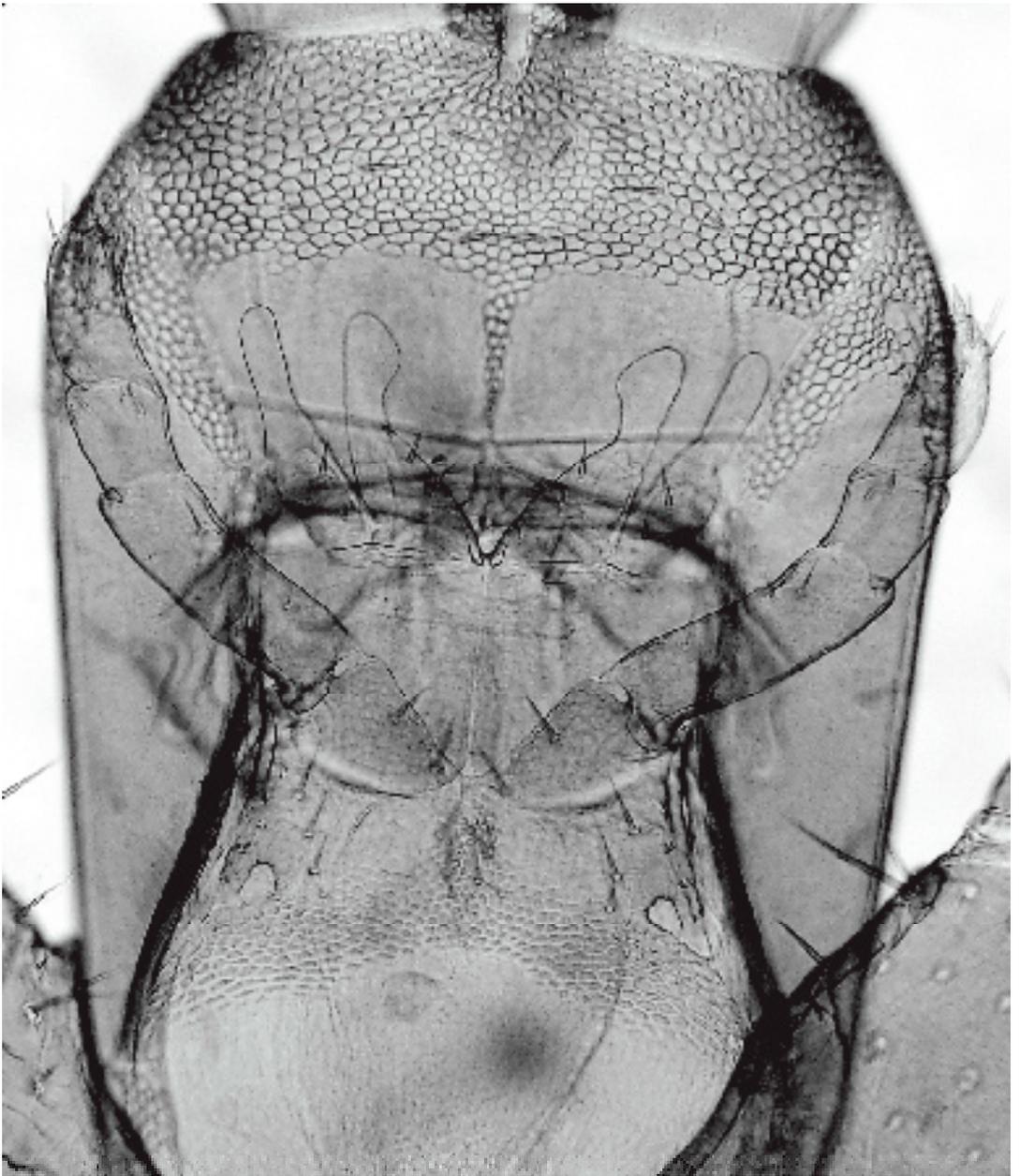
Figure 17. Ventral view of the head of *Taiwanella yanagiharai* showing buccae without spicula. The posterior clypeus has a linear mosaic area in the middle. The anterior and posterior clypeus is almost equal in size. The coxosternum of the first maxillae is divided medially. The coxosternum of the second maxillae is not divided.
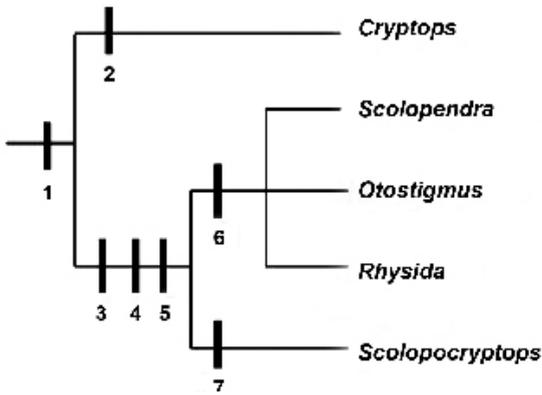
Figure 18. The relationships of the genera of Scolopendromorpha from Taiwan based on the characters of poison ducts. 1: Poison duct runs into trochanteroprefemur, 2: Round poison calyx, 3: Cylindrical poison calyx, 4: Poison calyx long, 5: Poison calyx with numerous pores from tarsungulum to trochanteroprefemur, 6: Arched calyx in trochanteroprefemur, 7: Serpentine calyx in trochanteroprefemur.

similar thick-bottomed shape, is different from the non-thick shaped calyx in *Esastigmatobius*, a member of Henicopidae.

In Geophilomorpha, Lewis (1996) described the poison calyx of *Ribautia arabica* as a sub-cordate type, and situated within tibia and femur. We found that *Scolioplanes maritimus japonicus* also has the same type of poison duct, and it provides evidence that both *Ribautia* and *Scolioplanes* belong to the family Geophilidae. Bonato et al. (2002) described a new species *Proterotaiwanella tanabei*, and suggested that *Taiwanella yanagiharai* Takakuwa, 1936 should be placed in the genus *Mecistocephalus* Newport, 1843 as *Mecistocephalus yanagiharai* (Takakuwa, 1936), n. comb. Recently, we found a specimen from Taiwan, which agreed with the description of *Taiwanella yanagiharai* (Takakuwa 1936, 1940a), and most importantly, its buccae were without spicula (Figure 17), a differential character of *Taiwanella* separating it from *Mecistocephalus*. In addition, the poison ducts of

Taiwanella yanagiharai and of *Proterotaiwanella tanabei* described by Bonato et al. (2002) are both cylindrical, extending from the basis of tarsungulum to the femur. Based on the above evidence, we consider that *Taiwanella* is still a valid genus. Furthermore, when Foddai et al. (2003) described the new species *Nannarrup hoffmani*, they drew a long, cylindrical, and nearly symmetric poison duct with the calyx located within the intermediate article. The same forms of poison duct are also present in *Mecistocephalus smithi*, *Mecistocephalus mikado* and *Taiwanella yanagiharai*. The evidence seems to support *Nannarrup, Mecistocephalus* and *Taiwanella* belonging to Mecistocephalidae.

In Scolopendromorpha, Lewis (1999 and 2002) described the poison calyxes of four species of *Cryptops*, including *C. doriae, C. mauritianus, C. decoratus and C. daszaki*, all the calyxes are situated at the anterior part of trochanteroprefemur. We found the same forms of poison ducts in *Cryptops japonicus* and *C. nigropictus*. All the above evidence discussed seems to suggest that the forms of the poison ducts are quite stable in higher taxa genera and families in Chilopoda. However, it is necessary to examine more species of centipedes to reach a firm conclusion.

Using the characters of poison ducts, we incline to divide the genera of Scolopendromorpha of Taiwan into three groups (Fig. 18). The short and unique form of the poriferous region of poison ducts in *Cryptops* separate the genus from all other genera of Scolopendromorpha examined. The same forms of poisons ducts of *Scolopendra, Otostigmus* and *Rhysida* suggests that they have a common ancestor, and the inclusion of the three into *Scolopendridae* (Attems 1930) seems to be supported. Furthermore, the Scolopocryptops, differs from the above three only in the length of the duct, seems to have a close relationship with Scolopendridae. The characters of poison ducts do not support *Cryptops* and *Scolopocryptops* being put together in Cryptopidae as in Attems (1930) system, neither *Cryptops* belonging to Scolopendridae in Schileyko's (1992, 1997) system. In this study, we tend to agree with

Shelley's (2002) treatment for Cryptopidae and Scolopocryptopidae as separate families. As herein making the first attempt to infer the relationships in Scolopendromorpha using the characters of the poison ducts, we consider that more data from other genera are needed to get a full picture of the evolution of the poison duct and the phylogenetic relationships within Chilopoda.

As the method making the specimens transparent, observations under light microscope for internal organs become much easier. The method also helps one to study other organs such as tracheal system, gizzards, etc., as the x-ray without dissecting the specimens. It also makes higher magnification observation on small structures such as the claws of second maxillae, and the antennal sensilla, etc. than the traditional method obtained under dissecting microscope.

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Structure and distribution of antennal sensillae in the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha)

Alfred Ernst, Jörg Rosenberg & Gero Hilken

Ernst, A., Rosenberg, J. & Hilken, G. 2006. Structure and distribution of antennal sensilla in the centipede *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha. Norw. J. Entomol. 53, 153-164.

Scanning electron microscopic investigations of the antennae of two larval stages and adults of *Craterostigmus tasmanianus* Pocock, 1902 show the presence of 6 types of cuticular sensillae: a single sensillum basiconicum and 8-13 tube-like sensilla at the top of the terminal antennal article, about 2 200 sensilla trichodea per antenna, some sensilla microtrichodea at the joint membranes of antennal articles, about 12 bottle-like sensilla at the distal edges of the antennal articles 2, 6, 11, and 16, and few sensilla coeloconica above the cuticular joint membranes of antennal articles. The structure and distribution of the six types of sensillae are compared with the antennal sensillae of other centipedes and diplopods. The possible functions of the sensillae are discussed.

Key words: antenna, antennal sensillae, scanning electron microscopy, Chilopoda, centipedes

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INTRODUCTION

Craterostigmus tasmanianus (Pocock, 1912) is a unique centipede, which is widely distributed in native forests and woodlands in Tasmania from sea level up to elevations of at least 1300 m (Mesibov 1995). Taxonomically, it is placed in the monotypic taxon Craterostigmomorpha (Lewis 1981, Dohle 1985, 1990, Borucki 1996). *C. tasmanianus* shows some special features which make this species unique among all other centipedes (Pocock 1902, Dohle 1990, Borucki 1996, Hilken 1997, 1998).

In Chilopoda, the antennae are equipped with numerous cuticular sensilla, which play an important role in the perception of the environment. Unfortunately, only few data are available on the sensillae of the antennae of some centipedes. Only in *Geophilus flavus* (De Geer, 1778) (=*"G. longicornis"* in Ernst (1976, 1979, 1981, 1983, 1997, 2000)) and *Lithobius forficatus* (Linné, 1758) (Keil 1975, 1976) distribution and fine structure of different antennal sensilla were studied. No data with regards to antennal sensillae are available for representatives of the Scutigeromorpha, Craterostigmomorpha, and Scolopendromorpha.
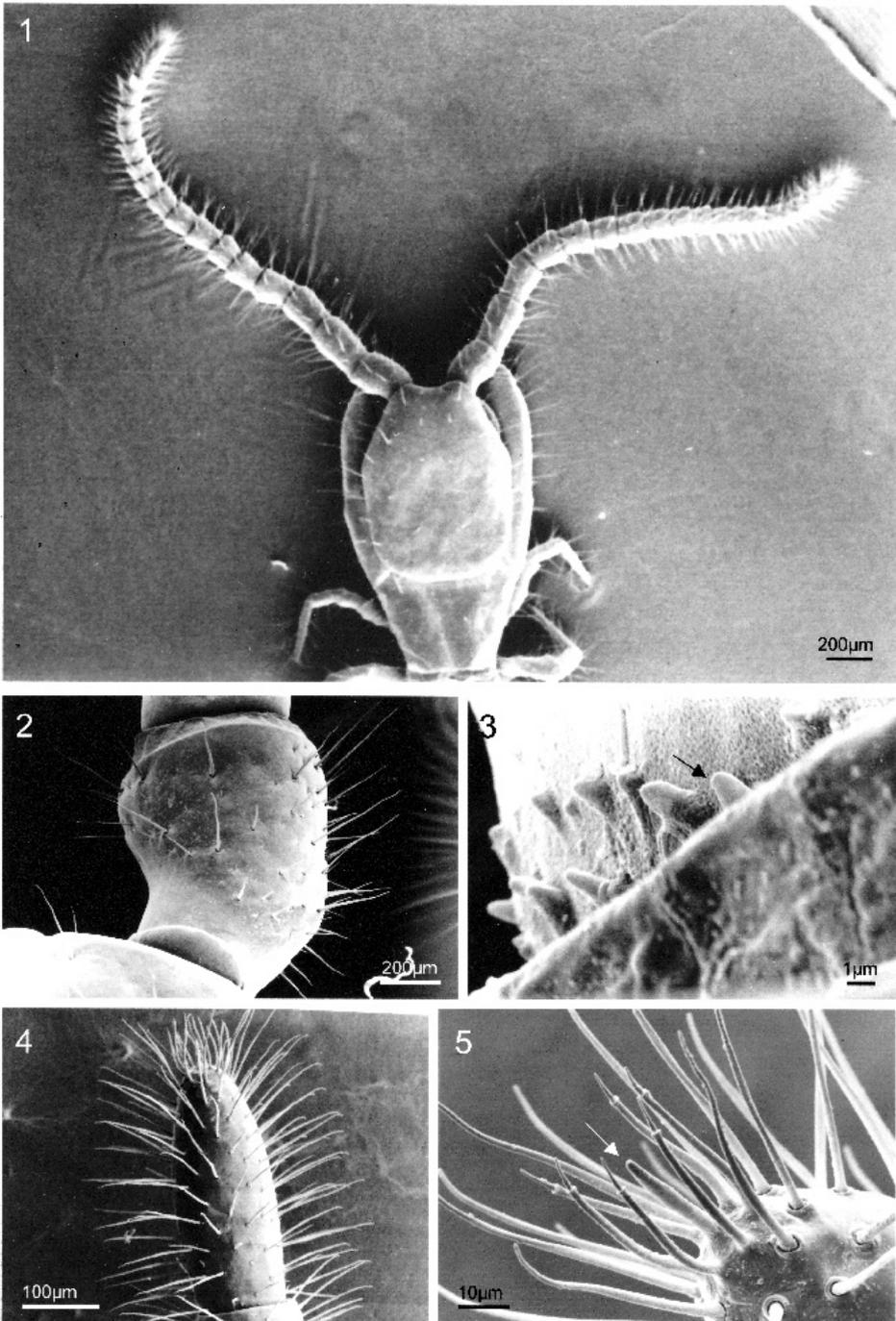
Figures 1-5. *Craterostigmus tasmanianus.* **1:** Dorsal side of the head with both antennae (larva I). **2:** Basal article of the left antennae with sensillae. **3:** Cuticular teeth (arrow) used for the fixation of retracted antennal articles. **4:** Terminal article of the right antenna with three different types of sensillae. **5:** Terminal article of the right antenna (larva I): Central sensillum basiconicum (arrow) surrounded by six tube-like sensillae and several sensilla trichodea.

Here, we present the first data on the distribution and classification of different antennal sensilla on the antennae of *C. tasmanianus* using scanning electron microscopy.

MATERIAL AND METHODS

Specimens of *Craterostigmus tasmanianus* were collected in an *Eucalyptus delagatensis*-forest in north-west Tasmania by R. Mesibov (Penguin, Tasmania). Heads of two larval stages (I and II) and adults of *C. tasmanianus* were preserved in 70% ethanol. After critical point drying, they were mounted on Leitz-Taps (Plano), sputter-coated with a 25 nm gold film (BAL-TEC SCD 005) and examined with SEM (LEO 1450 VP).

RESULTS

Structure of the antennae

The antennae of larval and adult specimens of *Craterostigmus tasmanianus* are composed of 18 antennal articles, which are connected by fine and movable cuticular joint membranes (Figure 1). Cuticular teeth at the base of the preceding article probably serve for the fixation of the retracted cuticular joint membranes (Figure 3). In adult specimens, the length of the antennae is about 8.9-10 mm (larva I: 1.3-1.4 mm; larva II: 2.1-2.4 mm).

The sensilla are differently distributed throughout the antenna. The basal antennal article (840-855 µm in length) bears only some sensillae (Figure 2), whereas the terminal article (240-260 µm in length) shows several and different types of sensillae (Figure 4). The highest number of sensillae is located on the antennal articles 5 to 10.

Six types of cuticular sensillae can be differentiated and classified:

Sensillum basiconicum
On top of the terminal antennal article only a single sensillum basiconicum is centrally located (Figures 5, 6, 10, 11). This sensillum is encircled and overtopped by several tube-like sensilla (see below). In adult specimens, the sensillum basiconicum reaches up to 49 µm in length (larva I: 27.2-30.1 µm; larva II: 33-37.4 µm), its basal diameter ranges from 8 to 8.3 µm (larva I: 4-4.1 µm; larva II: 4.2-4.3 µm). The base of the sensillum is connected to the antenna by a more or less folded cuticle, which possibly allows slight movement of the shaft (Figure 7). At the tip of the sensillum there is a terminal pore (Figure 8). The surface of the sensory shaft shows numerous small depressions (Figure 9).

Tube-like sensilla
A circle of 6 to 13 tube-like sensillae surround the single basiconic sensillum on the top of the terminal antennal article (Figures 5, 10). Each of the sensillae is composed of two parts, a long proximal collar-like shaft (larva 1: 50-62 µm; larva 2: 51-60 µm; adult: 71-87 µm) and an inserted distal conical flagellum (larva I: 7.7-8.0 µm; larva II: 7.0-8.0 µm; adult: 7.5-8.3 µm) (Figures 8, 11, 13). It is likely that the conical flagellum is movable. At its cone-shaped base (diameter 4 to 4.8 µm) the cuticle shows several cuticular stripes (Figure 12). The surface of the shaft is velvety with small pits, whereas the surface of the flagellum is smooth (Figure 13).

Sensilla trichodea
The most frequent type of sensillae are sensilla trichodea (about 1 100 per antenna (in adults) distributed over all antennal articles (Figure 14). The density of theses sensillae increases from the basal to the terminal antennal segment. Mostly, the sensillae trichodea are long and straight (50-390 µm in length), but in the central part of the antennal segments shorter and twisted sensilla trichodea are present (17.3-50 µm; Figure 15). The basal diameters range between 3.9 and 8.7 µm. The shaft of the trichoid sensillae is distinctively striated (Figures 16, 17, 18) and ends with a single terminal pore (Figures 16, 17). The base of each sensillum is inserted into antennal cuticle and is surrounded by a ring-like collar (Figure 18).

The shorter sensillae (15 to 40 µm in length) at the base of the antennal segments are termed as sensilla mesotrichodea.
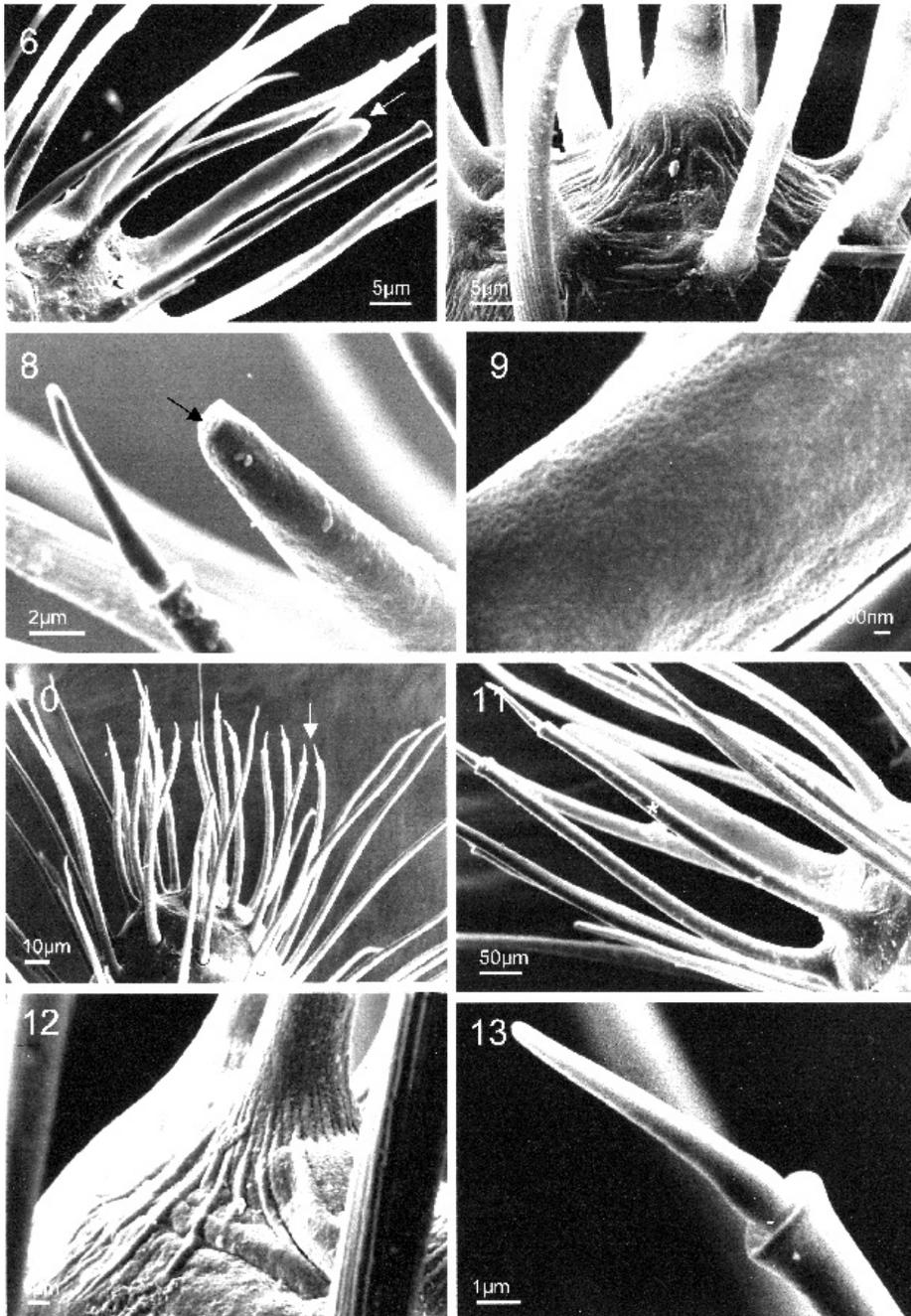
Figures 6-13. 6: Terminal article of the right antenna (larva II) with sensillum basiconicum (arrow) and surrounding tube-like sensilla. **7:** Base of basiconic sensilla with folded cuticle. **8:** Terminal pore (arrow) on the tip of a basiconic sensilla (larva I) and the distal conical flagellum of a tube-like sensillum. **9:** Sensory shaft of a basiconic sensilla with numerous small depressions. **10:** Terminal article of an antenna with 14th articles with 13 tube-like sensillae (arrow). **11:** Tube-like sensillum with a long shaft (*) and a conical flagellum (larva II). **12:** Base of a tube-like sensillum with several cuticular stripes. **13:** Tube-like sensillum (larva I) with its conical flagellum located in a small depression of the shaft.

Sensilla microtrichodea

The sensilla microtrichodea are located at the cuticular joint membranes of most of the antennal segments (Figures 23, 25). The conical sensory peg is probably movable, its surface is smooth (Figures 25-27). At the tip of the sensillum a single terminal pore is detectable (Figure 24). The length of the microtrichoid sensillae is up to 4.9 µm, their diameters ranges from 1.06 to 1.8 µm. The sensory peg will be turned off by retraction of the antennal segments (Figure 27).

Bottle-like sensilla

In adult specimens, dorsally 1-4 bottle-like sensilla are located only at the anterior edge of the antennal segments 2, 6, 11, and 16 (ventral side always only a single sensillum). In larval stages, the total number of bottle-like sensilla is lower. Each of the sensillum is composed of two parts: a high, but broad proximal collar-like shaft of different length (larva I: 14-18.2 µm; adult: 15-28 µm, up to 7.5µm in diameter) and an inserted distal conical flagellum of different length (larva I: 4.8-6.2 µm; adult: 5.6-8.1 µm), reminding to a bottle with a pointed bottleneck (Figures 19, 20, 22). Beside these long sensilla (Figures 19-21), short bottle-like sensilla (adult: up to 10µm in length, up to 5.2 µm in diameter) are distinguishable (Figure 22). The base of the bottle-like sensilla is inserted in a widened cuticular depression. Here, the cuticle is often slightly folded (Figures 19, 21).

Sensilla coeloconica

The conical sensilla coeloconica (5-8 per antenna) are located at the basal region of the antennal segments 1 to 13 nearby the cuticular joint membranes (Figures 28-31). The sensory peg with a rounded tip is 2.9 to 3.5 µm in length; the basal diameters range between 1.7 to 2.4 µm. Each sensillum is located in a rounded pit, which is surrounded by a distinct cuticular collar (Figure 31). The surface of the peg is smooth, sometimes small depressions are observable. The existence of a terminal pore could not be documented.

DISCUSSION

This study focuses on the structure and distribution of the different types of sensilla on the antenna of the centipede *Craterostigmus tasmanianus*. Investigations of cuticular sensilla in Chilopoda are rare and extremely complex. Here, we provide first results on different types of antennal sensilla in *C. tasmanianus* using SEM techniques. Six different types of sensilla can be documented, tube-like sensilla were not observed in centipedes before. By absence of ultrastructural and electrophysiological investigations on the sensilla it is difficult to estimate the function of the antennal sensilla. Therefore, we compare the types of the antennal sensillae of *C. tasmanianus* with the ultrastructurally investigated sensilla of the species *Geophilus flavus* (De Geer 1778) and *Lithobius forficatus* (Linnaeus 1758) (Ernst 2000, Keil 1975, 1976). Topographical and morphological similarities with the latter species may help to assume the function of the types of the antennal sensillae in *C. tasmanianus*.

Sensillum basiconicum

In *C. tasmanianus* only the single sensillum basiconicum is located centrally on the top of the terminal antennal segment. This sensillum has no direct contact to the soil, because it is overtopped by several surrounding tube-like sensilla. The wrinkled cuticle at the base of this sensillum implicates a restricted mobility. Beside a terminal pore the surface of the sensory shaft shows numerous small depressions. The latter remind to the pores of basiconic sensilla on the antennae of *G. flavus* (Ernst 1979). Due to the comparable structure, it is likely that the sensillum basiconicum of *C. tasmanianus* also has an olfactoric function.

In *G. flavus* several sensilla basiconica ("dünnwandige Zapfen", Fuhrmann 1922) are located on the terminal segment of the antennae. The surface of the shaft is covered with pores, which do not reach the lumen of the sensilla. The terminal pore connects the lumen of the cone with the environment. Ultrastructurally, the sensilla basiconica in *G. flavus* exhibit two types
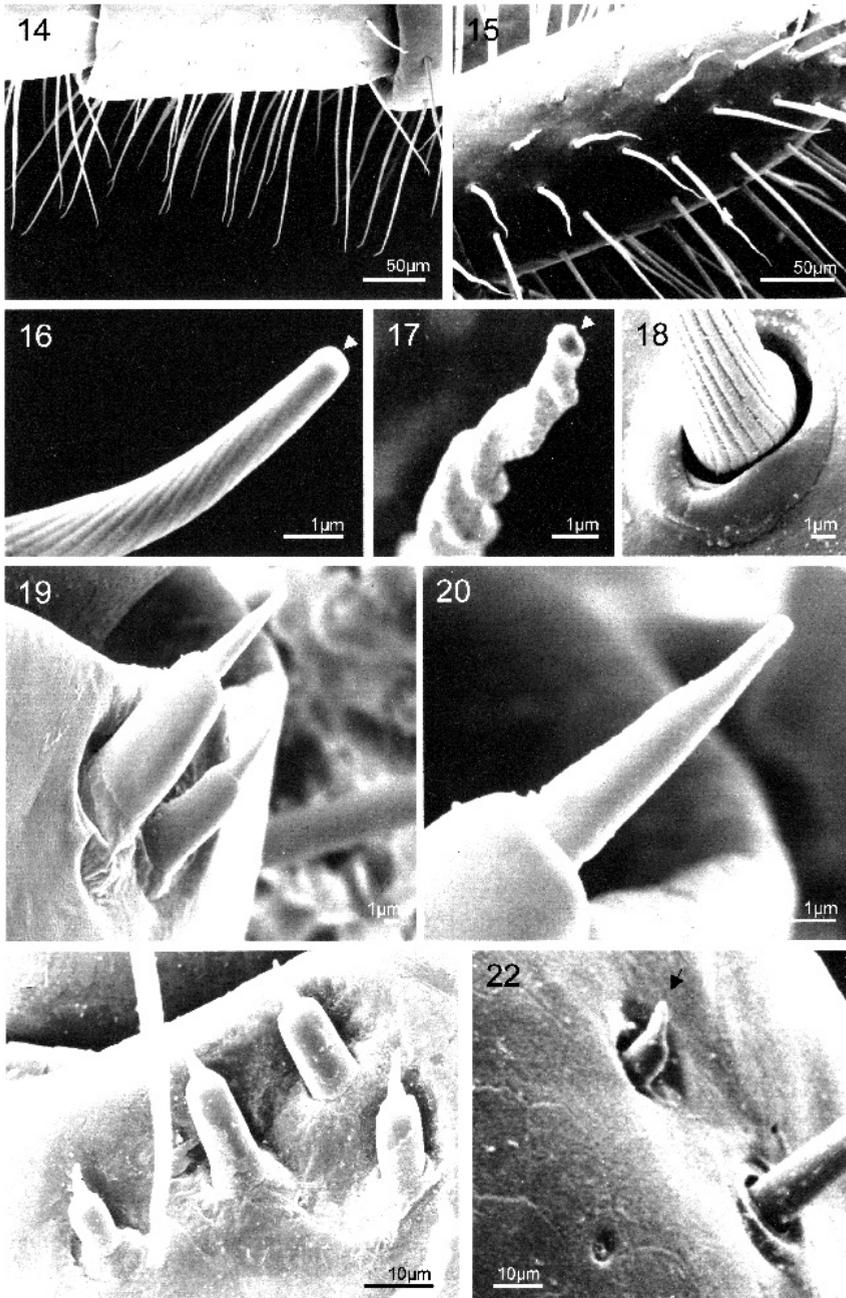
Figures 14-22. 14: Long sensilla trichodea at the margin of the 14th antennal article. **15:** Long sensilla trichodea at the margin and short twisted sensilla trichodea in the central part of the terminal antennal article. **16:** The striated shaft of a sensillum trichodeum with a terminal pore (arrow head). **17:** Terminal pore of a twisted sensillum trichodeum (arrow head). **18:** Bulbous base of a sensillum trichodeum. **19:** Two bottle-like sensilla at the anterior edge of the 11th antennal article. **20:** The distal conical flagellum of a bottle-like sensillum. **21:** Four bottle-like sensilla at the dorsal side of antennal article eleven. **22:** Small bottle-like sensilla (arrow) on the ventral side of second antennal article (larva II).

of dendritic outer segments. It is thought that the olfactory basiconic sensillae of *G. flavus* are able to differentiate between two scents (Ernst 1979, 1999, 2000). In *L. forficatus*, sensilla basiconica are also located on the dorsal side of the antennal terminal article nearby the top, but they are also present at the distal edges of the most antennal articles (1-2 per article, Keil 1975). The same distribution pattern are known from the antennal basiconic sensillae of *L. muticus* C. L. Koch, 1847 and *L. nodulipes* Latzel, 1880 (Ernst unpublished). Beside a terminal pore, the surface of the basiconic sensillae of *L. forficatus* is covered with many slits. They lead into a complex system of 'caves' inside the cuticle of the shaft. It is not known, whether these sensilla function as chemo- and/or as hygroreceptors.

In different species of millipedes antennal sensilla basiconica possesses uni- and biciliate sensory cells. Terminal pores are not described. (Nguyen Duy-Jacquemin (1982, 1985, 1989). In insects, basiconic sensilla show pores with pore tubuli on the surface of the sensory shaft, however, a terminal pore is not present (Ernst, K.-D. 1969, Steinbrecht & Müller 1971, Keil 1982, Keil & Steinbrecht 1984).

Sensillum trichodeum
The sensilla trichodea of *C. tasmanianus* are comparable in distribution and in shape with the sensilla trichodea of *G. flavus* (Ernst 1976, 1994, 1996, 1999, 2000), *L. forficatus* (Keil 1975, 1976), and *L. muticus* (Ernst, unpublished). In all these species, the movable hair shaft of the trichoid sensillae possesses a terminal pore and the surface of the shaft is striated.

In *G. flavus* and *L. forficatus*, the antennal sensilla trichodea show two types of sensory cells: 1. uniciliate sensory cells, whose dendritic outer segments extend into the lumen of the hair shaft near the terminal pore, 2. uniciliate (*L. forficatus*) or biciliate (*G. flavus*) sensory cells, whose dendritic outer segments terminate at the base of the hair shaft. This type of sensory cells possesses a tubular body, which is typical for mechanoreceptor cells. The tubular body

is involved in the stimulus transformation by mechanical bending of the hair shaft (Thurm 1964, 1965, 1982, Füller & Ernst 1975, 1977). The mobility of the base of the hair shaft and the presence of a terminal pore and a tubular body are indications of the bimodality (chemoreception and mechanoreception) of the sensilla trichodea. Uniciliate chemoreceptive sensory cells and a single biciliate mechanoreceptive neuron are also present in the antennal apical cones of different species of millipedes, but their cones consist of several subunits (Nguyen Duy-Jacquemin 1981, 1985, 1996, 1997, Schönrock 1981). The double function as contact chemoreceptor is also known from taste hairs of insects (Adams et al. 1965, Hansen & Heumann 1971). Therefore, it is thought that the sensilla trichodea in *C. tasmanianus* function as a contact-chemoreceptor.

Sensillum microtrichodeum
In *C. tasmanianus* only few sensilla micro- trichodea are located at the cuticular joint membrane between the antennal articles. The moveable peg with its terminal pore seems to be turned off by the retraction of the antennal articles and will provide information about the position of the antenna. Thus, it is thought that the sensilla microtrichodea of *C. tasmanianus* function as proprioreceptors. Due to the presence of a terminal pore, this type of sensillum may have a further chemoreceptive function. In *G. flavus* (Ernst 1983, 2000), in *L. forficatus* (Keil 1975, 1976), and in *L. muticus* (Ernst unpublished) sensilla microtrichodea are arranged in three rows (laterodorsal, mediodorsal, and lateroventral) at the base of the most antennal articles. They are miniaturized sensilla trichodea with terminal pores in *G. flavus*. A terminal pore is not described in *L. forficatus*. In *G. flavus,* the movable hair shaft houses two biciliate mechanoreceptive and 5-7 uniciliate chemoreceptive sensory cells. The dendritic outer segments of the chemoreceptive sensory cells have contact to the environment by means of the terminal pore. In *L. forficatus* these sensilla (= "kleine Borsten", Keil 1975) probably posses only two uniciliate mechanoreceptive sensory cells.
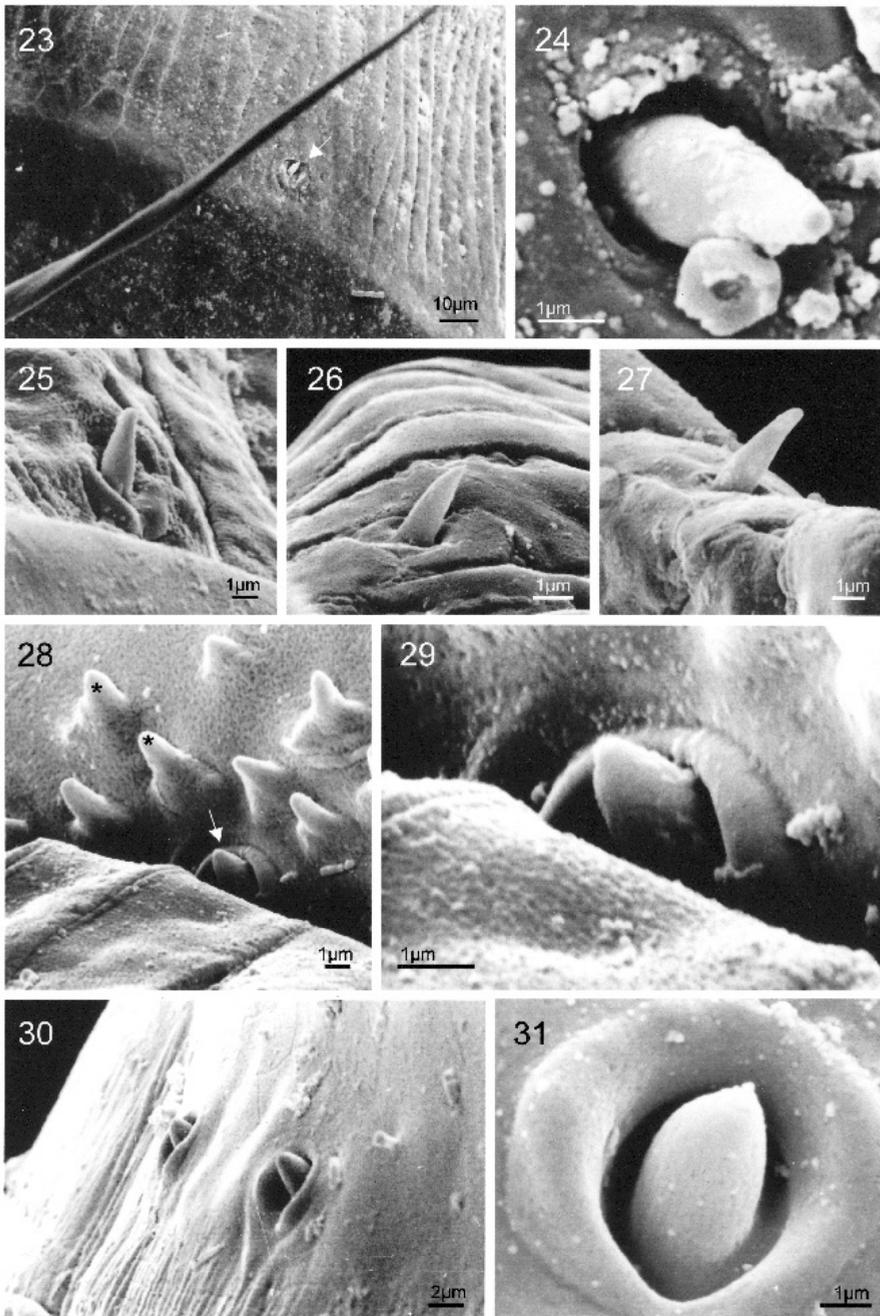
Figures 23-31. 23: A single sensillum microtrichodeum near the cuticular joint membrane (arrow). **24:** Sensillum microtrichodeum with a terminal pore. **25-26:** Sensillum microtrichodeum, located in a small cuticular pit. **27:** Sensillum microtrichodeum at the cuticular joint membrane. **28:** Sensillum coeloconicum (arrow) and cuticular teeth (*) near the cuticular joint membrane of the preceding antennal article. **29:** Detail of the sensillum coeloconicum of Fig. 28. **30:** Two sensilla coeloconica at the base of the 4th antennal article (ventral view). **31:** The peg of a sensillum coeloconicum is located in a rounded pit, surrounded by a cuticular collar.

Collared sensilla
(tube-like and bottle-like sensilla)
On different articles of the antennae of *C. tasmanianus* collared sensilla are observable. These sensilla are distinguished by a collar-like shaft and a tapered flagellum. The surface of the shaft and the flagellum is smooth. It is thought that the flagellum is movable. As shaft and flagellum are of different length and width, we make a distinction between sensilla with a long and slender shaft and a comparably shorter flagellum (tube-like sensilla) and sensilla with a bulgy shaft and a short and comparably thin flagellum (bottle-like sensilla). Tube-like sensilla are only situated at the top of the terminal antennal article of *C. tasmanianus*. They have never been described before in Chilopoda. Similar collared sensilla are described from the surface of antennal articles of *Scolopocryptops sexspinosus* Say, 1821, the length ration between shaft and flagellum is about 1:2, the sensillum is striated as in typical antennal trichoid sensilla (Edgecombe & Giribet 2004). Attems (1930, cited after Lewis 2000) described two-segmented sensilla in *Otocryptops* (=*Scolopocryptops)*. Lewis (2000) showed similar antennal sensilla in *Scolopocryptops ferrugineus* Linné, 1767 (length ratio between shaft and flagellum is about 1:2) and described those in Dinocryptops Crabill, 1953.

The bottle-like sensilla of *C. tasmanianus* occur in a short and a long subtype. In *C. tasmanianus* Edgecombe & Giribet (2004) showed both subtypes on the dorsal side at the anterior end of article 16 and a single long sensillum on the ventral side at the anterior end of article 16. Additionally, we can demonstrate both subtypes of bottle-like sensilla on the anterior edges of antennal articles 2, 6, and 11. Bottle-like antennal sensilla are hitherto not described in other Chilopoda. The function of the collared sensilla in Chilopoda remains unclear.

Sensillum coeloconicum
In *C. tasmanianus*, few sensilla coeloconica are situated near the cuticular joint membranes between the antennal articles. Each consists of a conical sensory peg, situated in a rounded pit. The existence of a terminal pore could not be proved. It is thought that these sensilla function as proprioreceptors involving in the perception of retraction movements of the antennal articles. Sensilla coeloconica are hitherto not described on antennal articles of other chilopods.

Antennal sensilla coeloconica are present in the millipede *Polyxenus lagurus* (Linné, 1758). A special feature of the fine structure is the existence of a lamellated dendritic segment beside of normal outer segments. The antennal sensilla coeloconica in *P. lagurus* are thought to be a thermo- and a hygroreceptor (Nguyen Duy-Jacquemin 1983, 1997). This sensillum belongs to the no-pore sensillae (Altner et al. 1983).

In Chilopoda sensilla coeloconica are present on the poison claws of the maxillipedes in all orders of centipedes (Ernst et al. 2002, Ernst & Rosenberg 2003). The sensory peg exhibit a terminal pore. Fine structural investigations on the sensilla coeloconica in *G. flavus* and *L. forficatus* show that long dendritic outer segments of the chemoreceptive sensory cells extent to the terminal pore of the sensory peg. Additionally, in *L. forficatus* shorter mechanoreceptive dendritic outer segments with tubular bodies terminate at the base of the cuticular channel (Ernst 1995, Ernst & Rosenberg 2001, 2003, Rosenberg & Ernst 2001). It is thought that the sensilla coeloconica on the maxillipedes of chilopodes function as contact-chemoreceptors.

CONCLUSIONS

It is difficult to estimate the functions of the antennal sensillae in *C. tasmanianus* without fine structural and electrophysiological methods. Correspondences in distribution and shape of antennal sensilla with other centipedes could only provide some indications on functional aspects. To clarify the structure and function of the different types of sensilla of *C. tasmanianus* investigations with other methods rather than SEM are required.

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Homology of lateral ocelli in the Pleurostigmophora? New evidence from the retinal fine structure in some lithobiomorph species (Chilopoda: Lithobiidae)

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Müller, C. H. G. & Rosenberg, J. 2006. Homology of lateral ocelli in the Pleurostigmophora? New evidence from the retinal fine structure in some lithobiomorph species (Chilopoda: Lithobiidae). Norw. J. Entomol. 53, 165-186.

The morphology of the lateral ocelli of adult lithobiid centipedes (*Eupolybothrus fasciatus* (Newport, 1844), *Lithobius forficatus* (Linnaeus, 1758), *L. dentatus* C.L. Koch, 1844 and *L. mutabilis* L. Koch, 1862) was examined by light and electron microscopy. In all species examined a triangular ocellar field with 11-24 lateral ocelli, arranged in 4-5 longitudinal rows, is present at both frontolateral cephalic borders. The lateral ocelli are cup-shaped and vary in diameters. Giant ocelli are found along the posteriodorsal margin of each ocellar cluster. A flat and pigmentless epithelium secretes a biconvex, sculpturated cornea. The retinula is made up of two photoreceptive cell types, distinguishable by cellular shape, orientation and rhabomeric arrangement. The distal retinula cells have a cubical or prismatic shape and are aligned in one or more transverse circles. The microvilli of the monodirectional distal rhabdomeres are always closely attached to each other and may emanate either from flattened (*Lithobius*) or fingerlike (circumapical rhabdomeres of *E. fasciatus*) apices. The proximal retinula cells are club-shaped, occupy the proximal half or third of the optic cup and show an epithelial arrangement. Their bidirectional rhabdomeres contain a fan-shaped hem of microvilli, which run perpendicular to those of overlying distal retinula cells. The rhabdomeres of all neighbouring proximal retinula cells interdigitate, producing a fused rhabdom, which, depending on ocellar size and species examined, appears star or net-like in cross sections. The entire retinula is surrounded by two different types of sheath cells. An inner multilayer of circumretinular sheath cells surrounds the retinula cells whereas the outer multilayer of interocellar sheath cells remains limited to the interocellar spaces. A thin basal matrix and subjacent sheet of external pigment cells cover the entire ocellar field. The re-described fine structure of the lateral ocelli of *E. fasciatus* and *Lithobius* differs considerably from earlier reports. Many characters speak for the homology of the lateral ocelli of the Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha. Complex morphological correspondencies between lithobiomorph (*E. fasciatus*) and scolopendromorph (*Scolopendra* spp.) eyes may be used as additional arguments for the monophyly of the Pleurostigmophora.

Keywords: Chilopoda, *Eupolybothrus, Lithobius*, dual type retinula, sheath cells, eye evolution, vision, phylogeny

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INTRODUCTION

Investigation of the lateral eyes in Chilopoda, and Lithobiomorpha in particular, have a long history and can be divided into two distinct phases. Referring to the lateral ocelli of the Lithobiomorpha, the classical histological epoch at the end of the 19th century brought out valuable data of the retinal anatomy (Sograff 1879, 1880, Grenacher 1880, Willem 1891a,b, 1892, Hesse 1901). These early studies were followed by the period of electron microscopical examinations, which started at the end of the 1960ies and provided an additional insight into the fine structure of the lateral ocelli of the lithobiid species *Lithobius forficatus* (Linnaeus, 1758) (see Joly 1969, Bähr 1971, 1972, 1974) and *Eupolybothrus fasciatus* (Newport, 1844) (see Bedini 1968). The relatively high number of papers let Lewis (1981, p. 112) conclude that "the eyes of lithobiids are better known than those of other centipedes".

In connection with the recently revived debate about the phylogenetic interrelationships among the Euarthropoda (Mandibulata: e.g. Edgecombe et al. 2003, Giribet et al. 2005; Paradoxopoda: e.g. Kadner & Stollewerk 2004, Mallatt et al. 2004) in general as well as the Mandibulata (Myriapoda: e.g. Edgecombe 2004, Giribet et al. 2005; Tracheata: e.g. Kraus 2001; Tetraconata: e.g. Dohle 2001, Richter 2002) and the Chilopoda (e.g. Borucki 1996, Edgecombe & Giribet 2002, 2004, Giribet & Edgecombe 2006) in particular, the structure and development of the lateral eyes of the Chilopoda became an important subject for morphological investigations and phylogenetic considerations (Paulus 1979, 2000, Müller et al. 2003b, Bitsch & Bitsch 2005, Harzsch et al. 2005, Müller & Meyer-Rochow 2006a,b). The homology of notostigmophoran ommatidia and pleurostigmophoran lateral ocelli are only weakly supported by the dual type retinula whereas many characters can be given for homologizing the lateral eyes of the eye-bearing Lithobiomorpha, Craterostigmomorpha and Scolopendromorpha. The lateral ocelli of *E. fasciatus* with its multi layered retinula is assumed to represent a combination of characters belonging to the ground pattern of the Pleurostigmophora. However, some characters that have been described in lithobiomorph eyes (absence of external pigment cells, lacking of proximal retinula cells in *E. fasciatus* (Bedini 1968), massive reduction of the formerly multi-layered system of distal retinula cells to one single layer in *L. forficatus* (Bähr 1974)) make it more difficult to explain the evolutionary transformation of lateral ocelli in the pleurostigmophoran stem lineage. Especially the described absence of a dual type retinula only in *E. fasciatus* appears to be doubtful.

In order to obtain a better understanding of the morphology and evolution of the lateral ocelli in the Pleurostigmophora and in particular the Lithobiomorpha we set out to re-investigate the fine structural organization of the lateral ocelli of *E. fasciatus* and several *Lithobius* species (including those of *L. forficatus)*. Furthermore, we evaluate our findings in terms of the still controversial phylogeny of the Chilopoda.

MATERIAL AND METHODS

Adult specimens of *Eupolybothrus fasciatus,* 26-38 mm in length, were sampled in June 2005 by Marzio Zapparoli and Abou Jaoudi under woody litter in a forest near the eastern side of Monte Fogliano (Provinzia Viterbo, Italy). Adult (15-25 mm in length) specimens of *Lithobius forficatus, Lithobius dentatus* C.L. Koch, 1844 and *Lithobius mutabilis* L. Koch, 1862 were collected in September 2003 by Karin Voigtländer in the soil of agricultural fields, under the bark of dead forest trees and under woody litter near-by Görlitz (Germany). Individuals were kept in spacious plastic boxes in a room exposed to natural light changes (12:12 rhythm). The individuals were decapitated *in vivo* under artificial light at 13.00 h after five hours of light adaptation and under dim red light at 02.00 h in a fully dark adapted state. Severed heads were split in halves along their sagittal planes and then fixed for 12 hours in a cold solution of Karnovsky's prefixative (1965), consisting of 2 % glutaraldehyde, 2 % paraformaldehyde, 1.52 % NaOH, and
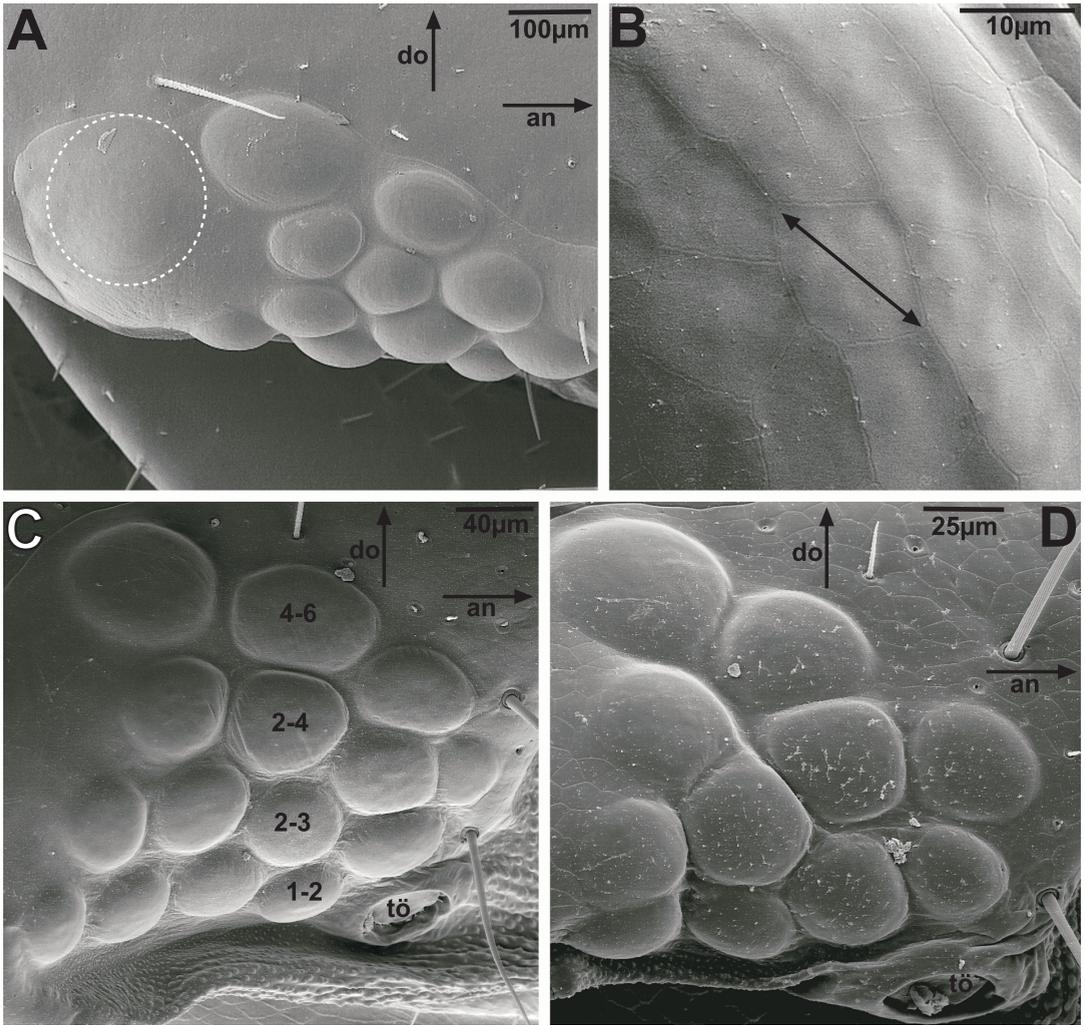
Figure 1 A-D. Outer appearance of lateral ocelli in Lithobiomorpha. SEM. **A.** Right ocellar field of *Eupolybothrus fasciatus*, the posterior, back-pointing ocellus is indicated by w*hite dashed circle*. **B.** Detailed view of the corneal surface pattern of a lateral ocellus situated in the middle of the right ocellar field of *Eupolybothrus fasciatus;* the *double arrows* illustrate the maximal extension (length) of a single corneal scute. **C.** Right ocellar field of *Lithobius dentatus*; the numeric ranges represent the number of distal retinula layers in a given lateral ocellus. **D.** Right ocellar field of *Lithobius mutabilis*.

an anterior body region, *do* dorsal body region, *SEM* scanning electron micrographs, *tö* organ of Tömösváry.
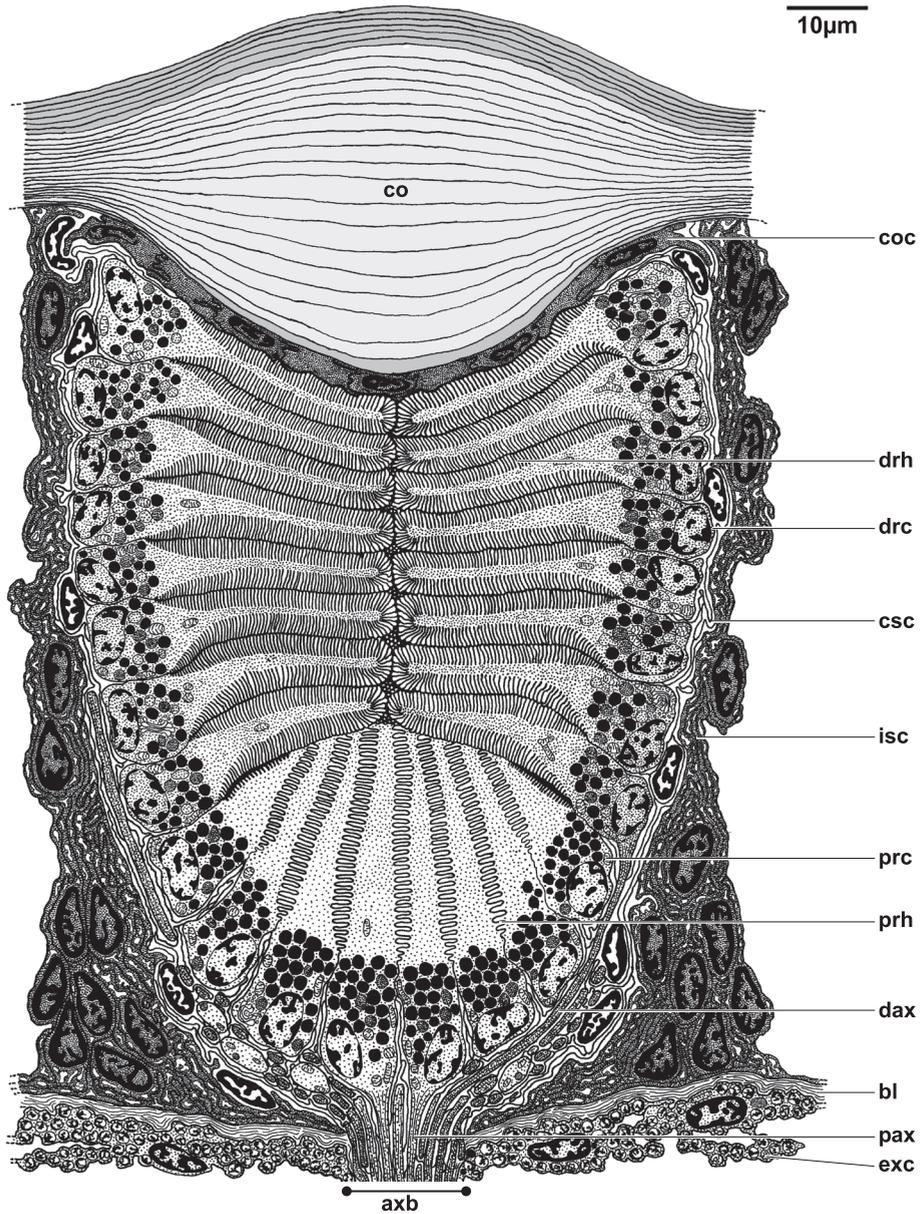
Figure 2. Semi-schematic, longitudinal reconstruction of a medially placed lateral ocellus in *Eupolybothrus fasciatus* including subjacent cell types. The cytoplasmic composition of the retinal constituents represents the dark-adapted state. For technical reasons the total number of the retinula cells (including the number of distal retinular layers) and the cornea-secreting epithelial cells have been reduced. The palisade-like system of perirhabdomeric ER in the distal retinula cells is not drawn.

axb retinular axon bundle, *bl* basal matrix, *co* cornea, *coc* cornea-secreting epithelial cell, *csc* circumretinular sheath cell, *dax* distal retinula axon, *drc* distal retinula cell, *drh* distal rhabdomere, *exc* external pigment cell, *isc* interocellar sheath cell, *pax* proximal retinula axon, *prc* proximal retinula cell, *prh* proximal rhabdomere.

1.2 g d-glucose, dissolved in 2.25 % Na-hydrogenphosphate buffer (pH 7.4). After washing in the same buffer, the specimens were then fixed for four hours in 1 % O_sO_4 solution (same buffer) at room temperature and, following dehydration in a graded series of acetone, embedded in epoxide resin (Araldite, FLUKA). Serial semithin sections (approximately 1 μm thick) were prepared and stained using 1 % toluidine blue in a solution of 1 % Na-tetraborate (borax). Serial ultrathin sections were stained with uranyl acetate and lead citrate for five minutes each and then examined under a Zeiss 902A transmission electron microscope, operated at 80 kV. Total number of distal and proximal retinula cells was counted by means of cross sections through the subretinal axonic bundles. Each axon included was marked digitally and counted by using the image analysis programm EsiVision (analySIS®). The number of sheath cells could only be estimated by analyzing complete series of semithin sections under a Olympus BH-2 light microscope. Some of the TEM-images shown (e.g. Figures 3E, 6B) were compound on the PC with the aid of Esivision, consisting of up to 12 single digital micrographs. For observations by scanning electron microscopy prefixed head-halves (see above) were critical point dried, coated with gold, and observed at an accelerating voltage of 15-30 kV under a Zeiss DSM 960A scanning electron microscope. Total number of cornea-secreting epithelial cells was determined by counting the polygonal "scutes" (term after Cals 1974) visible on the corneal surface. To distinguish epidermal from corneal "scutes" the length of up to 20 polygons were measured on the cornea around the ocellar tip and close-by the ocellar margins as well as on the surrounding cuticle. According to Müller & Meyer-Rochow (2006a), the maximal length of each polygon was given by the range between two opposing angles of maximal distance (see also Figure 1B). Statistical tests were carried out with SPSS-software to determine whether epidermal and corneal polygons differ signicantly (normal distribution: Kolmogorov-Smirnov test; significance: Student's t-test).

RESULTS

Topography and general organization

Eupolybothrus fasciatus and all of the examined *Lithobius* species bear a tringular field of 11-32 circular or elliptical eyes (Figures 1A,C-D), termed in the following "lateral ocelli", near the frontolateral edge of the cephalon and posterior to the antennae. These lateral ocelli, strongly varying in diameter, are densely packed and aligned in 3-5 vertical rows. Expressed as ocellar formulae, the following configurations were found: 1+2,4,4,3 in *E. fasciatus* (Figure 1A), 1+2,4,4,3,1 in *L. dentatus* (Figure 1C), 2+4,3,2 in *L. mutabilis* (Figure 1D) and 1+2,5,5,5,4,4,3,2,1 in *L. forficatus*. Generally, the smallest dimensions are associated with ocelli located at the anterioventral part of the ocellar field, near the organ of Tömösvary (diameter: 85-105 μm in *E. fasciatus*, 44-52 μm in *Lithobius* spp.), whereas the biggest diameters are measured in those eyes lining the posteriodorsal region of the ocellar field. The most posteriodorsal eye (with diameters of 126-190 μm in *E. fasciatus* and 74-80 μm in *Lithobius* spp.) is always the largest one (hence the name "giant ocellus"), which is either fully integrated into the ocellar field (*Lithobius*, see Figures 1C-D) or considerably distanced from the remaining eyes (*E. fasciatus*, see Figure 1A). In E. fasciatus the posterior interocellar epidermis produces a conspicuous, knob-like structure which let the visual field of the giant ocellus point away from those of the other ocelli (Figure 1A). As a result of the underlying corneagenous epithelium the corneal surface of all ocelli shows a distinct sculpturation of polygons (Figure 1B) or "scutes" (after Cals 1974). The corneal scutes look very similar to those on the head cuticle outside the ocellar field. In all species examined the corneal and interocellar (produced by sheath cells) scutes are nearly identical in length and significantly shorter than the scutes on the head cuticle (p<0.003).

A general view of the fine structural organization of the lateral ocelli of *E. fasciatus* and *Lithobius* spp. is given in Figures 2 and 5. The lateral ocelli of the three analysed *Lithobius* species do not show any interspecific discrepancies in gross and fine
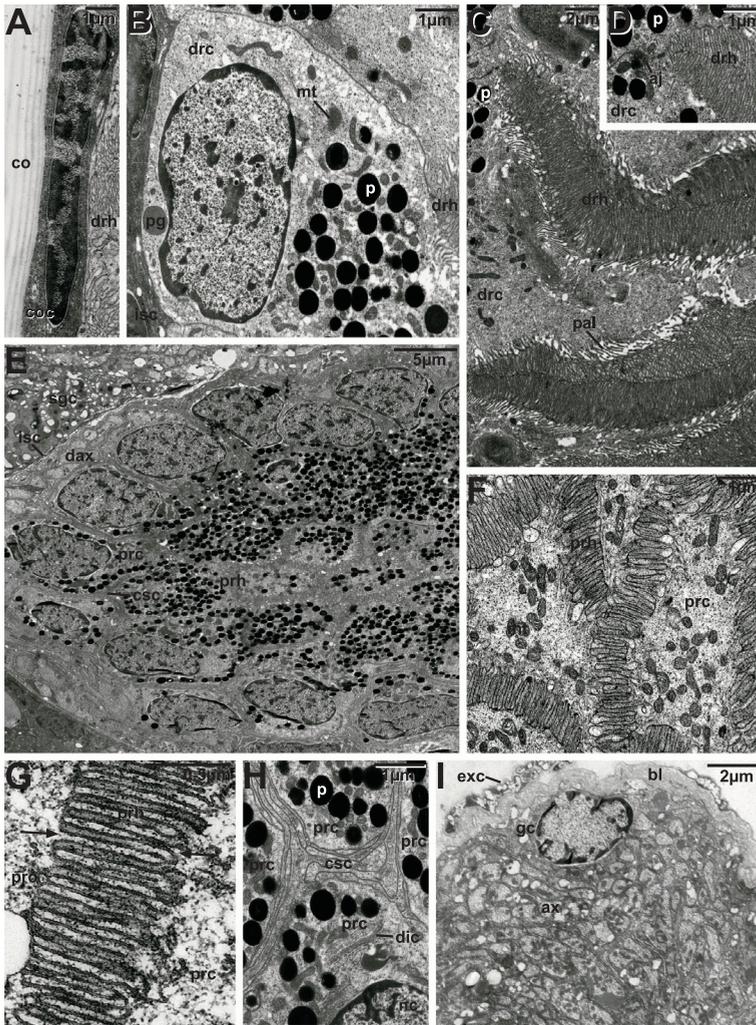
Figure 3 A-I. Fine structure of the cornea-secreting epithelium and dual type retinula of the lateral ocelli of *Eupolybothrus fasciatus*. TEM. **A.** Longitudinal section through the soma of an axially placed cornea-secreting epithelial cell (*coc*). **B.** Cytoplasmic composition of a single distal retinula cell (*drc*). Cross section. **C.** Multilayered distal retinula with compact circumapical rhabdomeres (*drh*) in longitudinal section. **D.** Detailed longitudinal view of the basal part of two circumapical rhabdomeres. **E.** Cross section through the nuclear zone of proximal retinula cells (*prc*) with net-like arrangement of proximal rhabdomeres (*prh*). **F.** Detailed view of the apical area of two proximal retinula cells showing bidirectional rhabdomeres. **G.** Longitudinal section through neighbouring proximal rhabdomeres with interdigitating microvilli (*arrows*). **H.** Middle part of the proximal retinula densely wrapped by numerous processes of circumretinular sheath cells (*csc*). Cross section. **I.** Axon bundle of the posterior giant ocellus in cross section.

aj adhering junction (*macula adhaerens*), *ax* retinular axons, *bl* basal matrix, *co* cornea, *dax* distal retinula axon, *dic* Golgi stack, *exc* external pigment cell, *gc* glial cell, *isc* interocellar sheath cells, *mt* mitochondrium, *nc* nucleus, *p* osmiophilic retinular pigment granule, *pal* perirhabdomeric ER-cisternae, *pg* moderately osmiophilic pigment granule, *sgc* secretory gland cell, *TEM* transmission electron micrographs.

morphology, only the total number of the cellular constituents seem to vary to small percentage (5-10 %). Each lateral ocellus appears cup-shaped and consists of a biconvex corneal lens secreted by a flattened corneagenous epithelium, a multi-layered retinula with two types of photoreceptor cells, two types of sheath cells as well as several layers of subjacent external pigment cells. Eyes situated in the centre of the ocellar field are delimited by a thin basal matrix only around their basal margin, whereas peripheral eye cups are also lined along their entire outer half. The basal matrix is produced from inside the eye by the peripheralmost lobes of the interocellar sheath cells as well as by the innermost layer of the external pigment cells (Figures 4A-B). Furthermore, tracheoles and granular hemocytes are occasionally observed being attached to the basal matrix from outside the eye (Figure 4A). Referring to adult specimens only, the lengths of the eye cups measure 100-180 µm in *E. fasciatus* and 60-110 µm in *Lithobius* species. The morphometric range is positively correlated to the particular position of one eye within the ocellar field and, moreover, seems to depend on the individual's age. The anteriorly and medially positioned ocelli show a coaxial arrangement, perpendicular to the cephalic cuticle, whereas the two posteriodorsal ocelli have their optical axes either obliquely or, as seen in the distanced giant ocellus of *E. fasciatus*, almost parallely to the head's cuticle. The interocellar space is sometimes interrupted by the openings of "interommatidial glands" (Müller et al. 2003a).

Cornea and cornea-secreting epithelium

A single-layered epithelium of 40-310 cells produces the corneal lens, which considerably varies in width (*E. fasciatus*: 35-70 µm; *Lithobius* spp.: 13-40 µm). Quantitative and morphometric variations are positively correlated with increasing diameters of a given ocellus and thus also depend on the particular position within the ocellar field. Each corneal lens appears bi-convex and asymmetrical in longitudinal sections. The internal vault of the lens is somewhat deeper curved (Figures 2, 5). The corneal endo- and exocuticle consists of up to 38 lamellae in *E. fasciatus* and

about 20 lamellae in various *Lithobius* species. Each lamella displays a highly osmiophilic lamina in which the microfibrilles are ordered in parallel layers and a less osmiophilic layer containing microfibrilles which turn 180° and abut to alternating laminae. The cornea-secreting epithelial cells look flattened from longitudinal perspective (0.5 µm in minimum width, Figures 3A, 6A,C) and show cubical outlines when seen in transverse sections. The cells abut directly to the cornea (Figures 3A, 6A). Neighbouring cornea-secreting epithelial cells interdigitate along their inferior cell borders. Apical cell-cell adhesion structures, like for example belt desmosomes (*maculae adhaerentes*), additionally stabilize the corneagenous epithelium (Figure 6A). The elongated and heterochromatin-rich nuclei are found in any position within the corneagenous epithelium (Figures 2, 5). In all species examined the cytoplasm of the cornea-secreting epithelial cells is very electron dense and granular. It houses a conspicuous network of rough ER, free ribosomes, partly bundled microtubules, some electron lucent vacuoles and several mitochondria of the cristaetype (e.g. Figure 6C).

Retinula cells and rhabdom

Depending on the species examined, the individual's age and the relative position of a lateral ocellus within the ocellar field, the retinulae of *E. fasciatus* and *Lithobius* spp. contain 36-750 photoreceptive cells. Two different sorts of retinula cells are found in the lateral ocelli of *E. fasciatus* and *Lithobius* spp.: a distal type with compact rhabdomeres and a proximal type with irregular rhabdomeres (Figures 2, 5).

Distal retinula cells

24-615 distal retinula cells can be counted in the lateral ocelli of a lithobiid centipede. Depending on the ocellar size, these cells may appear cubical (e.g. Figure 5) or cylindrical in shape (e.g. Figures 2, 6B). They are stably linked to each other by compact desmosomes (*maculae adhaerentes*, Figures 3D, 6D). The distal retinula cells are arranged in 1-12 horizontal circle(s) that occupy approximately 50-75 % of the optic cup (Figures 2, 5). In a lateral ocellus of a lithobiid
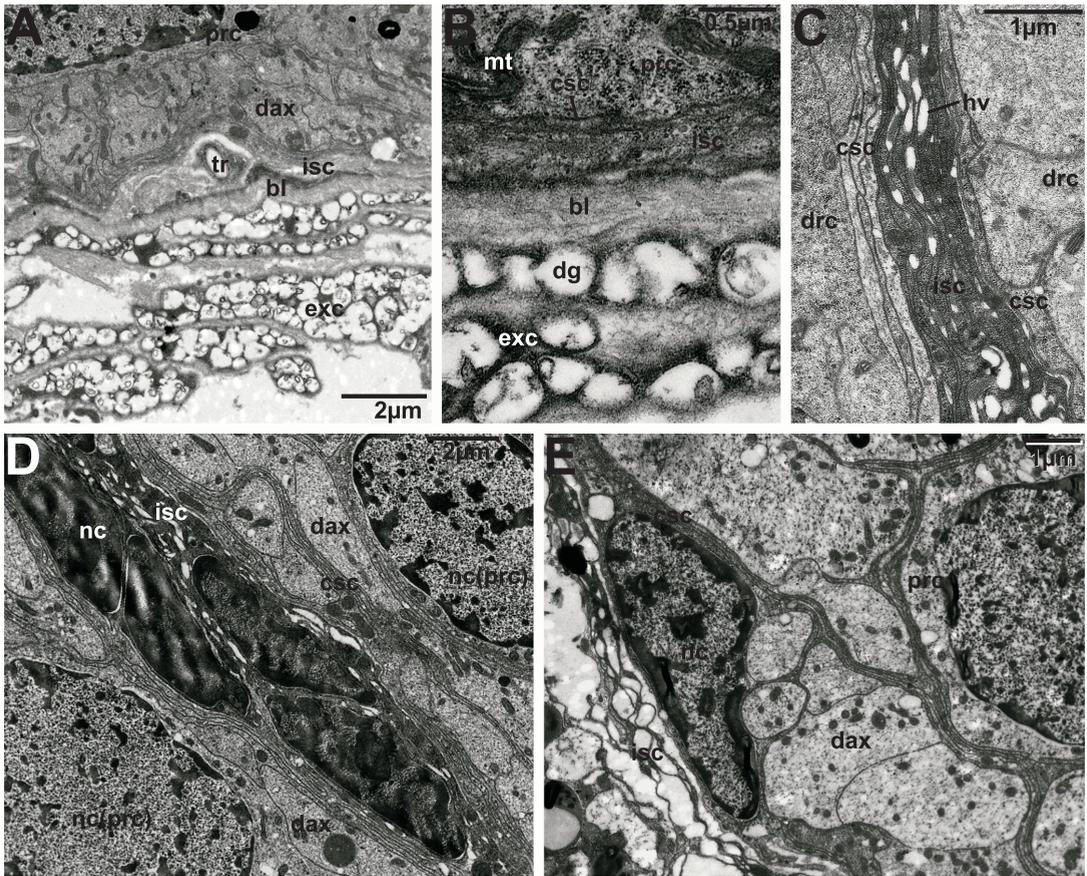
Figure 4 A-E. Fine structure of accessory pigment and sheath cells in the lateral ocelli of *Eupolybothrus fasciatus*. TEM. **A.** Longitudinal section through basal part of a frontally located lateral ocellus underlied by a thin basal matrix (*bl*) and external pigment cells (*exc*). **B.** Region around the basal matrix in detail. Longitudinal section. **C.** Cross section through the distal half of two neighbouring lateral ocelli showing the extensive sheath cell system. **D.** Proximal aggregation of the soma of interocellar sheath cells (*isc*). Longitudinal section. **E.** Longitudinal view of partly arborized circumretinular (*csc*, including one soma) and interocellar sheath cells associated with the proximal periphery of the posterior giant ocellus.

dax distal retinula axon, *dg* pigment granule (with desintegrated matrix), *drc* distal retinula cell, *exc* external pigment cell, *hv* hyaline vacuole, *mt* mitochondrium, *nc* nucleus, *prc* proximal retinula cell, *tr* tracheole.

centipede a distal retinula cell may be generally subdivided into four distinct compartments: (a) the axial region including the rhabdomere, (b) the perirhabdomeric region ("Schaltzone" after Hesse (1901), "intercalary zone" after Bähr (1974)), (c) the soma containing the nucleus and cytoplasmic organelles and (d) the terminal axonal region.

However, in the lateral ocelli of *E. fasciatus* and the three *Lithobius* species some of these regions may be either absent or considerably reduced in size.

In *E. fasciatus*, each distal retinula cell tapers into a fingerlike process extending towards the

centre of the eye (Figures 2, 3C). Each process, approximately 1-2 µm in diameter, forms the rhabdomere in a circumapical alignment. The rhabdomeres are compact with microvilli closely attached to each other. Opposing rhabdomeres are always separated by distinct radii (Figure 3D). All distal retinula cells produce a fused, but extensively ramified rhabdom which is widely circular in cross sections. The total number of distal retinula cells and distinct horizontal retinula cell layers show a strong regional variation. In the smallest ocelli, situated at the anteroventral margin of the ocellar field, one can count approximately 140 distal retinula cells which are fairly equally distributed among 4-6 layers; medially placed ocelli have about 270-345 distal retinula cells distributed among 7-9 layers whereas the posteriodorsal ocelli (including the irregular giant ocellus) possess 460-615 distal retinula cells spread over 9-12 layers. In *E. fasciatus*, the perirhabdomeric region, represented by dense palisades of mostly lengthened smooth ER cisternae, is rather compressed, inconspicuous and integrated into the thin axial projection (Figure 3C). The voluminous somatic part carries the large and spherical nucleus, weakly supplied with heterochromatin (Figure 3B). The soma of the distal retinula cells turns into an axonal process, with a diameter decreasing progressively from initially 1.5 µm to 0.5 µm subretinally and containing centrally placed microtubules (Figure 2). The distal retinular axons always run on a strict proximal course and remain lateral to the proximal retinula cells (Figures 4A, D-E). Just before breaking through the basal matrix all retinular axons of one particular ocellus become grouped together into a distinct bundle embedded by glial cells (Figure 3I).

In all *Lithobius* species the distal retinula cells are arranged in circles distributed among one or several layer(s) and display a straight apex from which almost rectangular rhabdomeres emerge. The compact structure of the rhabdomeres results in the formation of a fused rhabdom (Figures 5, 6B). The total number of distal retinula cells, distal retinula cells, the number of distinct the number of distinct horizontal layers as well as

the cross profile of the distal rhabdom change regionally (Figure 1C). 24-48 distal retinula cells, distributed among 1-2 layer(s) and building up a circular rhabdom, are found in the small anteroventral ocelli whereas medium-sized ocelli have their 70-220 cells organized in 2-4 layers producing a more elliptical rhabdom (Figure 6B). The two posteriodorsal ocelli (including the giant ocellus) are equipped with 242-336 distal retinula cells aligned in 4-6 layers; the rhabdom appears U-shaped in cross sections. The perirhabdomeric zone is conspicuous in *Lithobius* eyes, in particular if light adapted. The remarkable network of sac-like and electron lucent vacuoles (Figure 6C) is normally seen in direct vicinity of or merged into the likewise elaborated system of perirhabdomeric ER cisternae (Figure 6C). The voluminous cisternae are traversed by thin cytoplasmic bridges, which establish contacts between the main cytoplasm and the attenuated (submicrovillar) sheets from which the microvilli emerge (Figures 5, 6B-D). The photoperiodical increase (dark adaptation) or break-down (light adaptation) of the volume of the distal rhabdom in *Lithobius* species are in good accordance with the data already given by Bähr (1971, 1974). The structure and course of somatic (Figures 5, 6B) and axonal part (Figures 5, 6G-H) of each distal retinula cell in *Lithobius* fits well the description given for *E. fasciatus*.

In *E. fasciatus* and various *Lithobius* species the distal retinula cells, especially in their somatic and axonal part, are extraordinarily rich in different types of organelles which are embedded into a cytoplasm of moderate electron density (Figures 3B-C, 6B-D, 7B). Numerous small, partly branched mitochondria (cristae type), free or aggregated ribosomes, rounded and highly osmiophilic pigment granules (0.4-0.7 µm in diameter), small hyaline vacuoles of various shape and lipid droplets are always observed and do therefore not depend on a particular cytophysiological condition. On the other hand, many organelles known to be involved in the synthesis of membrane material, as multilayered cisternae of the rough ER, cisternae of the smooth ER in their vesicular form and Golgi

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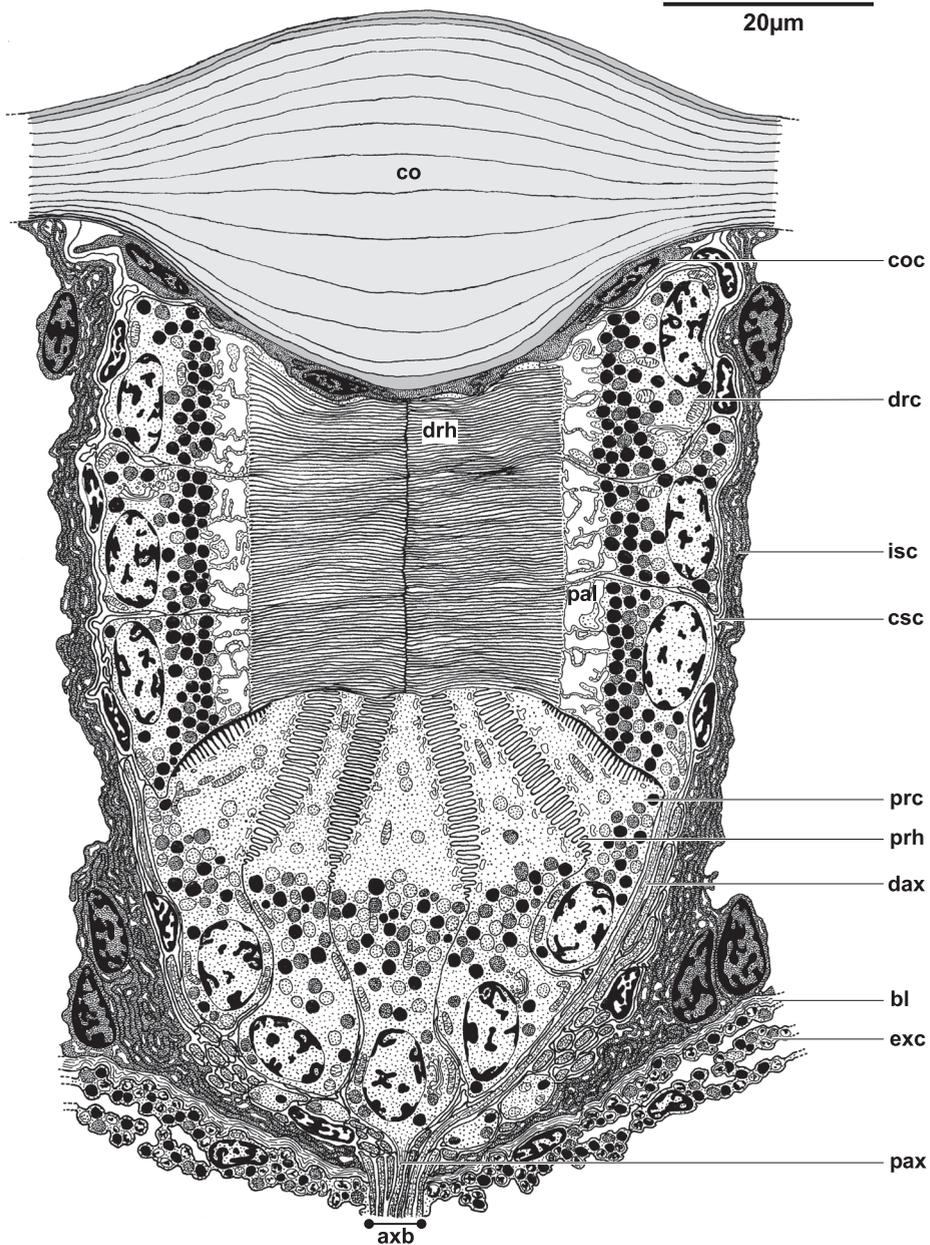
Figure 5. Semi-schematic, longitudinal reconstruction of a medially placed lateral ocellus in *Lithobius* spp. including subjacent cell types. The cytoplasmic composition of the retinal constituents represents the dark-adapted state. For technical reasons the total number of the proximal retinula cells has been reduced.

axb retinular axon bundle, *bl* basal matrix, *co* cornea, *coc* cornea-secreting epithelial cell, *csc* circumretinular sheath cell, *dax* distal retinula axon, *drc* distal retinula cell, *drh* distal rhabdomere, *exc* external pigment cell, *isc* interocellar sheath cell, *pal* perirhabdomeric ER, *pax* proximal retinula axon, *prc* proximal retinula cell, *prh* proximal rhabdomere.

stacks, are only found in dark adapted eyes. Different developmental stages of lysosomes (e.g., multi-vesicular and multilamellated bodies), peroxisomes, granular pigment granules (0.3-0.6 µm in diameter) as well as large polymorphic vacuoles (usually 1-2 µm in diameter) are predominant in the distal retinula cells when light adapted (Figures 6B, 7C). In dark-adapted eyes highly osmiophilic pigment granules aggregate and build up a screening shield around the entire retinula (Figures 2, 5). In *E. fasciatus* these "dark" pigment granules are concentrated around the basis of the axial process (Figures 3B,C), in *Lithobius* they tightly encompass the palisade system of the perirhabdomeric ER (Figure 6C).

Proximal retinula cells

The arrangement and ultrastructural organisation of the conical or club-shaped proximal retinula cells in the lateral ocelli of *E. fasciatus* and the various *Lithobius* species very much resemble each other (Figures 2, 5). Only the total number of cells may differ but can be explained by the double-sized dimensions of *Eupolybothrus*-ocelli in relation to *Lithobius*. In the lateral ocelli of *E. fasciatus* one can count 44-135 proximal retinula cells (15-30 % of the total retinula cell number) whereas 12-66 of them (15-40 % of the total retinula cell number) are present in *Lithobius* species. In all ocelli investigated the proximal retinula cells form a single layer, which occupies the entire bottom of the optic cup, tantamount to the proximal third in *E. fasciatus* (Figure 2) and the proximal half in *Lithobius* species (Figure 5). The elevated cell bodies of the lateroproximal retinula cells usually remain shorter than the most basal ones.

The most important ultrastructural pecularity of a proximal retinula cell is given by the bi-directional pectinate rhabdomeres with microvilli considerably distanced from each other. These proximal rhabdomeres always exceed a length of 5 µm and interdigitate with those of the neighbouring proximal retinula cells (Figures 3E-G, 6E-F). The proximal rhabdomeres are mainly oriented perpendicular to the overlying rhabdomeres of the distal retinula cells. The whole proximal retinular layer produces a more or less fused rhabdom which, in cross sections, appears star-like in smaller anteroventral eyes or lace-like in those eyes located in the centre and at the posteriodorsal part of the ocellar field (Figure 3E). In light adapted eyes the length of the rhabdomeric microvilli is reduced to approximately 50% of the night level. The apicalmost membrane of each cytoplasmic process is not equipped with a microvillar seam and therefore directly adjoins the rhabdomere of the proximalmost distal retinular layer (Figures 2, 5). The perirhabdomeric zone in a proximal retinula cell is weakly developed at any time as only some indistinct smmoth ER cisternae are visible (Figures 3G, 6F). The cytoplasmic composition (including the nuclear ultrastructure) of the proximal retinula cells generally resembles that of the distal retinula cells (Figures 3E-F,H, 6E, 7A), even though in dark adapted ocelli more pigment granules of high electron density seem to exist (Figures 2, 3E, 5). The axonal strands of the proximal retinula cells in any eye remain limited to the central areas of the related axon bundle (Figures 6G-H).

Sheath cells

In *E. fasciatus* and examined *Lithobius* species the distal and proximal retinula cells are tightly enveloped by approximately 50-350 sheath cells. Their exact number depends on the eye diameter (the particular position of the eye within the ocellar field, respectively) and the examined species. Sheath cells show two different compartments, the enwidened soma which contains the small and elongated nucleus and several, massively elongated cytoplasmic processes emanating from the soma in axial or vertical directions. Based on the retinal topography and the cytoplasmic composition, two different types of sheath cells can be distinguished in all examined lithobiomorphs (Figures 2, 5).

Circumretinular sheath cells

In the direct vicinity of the retinula cells (including the distalmost part of the retinular axons) one can find a dense sheet of approximately 20-150 extremely flattened cells, the so-called circumretinular sheath cells (Figures 2, 5). The arrangement of these cells does not seem to
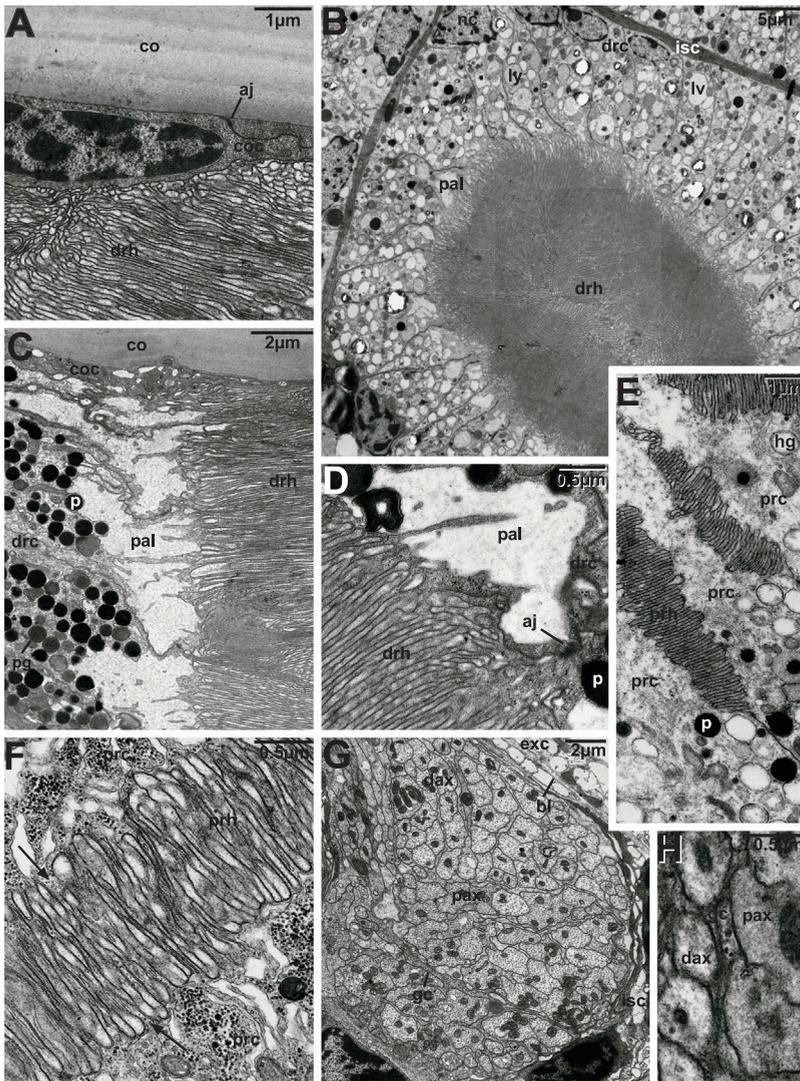
Figure 6 A-H. Fine structure of the cornea-secreting epithelium and dual type retinula of the lateral ocelli of various *Lithobius* species. TEM. **A.** Longitudinal section through the soma of an axially placed cornea-secreting epithelial cell (*coc*). **B.** Cross section through one layer of distal retinula cells (*drc*) in a medially positioned ocellus. **C.** Longitudinal view of the distal part of one posteriodorsal ocellus showing four distinct layers of distal retinula cells producing compact apical rhabdomeres (*drh*). **D.** Basal region of one distal rhabdomere accompanied by voluminous perirhabdomeric ER-cisternae (*pal*). Longitudinal section. **E.** Apical area of three proximal retinula cells (*prc*) forming bidirectional rhabdomeres (*prh*) in longitudinal section. **F.** Longitudinal section through two neighbouring proximal rhabdomeres with interdigitating microvilli (*arrows*). **G.** Crosssectioned axon bundle of a medially placed ocellus. **H.** Highly magnified cross section through one retinular axon bundle with smaller peripheral axons (*dax*) and wider central axons (*pax*).

aj adhering junction (*macula adhaerens*), *bl* basal matrix, *co* cornea, *exc* external pigment cell, *gc* glial cell, *hg* hyaline pigment granule, *isc* interocellar sheath cells, *lv* large polymorphic vacuole, *ly* lysosome, *nc* nucleus, *p* osmiophilic retinular pigment granule, *pg* moderately osmiophilic pigment granule.

follow a regular pattern, no clusters can be seen at any section level. The somatic part of each circumretinular sheath cell bears the nucleus which contains high concentrations of heterochromatin (Figure 4E). The circumretinular sheath cell tapers into (a) axial processes running towards the centre of the eye by being crammed into the infraretinular interspaces (Figures 3H, 4D-E) and (b) vertical ones covering the peripheral borders of numerous retinula cells (Figures 4C, 7C). In addition, the axial and vertical processes may arborize, which makes it difficult to assign every process to its mother soma. At those regions where the ramified processes meet the sheet of circumretinular sheath cells appears multilayered (Figures 3H, 4C, 7C). The very distal circumretinular sheath cells are attached to the interocellar cuticle and produce thin axial processes separating the cell bodies of the distalmost retinula cells from overlying corneageneous epithelium (Figures 2, 5, 7B). The most striking feature of the circumretinular sheath cells is their poorness in cytoplasmic organelles. Only a few mitochondria (cristae type), cisternae of rough ER, loosely arranged microtubules and translucent vacuoles can be observed in a moderately osmiophilic cytoplasm (Figure 4C).

Interocellar sheath cells
One can observe 30-200 interocellar sheath cells which build up the interocellar space and are located radially to the circumretinular sheath cell multilayer (Figures 2, 5). The somatic part of an interocellar sheath cell mostly has a cuneiform profile and includes an elongated or drop-shaped nucleus rich in heterochromatin (Figures 4D, 7B). In *Lithobius* species the somata of the interocellar sheath cells are aggregated in the most distal and proximal region of the interocellar space (Figures 5, 7B,D-E). In *E. fasciatus* a third nuclear zone is observed in the middle of the interocellar space (Figure 2). In all species investigated the majority of interocellar sheath cells is concentrated in the most proximal interocellar interstitium where they contribute to the formation of the basal matrix (Figures 2, 4D, 5, 7E). Axial projections running into the infraretinular space are never seen. As with the circumretinular sheath cells, vertical and oblique cytoplasmic processes, sometimes

smaller than 50 μm in diameter, emanate from the somatic part. These long-reaching distal and proximal processes may also ramify and then intertwine with neighbouring cells (Figures 4C, 6B, 7C). Thereby, the sheet of interocellar sheath cells looks multilayered - 6-10 parallel layers are usually visible-, even in their nuclear zone. The cytoplasm of the interocellar sheath cells is generally more electrondense than that of the aforedescribed circumretinular sheath cells and contains several small mitochondria (cristae type), minute osmiophilic granules (much likely lipid droplets), disorganised cisternae of the smooth and rough ER and dispersed microtubules. However, the shape and cytoplasmic composition of the interocellar sheath cells may strongly vary with the photoadaptational state of the eye. In dark adapted condition the entire cytoplasm is heavily endowed with polymorphic vacuoles of considerable size (0.5-1.2 μm in diameter) and weak osmiophyly (Figures 2, 4C, 5, 7D-E). In light adapted interocellar sheath cells these hyaline vacuoles are widely absent (Figures 6B, 7C).

External pigment cells
Numerous external pigment cells surround the entire ocellar field and extend from the posterior border of the antenna to the middle of the lateral cephalic fold. In all examined species the lobes of the external pigment cells are thin and utricular. They are arranged into a plexus of one or two contiguous rows subjacent to the basal matrix of the lateral ocelli and the neighbouring epidermis. External pigment cells also cover the optical nerve branching off the ocellar field's basis in its distal part. The innermost layer contributes to and usually adjoins the basal matrix (Figures 2, 4A-B, 5, 7A). Each pigment cell measures about 1-4 μm in thickness and contains a highly osmiophilic cytoplasm including a polymorphic but mostly elongated nucleus, only a few mitochondria of the cristae type, elliptical and granular pigment granules of moderate osmiophyly (0.2-0.4 μm in diameter) and unorderly distributed cisternae of rough ER (Figure 7A). Predominating organelles are, however, large polymorphic pigment granules (0.4-0.8 μm in diameter) whose inner matrix
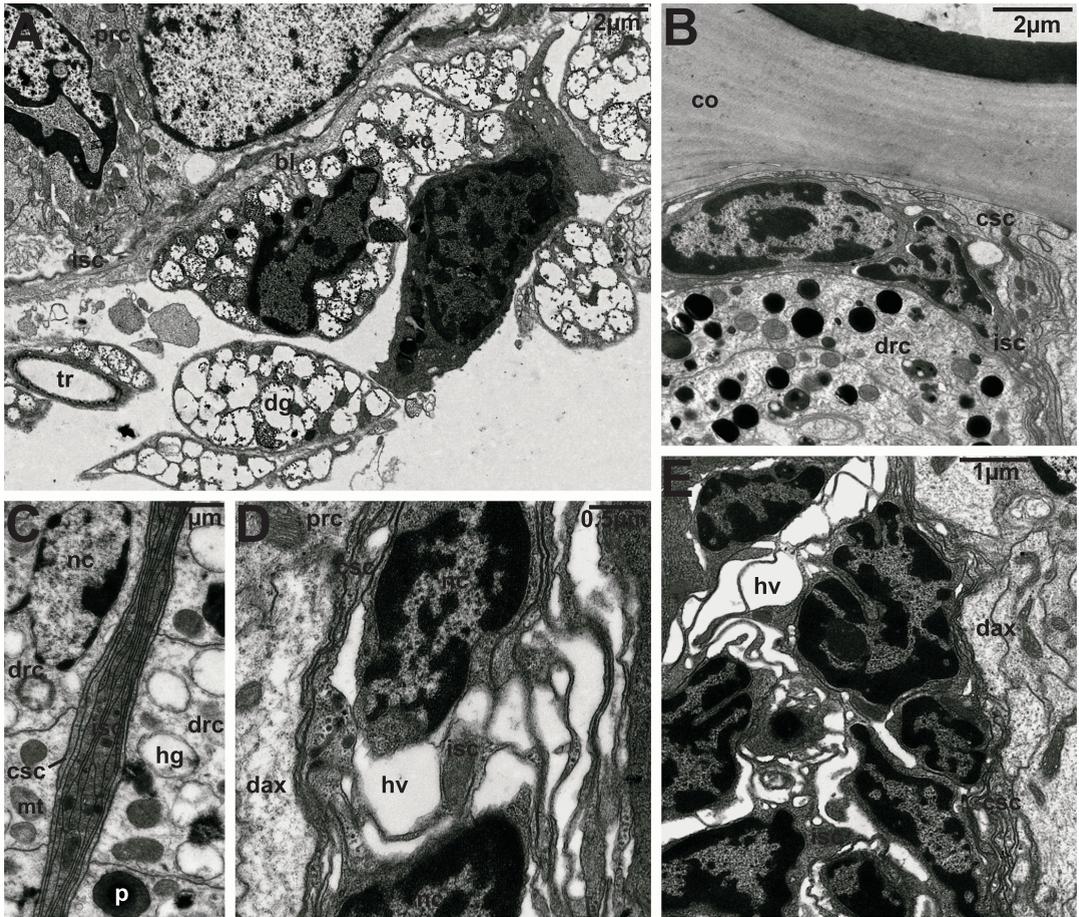
Figure 7 A-E. Fine structure of accessory pigment and sheath cells in the lateral ocelli of various *Lithobius* species. TEM. **A.** Longitudinal section through basal part of a lateral ocellus underlined by a thin basal matrix (*bl*) and thick sheath of external pigment cells (*exc*). **B.** Distalmost interocellar region with two soma of interocellar sheath cells (*isc*) and one circumretinular sheath cell process (*csc*) attaching to the periphery of the corneal lens (*co*). Longitudinal section. **C.** Crosscut multilayer of various sheath cell processes in mediodistal part of two neighbouring eyes. **D.** Detailed longitudinal view of different cytoplasmic compositions in both sheath cell types. **E.** Proximal aggregation of several interocellar sheath cell bodies containing massively broadened hyaline vacuoles (*hv*). Longitudinal section.

dax distal retinula axon, *dg* pigment granule (with desintegrated matrix), *drc* distal retinula cell, *exc* external pigment cell, *hg* hyaline pigment granule, *mt* mitochondrium, *nc* nucleus, *p* osmiophilic retinular pigment granule, *prc* proximal retinula cell, *tr* trachea.

appears to be disrupted or agglutinated, showing a central globule and radiating spokes of similar material (Figures 4A-B, 7A).

DISCUSSION

The lateral ocelli of the Lithobiomorpha: new vs. literature data

The fine structure of the lateral ocelli of various Lithobiomorpha (except Henicopidae) is presented with a special focus on comparative morphology. We investigated the lateral ocelli of altogether four representatives of the Lithobiidae: *Eupolybothrus fasciatus, Lithobius forficatus, L. dentatus* and *L. mutabilis*. The data presented here on the ocellar fine structure of *E. fasciatus* and various *Lithobius* species led to refinements or new interpretations of the lithobiomorph eye. Our re-examination also enables us to correct earlier morphological descriptions by Bedini (1968), Joly (1969) and Bähr (1971, 1972, 1974) with regard to details essential for phylogenetic considerations.

Ocellar diameter

The morphometric range of ocellar diameters in *E. fasciatus* according to Bedini (1968) (400-800 μm) is about four times greater than measured in our study. The maximal body length of *E. fasciatus* of about 45 mm (Brolemann 1930) does not differ considerably from our specimens. We therefore do not believe that the lateral ocelli of *E. fasciatus* reach the dimensions given by Bedini (1968). Even the lateral ocelli of the larger *Scolopendra cingulata* Latreille, 1789 barely exceed diameters of 300 μm (Müller & Meyer-Rochow 2006a).

Cornea and corneagenous epithelium

In *E. fasciatus* and the three *Lithobius* species the corneal surface displays a polygonal sculpturation which has not been described by previous authors (Bedini 1968, Joly 1969, Bähr 1971, 1974). Bähr (1971, 1974) found the somata of the cornea-secreting epithelial cells to be displaced only to the distolateral regions of the corneal lens in *L. forficatus*. However, this discontinuous arrangement could not be confirmed by our study as, in accordance with Hesse (1901), corneagenous

somata are regularly observed along the entire internal surface of the corneal lens. On the other hand, Bedini's (1968) illustration (see Figure 12, p. 41) of the corneagenous layer in *E. fasciatus* appears too idealized to reflect the real proportions of the cornea-secreting epithelial cells, which are spread out underneath the corneal lens.

Dual type retinula

The suspicion that a dual type retinula may also be present in *E. fasciatus* (Müller & Meyer-Rochow 2006a) has now become a fact. Bedini (1968) already illustrated the proximal retinula cells with their interdigitating bidirectional rhabdomeres (see Figures 2, 12, pp. 33, 41) but did not identify them correctly. In the lateral ocelli of *L. forficatus*, Bähr (1971) discovered only single- or bi-layered distal retinulae. However, in his following paper, Bähr (1974) presented a semischematic reconstruction of a *L. forficatus*-ocellus (Figure 1, p. 385) only equipped with one single layer of distal retinula cells (= "distal receptors or hair cells"). It has become now clear that in *Lithobius* species the distal retinula is normally multi-layered. The occurrence of several horizontal rings of distal retinula cells ("Haarzellen" after Grenacher (1880) in *L. forficatus*) has already been recorded and illustrated by Hesse (1901, see Figure 4 in Table 10), arranged in up to three layers of unequal size. The currently cited diagram of Hesse (1901) has been replaced by the scheme of Bähr (1974) by many review and textbook authors (Paulus 1979, 2000, Lewis 1981, Minelli 1993, Ax 1999). Perhaps Bähr's (1971, 1974) erroneous assumption of a single-layered distal retinula in *L. forficatus* resulted from studies focusing more on the anterior region of the ocellar field, where single- or bi-layered retinulae are occasionally realized in the smallest ocelli. This focus on a particular eye region might also explain why Bähr (1971, 1974) failed to mention the strongly elliptical or U-shaped diameter of the distal retinulae in the more posteriorly located ocelli.

Sheath cells

The characterisation and differentiation of the circumretinular and interocellar sheath cells which surround the retinulae of *E. fasciatus* and
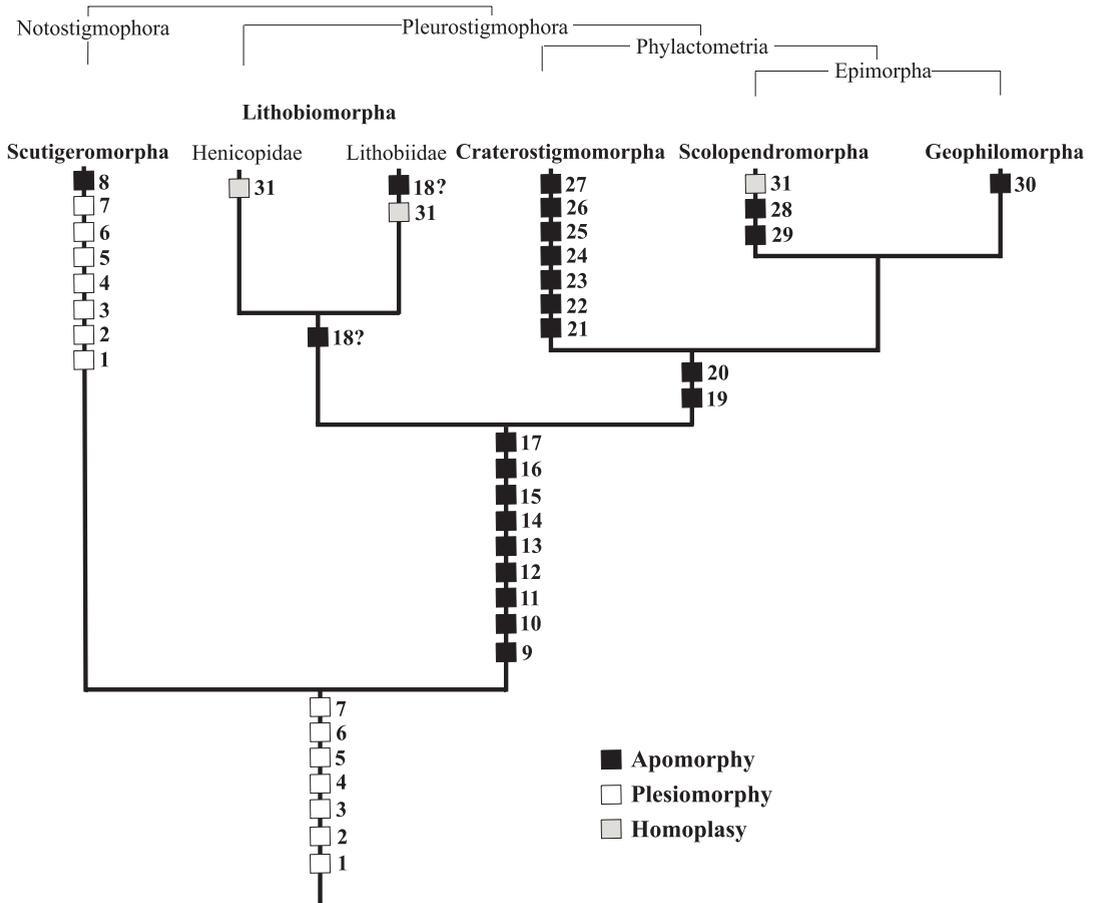
Figure 8. Eye characters mapped onto a tree depicting the Pleurostigmophora concept after Pocock (1902), Dohle (1985), Edgecombe & Giribet (2004) and Giribet & Edgecombe (2006). Details of all listed characters are given in the text. The assessment of eye characters has been modified from the phylogenetic evaluations of Edgecombe & Giribet (2004) and Müller & Meyer-Rochow (2006b). In the aim to reconstruct possible pathways of eye evolution in the Chilopoda, proposed retinal plesiomorphies, with respect to the Mandibulata, have been added to the ground pattern of the Chilopoda and Scutigeromorpha (= Notostigmophora).

the *Lithobius* species has never been done before. Indeed, previous studies have brought forward the existence of sheath cells in lithobiomorph eyes, like the "satellite cells" in *E. fasciatus* (Bedini 1968) as well as the "covering cells" (Bähr 1971, 1974), "cellules périphériques" (Joly 1969) or "cellules bordantes" (Joly & Herbaut 1968) in *L. forficatus*. In our opinion, all these terms should be regarded as synonyms for the circumretinular sheath cells because previous authors did not report on the extensive system of hyaline and polymorphic vacuoles which are typical for the interocellar sheath cells. In agreement with Land (1972), we propose that these hyaline vacuoles in dark adapted ocelli underline the tapetal function of the interocellar sheath cell multilayer. However, the occurrence of pigment or tapetal cells in *E. fasciatus* was denied by Bedini (1968).

Basal matrix
Joly (1969) and Bähr (1971, 1974) made no explicit comments on a basal matrix in *L.*

forficatus. The semischematic reconstruction (Figure 2, p. 33) of Bedini (1968) let us assume that each lateral ocellus in *E. fasciatus* is completely enveloped by a basal matrix. However, with the present study it could be demonstrated that in *E. fasciatus* and *Lithobius* species the basal matrix deliminates the whole ocellar field but not a single ocellus.

External pigment cells

The plexus of external pigment cells around the ocellar field of *E. fasciatus* and *L. forficatus* has not been noticed by Bedini (1968), Joly (1969) and Bähr (1971, 1974). The obvious difficulties previous authors had to trace these cells might be attributed to fixation artefacts as it is well known that accessory pigment cells in arthropod eyes are often badly affected by potential loss of osmotic pressure during the fixation and dehydration procedure (e.g. Gottlieb 1974). The external pigment cells were already seen by Grenacher (1880) but misinterpreted as a sort of basal matrix ("cuticulares Septum, durchbohrt von Opticusfaserbündeln", p. 442).

Interommatidial glands

Interommatidial glands, hitherto only described in *L. forficatus* (Müller et al. 2003a), were now also found in *E. fasciatus*, *L. dentatus* and *L. mutabilis*. These organs were already detected by Grenacher (1880) ("Pigmentzellen") and Joly & Herbaut (1968, see Figure 1, p. 595), but were not seen by Bedini (1968) and Bähr (1971, 1974).

In summary, our fine structural investigations revealed that the lateral ocellus of a lithobiid centipede possesses an unicorneal lens, built by a single-layered corneagenous epithelium, and a dual type retina, consisting of a multi-layered distal portion with horizontally arranged cells (circumapical rhabdomeres: *E. fasciatus*, simple apical rhabdomeres: *Lithobius* spp.) and a singlelayered proximal portion of obliquely or vertically arranged cells forming bidirectional and interdigitating rhabdomeres. The lateral ocelli are surrounded by a multilayered system of circumretinular and interocellar sheath cells. The entire ocellar field is covered by a thin

basal matrix and a subjacent network of external pigment cells.

Homology of the lateral eyes in Chilopoda

Based on the presence of a dioptric system, Müller et al. (2003b) defined two main classes of lateral eyes in Chilopoda: (a) plesiomorphic compound eyes with ommatidia, possessing a crystalline cone formed by four cone cells (Scutigeromorpha = Notostigmophora) (Müller et al. 2003b) and (b) derived lateral ocelli without a crystalline cone, but with an unicorneal lens (Lithobiomorpha: Bedini (1968), Joly (1969), Bähr (1971, 1974), this study; Scolopendromorpha: Paulus (1979), Müller & Meyer-Rochow (2006a); Craterostigmomorpha: Müller & Meyer-Rochow (2006b)). With the newly obtained fine structural data on lithobiid eyes the definition given above can now be substantially improved.

Except for the dual type retinula, the ommatidia of the Notostigmophora and the lateral ocelli of the Pleurostigmophora have almost nothing in common. However, even the value of this character for confirming a potential homology of these eye types is considerably reduced by differing modes of rhabdomeric interactions between proximal retinula cells (Müller et al. 2003a, Müller & Meyer-Rochow 2006a,b, this study). In contrast, our results show that the lateral ocelli of the Lithobiomorpha and Scolopendromorpha share many homologous structures. Such structures are the unicorneal lens which is more or less sunk into the eye cup, the singlelayered and pigmentless corneagenous epithelium, circumretinular sheath cells, and external pigment cells. The dual type retinulae consist of a multilayered system of horizontally oriented distal retinula cells and a single layer of proximal retinula cells at the basis of each eye cup. The specific quality of homologous fine structures seems to be particularly evident if one compares the lateral ocelli of *E. fasciatus* and *S. cingulata* (Müller & Meyer-Rochow 2006a). In both species the distal retinula cells produce axial processes with circumapical rhabdomeres. The distal retinula cells of *Lithobius* with its simple apical rhabdomeres are reduced in complexity and

thereby, despite its multi-layered appearance, more closely resemble the distal retinula arrangement seen in *Scutigera coleoptrata* Linnaeus, 1758 (Müller et al. 2003b). A "bi-layered retinula" with distal and proximal retinula cells being arranged in each one single horizontal layer (Müller et al. 2003b), is only regularly found in scutigeromorph ommatidia. Similar to *S. coleoptrata*, the strict parallel and unidirectional course of microvilli within the distal retinula rhabdomeres enables *Lithobius* to perceive lineary polarised light (see chapters 16.7.2.-5. in Horváth & Varjú 2004). This specific quality of vision is unique among all other scototactical Pleurostigmophora whose eye structures have been analysed so far. A high polarisation sensitivity would imply that vision in general and the orientation in the illuminated field in particular plays an important role in the life of a *Lithobius* (cf. Hosey et al. 1985). In addition, the ocellar clusters of lithobiid centipedes may functionally work as compound eyes. The enhanced visual capability of lithobiid eyes might have evolved in adaptation to diurnal activity and to the necessity of seasonal or weather-induced movements between variously illuminated microhabitats (e.g. Monteith 1976).

Interocellar sheath cells and "interommatidial glands" (Müller et al. 2003a) are not associated with the lateral ocelli of *Scolopendra* (Müller & Meyer-Rochow 2006a) and *Craterostigmus tasmanianus* Pocock, 1902 (Müller & Meyer-Rochow 2006b).

Possible evolution of retinal characters and their importance for chilopod phylogeny

The present data on the ultrastructure of the lateral ocelli of *E. fasciatus* and *Lithobius* spp. (Lithobiomorpha) as well as recently documented data of the lateral eyes of other eye-bearing chilopod representatives (Scutigeromorpha, Craterostigmomorpha, Scolopendromorpha) now enable us to use retinal characters for a phylogenetic reconstruction of the Chilopoda (Müller et al. 2003a,b, Harzsch et al. 2005, Müller & Meyer-Rochow 2006a,b). The given set of eye characters seems to be most compatible with the

'Pleurostigmophora-concept' of Pocock (1902), which has found general acceptance by authors using morphological (Dohle 1985, Borucki 1996, Wirkner & Pass 2002), molecular genetic (Giribet et al. 1999) and combined cladistic approaches (Edgecombe & Giribet 2002, 2004, Giribet & Edgecombe 2006). By developing further the phylogenetic views of Müller et al. (2003b), Müller & Meyer-Rochow (2006b) and Harzsch et al. (2006) (see cladogram in Figure 8), we propose that the stem species of the Chilopoda and, subsequently, also the last common ancestor of the Scutigeromorpha (Notostigmophora) has retained compound eyes with ommatidia containing (1) several dozens of contributing cells, (2) some cell types with fixed numbers, (3) dual type retinulae primarily arranged in two distinct layers, (4) crystalline cones of four cone cells producing four infraretinular proximal processes, (5) pigmented corneagenous cells ("primary pigment cells"), (6) interommatidial pigment cells and (7) interommatidial organs (glands) from the ground pattern of the Mandibulata (numbers refer to character ordering given in Figure 8). The (8) presence of distal cytoplasmic cone cell processes each branching into two secondary processes and being responsible for the formation of two cone compartments (see Müller et al. 2003b) may be considered an apomorphy of the Scutigeromorpha.

A lateral ocellus of the last common ancestor of the Pleurostigmophora was most likely (9) cup-like and (10) had no crystalline cone. As other apomorphies are known: (11) a flat and pigmentless corneagenous epithelium, (12) a multi-layered distal retinula with cells forming compact, primarily circumapical rhabdomeres, (13) a single-layered proximal retinula with cells forming bi-directional and interdigitating rhabdomeres (star- or net-like rhabdom), (14) unpigmented circumretinular sheath cells, and (15) a thin and homogeneous basal matrix. Furthermore, (16) the presence of a subretinal plexus of external pigment cells, and (17) of a sculptured corneal surface ("scutes"), formerly believed to define the Phylactometria (Müller & Meyer-Rochow 2006b), have now to be reassessed

additional apomorphies of the Pleurostigmophora. Since all representatives of the non-lithobiid Lithobiomorpha, the Henicopidae, lack ocellar clusters (Edgecombe et al. 2002), it is still impossible to decide whether the (18) possession of interocellar sheath cells may be regarded as an apomorphic character of the Lithobiomorpha or of the Lithobiidae alone. By following the principle of parsimony it seems however reasonable to assume that this cell type has evolved in the stem lineage of the Lithobiidae. Generally, there are functional morphological and phylogenetic arguments (Edgecombe & Giribet 2004, Figure 14) to maintain that in the Lithobiidae the lateral ocelli of the *Lithobius*-type represent the derived condition. However, both hypotheses remain preliminary as long as substantial data on ocellar fine structure of representatives of the assumed sister group Henicopidae (Edgecombe & Giribet 2004) are not included.

With respect to eye structures, the more derived Phylactometria, which include the Craterostigmomorpha and Epimorpha (Scolopendromorpha + Geophilomorpha) as sister groups (Edgecombe & Giribet 2004) shall now be defined by (19) the presence of large lateral ocelli with extraordinarily high cell numbers (retinula: > 1000 cells) and (20) proximal retinula cells partly with monodirectional rhabdomeres (Müller & Meyer-Rochow 2006a,b).

The Craterostigmomorpha bear strongly derived eyes with many structures not to be found in other Chilopoda (Müller & Meyer-Rochow 2006b). Therefore, (21) a bipartite eye cup, (22) intraocellar epidermal glands, (23) inverse photoreceptor cells, (24) distal retinula cells with bilobed apices (forming an irregular, vertically partioned and arborized rhabdom), (25) proximal retinula cells being separated into dual cell units, (26) retinular axon bundles running through the center of the optic cup, and (27) peripheral, wedge-shaped aggregations of sheath cell somata should have already been present in the stem species of the Craterostigmomorpha.

The Scolopendromorpha show the following retinal apomorphic features: (28) differentiation of the corneagenous epithelium into extremely flattened proximal cells and more cubical distal cells producing specific attachment structures to the cornea as well as (29) an enormously developed and ramified basal matrix.

The (30) complete absence of eyes is interpreted as an apomorphy of the Geophilomorpha, whereas (31) the partial lack of eyes in some remaining chilopod groups (on the subordinal, generic or species level), as reported from some cavernicolous Lithobiidae (Lithobiomorpha), few Henicopidae and all Cryptopidae (Scolopendromorpha) (Lewis 1981, Edgecombe et al. 2002, Edgecombe & Giribet 2004), may be understood as a derived, homoplasic character.

Alternative views on the phylogenetic inter-relationships among centipedes exist indeed, but seem to be implausible with respect to eye structures as in too many cases the convergent development of retinal characters would have to be accepted. However, this would in a variety of ways contradict the principle of parsimony. The 'Anamorpha-concept' (Haase 1881), which presumes the Scutigeromorpha and Lithobiomorpha to be sister taxa, implies an independent evolution of either scutigeromorph ommatidia or lateral ocelli of the pleurostigmophoran type in the stem lineage of the Anamorpha. But it becomes clear that the lateral ocelli of the lithobiid *E. fasciatus* and of the scolopendrid *Scolopendra. cingulata* (Müller & Meyer-Rochow 2006a) share many homologous features, which appear too complex to be considered merely the result of convergence. The acceptance of the 'Heteroterga-concept' (Ax 1999) requires that ommatidia, homologous to those of insects and crustaceans, must have been re-invented in the then mostly derived taxon, the Scutigeromorpha.

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Eye development in Myriapoda: implications for arthropod phylogeny

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Harzsch, S., Melzer, R. R. & Müller, C. H. G. 2006. Eye development in Myriapoda: implications for arthropod phylogeny. Norw. J. Entomol. 53, 187-190.

In order to gain new insights into eye formation in Myriapoda we examined the arrangement of proliferating cells in the developing eyes by *in vivo* labelling with the mitosis marker bromodeoxyuridine (BrdU) in three representatives of the Myriapoda, the diplopod *Archispirostreptus gigas* (Peters, 1855) and the two chilopods *Scolopendra oraniensis* Lucas, 1846 and *Scutigera coleoptrata* (Linnaeus, 1758). Our results confirm earlier reports that had indicated that during eye growth in many Myriapoda new elements are added to the side of the eye field and elongate the rows of earlier generated optical units. This pattern of a "row-by-row" growth is clearly different from the "morphogenetic furrow" type of eye development in Hexapoda and Crustacea but closely resembles that in Xiphosura and Trilobita. We suggest that the trilobite, xiphosuran, and myriapod mechanism of eye growth represents the ancestral arthropod mode of visual system formation and hence, that the eyes of Myriapoda may not be secondarily reconstructed insect eyes.

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INTRODUCTION

In the discussion on the phylogenetic relationships of Arthropoda, structure and development of the lateral eyes have always played pivotal roles (e.g. Melzer et al. 1997, Müller et al. 2003, Harzsch 2006; see also contribution by Müller in this volume). The lateral eyes of Crustacea and Insecta consist of many single optical units, the ommatidia that are composed of a small, strictly determined and evolutionarily conserved set of cells. Contrary, the eyes of Myriapoda are fields of optical units, the lateral ocelli which are composed of up to several hundreds of cells. For many years these striking differences between the lateral eyes of Crustacea/Insecta *versus* Myriapoda

have puzzled evolutionary biologists (discussed in Müller et al. 2003, Harzsch et al. 2005) since the Myriapoda are traditionally considered to be closely related to the Insecta. The prevailing hypothesis to explain this paradox has been that the myriapod fields of lateral ocelli derive from insect compound eyes by disintegration of the latter into single ommatidia and subsequent fusion of several ommatidia to form multicellular ocelli. Harzsch et al. (2005) recently challenged this hypothesis and instead suggested an evolutionary scenario that followed the opposite direction. They proposed the multicellular eye subunits of Chelicerata/Xiphosura with their high and variable cell number to be plesiomorphic for the Euarthropoda. Some taxa of Progoneata and
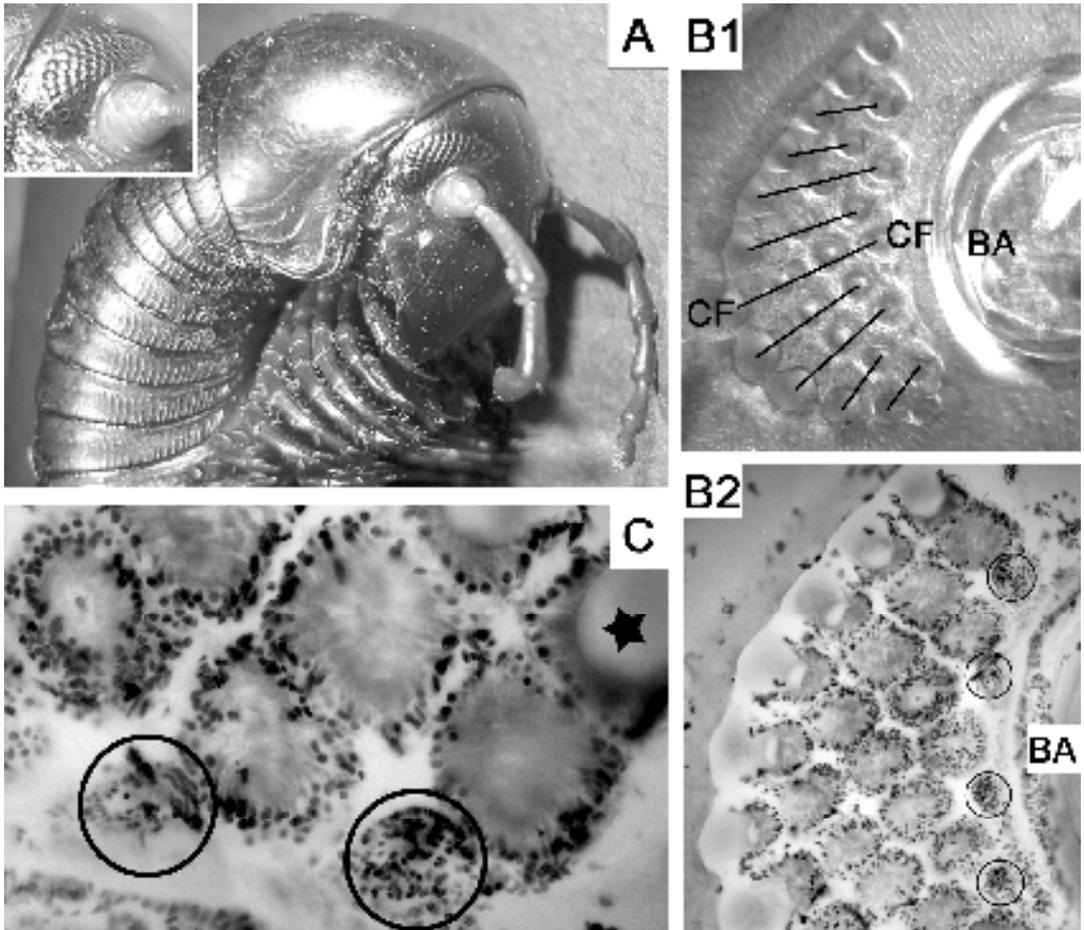
Figure 1 A: An adult specimen of the diplopod *Archispirostreptus gigas* (Peters, 1855). **B1, 2:** An eye field of a juvenile *A. gigas* with 35 ocellar ommatidia labelled with the proliferation marker bromodeoxyuridine (for orientation of the images compare with the adult specimen in **A;** B1 - Normarski interference contrast; B2 - bright field illumination). Abbreviation: BA - base of the antenna. **C:** Higher magnification from B. Circles identify the protoommatidia which are being added to the side of the eye field. Asterisks identify an ommatidium at the side of the eye field which is slightly tilted thus provides a side view.

Chilopoda (genera *Scutigera, Polyxenus*) have reduced the number of cells of which each eye subunit is composed and some cell types occur in constant numbers. In the new model of Harzsch et al. (2005) they represent an intermediate on the pathway towards the Tetraconata in which the eye subunits have a fixed architecture with a relatively low, constant cell number.

RESULTS AND DISCUSSION

Despite an extensive body of literature on eye structure, the mechanisms of eyes growth have not yet been explored systematically across the Euarthropoda. Concerning eye formation in Myriapoda, one would expect that some residual evidence of the evolutionary pathway suggested by the prevailing hypothesis on eye evolution in this

group should be betrayed by the developmental program by which the generation of the eyes in recent Myriapoda is governed. However, such evidence is lacking so far.

Therefore, we analysed the formation of new visual units and their integration into the eyes in four representatives of the Myriapoda and compared these mechanisms with those in other Arthropoda representing different types of eye architecture in order to gain new insights into the evolutionary relationship of myriapod eyes with respect to the competing scenarios (Harzsch et al., 2006a).

Specifically, we mapped the pattern in which new visual units are added to the existing eye field in the diplopod *Cylindroiulus truncorum* (Silvestri, 1896). Furthermore, the arrangement of proliferating cells in the developing eyes was monitored by *in vivo* labelling with the mitosis marker bromodeoxyuridine (BrdU) in the diplopod *Archispirostreptus gigas* (Peters, 1855) and the two chilopods *Scolopendra oraniensis* Lucas, 1846 and *Scutigera coleoptrata* (Linnaeus, 1758). As an example for our studies, Figure 1B shows an eye field of a juvenile *A. gigas* with 35 ocellar ommatidia labelled with the proliferation marker bromodeoxyuridine (BrdU; for orientation of images compare with the adult specimen in **A**). In B1 the specimen is viewed with Normarski interference contrast to show the surface of the eye field. The black lines connect the ocellar ommatidia of one file. The central file (CF) with four mature units is on both sides is flanked by a file composed of three mature ocellar ommatidia plus a protoommatidium (see circles in B2). B2 shows the same specimens as in B1 viewed with bright field illumination to show the BrdU labelled nuclei. Circles identify protoommatidia which appear as clusters of numerous black labelled nuclei. A new row of protommatidia is added to the eye field from the side where the base of the antenna (BA) adjoins the eye. Furthermore, all existing units within the eye field are surrounded by a distinct rim of mitotic cells. Figure 1C is a higher magnification from B. Circles identify the protoommatidia which are being added to the side

of the eye field. The protoommatidia at this stage are clusters of mitotic nuclei all of which appear to be of a uniform size. Note the mitotic cells which surround the base of existing ocellar ommatidia and are located within the layer of retinula cells. Asterisks in Figure 1C identify an ommatidium at the side of the eye field which is slightly tilted thus provides a side view.

Our results confirm that, in accordance with previous reports on Diplopoda (Enghoff et al. 1993), during eye growth in many Myriapoda new elements are added to the side of the eye field and elongate the rows of earlier generated optical units. This pattern closely resembles that in horseshoe crabs (Xiphosura, Chelicerata; Harzsch et al. 2006b) and Trilobita. We conclude that the trilobite, xiphosuran, diplopod and chilopod mechanism of eye growth represents the ancestral arthropod mode of visual system formation which raises the possibility that the eyes of Diplopoda and Chilopoda may not be secondarily reconstructed insect eyes.

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Effects on a community of centipedes (Chilopoda) of cadmium accidentally released

Andrés García Ruiz

This is the first study on the possible effects on centipedes of the accidentally released cadmium in the area of Monte de las Nieves (Madrid province). The heavy metal seems to produce modifications in the communities of centipedes, and it has also caused structural abnormalities, for example abnormalities in the last pair of legs, abnormal forcipular coxosternite, abnormal eye structure and abnormally sized antenna.

Key words: Pollution, cadmium, centipedes, Chilopoda, abnormalities

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INTRODUCTION

Among the large quantities of centipedes studied during the recent years we have found several specimens with malformed structures. Minelli & Pasqual (1986) described eight structurally abnormal centipedes and listed the previously recorded cases. They distinguished the three most frequent, principal types of abnormality: spiral segmentation, homeotic mutations and schistomely (bifurcation).

Lewis (1987) discussed the problem of determining whether an anomaly is due to errors in development or to effects due to regeneration after damage. Numerous cases of abnormal structures of centipedes of the Iberian Peninsula have also been described (García Ruiz 1994, 1995, 1997).

The present study describes the effects of cadmium, on the centipede fauna in the area Monte de las Nieves. The accident took place in February 1995. Monte de las Nieves, is located in the county of Madrid, between the towns of Torrelodones and Hole of Orchards. It covers a total area of nine square kilometres. The specimens were captured in the polluted area in 1996 and 1997.

DESCRIPTION OF THE STUDIED CASES

Abnormal size of left antennae in *Pseudohimantarium* mediterraneum Meinert, 1870

A female *Pseudohimantarium mediterraneum* captured by hand 12 October 1996 shows antennas of different dimensions (Figure 1) The two antennae both have the complete number of articles, but the left is shorter than the right. This is caused by each antennal article being shorter than the equivalent on the normal antenna. This is probably a developmental abnormality.

García Ruiz (1995, 1997) reported similar cases in individuals of *Scolopendra cingulata* and *Cryptops hispanus*.
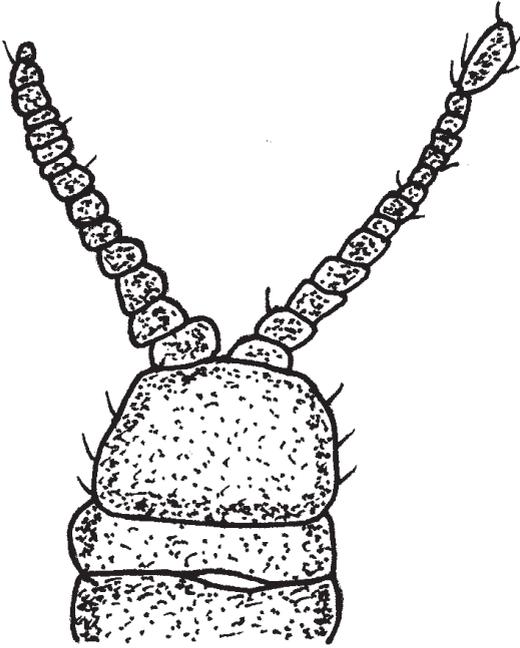
Figure 1. Dorsal view of head and antennae of a *Pseudohimantarium mediterraneum*
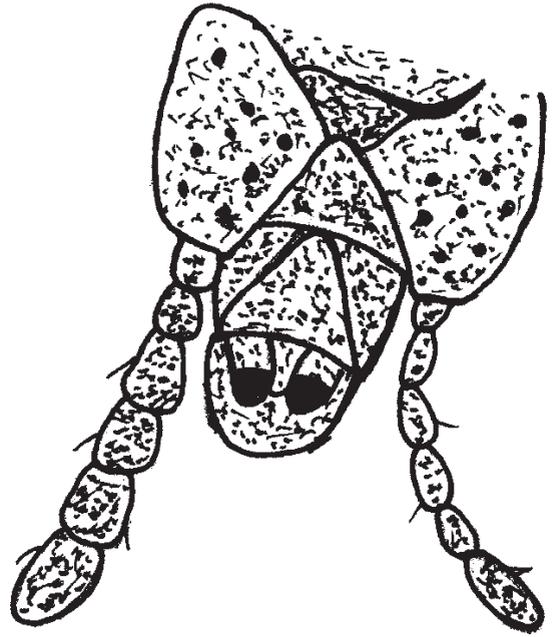
Figure 2. Ventral view of last pair of legs of a *Pseudohimantarium mediterraneum*
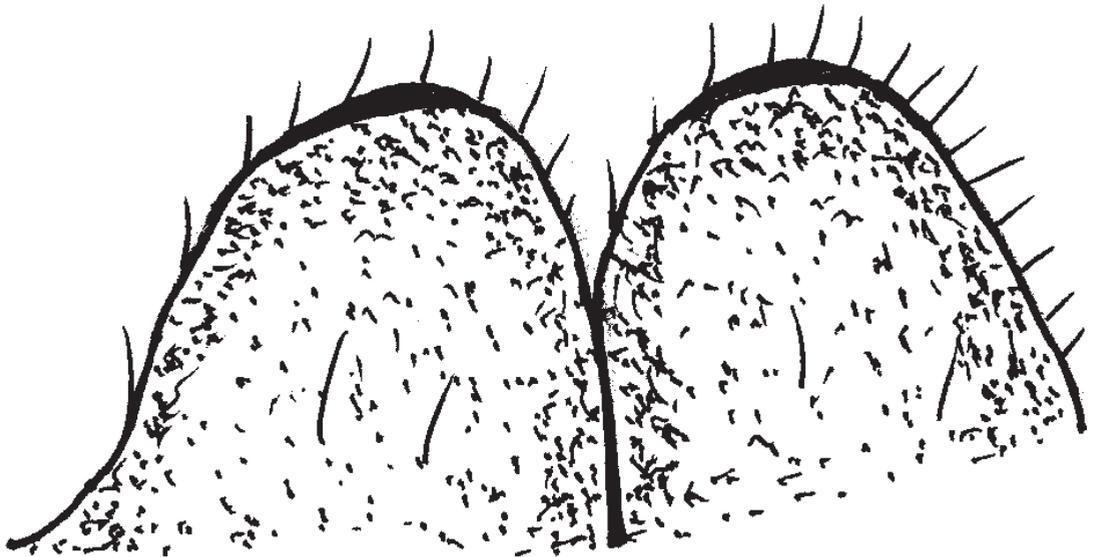
Figure 3. Forcipular coxosternite of a *Lithobius calcaratus*
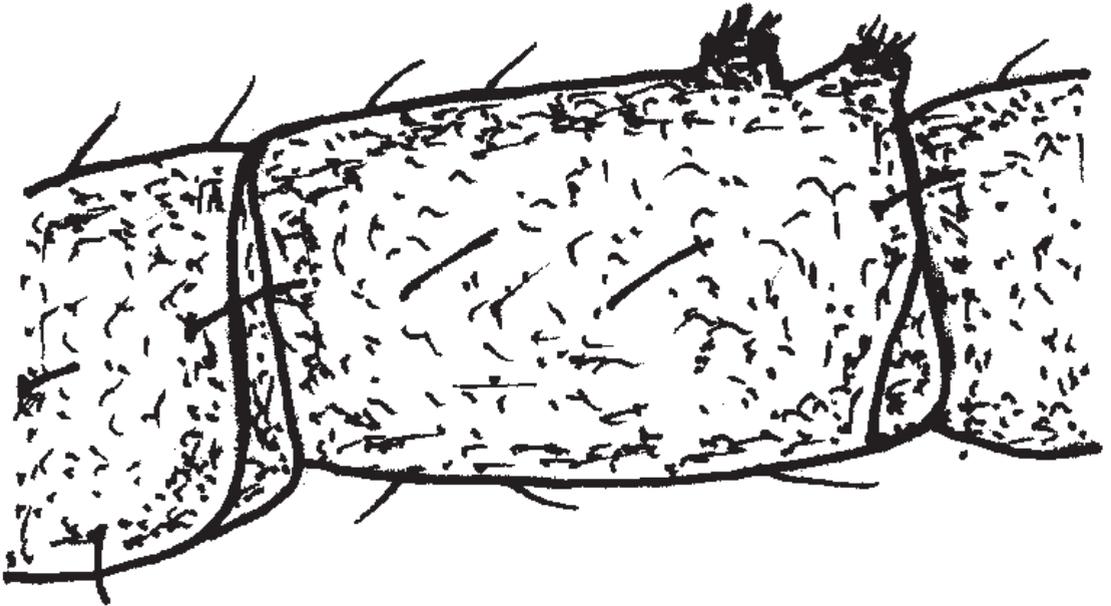
Figure 4. Lateral view exterior of left leg of a *Lithobius calcaratus*

Abnormalities in the last pair of legs in *Pseudohimantarium mediterraneum* Meinert, 1870

Two females of *Pseudohimantarium mediter-raneum* captured by hand 7 March 1997 have their last pair of legs of different sizes (Figure 2). The two legs have the complete number of telopodites, but the left leg has smaller tarsus and pretarsus and the leg seems much slimmer.

Abnormal forcipular coxosternite in *Lithobius calcaratus* C. Koch, 1844

Two males of *Lithobius calcaratus* captured by hand 4 October 1996 and 7 March 1997 respectively have the anterior border of the forcipular coxosternites almost straight, without any teeth (Figure 3). Normally there are two on each coxosternite.

Abnormal wart-like process on the femur of the last pair legs in *Lithobius calcaratus* C. Koch, 1844

Two males of *Lithobius calcaratus*, captured by hand 21 April 1996 and 7 March 1997 respectively, have on the femur of the last left leg two wart-like processes in stead of the characteristic one (Figure 4).

Abnormal ocelli in *Lithobius variegatus* rubriceps Newport, 1845

A female of *Lithobius variegatus rubriceps* captured by hand 4 October1996 has on the left side of the head only one small ocellus, instead of the characteristic number for this species that varies between 13 and 21. Normally the ocelli are arranged in 4 to 5 more or less regular lines, with a bigger one placed separately (Figure 6).

Abnormal forcipular coxosternite in *Lithobius variegatus rubriceps* Newport, 1845

Two male *Lithobius variegatus rubriceps*, captured by hand in March 1997, have the anterior border of the left forcipular coxosternite almost straight, without teeth (Figure 5).

DISCUSSION

We think that the six cases of abnormal structures described here are due to abnormal development rather than regeneration, because there is no sign of damage on any of the six specimens.
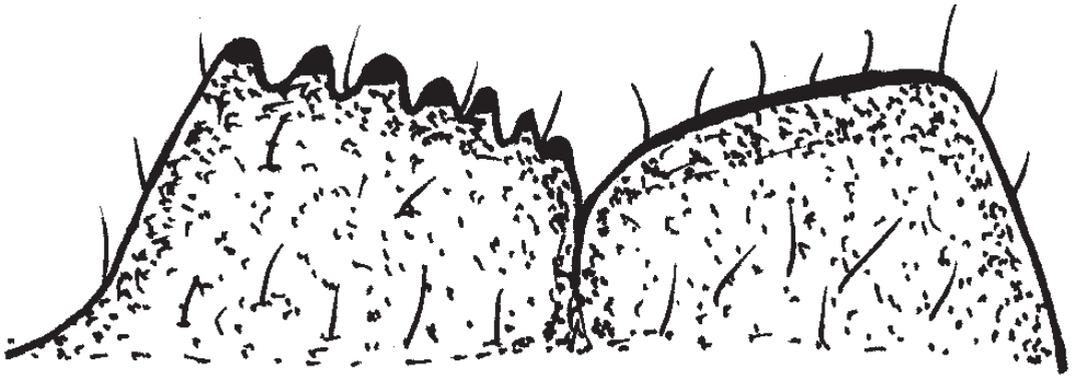
Figure 5. Forcipular coxosternite of a *Lithobius variegatus rubriceps*
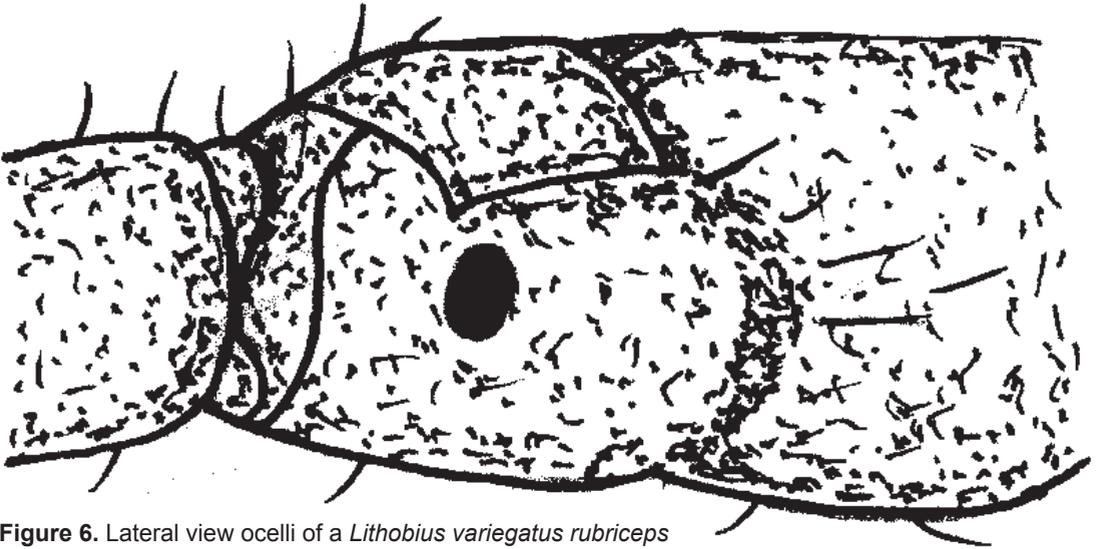
Figure 6. Lateral view ocelli of a *Lithobius variegatus rubriceps*

This is the first case for chilopods, where the appearance of structural abnormality may be related to pollution by a heavy metal (Cadmium). We consider it necessary to carry out more studies on this topic.

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Haemocytes in Diplopoda and Chilopoda (Arthropoda, Myriapoda): Types, structures and numbers

Willi E. R. Xylander & Lutz Nevermann

Xylander, W. E. R. & Nevermann, L. 2006. Haemocytes in Diplopoda and Chilopoda (Arthropoda. Myriapoda): Types, structures and numbers. Norw. J. Entomol. 53, 195-209.

A review of the different types of haemocytes in Diplopoda and Chilopoda is given with special reference to their ultrastructure and spreading behaviour. Thus, five types of haemocytes can be distinguished within these taxa: prehaemocytes, plasmatocytes, granular haemocytes, spherulocytes and discoid haemocytes; of these the three types mentioned first occur in all groups whereas the others were found in one group each. Furthermore, coagulocytes where described which may be plasmatocytes. The number of haemocytes per volume (total haemocyte count) is significantly lower in Diplopoda than in Chilopoda. Comparing the quantity of different haemocyte types (differential haemocyte count) granular haemocytes comprise more than half of the haemocytes, plasmatocytes between 27 % and 39 %. The results are discussed with reference to the characteristics of other arthropod groups.

Key words: Haemocytes, Myriapoda, Arthropoda, ultrastructure, immune defense, total haemocyte count, differential haemocyte count.

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INTRODUCTION

Haemocytes belong to the most important cell types for immune response in arthropods and seem to represent the most original elements of self recognition and defence (Gupta 1986, Millar & Ratcliffe 1989, Xylander 1994). In arthropods they may phagocytise smaller xenografts and encapsulate larger ones. They produce and store phenoloxidase in its inactive form, the prophenoloxidase (Xylander & Bogusch 1992, 1997, Xylander & Nevermann 1993), as well as antibacterial substances (Xylander et al. 1997), lectins and hemolysins (Xylander 1992b). Furthermore, they are involved in haemolymph clotting and wound closure after injury (e. g. Hilken et al. 2003b, Xylander 1994).

The haematogram, the contribution of the different haemocyte types to the total haemocyte count, differs according to the taxon investigated. Also the methods of obtaining the haemolymph, in vitro-preparation (e.g. Xylander et al. 2003), fixation as well as staining techniques applied have influence on the reactions and thus on the characteristics of haemocytes. So in the last 100 years nomenclature of haemocytes had developed into a confusing set of more than 50 termini for – at least partly – homologous cell types. These were reconsidered by Jones (1962) and Ratcliffe & Price (1974) resulting in a practical new nomenclature for (more or less) all arthropod taxa.

Investigation on haemocytes of myriapods started with the same dilemma: The first systematic investigations by Gregoire (1955), Gupta (1968),
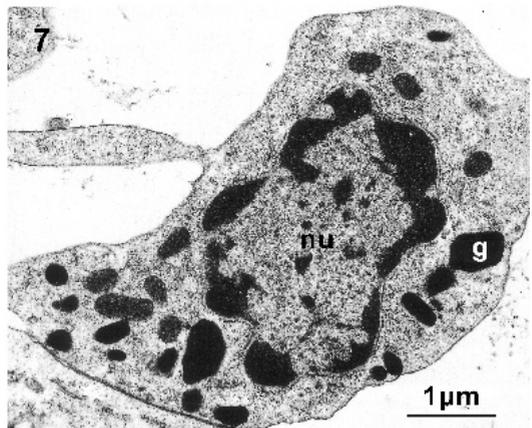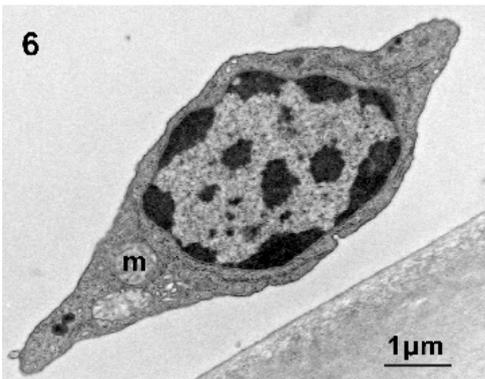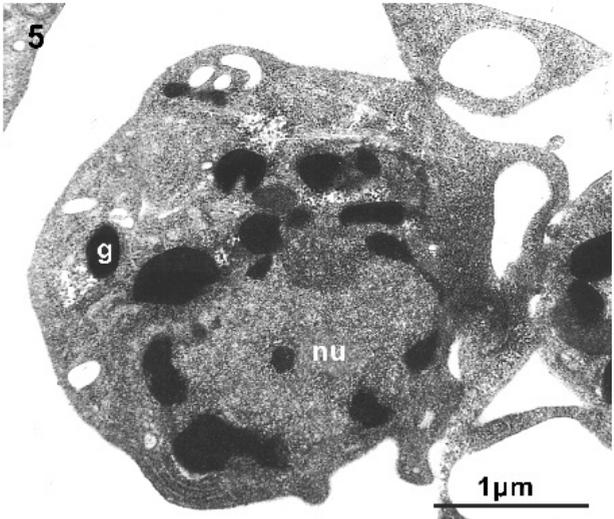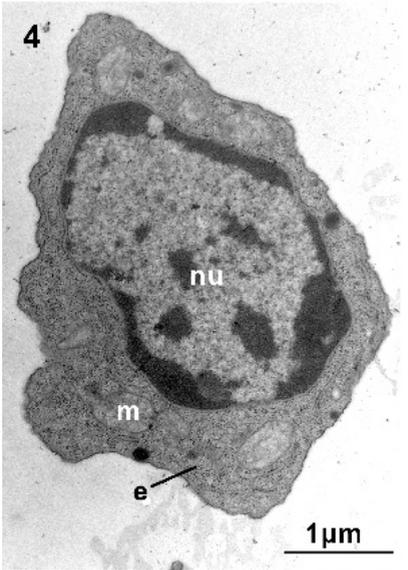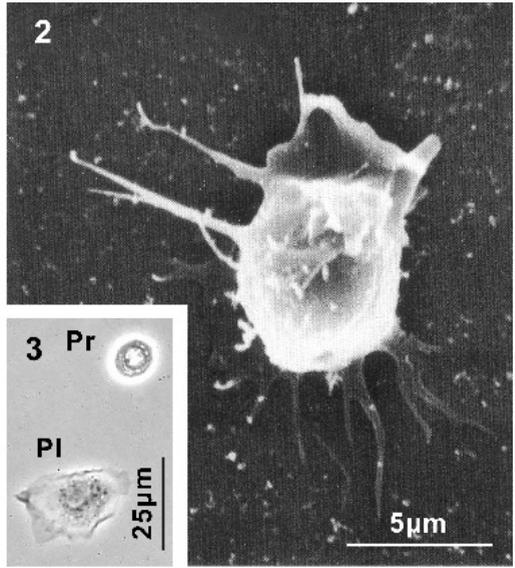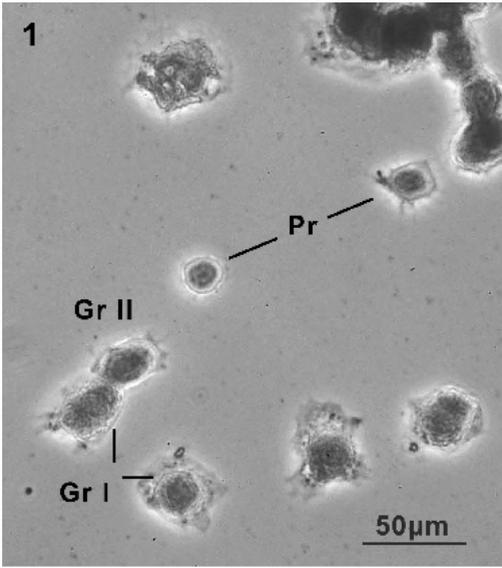
Ravindranath (1973, 1977, 1981) and Rajulu (1971) led – in close relation to investigations in insects – to the description of at least 7 different haemocyte types (prehaemocytes, granular haemocytes, plasmatocytes, cystocytes, sphaeulocytes, adipohaemocytes and oenocytoids).

More recently the investigations on chilopods using TEM techniques by Nevermann (1996), Nevermann & Xylander (1996), Nevermann et al. (1991, 1996), Hilken et al. (2003a) described haemocyte types with a major focus on their function, e.g. in immune defense. Xylander (1992), Xylander & Bogusch (1997) gave further indications on the haematogram of diplopods using light-microscopy. These investigations showed a less complex haematogram.

The purpose of this paper is to compare light and electron microscopic investigations on various myriapods using light microscopic, in vitro and TEM techniques. Some of the data described review results published earlier whereas some are new to science.

MATERIAL AND METHODS

Animals used in the present study

The new data presented here are based on investigations of numerous specimens of the two diplopods *Rhapidostreptor virgator* (Attems) and *Chicobolus* sp. as well as the chilopods *Scolopendra cingulata* and *Lithobius forficatus*. The origin and rearing of chilopods and diplopods have been described earlier elsewhere (Nevermann et al. 1991, Nevermann & Xylander 1996, Xylander & Nevermann 1990).

Figures 1-7. Prehaemocytes.
Figure 1. *Rhapidostreptus virgator* (Diplopoda). Haemocytes: Small prohaemocytes, granular haemocytes (left) and plasmatocytes (right, bottom). Pure haemolymph, spread on glass slides for 10 min, fixed in Karnoffsky´s fixative, subsequent May-Grünwald/Giemsa-staining, phase contrast.
Figure 2. *Lithobius forficatus* (Chilopoda). Pseudopodia of prehaemocytes are formed after incubation. 1 h in Grace´s medium on cellophane, SEM. Modified from Nevermann et al. (1991).
Figure 3. *Chicobolus spec*. (Diplopoda). Prehaemocyte and plasmatocyte. Pure haemolymph, unfixed, spread on glass slide, phase contrast.
Figure 4. *Scolopendra cingulata* (Chilopoda). Prehaemocyte. Fixed 3 h after incubation in Grace´s medium on cellophane, TEM.
Figure 5. *R. virgator.* Prehaemocyte. Pure haemolymph, fixed after 20 min on cellophane, TEM.
Figure 6. *S. cingulata*. Prehaemocyte. TEM, preparation as in Figure 4.
Figure 7. *L. forficatus*. Prehaemocyte with several grana. Preparation as Figure 2, TEM. Modified from Nevermann et al. (1991).

Abbreviations used in the figures:
c – cytoplasmic process
d - dictyosom
e or er – endoplasmic reticulum
g – grana/granulum
G I or Gr I – granular haemocytes of type I in Diplopoda
G II or Gr II – granular haemocytes of type II in Diplopoda
m - mitochondrium
nu – nucleus
Pl - plasmatocyte
Pr – prehaemocytes
SEM – scanning electron microscopy/micrograph
sv – tubular structure inside a vesicle of plasmatoctyes
TEM – transmission electron microscopy/micrograph
va - vacuole
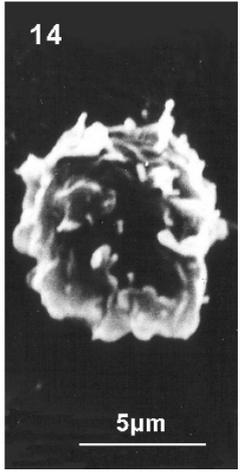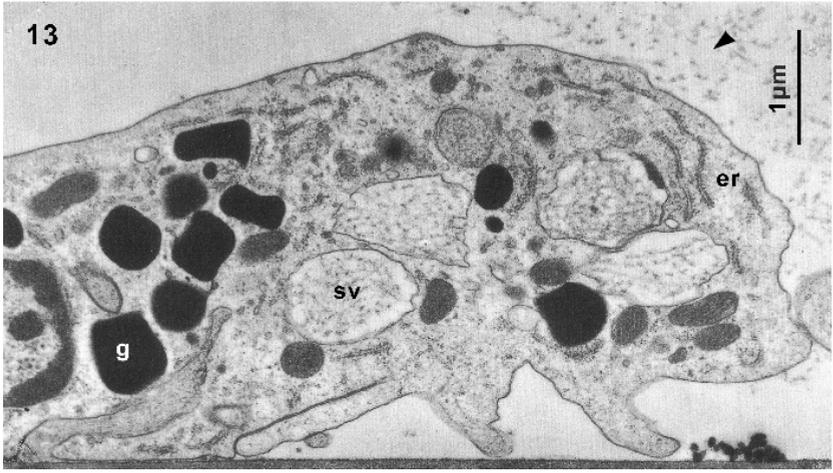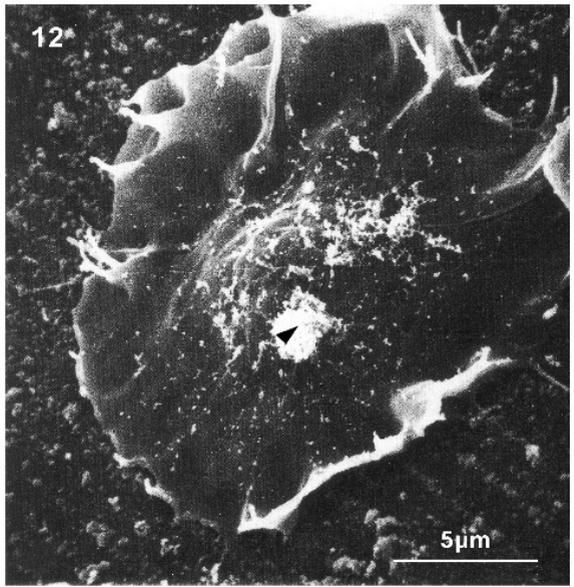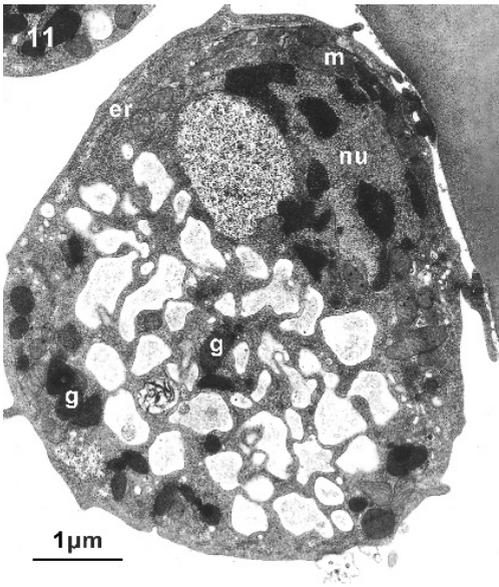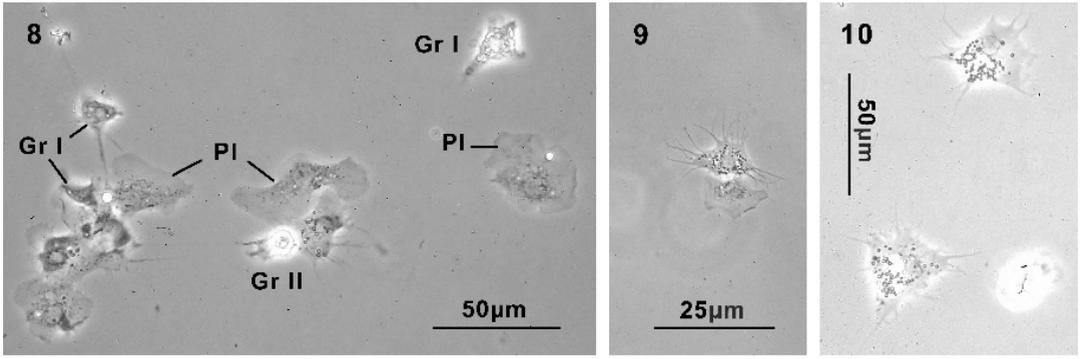
Staining and histochemistry for light microscopy

Haemolymph was investigated undiluted (in unstained samples) or diluted in small amounts of insect-ringer (K-saline: 5 g NaCl, 6.7 g KCl per l aq. dest.) and applied to a glass slide which has been carefully cleaned with EtOH and dried previously. Slides were kept in a moist chamber to let the haemocytes attach and spread on the glass surface for 5 to 30 minutes. Haemocytes were fixed before staining. Haemocyte not stained were not fixed.

Preparation for electron microscopy

Prior to fixation haemocytes attached to different substrates suspended in Ringer-solutions. Substrate and attached haemocytes were fixed in the cold for at least 2 h in a modified Karnoffsky´s fixative (2.5% glutaraldehyde, 2 % paraformaldehyde in 0.05 M cacodylate buffer, pH 7.2, osmolarity: 1000 mOsm) or in 2.5% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.2, osmolarity: 182 mOsm). Samples were washed and postfixed for 1-2 h in 2% (w/v) OsO^4 and dehydrated in an acetone series. After OsO^4-fixation samples were subdivided (with a small scissors). For transmission electron microscopy samples were embedded into araldite (via an acetone:araldite series) and sectioned on a Reichert OmU 3 microtome. Semithin sections were done using glass knives, ultrathin sections with a diamond knife. Sections were mounted on coated copper grids and double stained with uranyl acetate and lead citrate (if not otherwise indicated); investigations were done mainly on a Zeiss EM 9A at 60 kV. For scanning electron microscopy samples were critically point dried and sputtered with gold. SEM investigations were done on a JEOL or Cambridge Stereoscan S4 SE-microscope.

Haemocyte counts

For determination of the numbers of haemocyte per volume unit of haemolymph a Buerkner-chamber was used (depth 0.02 mm). Haemocytes from at least 20 "medium" squares (each with a volume of 0.8 nl) were counted and the mean and standard deviation were calculated.

RESULTS

Haemocyte types

Six types of haemocytes could be differentiated by light and electron microscopy in the diplopod and chilopod taxa mentioned above as well as in *Scutigera coleoptrata* investigated by TEM and SEM as well as cytochemical and in vitro techniques within the last years. Three types occur in all taxa investigated: Prehaemocytes, plasmatocytes and granular haemocytes.

Furthermore, spherulocytes, coagulocytes, and discoid cells have been described in different

Figures 8-14. Plasmatocytes.
Figures 8-10. *Chicobolus* spec. (Diplopoda). Preparation as Figure 3, phase contrast.
Figure 8. Plasmatocytes and different granular haemocytes.
Figure 9. The two different types of plasmatocytes with and without pseudopodia.
Figure 10. Two plasmatocytes spreading as "star-type" with few grana.
Figure 11. *Rhapidostreptus virgator (*Diplopoda). Plasmatocyte with numerous vacuoles filled with flocculent material and several grana located mainly at the periphery. Preparation as Figure 5, TEM.
Figures 12 and 13: *Lithobius forficatus* (Chilopoda). Preparation as Figure 2. Modified from Nevermann et al. (1991).
Figure 12: Plasmatocyte in "fried-egg"-spreading. Arrowhead points to coagulated plasma protein. SEM.
Figure 13: Plasmatocyte with grana and vacuoles containing filamentous material. Arrowhead indicates extracellular material which was probably exocytosed. TEM.
Figure 14: *R. virgator:* Plasmatocyte with numerous extensions of the cell surface. Preparation as Figure 5, TEM.
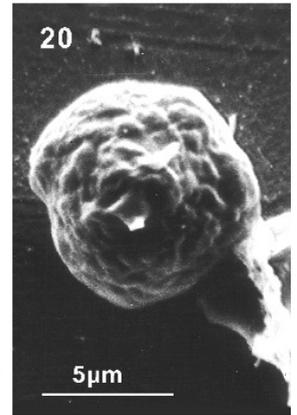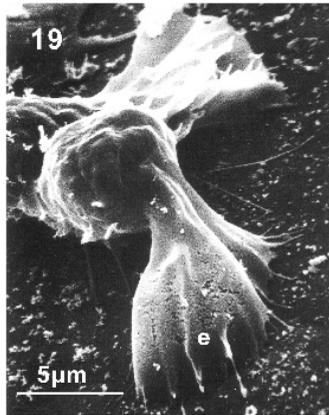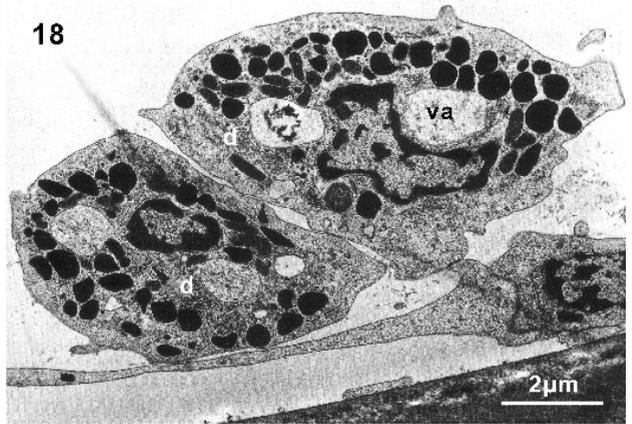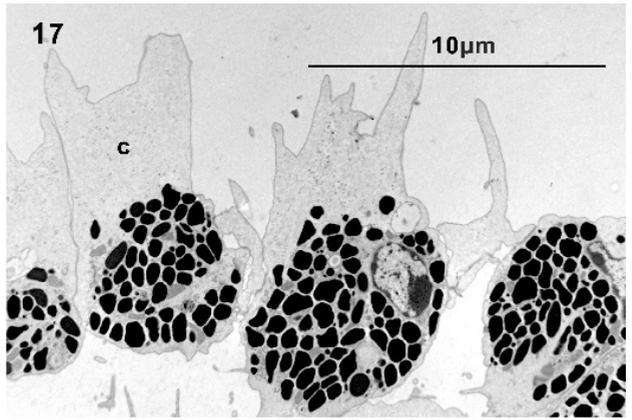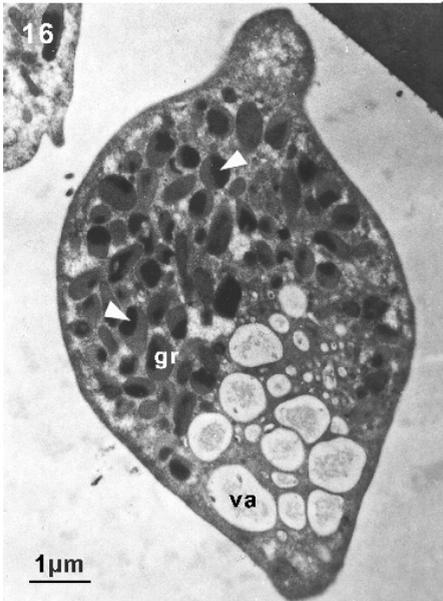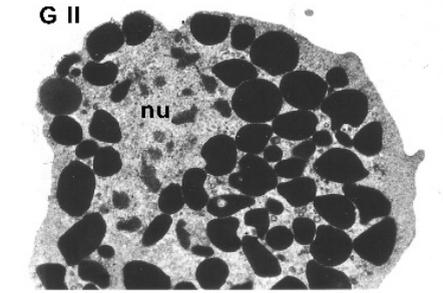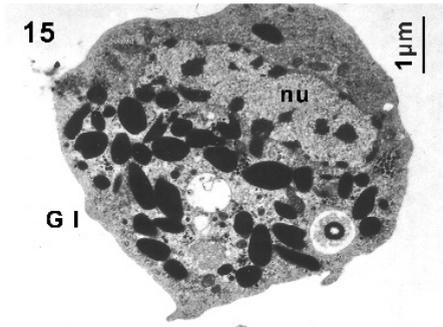
chilopod taxa. These haemocytes are to be described and characterised.

In the following, the haematocyte types of Diplopoda and (partly) Chilopoda are described according to own new results and directly compared and discussed with reference to results for the same types of haemocytes from further species and authors. A more comprehensive discussion also referring to other taxa of arthropods follows in the discussion section.

Prehaemocytes (Figures 1-7)
Prehaemocytes comprise 3 to 10% of all haemocytes in the diplopods and chilopods investigated (Figure 5). They are spherical and the smallest cells of all among the haematogram (Figure 1). Their nucleus-plasma-ratio is large (Figures 1, 3, 4-7). The nucleus is located in the centre of the cell. In vitro, these cells start spreading quite late (Figures 2 and 5); until that time their plasma occurs faint blue in phase contrast (Figure 3). Few small grana may occur in the plasma (Figures 5 and 7) and the phenoloxidase activity is mostly weak.

Plasmatocytes (Figures 8-14)
Plasmatocytes (PL) are much larger than the prehaemocytes with a mean size of 30 to 70 μm; they are characterized by their well developed spreading capabilities, their plasma bears no or

very few grana (Figures 9, 11, 13) and is greyish in phase contrast. PL´s contain no or very little prophenoloxidase and do not (or hardly) stain when incubated with DOPA (Figures 21 and 22). The nucleus is mostly located non-centrically and its appearance is larger in spread plasmatocytes than in any other haemocyte type (Figure 9). PL´s are spherical to spindle-shaped briefly after obtaining the haemolymph but flatten and attach to glass slides forming pseudopodia within 8 to 10 min (in an undiluted haemolymph sample) (Figures 8-10, 12). Two types of spreading have been observed:

a) the "fried-egg-type" - here cells flatten und spread homogeneously without formation of many pseudopodia; these PL show no or fewer grana (Figures 8, 9 and 12).

b) the "star-type" - these cells have many thin peripheral pseudopodia and increase in diameter continuously during spreading; in plasmatocytes of this type several small grana can be found frequently in the cytoplasm which are bluish in phase contrast (Figures 9, 10, 14).

In TEM, the plasmatocytes in Chilopoda contain electron translucent vacuoles with moderately electron dense filamentous material (Hilken et al. 2003a,b, Nevermann et al. 1991) (Figure 13). In Rhapidostreptus virgator comparable vacuoles have been found, but their content was rather

Figures 15-20. Granular haemocytes.
Figures 15, 16 and 20. *Rhapidostreptus virgator* (Diplopoda).
Figure 15. Granular haemocytes of type I (G I, top) with irregularly shaped mostly ellipsoid grana and granular haemocytes of type II (G II, bottom) with rounded grana. Preparation as Figure 5, TEM.
Figure 16. Granular haemocyte of type I with vacuoles. Preparation as Figure 15, but sections were not double stained with uranyl acetate and lead citrate, TEM.
Figure 17. *Scolopendra cingulata* (Chilopoda). Granular haemocytes with numerous closely packed grana in the central cytoplasm and elaborated cytoplasmic extensions which are free of grana; these granular haemocytes are located at the periphery of a nodule surrounding a xenograft. Fixed 85 min after incubation in Grace´s medium on cellophane, TEM.
Figures 18 and 19. *Lithobius forficatus* (Chilopoda). Preparation as Figure 2. Modified from Nevermann et al. (1991).
Figure 18. Granular haemocytes with vacuoles, extended endoplasmic reticulum (arrow head) and grana. TEM.
Figure 19. Granular haemocyte with the typical cytoplasmic extension. SEM.
Figure 20. Granular haemocyte of type II with grana bulging the cell surface. SEM.
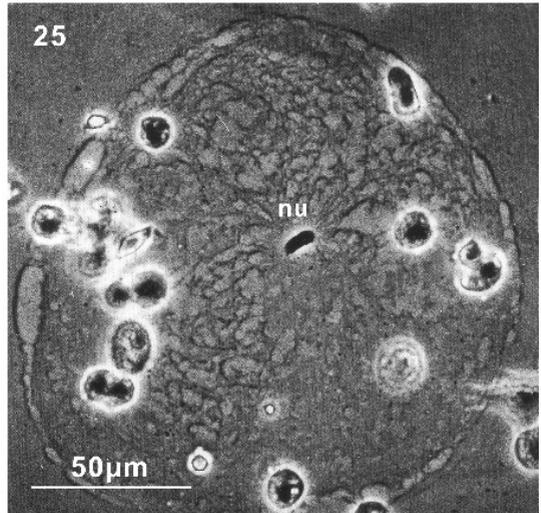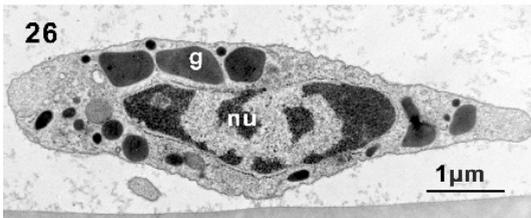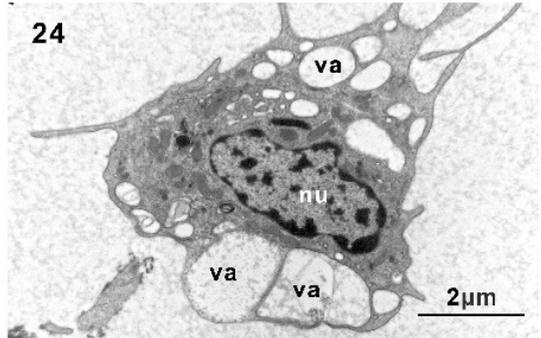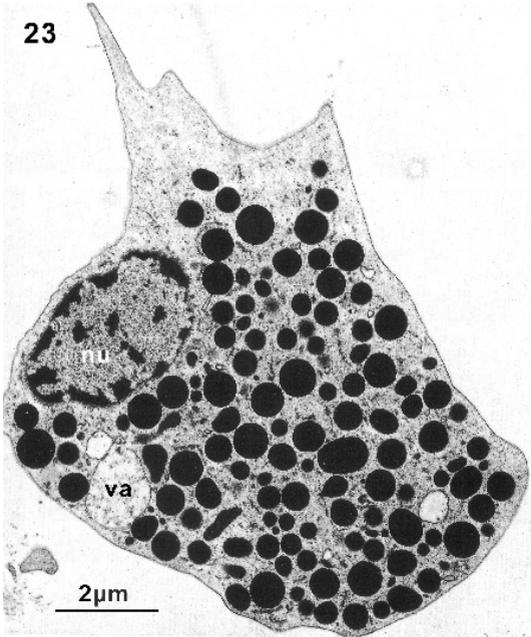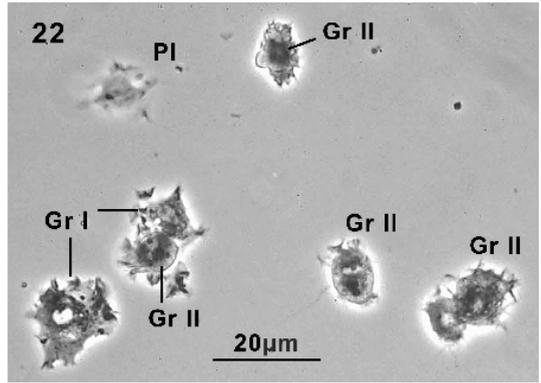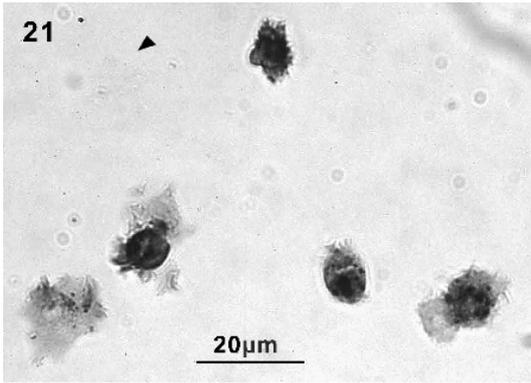
flocculent than filamentous (Figure 11). This material has been documented to be discharged some time after the start of in vitro-incubation and discharging could be stimulated by xenografts. Then, this material seems to attract other cell types to become involved in the immune response reaction (opsonisation effect).

Granular haemocytes (Figures 8, 15-22)
Granular haemocytes (GR) are the most frequent haemocytes in the haemolymph of Myriapoda (see for Diplopoda Figure 26) and contain numerous electron dense grana and some vacuoles (Figures 15-18). They are medium sized and all phenoloxidase active (Xylander 1992 a, 1996, Xylander & Bogusch 1997, Xylander & Nevermann 1993) (Figures 21 and 22). When taken from the haemolymph GR are spherical but slightly flatten within 15 min in vitro; nevertheless, they can be easily distinguished from PL for more than 1 h in light microscopy as they show significantly lower spreading capabilities (Figure 8). During spreading these haemocytes often form a unidirectional process (Figures 8, 17 and 19). But intermediate forms between granular haemocytes and PL may be found indicating that PL may be a transitional stage of differentiation (Nevermann et al. 1991, Hilken et al. 2003a) (at least of GR of type I, see below).

In the diplopods *Chicobolus* spec. and *Rhapidostreptus virgator* two different types of GR were encountered. Granular haemocytes of type I (GR I) differ from those of type II (GR II) in their higher spreading capabilities (Figures 8 and 22). They contain fewer and smaller grana and occur bluish or greenish in phase contrast; in TEM the grana are seen to be irregularly shaped (Figure 15). After spreading the grana of GR I arrange more or less concentrically around the nucleus; so the nucleus remains mostly visible. The phenoloxidase activity of this haemocyte type is moderate (and significantly lower than in GR II) (Figures 21 and 22). In unstained TEM-sections the grana can be subdivided into an electron dense and a more translucent part (Figure 16); the unstained part represents an non-centric core of the granule (Figure 16).

Granular haemocytes of type II are smaller in size in undiluted haemolymph samples than PL and GR I as they spread moderately and so – "looked from the top" have a smaller diameter (Figures 8 and 22). Their volume, however, differs hardly from the GR I and PL. GR II often form a unidirectional protrusion (Figure 8). Due to the higher number of grana GR II occur yellowish in phase contrast. The grana of this haemocyte type are larger and spherical; they may bulge

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Figures 21-26. Granular haemocytes, spherulocutes, discoid cells, coagulocytes.
Figures 21 and 22. *Rhapidostreptus virgator* (Diplopoda). Pure haemolymph, spread on glass slides for 20-30 min, fixed in Karnoffsky´s fixative, washed, activated by briefly rinsing with EtOH, incubated with DOPA as described by Xylander & Bogusch (1997).
Figure 21. Bright field. Granular haemocytes of type II are dark brown due to the phenoloxidase reaction, granular haemocytes of type I stain significantly weaker. Plasmatocytes (indicated by the arrowhead) do not stain at all and are invisible in this picture.
Figure 22. Phase contrast. All haemocytes are visible.
Figure 23. *Lithobius forficatus* (Chilopoda). Spherulocyte with regularly rounded grana which are phenoloxidase inactive. Preparation as Figure 2. Modified from Nevermann et al. (1991).
Figure 24. *Scolopendra cingulata* (Chilopoda). Strongly vacuolated coagulocyte (or plasmatocyte?) immediately fixed after sampling of haemolymph (dropping haemolymph sample into the fixative). TEM
Figure 25. *L. forficatus*. Remnants of a putative coagulocyte with a concentrical coagulation zone. Pure haemolymph on glass slide, fixed in formaldehyde vapour. Modified from Nevermann et al. (1991).
Figure 26. *S. cingulata*. Discoid cell characterized by concentrically arranged bundles of microtubules at the cell periphery. Fixed 30 min after incubation in K-Ringer (5 g NaCl, 6.7 KCl l^{-1}) on cellophane, TEM.

Table 1. A comparison of different haemocyte types within the Arthropoda. PH = prehaocutes, PL = plasmatocytes, GR = granular haemocytes, SPH = spherulocytes, COA = coagulocytes, DISC = discoid haemocytes, ADI = adipohaemocytes, CYST = cystocytes, OEN = oenocytoids, CYAN = cyanocytes.

Taxon	PH	PL	GR	SPH	COA	DISC	ADI	CYST	OEN	CYAN
Rhapidostreptus virgator	X	X	X		?		?			
Chicobolus spec.	X	X	X				?			
Lithobius forficatus	X	X	X	X	(X)		?			
Scolopendra cingulata	X	X	X			X	?			
Scutigera coleoptrata	X	X	X	X						
INSECTA	X	X	X	X			X	X	X	
CRUSTACEA	X	X	X				X			X
XIPHOSURA	?	X	X							X
SCORPIONES	X	X	X	X			X	X		?
ARANEA	X	X	X					?	X	X

Figure 27. Differential haemocyte counts in the millipeds *Rhapidostreptus virgator* (upper part) and *Chicobolus* sp. (lower part).

the surface of the haemocytes. GR II react much stronger when incubated with DOPA and stain dark brown (Figures 21 and 22).

Spherulocytes
In *Lithobius forficatus* and *Scutigera coleoptrata* a haemocyte type was found which is characterised by regularly shaped spherical grana (Nevermann et al. 1991, Hilken et al. 2003 a) (Figure 23). It was referred to as spherulocyte by Nevermann et al. (1991). This haemocyte could not be found in the Diplopoda (e.g. by Xylander 1992a) and *Scolopendra cingulata* (Nevermann 1996). Spreading capability of these cells is low and they are completely phenoloxidase inactive (Nevermann et al. 1991). They may form an ectoplasmic protrusion which completely lacks grana. No intermediate forms between spherulocytes and granular haemocytes or plasmatocytes have been found in L. forcipatus and S. coleoptrata.

Although there are some similarities in GR II and spherulocytes (spherical grana, ectoplasmic protrusion, moderate spreading capabilities) we consider these two to be disctinct haemocyte types as
1) no intermediate forms occur for spherulocytes whereas there are in GR I and GR II,
2) spherulocytes are PO inactive.

Coagulocytes

Nevermann et al. (1991) found coagulations zones in haemolymph preparations from *Lithobius forficatus* and discussed this to be the result of a possible coagulocyte (see Figure 25). This cell type has been considered to be extremely unstable and to disintegrate immediately when obtaining the haemolymph; so it is very infrequently found in haemocyte preparation. More recently Nevermann (1996) described a disintegrating haemocyte after dropping haemolymph directly into a fixative (Figure 24). These haemocytes had large vacuoles with flocculent material inside (as an indication of disintegration); they resembled plasmatocytes containing only few electron dense grana and vacuoles (Figure 24). So Nevermann (1996) speculated coagulocytes to be just "stressed plasmatocytes". A naked nucleus and remnants of cells (like isolated membranes) were also found in capsules around xenografts in Rhapidospreptus virgator; they may also constitute remnants of coagulocytes.

Discoid haemocyte

For Scolopendra cingulata Nevermann (unpublished thesis) described a haemocyte type (Figure 26) characterised by peripheral circular bundles of microtubules. These microtubules disintegrate briefly after attachment to any substrate and are subsequently not visible any more. Such bundles of microtubules have recently been desbribed also from granular haemocytes of *Scutigera coleoptrata* (Hilken et al. 2003a) and it is possible that circular peripheral bundles of microtubules are a trait native to plasmatocytes and granular haemocytes in vivo, too.

Cystocytes

Cystocytes were described to occur in the haemolymph of diplopods by Ravindranath (1981). Nevermann et al. (1991) showed, however, that this cell type can only be found in cell preparations where the cells have undergone mechanical stress (e. g. by sucking haemocytes into the narrow slit under a cover slip). For this reason cystocytes most probably represent preparation artefacts.

Adipohaemocytes

In very few cases cells have been found circulating in the haemolymph which contained numerous and large lipid grana, the outstanding character of adipohaemocytes. But such observations were infrequent and not reproducible with other specimens of the same species. It seems likely that these cells were set free from the fat body when puncturing the animals to obtain the haemolymph. They, therefore, may represent also an artifact originating from preparation and may not constitute a genuine haemocyte type.

Oenocytoids

In none of the diplopod and chilopod species investigated by our group oenocytoids have ever been encountered. However, oenocytoids are considered to be involved in the moulting process and their number may increase prior to moulting. As none of the specimens investigated was in the process of moulting, this may be the reason for the absence of oenocytoids in the haemolymph samples investigated. No definitive conclusion regarding the occurrence of oenocytoids in chilopods and diplopods can be drawn from our studies.

Differential haemocyte counts

In *Rhapidostreptus virgator* and *Chicobolus* sp. the haemocyte type with the highest abundance in the haemolymph are granular haemocytes of type I (38 and 39 %) whereas GR II comprised 30 % in *R. virgator* and 17 % in *Chicobolus* (Figure 27); plasmatocytes made up 27 % in *R. virgator* and 39 % in *Chicobolus* (Figure 27). In both species prehaemocytes were represented by about 5 % of all haemocytes (Figure 27).

Total haemocyte counts

A striking result regarding total haemocyte counts in myriapods is the fact that chilopods have about tenfold higher haemocyte numbers than diplopods (Table 2). So in Lithobius forficatus 45.000 haemocytes per µl haemolymph had been counted, in Scolopendra cingulata 31.500 and in S. oraniensis about 50.000 (only a single specimen could be investigated) (Table 2).

In R. virgator there were 2.450 and in Chicobolus

Table 2. Total haemocyte counts (THC in haemocytes µl -1) in different taxa of arthropods. (4 d and 5 d in Drosophila melanogaster refers to the age of larvae in days, L5 in Manduca sexta and Galleria mellonella to the fifth instar larval stage).

	THC [hc/µl]	References
Myriapoda		
Rhapidostreptus virgator	2.500	this paper
Chicobolus sp.	6.500	this paper
Scolopendra cingulata	31.000	Nevermann (1996)
Scolopendra oraniensis	ca. 50.000	this paper
Lithobius forficatus	45.000	Nevermann (1996)
Crustacea		
Astacus leptodactylus	ca. 500	Ullrich (1993)
Procambarus clarkii	ca. 580	Ullrich (1993)
Crangon crangon	800-1200	Smith & Johnston (1992)
Insecta		
Blatella germanica	23.000	Gupta (1986)
Periplaneta americana	60.000	Crossley (1975)
Chironomus thummi	1000-3000	Götz & Vey (1974)
Drosophila melanogaster (2d)	2000	Rizki & Rizki (1992)
Drosophila melanogaster (4d)	23.000	Rizki & Rizki (1992)
Manduca sexta (L5)	4.500	Horohov & Dunn (1982)
Galleria melonella (L5)	25.000	Chain & Anderson (1982)
Arachnida		
Limulus polyphemus	30.000	Sherman (1981)
Arenea sp.	11.000	Sherman (1981)

spec. 6.500 haemocytes per µl haemolymph (Table 2).

A brief review of functions of haemocytes in immune response

Haemocytes are involved in the following immune reaction:

a) phagocytosis and intracellular degradation of bacteria and other microbial invaders (Nevermann & Xylander 1996).

b) nodule formation and extracellular degradation of bacteria (see Nevermann & Xylander 1996).

c) encapsulation of larger xenografts (e. g. parasites) (Nevermann 1989, Xylander 1992a).

d) opsonisation to attract further immune cells to accelerate the process of immune defense (Nevermann 1996, Nevermann et al. 1996).

e) wound closure and clott formation (Hilken et al. 2003b, Xylander 1994).

f) melanisation of clotts after wounding.

g) production and storage of antibacterial substances (Nevermann 1996).

h) production and storage of prophenoloxidase and discharge of this enzyme onto xenografts (Xylander 1996, Xylander & Bogusch 1997, Xylander & Nevermann 1993).

DISCUSSION

Haemocyte types – a comparison within and outside the Myriapoda

Up to date representatives of three major taxa of myriapods have been investigated with regard to their haemocytes: Chilopoda, Diplopoda and Symphyla. Prehaemocytes, plasmatocytes and granular haemocytes occur in representatives of all three taxa. Other types described so far seem to be restricted to specific subtaxa or are considered to be artefacts. The ultrastructure of myriapod haemocytes (as far as investigated) corresponds largely to that found in insects and other arthropods (e.g. Bauchau (1981), Jones (1962), Ravindranath (1974), Sherman (1981), and Xylander (1992)).

Although homology (or exclusion of analogy) of haemocytes within the arthropods has not yet been definitively proven, the correspondence of characters (up to the ultrastructural level) indicates that usage of a common nomenclature for haemocytes is reasonable due to comparative-morphological, functional and pragmatic reasons (except for the haemocyte types of decapod crustaceans, see e. g. Bauchau (1981), Xylander et al. (2003)).

At least 9 different types of haemocytes seem to occur in the arthropods (Table 1). Those found in all groups of myriapods investigated can be found in other groups of Arthropoda (for references see Bauchau (1981), Jones (1962), Ravindranath (1974), Sherman (1981) and Xylander (1992)). Five other types are restricted to few taxa. Arthropods which use respiratory pigments (and not primarily trachea) for oxygen transfer have cyanocytes.

For these reasons, in the ground pattern of arthropods at least 4 different haemocyte types may be postulated: the undifferentiated prehaemocytes, the plasmatocytes capable for phagocytosis, the multifunctional granular haemocytes and the cyanocytes (responsible for production and storage of the respiratory pigments which do not occur in Myriapoda). Possibly there is also a specialised type of granular haemocytes

which easily disintegrated on contact to air or xenografts releasing grana and initiating plasma coagulation. After the change to terrestrial life and the formation of trachea, respiratory pigments and the cell type responsible for its production was reduced. The major tasks of the remaining haemocyte type are immune defense, wound closure and haematopoesis.

Total haemocyte counts

The number of haemocytes per volume of haemolymph is quite variable among the arthropods ranging from 500 haemocytes per µl (in decapod crustaceans) to 60 000 (in cockroaches) (Table 2). Whereas the diplopods range among those with fewer haemocytes the chilopods are among those with the highest number, but ontogenetical stages differed in their total haemocyte counts even within a single species (see references in Table 2).

An explanation for the variability among the haemocytes counts is hardly possible. But often species which are protected by hard and calcified cuticles and passive strategies of protection against predators (e. g. the defensive glandular products of many diplopods) show lower numbers of haemocytes (e. g. the diplopods investigated and decapod crustaceans); here the risk of injuries and – secondarily - infections may be lower. Thus, the demand for haemocytes for wound closure and immune defense is lower. For predatory taxa with a thin cuticle (reducing body weight and enabling more effective scavenging) or taxa with higher risk of injury and infection due to their life style (e. g. chilopods, cockroaches, dipteran larvae) higher haemocyte numbers may be expected. So Fründ (1992) showed that 28 to 60 % of all specimens of *Lithobius forficatus* from different habitats showed melanised scares or lost legs. Thus – at least for the Chilopoda – the high total haemocyte count probably constitutes an adaptation to their predatory life style meaning a higher risk for attacks and injuries.

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Redescription of Phryssonotus novaehollandiae (Silvestri, 1923) with details of post-embryonic stadia

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Short, M. & Huynh, C. 2006. Redescription of *Phryssonotus novaehollandiae* (Silvestri, 1923) with details of post-embryonic stadia. Norw. J. Entomol. 53, 211-222.

Phryssonotus novaehollandiae (Silvestri, 1923), a millipede species in the family Synxenidae (Diplopoda, Penicillata, Polyxenida), first described from a juvenile specimen at stadium V, is redescribed from adults collected in Victoria and South Australia. All ten post-embryonic stadia for this species were collected and Stadium V juveniles compared with the type description by Silvestri. All synxenid milllipedes collected were confirmed to be *P. novaehollandiae* which was found to occur in two reproductive forms: thelytokous (parthenogenetic) and sexual. No males were found in the thelytokous populations.

Keywords: *Phryssonotus novaehollandiae*, Diplopoda, Synxenidae, parthenogenesis, post-embryonic stadia

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INTRODUCTION

Millipedes in the subclass Penicillata (Latreille, 1831) are found world wide. All Penicillates are contained in a single order Polyxenida Verhoeff, 1934, and although phylogenetic relationships have not been completely elucidated, the majority of trees based on morphological and developmental characters have penicillates as the basal millipede clade (Sierwald, et al. 2003). There are four families: Polyxenidae (with 21 genera), Lophoproctidae (5 genera), Synxenidae (2 genera) and Hypogexenidae (1 genus with just 1 species). Until recently *Phryssonotus* (Scudder, 1885) was thought to be the sole genus in the family Synxenidae. The second genus *Condexenus* is described elsewhere in this volume (Nguyen Duy-Jacquemin 2006).

The genus *Phryssonotus* (Scudder 1885) was first described from fossil specimens found in Eocene Baltic amber (Menge, 1854). Live specimens were first collected in 1899 by Silvestri who

described a new genus *Synxenus* to accommodate them (Silvestri 1900). Silvestri placed six species in the genus *Synxenus* (Silvestri 1923, 1948). The genus was eventually synonymised under *Phryssonotus* by Condé in 1954. Altogether eight species are now described within the genus. The taxon is not only an ancient lineage but has a global distribution in the fossil record with species in the genus *Phryssonotus* being found in Eocene Baltic amber (*Phryssonotus hystrix* (Menge, 1854)), Cretaceous amber from France (species not identified (Nguyen Duy-Jacquemin & Azar, 2004)), as well as in Burmese amber also dated from the Cretaceous era (*Phryssonotus burmiticus* (Cockerell, 1917)).

Extant species in the genus have been collected in Africa, Australia, New Guinea, Spain, Sicily and South America. Of the 6 extant species, Condé (1971) believed the two South American species may be conspecific while there has also been doubt about the distinctness of the two species identified in Australia (Condé & Nguyen Duy-
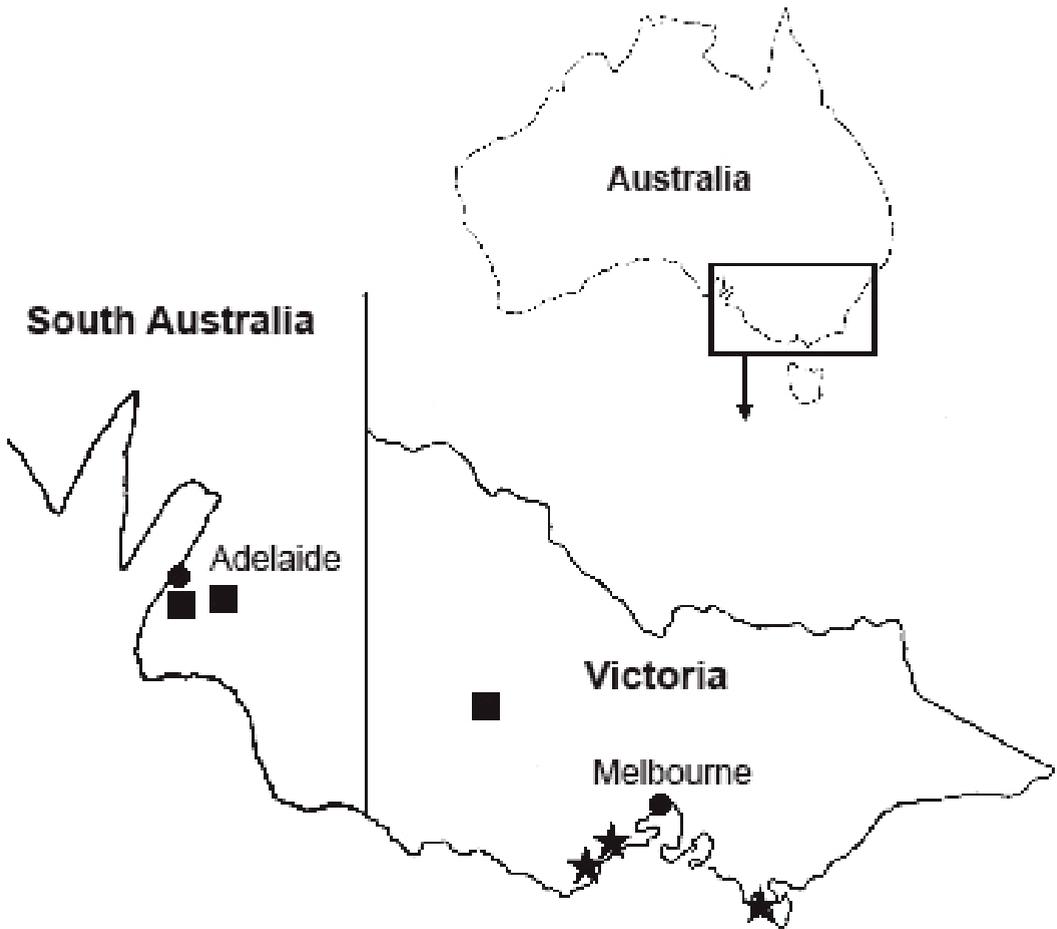
Figure 1. Map showing sites in Victoria and South Australia where *P. novaehollandiae* has been collected. ☐ = sites where only females have been collected, ☐ = sites where both males and females have been collected. ☐ = locations of the cities of Melbourne and Adelaide.

Jacquemin 1984; Rasnitsyn & Golovatch 2004). The task of determining and describing species within this genus has been difficult for two reasons. In past studies the limited availability of material has led to species descriptions being based on small numbers of specimens. Secondly the genus is highly conserved with little to distinguish one species from another. The genus itself is easily identifiable with striated scale-shaped tergal trichomes or setae, 17 pairs of legs with the last two pairs having pads rather than claws, and elongated vulvae in females. The two fossil species have not been able to be fully described due to incompleteness or inability to

view important differentiating structures, hence they cannot be compared with the extant species.

In this study, specimens of *Phryssonotus* from both Victoria and South Australia were examined in order to determine if they were populations of *P. novaehollandiae* (Silvestri, 1923) the only synxenid millipede previously described from Southern Australia. As the species was originally described from stadium V juveniles, it was necessary to compare specimens from the same stadium with Silvestri's description to confirm the identity of the millipedes in this study as *P. novaehollandiae*. This paper redescribes *P.*
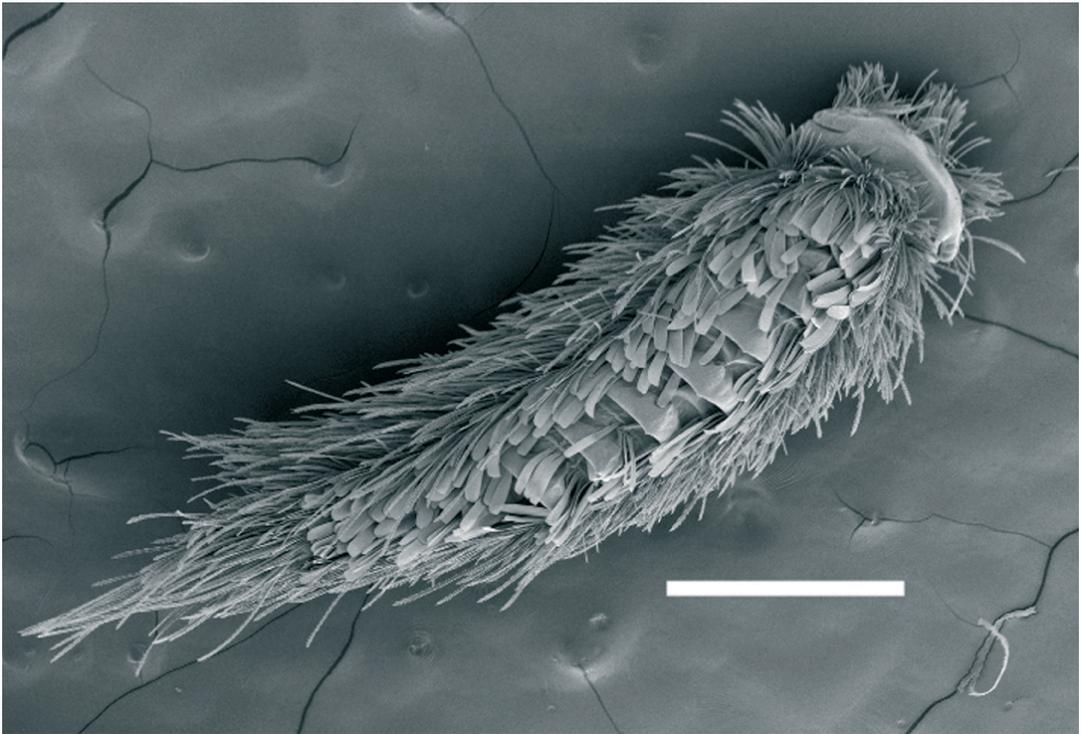
Figure 2. Dorsal view of adult female *P. novaehollandiae* from Point Addis, Victoria, showing two rows of scale -shaped tergal trichomes on each tergite. Scale bar = 1mm.

novaehollandiae using the adult material now available. In contrast to other published studies on this genus, abundant material both preserved and living was available.

Specimens of *Phryssonotus* were collected from a number of sites in Southern Australia (Figure 1). Collections were made from heath, heathy woodland and sand dune habitats along the coastline from Point Addis to Fairhaven, and at Tidal River in Wilsons Promontory National Park in Victoria. Inland, specimens were collected from a Box Ironbark Forest habitat at Deep Lead Flora Reserve, Stawell, Victoria. The South Australian specimens were collected from sand dunes at Hallett Cove Conservation Park and in eucalypt woodland at Scott Creek in the Mt Lofty Ranges National Park. Collections were made under the following research permit numbers: 10003354 (Victoria) and Y24944 –1 (South Australia). A small number of specimens in collections held

at the South Australian Museum and Museum Victoria were also examined.

Millipedes were collected using a combination of sieving and Tullgren funnel extraction and preserved in 70 - 80% ethanol. Specimens were then examined with light and scanning electron microscopy. Preserved material was mounted on slides with Fast Green (Horobin & Kiernan, 2002) as a stain for observing characteristics of the cuticle and ocelli. Representative adults of both sexes have been lodged in both the South Australian Museum and Museum Victoria.

SYSTEMATIC DESCRIPTION

Class **Diplopoda** de Blainville in Gervais, 1844
Subclass **Penicillata** Latreille, 1831
Order **Polyxenida** Verhoeff, 1934
Superfamily **Synxenoidea** Silvestri, 1923
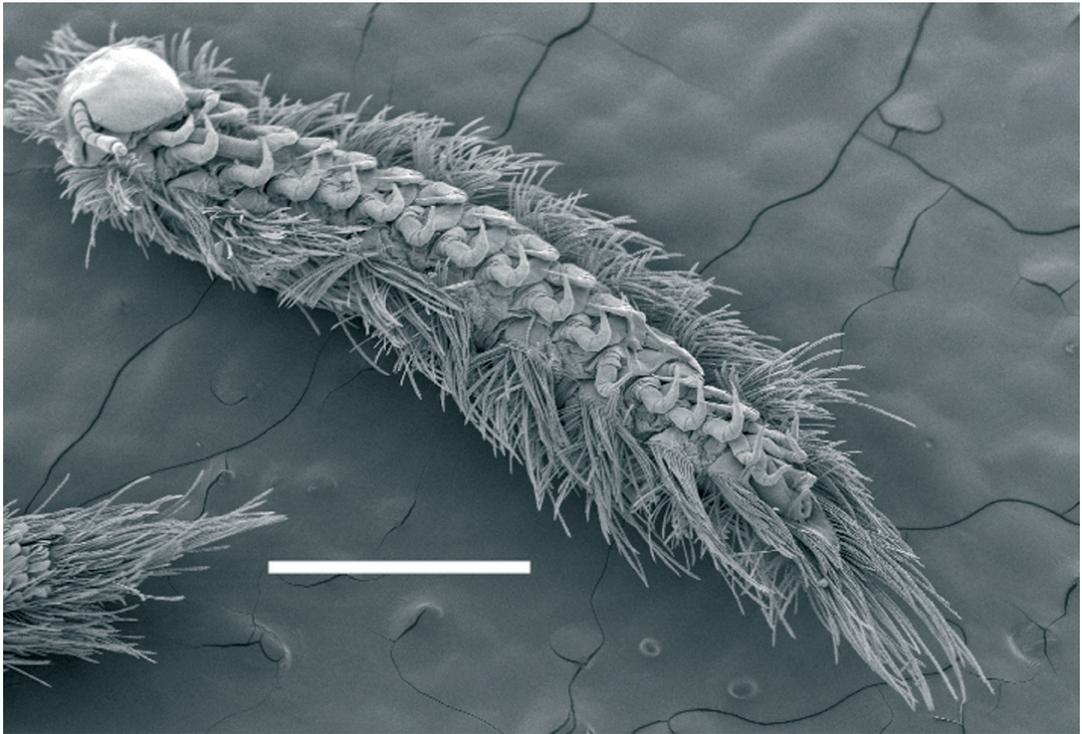
Figure 3. Ventral view of adult female *P. novaehollandiae* from Point Addis, Victoria showing 17 pairs of legs. Scale bar = 1mm.

Family **Synxenidae** Silvestri, 1923
Genus **Phryssonotus** Scudder, 1885

(= *Lophonotus* Menge, 1854 non Stephens, 1829, nec Macquart, 1839, type species: *Lophonotus hystrix* Menge, 1854, fossil from amber, by monotypy: = *Synxenus* Silvestri, 1900, type species: *Synxenus orientalis* Silvestri 1900, Uraguay, by original designation: = *Schindalmonotus* Attems, 1926, type species: *Schindalmonotus hystrix* Attems, 1926, South Africa, by monotypy: = *Kubanus* Attems, 1926, type species: *Polyxenus platycephalus* Lucas, 1846, Algeria, by subsequent designation of Jeekel (1970:2): = *Koubanus* Attems, 1928, type species: *Polyxenus platycephalus* Lucas, 1846, Algeria, by original designation)

Phryssonotus novaehollandiae Silvestri
Synxenus novaehollandiae Silvestri, 1923: 14-15.

Holotype
Juvenile stadium V, Mt Lofty, South Australia in 1913, possibly in the Silvestri type collection formerly housed at Portici, now moved to the Museum of Genoa, Italy (B. Espinosa, pers. comm.) not examined.

Material examined
516 specimens from 6 unique locations in Southern Australia: Point Addis, Aireys Inlet, Tidal River and Deep Lead in Victoria; Hallett Cove and Scott Creek in South Australia.

Diagnosis
Differs from all other extant species in the genus *Phryssonotus* in having 5 short frontal trichomes B and 11 ocelli. Comparison with the two fossil species was not possible due to incomplete preservation of the fossils.
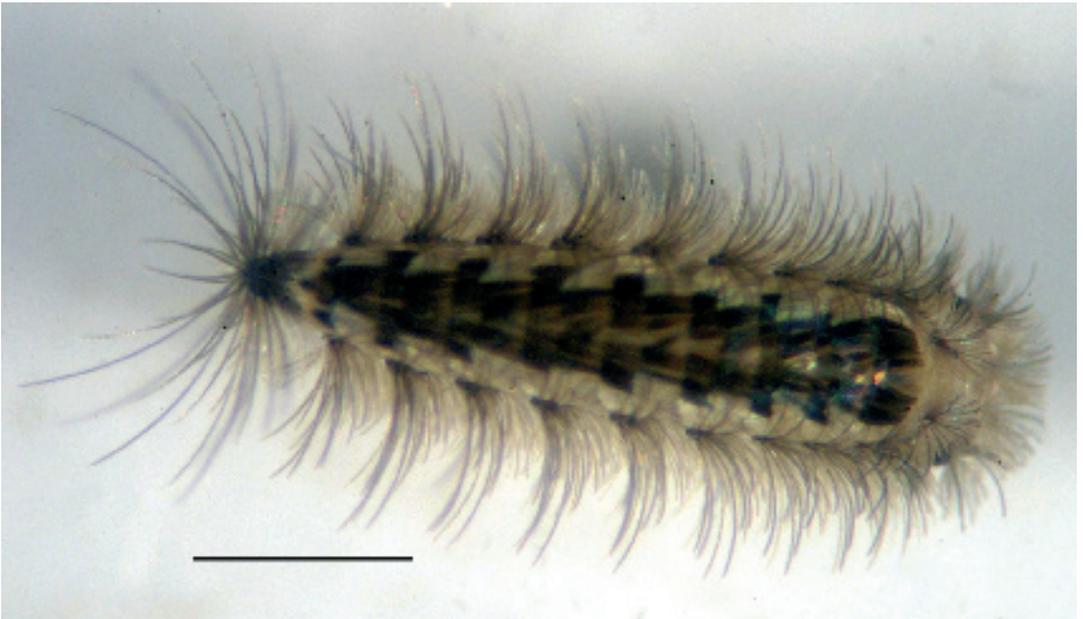
Figure 4. Dorsal view of live adult female *P. novaehollandiae* from Point Addis, Victoria showing the distinctive colour pattern. Dark brown pigmented tergal trichomes are positioned centrally on each tergite with unpigmented tergal trichomes either side. Scale bar = 1mm.

Description

General appearance: Adults of both sexes with 12 tergites (including collum and telson) and 17 leg pairs (Figures 2 and 3). Overall colour of adults brown with distinctive white stripes down each side of the dorsal surface (Figure 4). The pigment where present is contained in the trichomes.

Measurements: Length 3.49 ± 0.02 mm (adult females preserved in 80% ethanol, n = 10), width at head just anterior to ocelli 0.63 ± 0.05 mm.

Head: Eyes with eleven ocelli (Figure 5), antennae with eight articles and four conical sensillae at the top of the terminal articles. A group of three trichobothria occur posterior to the eyes on each side, with the anterior one (referred to as trichobothrium c) possessing a shorter sensory hair than the other two. Associated with the anterior trichobothrium on each side is a distinctively long outwardly curving trichome referred to as the long frontal trichome A, and a row of 5 shorter frontal trichomes B (Figure 6). The notations A and B

were first given to these structures by Silvestri (1923). A pair of circular Tömösvary organs is positioned adjacent to eleventh ocellus on each side (Figure 5).

Trunk - dorsal: Long trichomes on collum are arranged in two rosettes. All post-collum tergites are covered with scale-shaped trichomes which are striated and arranged in two transverse rows (Figure 2). Lateral to the scale-shaped trichomes are pleural bundles of long thin pigmented trichomes arching up as well as outwards.

Trunk - ventral: Legs are short with all but last two pairs possessing claws; last two pairs of legs lack claws, and point posteriorly (Figure 7). These two pairs of legs end in hairy pads which are possibly used to produce a pushing or jumping movement to escape predation. Large vulvae are present in female from the second pair of coxal plates (Figures 7a and 8), while males have penes in the same position (Figure 7b) together with 3 pairs of coxal glands associated with the 9th, 10th
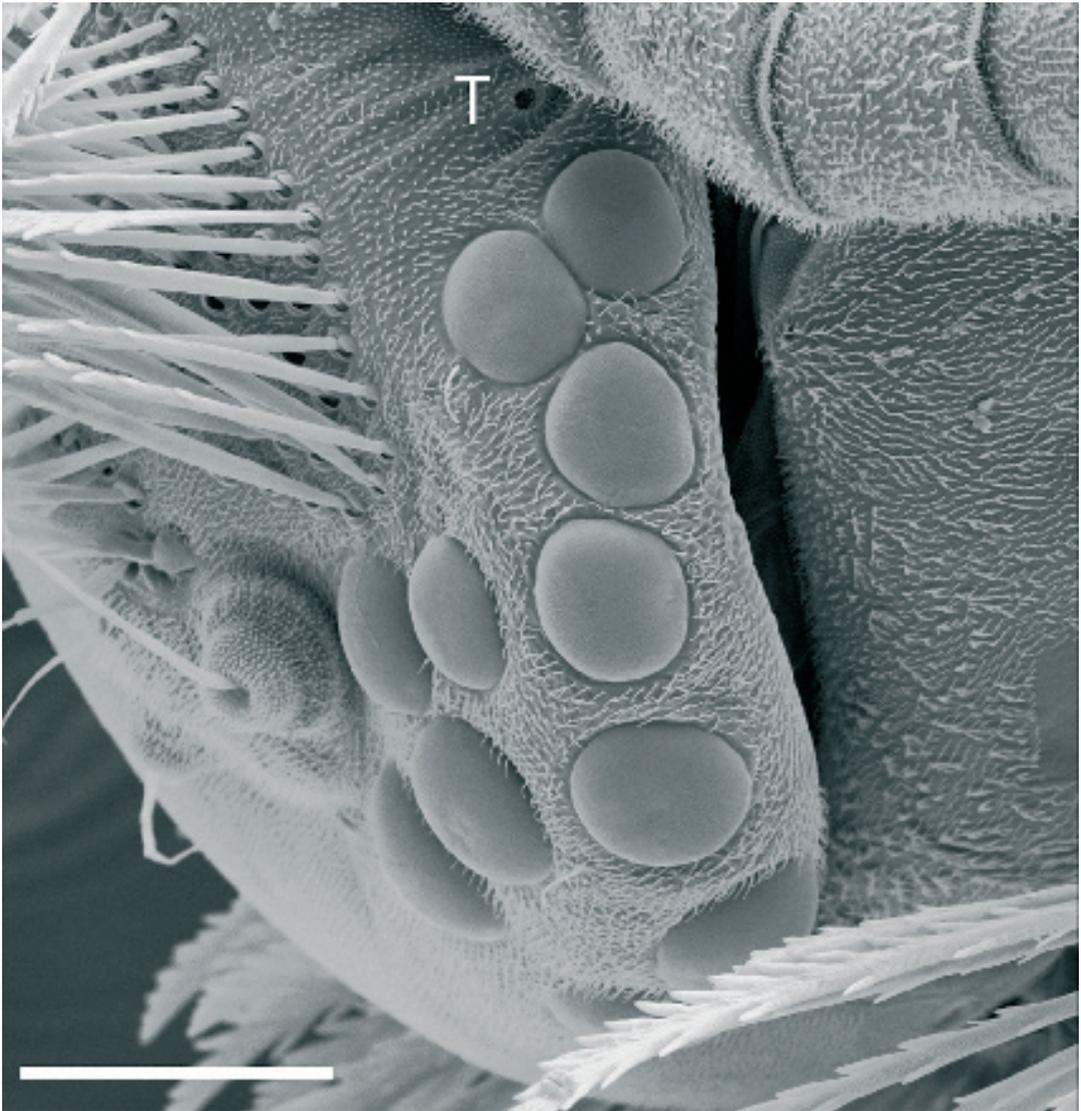
Figure 5. Lateral view of the head of an adult *P. novaehollandiae* from Point Addis, Victoria showing detail of the ocelli. Note that the circular Organ of Tömösvary (T) is visible. Scale bar = 50µm.

and 11th leg pairs. Penes distinguishable as shorter and more pointed in shape than the vulvae.

Telson: cone shaped and covered anteriorly with one row of the scale-shaped trichomes as well as a thick coverage of uniformly long thin dark brown trichomes.

Immature stadia: Specimens of *Phryssonotus* at all stages from the newly emerged stadium I with 3 pairs of legs through to the adult stadium X were observed and distinguishing features recorded (Table 1). At each of the first 3 moults, just one pair of legs was added, with 2 pairs of legs added at each moult from stage IV to IX. One pair of legs is added in the final moult. New leg pairs were present and visible as external buds prior to each moult. A tergite with one pair of pleural bundles

Table 1. Selected characteristics of post-embryonic stadia of *P. novaehollandiae* collected at Point Addis, Victoria. Although early juvenile stadia cannot be sexed it is assumed all are female as no males have been collected at this site. * Number of tergal plates includes collum and telson.

| Characteristics | Stadium | | | | | | | | | |
	I	II	III	IV	V	VI	VII	VIII	IX	X
Mean length (mm) n=5	0.50	0.65	0.77	1.16	1.40	1.56	1.90	2.60	3.00	3.31
No. tergal plates *	5	5	6	7	8	9	10	11	12	12
No. pleural bundles	3	3	4	5	6	7	8	9	10	10
Pairs of legs	3	4	5	6	8	10	12	14	16	17
No. antennal articles	5	5	5	7	8	8	8	8	8	8
Ocelli	5	5	7	7	10	11	11	11	11	11
Dorsal colour pattern	none	simple	simple	simple	simple	dual	dual	dual	dual	dual
Vulvae present	no	no	no	no	buds	yes	yes	yes	yes	yes
No. trichomes B	1	1	1	2	2	3	3	4	4	5

of trichomes was added each moult from stadium II to stadium IX. Antennal articles were added at two moults with adult number being achieved at stadium V. Number of ocelli and short frontal trichomes B increased at some but not all moults. Stadium I hatchlings were unpigmented and lacked scale-shaped tergal trichomes. The next four stadia had uniform brown tergal trichomes (described as "simple" in Table 1). Stadia VI –X had a distinctive dorsal colour pattern with bands of unpigmented scaled-shaped trichomes either side of central dark brown tergal trichomes.

Parthenogenetic populations
No males have been collected from populations of *P. novaehollandiae* at Victorian coastal sites: Point Addis, Aireys Inlet, Tidal River (Figure 1). As all post-embryonic stadia were collected from these populations, it appears that reproduction is parthenogenetic. The remaining populations both inland and coastal contained both males and females. No discernible or measurable morphological differences were observed between females of each type of population.

Distribution and ecology
Phryssonotus novaehollandiae appears to be widespread throughout drier habitats in south eastern Australia. This species was collected from sandy well-drained coastal habitats as well as inland dry sclerophyll forests. The species

appears to prefer well drained, dry locations, and specimens were collected from eucalypt bark and litter as well as leaf litter beneath coastal *Boobialla* and *Melaleuca* trees. There appeared to be no morphological variation between *Phryssonotus* collected at different sites. The first stadium was abundant in dry litter in late spring (October & November). The next 3 stadia have only been collected over summer, while stadia 5 - 8 were collected throughout the year, most commonly in bark of live trees between 0 - 0.5 m from the ground. Relatively few examples of stadium IX or X (adults) have been found to date.

Remarks
Two species of *Phryssonotus* have been identified in Australia. Silvestri (1923) described a new species *P. novaehollandiae* from one juvenile specimen with 8 pairs of legs (Stadium V). Condé and Nguyen Duy-Jacquemin (1984) identified a specimen collected from Buderim, Queensland with 16 pairs of legs (Stadium IX) as being *Phryssonotus capensis* (Silvestri, 1923), originally described from specimens collected in South Africa. Silvestri (1923) used two characteristics to distinguish species of *Phryssonotus*: number of ocelli and number of short frontal trichomes B.

As can be seen in Table 1, the characteristics described for stadium V specimens collected in this study (8 pairs of legs, ten ocelli and 2
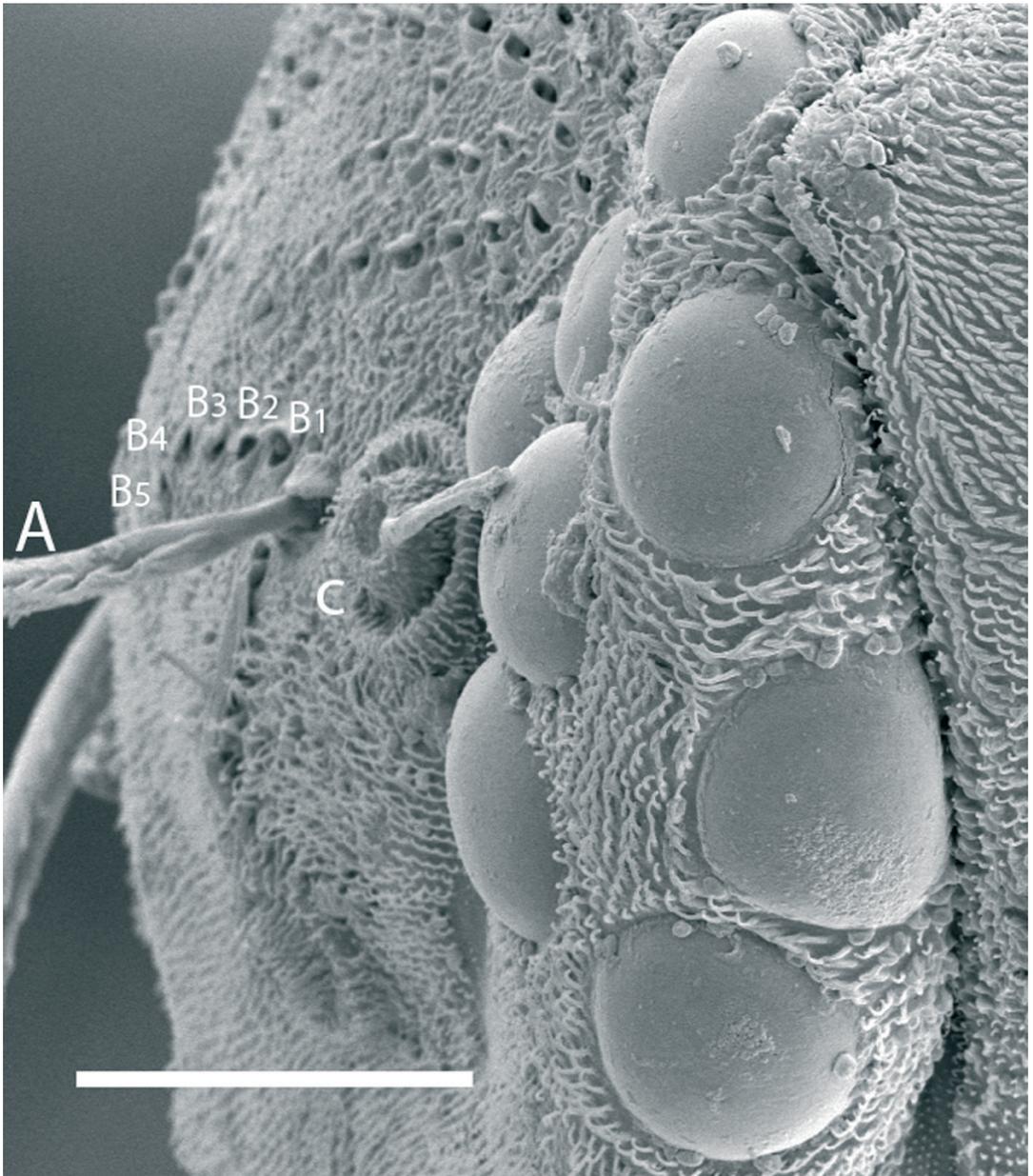
Figure 6. Lateral view of the head of adult female *P. novaehollandiae* from Point Addis, Victoria showing detail of the frontal trichomes. The single long frontal trichome (A) is adjacent to the trichobothrium c (c). The five short frontal trichomes are indicated with the notations B1 –B5. Scale bar = 43µm.

Figure 7. Ventral view of live adult specimens of *P. novaehollandiae* from Hallett Cove, South Australia showing genital structures associated with the second coxal plates.
Female (a), Male (b). The female is 3.50mm in length from head to tip of the telson, while the male is 3.65mm. Note that the final two leg pairs in the female are damaged.
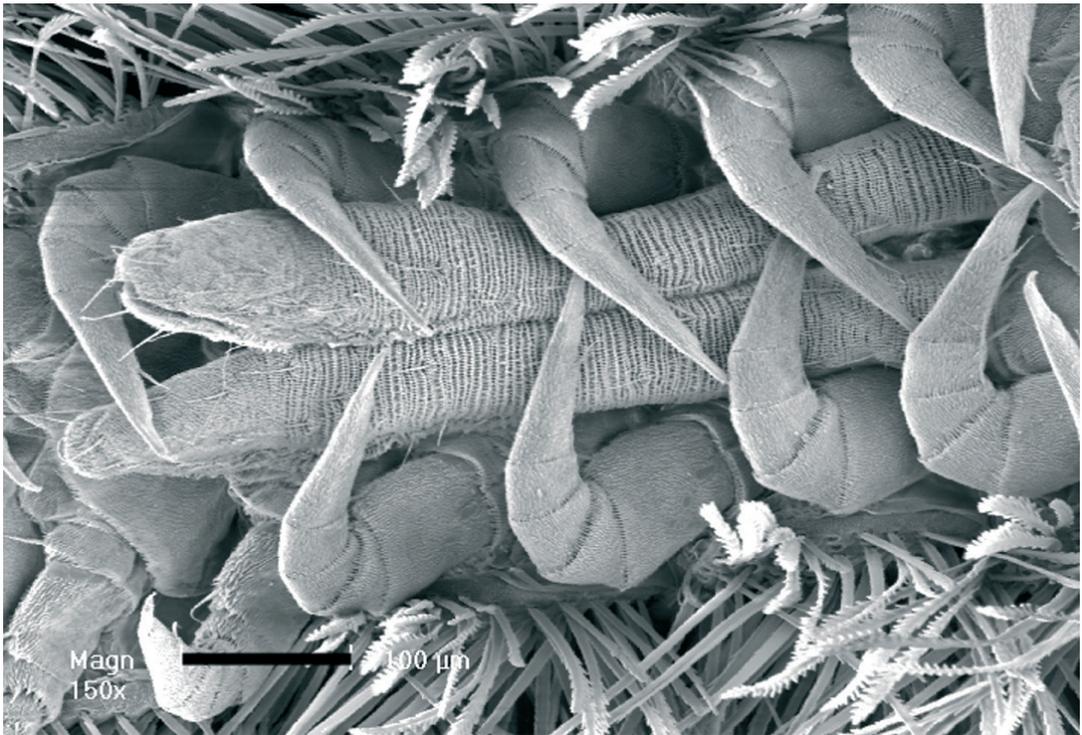
Figure 8. Ventral view of adult female *P. novaehollandiae* from Point Addis, Victoria showing detail of vulvae. Scale bar = 100μm.

short frontal trichomes B associated with each of the trichobothria c) match Silvestri's (1923) description of the type specimen (Figure 9). All *Phryssonotus* specimens examined in the course of this study from Southern Australia are therefore identified as *Phryssonotus novaehollandiae*. It should be noted that while *P. capensis* and *P. novaehollandiae* are very similar with five short frontal trichomes B, Silvestri described adult *P. capensis* as having ten ocelli. It is most unlikely that Silvestri overlooked an eleventh ocellus in his description of adult *P. capensis*, as in the same paper he describes adult *Phryssonotus platycephalus* (Silvestri, 1923) with eleven ocelli (Silvestri 1923).

A REVISED KEY TO THE EXTANT SPECIES OF THE GENUS *PHRYSSONOTUS.*

This key uses the same characteristics as Silvestri (1923) whose key has been the only one available for extant *Phryssonotus* species until now. The key includes species mentioned above together with *Phryssonotus orientalis* (Silvestri, 1900).

1. One short frontal trichomes B present 2
-   Five or six short frontal trichomes B present ..3
2. Nine ocelli present in adult...........*P. orientalis*
- Eleven ocelli present in adult....*P. platycephalus*
3. Ten ocelli present in adult...............*P. capensis*
- Eleven ocelli present
in adult....................................*P. novaehollandiae*

The two remaining species in the genus, *Phryssonotus chilensis* (Silvestri, 1948) (collected
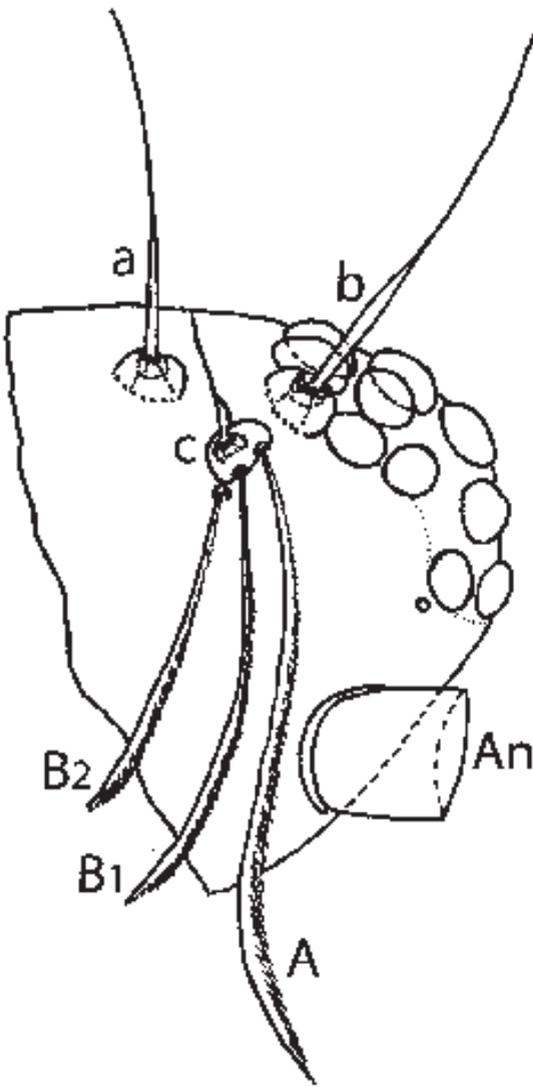
Figure 9. View of the head of a stadium V juvenile redrawn from Silvestri (1923) showing characters used in the original description of *P. novaehollandiae*. These characters are tricho-bothria a, b and c, long frontal trichome A, and two short frontal trichomes B1 and B2. The base of the antenna is indicated (An). No scale was given in the original drawing.

in Chile) and *Phryssonotus cubanus* (Silvestri, 1948) (collected in Cuba), cannot be included in the key with confidence due to the incomplete descriptions and lack of illustrations (Silvestri 1948). It should be noted that Condé (1971) identified *Phryssonotus* specimens collected from ant nests in Brazil, South America as *P. orientalis* with some reservation, commenting on the summary nature of Silvestri's description of *P. chilensis* and the absence of illustrations. Silvestri did not clarify why he was placing the *Phryssonotus* specimens collected in Chile as a new species. Silvestri described *P. chilensis* and *P. cubanus* as being very similar to *P. orientalis*, so in the absence of further information it is assumed that these species both had just one short frontal trichome B like *P. orientalis*. This being so, the presence of 9 ocelli in *P. chilensis* would mean that it would be bracketed with *P. orientalis* if placed in the key above, while *P. cubanus* with 8 ocelli would key out separately.

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Robert Latzel – his life-work and importance for Myriapodology

Verena Stagl

Stagl, V. 2006. Robert Latzel - his life-work and importance for Myriapodology. Norw. J. Entomol. 53, 223-236.

Robert Latzel, one of the greatest European pioneers in Myriapodology was born in 1845 in Austrian Silesia, part of the Austro-Hungarian Monarchy, in today's Czech Republic. After his studies in Vienna he became a teacher of natural history at high schools and later was appointed as the principal of the main grammar school in Klagenfurt, Carinthia. Since 1875 he focused on myriapods. He published his main work "Die Myriopoden der österreichisch-ungarischen Monarchie" – "Die Chilopoden" in 1880 and "Die Symphylen, Pauropoden, Diplopoden" in 1884 – a classic opus for taxonomic and systematic research both then and today. Especially the latter became a basic work for systematic research because Latzel recognised the importance of gonopods as the key diagnostic factor of the single species. He sold large collections to the Viennese Museum in 1884 and in 1919, the year of his death. The exact localities, registered by Latzel himself, are provided only in the museum's book of acquisitions for 1884. These are now published here for the first time. The complete list of Latzel's publications on myriapods is compiled and all the new taxa described and assigned by him are listed.

Key words: Robert Latzel, myriapod collection, museum history

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CURRICULUM VITAE

Robert Latzel was born on 28 October 1845 in Sörgsdorf, situated in the NW part of Austrian Silesia, part of the Austro-Hungarian Empire. This is present-day Uhelná, located in the NE part of the Czech Republic, close to the Polish border.

The family was very poor; they were farmers and he was the tenth of fourteen children. Since earliest childhood, he was accustomed to hard work (Bendl 1921). Nevertheless, he got the opportunity to visit grammar school in Troppau (Opava today) between 1858 and 1866. During his school years he started his first activities in the natural sciences at the local museum, determining and ordering beetles and plants. After his primary certification he studied natural sciences in Vienna. His intention was to become a school teacher. Latzel took his exams for the teaching profession in 1870, and in 1872 he received his Doctor's degree at the University in Vienna. For the next 17 years, he worked as a teacher in Vienna. Robert Latzel was a hard-working and dutiful teacher; he published several important schoolbooks in biology and instructed many candidates for the teaching profession. In 1873 he married Hedwig Horrakh. Two children, a son and a daughter, were born.

In August 1889 the government appointed him as a principal of the main grammar school in Klagenfurt, Carinthia, a very honourable assignment, but connected with many bureaucratic

obligations. Under his guidance a new school building had to be planned and built. Latzel was a highly revered and well-known personality in Klagenfurt, one who contributed much to the exploration of the local fauna and flora (Stagl & Mildner 2001). Several papers he wrote made an important contribution to the exploration of the Carinthian local fauna (Bendl, 1921).

After his retirement in 1810, Latzel was still very busy as a member of several societies in Klagenfurt, and he was the president of the so-called Society of the Landesmuseum there. He was also active in humanitarian associations. In 1915 he fell ill with a severe pulmonary disease, after which he gave up all his duties and rarely left home. Robert Latzel died on 15 December 1919 in Klagenfurt.

Robert Latzel, oil-painting, O. von Pistor, 1916 in the office of the "Naturwissenschaftlichen Verein für Kärnten" in Klagenfurt, photo K. Allesch.

THE SCIENTIST - PIONEER IN MYRIAPODOLOGY

According to his own account, beginning in 1875 while teaching in Vienna, he started to focus on centipedes, diplopods, pauropods and symphylans.

Latzel published the first half of his main work in 1880: "Die Myriopoden der österreichisch-ungarischen Monarchie" – "Die Chilopoden" and the second half in 1884 "Die Symphylen, Pauropoden, Diplopoden". Mainly the latter became a basic work for systematic research because Latzel recognised the importance of gonopods as the key diagnostic factor of the single species. Richard Hoffman (1980) described it as "an epochal work". Carl Attems (1901) characterised his scientific work as a turning point in millipede systematic research.

For his studies, Latzel travelled extensively in many parts of the Austro-Hungarian Empire. He travelled at his own expense, mostly during the school vacations. He never received financial support. He collected in Hungary, Bohemia, Moravia, Austrian Silesia, Slavonia (Croatia), Lower Austria, Upper Austria, Salzburg, Tyrol, Carinthia, Styria, Carniola, Northern Italy and Istria ("österreichische Küstenlande"). Latzel never had the opportunity to visit Galicia, Bucovina and parts of Dalmatia, but he received enough specimens from colleagues (Latzel 1884b). Only Vorarlberg and Transylvania (Siebenbürgen), also territories of the Empire, were not included in his studies because he had no material. He extended his investigations to myriapods from Normandy, from the surroundings of Hamburg, from caves in Liguria, from the Azores, Madeira, the Canaries and Selvages, from North Africa and from Tahiti. While he himself did not collect in these areas, he was sent material by colleagues, among others from M. J. Chalande, H. Gadeau de Kerville, C.O. Porat and K. Kraepelin.

Latzel published his myriopod studies in a total of 33 articles/papers/books. During the last years of his life he focused on collembolans; the

Table 1. Citation of taxa described by Robert Latzel

Genus	Subgenus	Species	Variation	Citation
Glomeris		*klugii*	*pentasticha*	Latzel 1876/101
Lithobius	*Archilithobius*	*cyrtopus*		Latzel 1880a/225
Lithobius	*Lithobius*	*nodulipes*		Latzel 1880a/225
Notiphilides				Latzel 1880b/ 20
Poylbothrus				Latzel 1880b/ 35
	Oligobothrus			Latzel 1880a/ 36
Lithobius	*Neolithobius*	*leptopus*		Latzel 1880b/ 53
Lithobius	*Lithobius*	*dalmaticus*		Latzel 1880b/ 60
Lithobius	*Lithobius*	*peregrinus*		Latzel 1880b/ 63
Lithobius	*Lithobius*	*nigrifrons*		Latzel & Haase 1880b/ 71
Lithobius	*Lithobius*	*aulacopus*		Latzel 1880b/ 84
Lithobius	*Lithobius*	*pygmaeus*		Latzel 1880b/ 86
Lithobius	*Lithobius*	*anodus*		Latzel 1880b/ 88
Lithobius	*Archilithobius*	*subtilis*		Latzel 1880b/ 91
Lithobius	*Archilithobius*	*mutabilis*	*hungaricus*	Latzel 1880b/101
Lithobius	*Archilithobius*	*mutabilis*	*transalpinus*	Latzel 1880b/101
Lithobius	*Archilithobius*	*mutabilis*	*sudeticus*	Latzel & Haase 1880b/101
Lithobius	*Archilithobius*	*pusillus*		Latzel 1880b/108
Lithobius	*Archilithobius*	*stygius*		Latzel 1880b/113
Lithobius	*Archilithobius*	*illyricus*		Latzel 1880b/115
Geophilus		*gorizensis*		Latzel 1880b/170
Geophilus		*strictus*		Latzel 1880b/174
Geophilus		*flavidus*	*carynthiacus*	Latzel 1880b/178
Geophilus		*longicornis*	*austriacus*	Latzel 1880b/182
Geophilus		*pygmaeus*		Latzel 1880b/182
Stigmatogaster				Latzel 1880b/ 20, 211
Lithobius		*tylopus*		Latzel 1882a/223
Lithobius	*Eulithobius*	*transsylvanicus*		Latzel 1882b/ 2
Glomeris		*carpathica*		Latzel 1883a/281
Polydesmus		*tatranus*		Latzel 1883a/281
Craspedosoma	*Megalosoma*	*carpathicum*		Latzel 1883a/282
Lysiopetalum		*fasciatum*		Latzel 1883a/282
Iulus	*Typhloiulus*	*strictus*		Latzel 1883a/282
Craspedosoma		*flavescens*		Latzel 1883b/235, 1884b/206
Eurypauropus		*ornatus*		Latzel 1884a/127
Eurypauropus		*cycliger*		Latzel 1884a/127
Scolopendrella		*notacantha*	*munda*	Latzel 1884b/ 15
Scolopendrella		*immaculata*	*maior*	Latzel 1884b/ 18
Scolopendrella		*immaculata*	*minor*	Latzel 1884b/ 18
Polyxenus				Latzel 1884b/ 70
Gervaisia		*costata*	*acutula*	Latzel 1884b/ 89

Table 1. continued

Genus	Subgenus	Species	Variation	Citation
Gervaisia		*costata*	*gibbula*	Latzel 1884b/ 89
Glomeris		*minima*		Latzel 1884b/ 94
Glomeris		*tyrolensis*		Latzel 1884b/ 97
Glomeris		*cingulata*	*intercedens*	Latzel 1884b/100
Glomeris		*pustulata*	*norica*	Latzel 1884b/106
Glomeris		*connexa*	*carpathica*	Latzel 1884b/110
Glomeris		*connexa*	*tenebrosa*	Latzel 1884b/110
Glomeris		*connexa*	*alpina*	Latzel 1884b/110
Glomeris		*hexasticha*	*quadrimaculata*	Latzel 1884b/113
Glomeris		*hexasticha*	*formosa*	Latzel 1884b/113
Glomeris		*hexasticha*	*mniszechii*	Latzel 1884b/113
Glomeris		*hexasticha*	*rubiginosa*	Latzel 1884b/113
Glomeris		*tridentina*		Latzel 1884b/118
Glomeris		*conspersa*	*excellens*	Latzel 1884b/123
Glomeris		*conspersa*	*coccinea*	Latzel 1884b/123
Brachydesmus		*filiformis*		Latzel 1884b/129
Brachydesmus		*superus*		Latzel 1884b/130, 1883b/236
Brachydesmus		*dalmaticus*		Latzel 1884b/132
Brachydesmus		*inferus*		Latzel 1884b/135
Polydesmus		*tridentinus*		Latzel 1884b/140
Polydesmus		*noricus*		Latzel 1884b/144
Polydesmus		*falcifer*		Latzel 1884b/146
Polydesmus		*subscabratus*		Latzel 1884b/147
Polydesmus		*rangifer*		Latzel 1884b/148
Polydesmus		*complanatus*	*constrictus*	Latzel 1884b/153
Polydesmus		*complanatus*	*monticola*	Latzel 1884b/153
Polydesmus		*tatranus*	*balcanus*	Latzel 1884b/157
Polydesmus		*polonicus*		Latzel 1884b/160
Rhiscosoma				Latzel 1884b/173
Rhiscosoma		*alpestre*		Latzel 1884b/174
Rhiscosoma		*alpestre*	*illyricum*	Latzel 1884b/175
Atractosoma		*meridionale*	*alpinum*	Latzel 1884b/180
Craspedosoma	*Scotherpes*			Latzel 1884b/190, 209
Craspedosoma		*oribates*		Latzel 1884b/194
Craspedosoma		*stygium*		Latzel 1884b/196
Craspedosoma		*moniliforme*		Latzel 1884b/197
Craspedosoma		*mutabile*		Latzel 1884b/199
Craspedosoma		*mutabile*	*nigrescens*	Latzel 1884b/202
Craspedosoma		*mutabile*	*fasciatum*	Latzel 1884b/203
Craspedosoma		*mutabile*	*punctulatum*	Latzel 1884b/203
Craspedosoma		*crenulatum*		Latzel 1884b/205

Table 1. continued

Genus	Subgenus	Species	Variation	Citation
Craspedosoma	*Scotherpes*	*troglodytes*		Latzel 1884b/209
Lysiopetalum		*degenerans*		Latzel 1884b/218
Lysiopetalum		*illyricum*		Latzel 1884b/221
Lysiopetalum		*illyricum*	*troglobium*	Latzel 1884b/225
Lysiopetalum		*anceps*		Latzel 1884b/232
Lysiopetalum		*cognatum*		Latzel 1884b/234
Iulus	*Typhloiulus*			Latzel 1884b/260
Iulus	*Typhloiulus*	*psilonotus*		Latzel 1884b/261
Iulus	*Allaiulus*	*nanus*		Latzel 1884b/264
Iulus	*Typhloiulus*	*strictus*	*nematodes*	Latzel 1884b/264
Iulus	*Allaiulus*	*pelidnus*		Latzel 1884b/267
Iulus	*Allaiulus*	*nanus*	*pannonicus*	Latzel 1884b/267
Iulus	*Allaiulus*	*dicentrus*		Latzel 1884b/270
Iulus	*Allaiulus*	*dicentrus*	*devius*	Latzel 1884b/272
Iulus	*Allaiulus*	*imbecillus*		Latzel 1884b/274
Iulus	*Ommatoiulus*			Latzel 1884b/277
Iulus	*Ommatoiulus*	*italicus*		Latzel 1884b/289
Iulus	*Ommatoiulus*	*platyurus*		Latzel 1884b/294
Iulus	*Ommatoiulus*	*luridus*	*fulviceps*	Latzel 1884b/294
Iulus	*Ommatoiulus*	*austriacus*		Latzel 1884b/296
Iulus	*Ommatoiulus*	*austriacus*	*erythronotus*	Latzel 1884b/299
Iulus	*Ommatoiulus*	*podabrus*		Latzel 1884b/300
Iulus	*Ommatoiulus*	*austriacus*	*nigrescens*	Latzel 1884b/300
Iulus	*Ommatoiulus*	*montivagus*		Latzel 1884b/308
Iulus	*Ommatoiulus*	*montivagus*	*elucens*	Latzel 1884b/310
Iulus	*Ommatoiulus*	*longabo*	*exilis*	Latzel 1884b/316, 1884c/271
Iulus	*Ommatoiulus*	*fallax*	*chilopogon*	Latzel 1884b/321
Iulus	*Ommatoiulus*	*fallax*	*noricus*	Latzel 1884b/321
Iulus	*Ommatoiulus*	*fallax*	*oribates*	Latzel 1884b/321
Iulus	*Ommatoiulus*	*fallax*	*vagabundus*	Latzel 1884b/321
Iulus	*Ommatoiulus*	*scandinavius*		Latzel 1884b/322
Iulus	*Ommatoiulus*	*sabulosus*	*exstinctus*	Latzel 1884b/331
Iulus	*Ommatoiulus*	*sabulosus*	*hispanicus*	Latzel 1884b/331
Iulus	*Ommatoiulus*	*fuscipes*	*leuconotus*	Latzel 1884b/336
Iulus	*Ommatoiulus*	*fuscipes*	*subcrassus*	Latzel 1884b/336
Iulus	*Ommatoiulus*	*mediterraneus*		Latzel 1884b/337, 1884c/270
Iulus	*Ommatoiulus*	*cattarensis*		Latzel 1884b/342
Cryptops		*hortensis*	*paucidens*	Latzel 1884c/267
Glomeris		*hexasticha*	*intermedia*	Latzel 1884c/267
Polydesmus		*complanatus*	*angustus*	Latzel 1884c/267
Polydesmus		*gallicus*		Latzel 1884c/268

Table 1. continued

Genus	Subgenus	Species	Variation	Citation
Polydesmus		*subinteger*		Latzel 1884c/268
Polydesmus		*inconstans*		Latzel 1884c/269
Chordeuma		*gallicum*		Latzel 1884c/269
Iulus		*luridus*	*gracilis*	Latzel 1884c/271
Brachypauropus				Latzel 1884c/ 28
Brachypauropus		*hamiger*		Latzel 1884c/ 30
Julus		*belgicus*		Latzel 1884d/CCXLIX
Lithobius		*oligoporus*		Latzel 1885b/254
Lithobius		*typhlus*		Latzel 1886a/169
Lithobius		*microdon*		Latzel 1886a/170
Henicops		*numidica*		Latzel 1886a/171
Himanarium		*dimidiatum*	*angustum*	Latzel 1886a/173
Schendyla		*eximia*	*oraniensis*	Latzel 1886a/173
Himantarium		*mediterraneum*	*tenue*	Latzel 1886a/174
Glomeris		*pyrenaica*		Latzel 1886a/174
Strongylosoma		*pallipes*	*gallicum*	Latzel 1886a/175
Blaniulus		guttulatus	troglobius	Latzel 1886a/175
Iulus		*luscus*	*homalopsis*	Latzel 1886a/176
Scolopendrella		*immaculata*	*italica*	Latzel 1886b/308
Glomeris		*connexa*	*ligurica*	Latzel 1886b/308
Glomeris		*connexa*	*ligurica xantopyge*	Latzel 1886b/308
Glomeris		*connexa*	*ligurica nycthemera*	Latzel 1886b/308
Glomeris		*conspersa*	*genuensis*	Latzel 1886b/308
Strongylosoma		*italicum*		Latzel 1886b/309
Lithobius		*troglodytes*		Latzel 1886c/104
Iulus		*cognatus*		Latzel 1886c/105
Iulus		*psilopygus*		Latzel 1886c/106
Iulus		*albolineatus*	*confundens*	Latzel 1887a/ 14
Lithobius		*scotophilus*		Latzel 1887b/507
Atractosoma		*angustum*		Latzel 1887b/507
Atractosoma		*angustum*	*hebescens*	Latzel 1887b/508
Atractosoma		*angustum*	*caecum*	Latzel 1887b/508
Lithobius		*grossipes*	*bosniensis*	Latzel 1888a/ 93
Lithobius		*spiniger*		Latzel 1888a/ 93
Julus		*podabrus*	*bosniensis*	Latzel 1888a/ 94
Polydesmus		*distractus*		Latzel 1888b/LXXXV
Lithobius		*tricuspis*	*mononyx*	Latzel 1888b/LXXXV
Iulus		*luridus*	*oedurus*	Latzel 1888b/LXXXVI
Lithobius		*grossipes*	*debilis*	Latzel 1889a/360
Glomeris		*inferorum*		Latzel 1889a/360
Polydesmus		*troglobius*		Latzel 1889a/360

Table 1. continued

Genus	Subgenus	Species	Variation	Citation
Polydesmus		*barberii*		Latzel 1889a/361
Atractosoma		*hyalops*		Latzel 1889a/361
Brachydesmus		*proximus*		Latzel 1889b/405
Glomeris		*marginata*	*lucida*	Latzel 1890/367
Iulus		*ligulifer*		Latzel & Verhoeff 1891/152
Spirobolus		*nannodes*		Latzel 1892/186
Glomeris		*kervillei*		Latzel 1895a/219
Glomeris		*perplexa*		Latzel 1895b/107
Paradesmus		*albonanus*		Latzel 1895b/107
Iulus		*pusillus*	*acutulus*	Latzel 1895b/108
Spirobolus		*dictyonotis*		Latzel 1895b/108
Lithobius		*orotavae*		Latzel 1895c/117
Lithobius		teneriffae		Latzel 1895c/118
Cryptops		*canariensis*		Latzel 1895c/119
Geophilus		*madeirae*		Latzel 1895c/120
Iulus		*kraepelinorum*		Latzel 1895c/120
Iulus		*salvagicus*		Latzel 1895c/121
Iulus		*schneideri*		Latzel 1900/521
Craspedosoma		*blaniulides*		Latzel 1900/521

Names without any status in nomenclature

Megopisthus				Latzel 1880b/145
Craspedosoma		*terreum*		Latzel 1883b/187
Geophilus		*proximus*	*minor*	Latzel 1883b/232
Scolopendrella		*pilosula*		Latzel 1883b/233
Dolichostenus				Latzel 1884b/ 68
Zygopus				Latzel 1884b/190

monograph he began remained incomplete and unpublished.

The new taxa described by Robert Latzel are listed in Table 1, together with names without any status in nomenclature such as *Megopisthus, Dolichostenus* and *Zygopus* (see Jeekel 1970, 2005). Three species names are nomina nuda, lacking any description by Latzel in Justyn Karlinski´s paper (Latzel 1883b).

Altogether, Latzel described 43 new chilopod taxa (2 genera, 29 species and 12 variations), 128 diplopods (1 genus, 2 subgenera, 69 species and 56 variations) and 4 new taxa of symphylans (4 variations) and pauropods (1 genus, 3 subspecies). Most of the species are still valid, and some of the variations have now been elevated to good species.

ROBERT LATZEL´S COLLECTION

Latzel was in contact and exchange with several European scientific institutions, but he sold the main part of his large collection, with many types,

to the Hofmuseum in Vienna – the Natural History Museum of today. The museum got the first part – 125 series with 1098 specimens – in 1884 for 80 florins (equivalent to about 770 €). The second part, 420 series with 7000 specimens, was sent to the museum by Robert Latzel's wife only a few days before his death in late 1919. The purchase was arranged several months previously between Latzel and Attems, with whom he had an amicable and cooperative relationship, clearly evident in letters and postcards stored in the museum's archive. Concerning the fee, Latzel had absolute trust in Attems, who evaluated the collection at 10 000 crowns. The present equivalent value can not be stated, because the economic crisis after the first world war resulted in severe inflation. In January 1920 the widow received an advance payment of 3000 crowns. For that payment she could only buy a bit more than one loaf of bread.

Latzel did not specify localities in his main work (1880b, 1884b), neither in the original description of new species and variations, nor on the labels in the jars of his collection. He gave only general data about the regions from which the specimens were collected, for instance "österreichische Küstenlande, Kärnten, Niederösterreich". Only in the book of acquisitions for 1884 is information on the exact localities provided, written in red ink by Latzel himself (Stagl 2001, Stagl & Mildner 2001, Wirkner et al. 2002, Stagl & Stoev 2005), published here for the first time (Table 2).

PUBLICATIONS OF ROBERT LATZEL CONCERNING MYRIAPODS

Latzel, R. 1876. Beiträge zur Fauna Kärntens. Jahrbuch des naturhistorischen Landes-Museums von Kärnten. Herausgegeben von J.L. Canaval. 12. Heft, 91-124.

Latzel, R. 1880a. Zwei neue mitteleuropäische Arten der *Gattung Lithobius* Leach. Zoologischer Anzeiger, III, No. 55: 225-226.

Latzel, R. 1880b. Die Myriopoden der Österreichisch-Ungarischen Monarchie. Erste Hälfte: Die Chilopoden. – Hölder, Wien. 228 pp., 10 lith. Tafeln mit 98 Fig.

Latzel, R. 1880c. Beitrag zur Kenntnis der Geophiliden. Zoologischer Anzeiger, III, No. 68: 546-547.

Latzel, R. 1882a. Descrizione di un nuovo litobio italiano. Bullettino della Società Entomologica Italiana, Firenze, Anno XIV, p. 223.

Latzel, R. 1882b. Ein neuer Lithobier aus Ungarn und Serbien. Zoologischer Anzeiger, V. Jahrgang 1882 1p.

Latzel, R. 1883a. Beitrag zur Myriopodenkenntnis Österreich-Ungarns und Serbiens. Verhand-lungen der k.k. zoologisch-botanischen Gesell-schaft in Wien, Jahrg. 1882, XXXII. Band, 281-282.

Latzel, R. 1883b. in: Justyn Karlinski. Materjaly do fauny wijów Galicyi zachodniéj z r. 1878-1882. Sprawozdanie Komisyi Fizyjograficznéj, 17: 226-238.

Latzel, R. 1884a. Die Pauropoden Österreichs. Verhandlungen der zoologisch-botanischen Gesellschaft in Wien, Jahrg. 1883, 123-128.

Latzel, R. 1884b. Die Myriapoden der öster-reichisch-ungarischen Monarchie. 2. Hälfte: Die Symphylen, Pauropoden und Diplopoden. – Hölder, Wien. 414 pp., 16 lith. Tafeln mit 209 Fig.

Latzel, R. 1884c. Suivie de diagnoses d´espèces et des variétés nouvelles des Myriopodes, dans „Les Myriopodes de la Normandie, 1ʳᵉ liste", par H. Gadeau de Kerville. Rouen. Bulletin de la Société des Amis des Sciences naturelles de Rouen (année 1883) 251-272, 1 lith. Taf., 7 figs.

Latzel, R. 1884d. Description d´une espèce nouvelle du genre Julus in: Preudhomme de Borre; Note sur les Julides de Belgique. Annales de la Société Entomologique de Belgique. Tome 28, p. CCXLIX.

Latzel, R. 1885a. Die Myriopoden Kärntens. Jahrbuch des naturhistorischen Landesmuseums von Kärnten. 17. Heft, 14pp.

Latzel, R. 1885b. Lithobius oligoporus n. sp in Costa 1885: Diagnosi di nuovi Artropodi della Sardegna (1). Bullettino della Società entomologica italiana 17: 240-255.

Latzel, R. 1886a. Suivie de diagnoses d´espèces et de variétées nouvelles (des Myriopodes) de France, Algérie et Tunisie, dans „Les

Table 2. The acquisition of 1884 by the Naturhitorisches Museum, Wien with specified localities in square brackets

	Species	Locality
1.	*Lithobius grossipes* C. Koch, 1847	Kärnten [Klagenfurt]; Krain [Krainburg]; Tirol [Bozen]
2.	*Lithobius grossipes* C. Koch var.	Dalmatien [Zara]
3.	*Lithobius transsylvanicus* Latzel, 1882	Banate [Orsova]
4.	*Lithobius validus* Meinert, 1872	Kärnten [Villach]; Steiermark [Leoben]; Oberösterreich (= OÖ) [Gmunden]
5.	*Lithobius leptopus* Latzel, 1880	Kärnten [Millstadt]; Steiermark [Gesäuse, Hieflau]
6.	*Leptopus piceus* L. Koch, 1862	Niederösterreich (=NÖ) [Mauerbach]; Oberösterreich [Kirchdorf]; Salzburg [Salzburg]; Tirol [Kufstein]
7.	*Lithobius nodulipes* Latzel, 1880	Böhmen [Elbgrund]; Mähren [Adamsthal]; NÖ [Purkersdorf]; Steiermark [Eisenerz]; Küstenlande [Triest]
8.	*Lithobius nigrifrons* Latzel & Haase 1880	Kärnten [Raibl]; Galizien [Limanova]
9.	*Lithobius glabratus* C. Koch, 1847	Niederösterreich [Wien]; Ungarn [Szegedin]
10.	*Lithobius tricuspis* Meinert, 1872	Tirol [Achensee]; Kärnten [Bleiberg]
11.	*Lithobius agilis* C. Koch, 1847	Tirol [Kufstein]; Kärnten [Klagenfurt]; Krain [Adelsberg]
12.	*Lithobius dentatus* C. Koch, 1847	Niederösterreich [Schönbrunn]; Oberösterreich [Ischl]; Salzburg [Zell am See]
13.	*Lithobius aulacopus* Latzel, 1880	Oberösterreich [Kirchdorf]; Salzburg [Untersberg]; Steiermark [Graz]
14.	*Lithobius pygmaeus* Latzel, 1880	Kärnten [Loibl]
15.	*Lithobius cyrtopus* Latzel, 1880	Böhmen [Schneekoppe]; Mähren [Tessthal]; Schlesien [Altvater]; Oberungarn [Tatra]
16.	*Lithobius pelidnus* Haase, 1880	Oberösterreich [Kirchdorf]; Salzburg [Scharfling]
17.	*Lithobius mutabilis* L. Koch, 1862	Böhmen [Nachod]; Mähren [Adamsthal]; Schlesien [Freiwaldau]; Ungarn [Kaschau]
18.	*Lithobius latro* Meinert, 1872	Tirol [Patscherkofel]
19.	*Lithobius calcaratus* C. Koch, 1844	Normandie [Rouen]
20.	*Lithobius lapidicola* Meinert, 1872	Alpenländer Österreichs [Riva, Klagenfurt, Kirchdorf in Oberösterreich]
21.	*Lithobius stygius* Latzel, 1880	Adelsberger Grotte in Krain
22.	*Lithobius illyricus* Latzel, 1880	österreichische Küstenlande [Görz]
23.	*Lithobius muticus* C. Koch, 1847	Ungarn [Schemnitz]; NÖ [Brühl]; OÖ [Kirchdorf]; Salzburg [Untersberg]; Kärnten [Pörtschach]
24.	*Lithobius lucifugus* L. Koch, 1862	Oberösterreich [Wascheneck]; Salzburg [Schafberg]; Tirol [Brenner]
25.	*Lithobius audax* Meinert, 1872	Krain [Jauerburg]; Kärnten [Villach]
26.	*Lithobius aeruginosus* L. Koch, 1862	Oberösterreich [Gmunden]; Salzburg [St. Wolfgang]
27.	*Lithobius crassipes* L. Koch, 1862	Ungarn [Kaschau]; Niederösterreich [Prater bei Wien]; Kärnten [Klagenfurt]
28.	*Lithobius curtipes* C. Koch, 1847	Böhmen [Riesengebirge]; Mähren [Tessthal]; Schlesien [Karlsbrunn]
29.	*Henicops fulvicornis* Meinert, 1868	Niederösterreich [Ufer der Wien]; Böhmen [Elbgrund]; Schlesien [Jauernig]

Table 2. continued

Species	Locality
30. *Scolopendra cingulata* Latreille, 1829	österreichische Küstenlande [Görz, Pola]
31. *Cryptops punctatus* C. Koch, 1847	Croatien [Agram]; Ungarn [Temesvár]; Niederösterreich [Brühl]
32. *Cryptops hortensis* Leach, 1814	Oberösterreich [Gmunden]; Salzburg [Schafberg]; Kärnten [Villach]; Steiermark [Mürzthal]
33. *Mecistocephalus carniolensis* C. Koch, 1847	Tirol [Lienz]; Kärnten [Villach]; Steiermark [Leoben]; Krain [Laibach]; Croatien [Agram]
34. *Geophilus mediterraneus* Meinert, 1870	Tirol [Bozen]
35. *Geophilus strictus* Latzel, 1880	österreichische Küstenlande [Pinguente]
36. *Geophilus longicornis* Leach, 1814	Niederösterreich [Pittenthal]; Böhmen [Prag]; Mähren [Blansko]; Schlesien [Freiwaldau]
37. *Geophilus longicornis var. austriacus* Latzel, 1880	Niederösterreich [Geisberge]; Böhmen [Nachod]; Mähren [Blansko]
38. *Geophilus pygmaeus* Latzel, 1880	österreichische Küstenlande [Tarnowaner Wald bei Görz]; Kärnten [Loiblthal]
39. *Geophilus proximus* C. Koch, 1847	Schlesien [Altvater]; Böhmen [Prag]; Oberösterreich [Kirchdorf]; Steiermark [Graz]
40. *Geophilus electricus* Linneus, 1758	Böhmen [Eger]; Schlesien [Freiwaldau]
41. *Geophilus linearis* C. Koch, 1835	Kärnten [Klagenfurt]; Ungarn [Leythagebirge]
42. *Scolioplanes acuminatus* Leach, 1814	Böhmen [Riesengebirge]; Mähren [Tessthal]; Schlesien [Karlsbrunn]; Galizien [Krakau]; Salzburg [Zell/See]
43. *Scolioplanes crassipes* C. Koch, 1835	Galizien [Przemysl]; Steiermark [Mürzthal]; Küstenland [Görz]; Tirol [Innsbruck]
44. *Schendyla nemorensis* C. Koch, 1837	Alpenländer [Eisenerz]; Wien [botan. Garten]; Böhmen [Nachod]; Schlesien [Freiwaldau]
45. *Chaetechelyne vesuviana* Newport, 1844	Tirol [Bozen]
46. *Scotophilus illyricus* Meinert, 1870	Ungarn [Ofen-Pest]; Niederösterreich [Brühl]; Küstenlande [Triest]
47. *Scotophilus bicarinatus* Meinert, 1870	aus dem Küstenlande [Görz]
48. *Dignathodon microcephalum* Lucas, 1846	Dalmatien [Zara]; österreichische Küstenlande [Triest]
49. *Stigmatogaster gracilis* Meinert, 1870	Dalmatien [Cattaro]; und dem österreichischen Küstenlande [Pola]
50. *Scolopendrella nivea* Scopoli, 1763	Kärnten [Klagenfurt]; Steiermark -?-; Niederösterreich [Pittenthal]
51. *Scolopendrella immaculata* Newport, 1845	Böhmen [Riesengebirge]; Kärnten [Friesach]; Ungarn [Tatra]
52. *Pauropus huxleyi* Lubbock, 1867	Niederösterreich [Pittenthal]; Kärnten [Kreuzberg bei Klagenfurt]
53. *Brachypauropus hamiger* Latzel, 1884	Kärnten [zwischen Klagenfurt und Pörtschach]
54. *Eurypauropus ornatus* Latzel, 1884	Niederösterreich [Pittenthal]
55. *Eurypauropus cycliger* Latzel, 1884	Niederösterreich [Pittenthal]; Kärnten [zwischen Klagenfurt und Pörtschach]
56. *Polyxenus lagurus* (Linnaeus, 1758)	Niederösterreich [Neuwaldeck]; Kärnten [Kreuzberg bei Klagenfurt]
57. *Gervaisia costata* Waga, 1857	Ungarn [Rutek]; Mähren [Adamsthal]; Niederösterreich [Pittenthal]; Kärnten [Satnitz]
58. *Glomeris minima* Latzel, 1884	Oberösterreich [Kirchdorf]
59. *Glomeris marginata* (Villers, 1789)	Normandie [Rouen]

Table 2. continued

60. *Glomeris cingulata* C. Koch, 1847	österreichische Küstenlande [Isonzothal]
61. *Glommeris connexa var. alpina* Latzel, 1884	Kärnten [Karawanken]; Tirol [Innsbruck]
62. *Glommeris connexa var. carpathica* Latzel, 1882	Galizien [Rabka]; Oberungarn [Tatra]
63. *Glomeris ornata* C. Koch, 1847	österreichische Küstenlande [Tschitschenboden]
64. *Glomeris tridentina* Latzel, 1884	Südtirol [Riva]
65. *Glomeris conspersa* C. Koch, 1847	Kärnten [Satnitz]; österreichische Küstenlande [Görz]
66. *Glomeris conspersa var. excellens* Latzel, 1884	österreichische Küstenlande [Görz]
67. *Brachydesmus superus* Latzel, 1884	Niederösterreich [Prater bei Wien]
68. *Brachydesmus subterraneus* Heller, 1857	Adelsberger Grotte in Krain
69. *Brachydesmus inferus* Latzel, 1884	Vodena Jama in der Militärgrenze
70. *Polydesmus denticulatus* C. Koch, 1847	Ungarn [Pressburg]; Niederösterreich [Prater bei Wien]; Oberösterreich [Gmunden]
71. *Polydesmus rangifer* Latzel, 1884	Kärnten -?-; österr. Küstenlande [Görz]
72. *Polydesmus edentulus* C. Koch, 1847	Kärnten [Klagenfurt]
73. *Polydesmus tatranus* Latzel, 1882	Oberungarn [Kohlbachthal]; Galizien [Galizische Tatra]
74. *Paradesmus gracilis* C. Koch, 1847	Margarethen Insel bei Ofen [Pest]
75. *Strongylosoma iadrensis* Pregl, 1883	Dalmatien [Zara]
76. *Atractosoma meridionale* Fanzago, 1876	Tirol [Patscherkofel]; Kärnten [Villacher Alpe]; Küstenlande [Görz]
77. *Craspedosoma carpathicum* Latzel, 1882	Galizische und ungarische Tatra
78. *Atractosoma athesinum* Fedrizzi, 1877	Ungarn [Herkulesbad]; Kärnten [Satnitz]; Oberösterreich [Kirchdorf]
79. *Atractosoma bohemicum* Rosický, 1876	Mähren; Niederösterreich; Oberösterreich
80. *Craspedosoma rawlinsii* Leach, 1814	Oberösterreich [Kirchdorf]; Niederösterreich [Kierlingsthal]
81. *Craspedosoma oribates* Latzel, 1884	Oberösterreich [Gradenalm]
82. *Craspedosoma stygium* Latzel, 1884	Adelsberger Grotte in Krain
83. *Craspedosoma mutabile + var. fasciatum* Latz., 1884	östliche Alpenländer [Klagenfurt]; Ungarn [Rutek]
84. *Craspedosoma mutabile var. punctulatum* Latz., 1884	Schlesien
85. *Craspedosoma flavescens* Latzel, 1884	Niederösterreich [Schönbrunn]; Oberösterreich [Kirchdorf]
86. *Chordeuma silvestre* C. Koch, 1847	Tirol [Bozen]
87. *Lysiopetalum degenerans* Latzel, 1884	Serbien ?
88. *Lysiopetalum illyricum* Latzel, 1884	österreichische Küstenlande [Görz; Pola]
89. *Lysiopetalum carinatum* Brandt, 1840	Dalmatien [Zara; Cattaro]

Table 2. continued

Species	Locality
90. *Lysiopetalum fasciatum* Latzel, 1883	Banate [Herkulesbad]; Serbien ?
91. *Lysiopetalum anceps* Latzel, 1884	österreichische Küstenlande [Triest]
92. *Isobates varicornis* C. Koch, 1847	Niederösterreich [Pittenthal]; Kärnten [Südufer des Wörthersees]
93. *Blaniulus venustus* Meinert, 1868	Niederösterreich [Prater bei Wien]
94. *Blaniulus fuscus* Am Stein, 1857	Tirol [Achensee]
95. *Blaniulus guttulatus* Bosc, 1792	Niederösterreich [Pittenthal]; Böhmen [Eger]
96. *Iulus strictus* Latzel, 1883	Serbien ?
97. *Iulus nanus* Latzel, 1884	Oberösterreich [Kirchdorf]; Galizien [Krakau]
98. *Iulus pelidnus* Latzel, 1884	Kärnten [Tarvis]; Steiermark [Eisenerz]
99. *Iulus dicentrus* Latzel, 1884	Kärnten [Loiblthal]; Küstenlande [Tarnowaner Wald]
100. *Iulus molybdinus* C. Koch, 1847	Oberösterreich [Rossleithen]; Salzburg [Untersberg]; Kärnten [Südufer des Wörthersees]
101. *Iulus imbecillus* Latzel, 1884	Oberösterreich [Kirchdorf]
102. *Iulus pusillus* Leach, 1814	Niederösterreich [Prater bei Wien]
103. *Iulus luscus* Meinert, 1868	Niederösterreich [Prater bei Wien]
104. *Iulus boleti* C. Koch, 1847	Oberösterreich [Kirchdorf]; Niederösterreich [Pittenthal]; Croatien [Agram]
105. *Iulus luridus* C. Koch, 1847	Niederösterreich [Payerbach]; Steiermark [Eisenerz]; Kärnten [Friesach]; Tirol [Kufstein]
106. *Iulus platyurus* Latzel, 1884	Serbien ?; Ungarn [Herkulesbad]
107. *Iulus austriacus* Latzel, 1884	Kärnten [Sattnitz]; Krain [Adelsberg]; Mähren [Adamsthal]; Schlesien [Freudenthal]
108. *Iulus austriacus var. erythronotus* Latzel, 1884	Südungarn [Herkulesbad]
109. *Iulus austriacus var. nigrescens* Latzel, 1884	Galizien [Przemysl]; Mähren [Schönberg]
110. *Iulus podabrus* Latzel, 1884	Dalmatien [Cattaro]
111. *Iulus albolineatus* Lucas, 1845	Südtirol [Rovereto]
112. *Iulus montivagus* Latzel, 1884	Niederösterreich [Baden]
113. *Iulus trilineatus* C. Koch, 1847	österr. Küstenlande [Görz]; Dalmatien [Zara]; Südtirol [Riva]
114. *Iulus longabo* C. Koch, 1847	Niederösterreich [Pittenthal]; Oberösterreich [Kirchdorf]; Steiermark [Judenburg]
115. *Iulus fallax* Meinert, 1868	Schlesien [Altvater]; Galizien [Rabka]; Oberungarn [Tatra]; Niederösterreich [Brühl]; Tirol [Innsbruck]
116. *Iulus fallax var. oribates* Latzel, 1884	Kärnten [Villacher Alpe]; Tirol [Sonnwendjoch]
117. *Iulus scandinavius* Latzel, 1884	Oberösterreich [Kirchdorf]; Niederösterreich [Prater bei Wien]
118. *Iulus sabulosus* Linnaeus, 1758	Galizien [Krakau]; Niederösterreich [Brühl]; Tirol [Zillerthal]

Table 2. continued

119. *Iulus sabulosus var. apunctulatus* Fedrizzi, 1877	Südtirol [Bozen]
120. *Iulus fuscipes* C. Koch, 1847	Dalmatien [Zara]; österreichische Küstenlande [Görz; Triest]
121. *Iulus mediterraneus* Latzel, 1848	Spanien [Andalusien]; Frankreich [Vichy]; Oberitalien [Lombardei]
122. *Iulus cattarensis* Latzel, 1848	Dalmatien [Cattaro]
123. *Iulus flavipes* C. Koch, 1847	Dalmatien [Lissa]: Küstenlande [Lussin grande]
124. *Iulus varius* Fabricius, 1781	öster. Küstenlande [Görz; Triest]
125. *Polyzonium germanicum* Brandt, 1831	Galizien [Rabka]; Ungarn [Kaschau]; Croatien [Agram]

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Condexenus, a new genus of the millipede family Synxenidae (Diplopoda, Polyxenida) from Namibia

Monique Nguyen Duy-Jacquemin

Nguyen Duy-Jacquemin, M. 2006. *Condexenus*, a new genus of the millipede family Synxenidae (Diplopoda, Polyxenida) from Namibia. Norw. J. Entomol. 53, 237-248.

A second genus of Synxenidae, *Condexenus* gen. n., is described, for a new species *Condexenus biramipalpus* sp. n., discovered in Namibia. It differs from *Phryssonotus* Scudder, 1885 in the structure of the scale-like tergal trichomes and, especially, in having only 11 tergites, i.e. one less diplosegment than Phryssonotus. In the latter respect, *Condexenus* appears to occupy an intermediate position between Polyxenoidea (maximum of 11 tergites) and *Phryssonotus*, (as many as 12 tergites), thus supporting the hypothesis of a trend towards a shortened postembryonic development in the evolution of Polyxenida.

Key words: Synxenoidea, Polyxenoidea, Synxenidae, *Phryssonotus, Condexenus*, new species, postembryonic development, tergite.

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INTRODUCTION

Among the three known families of Penicillata (the fourth, Hypogexenidae Schubart, 1947, being insufficiently described), Synxenidae have higher number of leg pairs (17 instead of 13) and show specializations absent in other Penicillata: last two pairs of legs adapted for jumping, scale-shaped trichomes, and long vulval sacs. Since Silvestri's erection of the Synxenidae (1923) and Synxenoidea (1948a), these taxa have remained monogeneric. The family was originally based on the genus *Synxenus* Silvestri, 1900, which included several Recent species, but this was later synonymized with the fossil genus *Phryssonotus* Scudder, 1885 by Condé (1954). The six known extant species of *Phryssonotus* are all Neotropical: *orientalis* (Silvestri, 1900), from Uruguay; *chilensis* (Silvestri, 1948b), from Chile; *cubanus* (Silvestri, 1948b), from Cuba; *capensis*

(Silvestri, 1923) from the Republic of South Africa, Mozambique, Madagascar and Papua-New Guinea; *novaehollandae* (Silvestri, 1923), from Australia; and *platycephalus* (Lucas, 1846), from Mediterranean North Africa, Sicily and Spain. The identification of species is difficult, the two principal characters of Silvestri's key (1923) – number of ocelli and number of trichomes arranged in a row, near the internal short trichobothrium – are not always clear, particularly in fossil species such as *Phryssonotus hystrix* (Menge, 1854) from the Eocene Baltic amber, *Phryssonotus burmiticus* (Cockerell, 1917) (Rasnitsyn & Golovatch 2004) from Cretaceous Burmese amber and *Phryssonotus* sp. (Nguyen Duy - Jacquemin & Azar 2004) from amber of France.

Here a new genus of Synxenidae is described, based on a new species from Namibia, representing the first new genus of Synxenidae to be discovered for over a century.
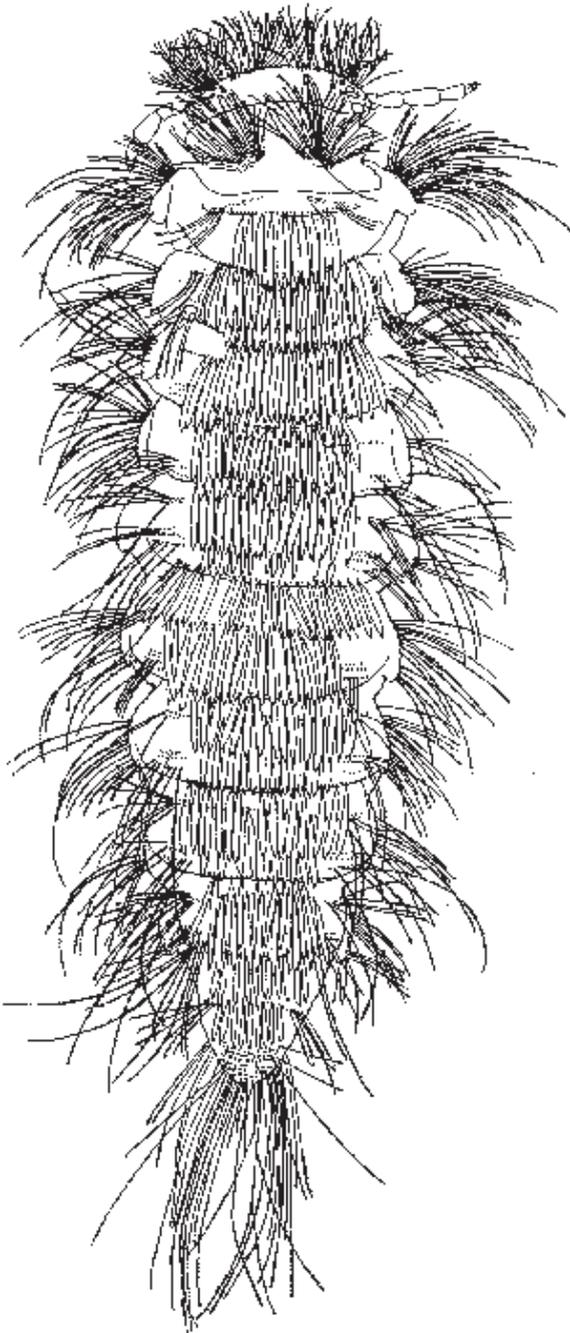
Figure 1. *Condexenus biramipalpus* n. sp., holotype subadult male, habitus, dorsal view, body length: 3mm.

MATERIAL AND METHODS

The material examined was found in Namibia: 23-24 km north-west of Keetmanshoop, in pitfall traps, in savannah (Nama-Karoo) with dwarf shrubs. The specimens formed part of the material of Penicillata collected by Katrin Vohland and Tharina Bird during the "BIOTA Programme". Details of the collections are as follows (p.l. = pair of legs):

– Distr. Gellap 0st 3, 23 km NW Keetmannshoop, 26°24'11.8"S/18°00'22.8"E, pitfall trap E6. 13.-21.x.2001 leg. A. Hoffmann: one male holotype with 14 pairs of legs; 26°24'12.8°S/18°00'22.8"E, same data, same collector, different pitfall traps: one female 14 p.l., 4 ind. 8 p.l., 4 ind. 5 p.l., 1 ind. 4 p.l., 27.ii-6.iii.2003: 2 ind. 10 p.l., 4 ind. 8 p.l.; 26°24'13.3"S, 18° 00'22.9"E, pitfall trap E3. 16.-23.x. 2002 leg. A. Hoffmann: 1 ind. 6 p.l.., 26°24'30.2"S/19°00'28.5"E, pitfall traps: outcrop (ZMHB4964), 4.-8.vi.2002, leg. M. Uhlig: one male with 14 pairs of legs.; – Distr. Nabaos, 7 (Nuwe Fontein) 24 km NW Keetmannshoop, 26°23'36.1"S/17°59'43.9"E, pitfall trap. 4.-8. iv. 2002 leg. M. Uhlig: 2 ind. 12 p.l. and 2 ind. 10 p.l.

SYSTEMATICS

Superfamily Synxenoidea Silvestri, 1923
Family Synxenidae Silvestri, 1923
Genus *Condexenus* n. gen.

Type species
Condexenus biramipalpus n. sp. (Figure 1)

Etymology
Condexenus is dedicated to the late Prof. Bruno Condé, who made many important contributions to the systematics of Penicillata.

Diagnosis
Head: Numerous ocelli. Insertion of head trichomes in 4 distinct areas. Antennal sensilla basiconica thick and short: two apical and others more basal on antennal article VI; two on article

VII. Three trichobothria of equal size with cylindrical funiculi (Figure 9). Entire surface of labrum with numerous papillae of different sizes, armed with lamellate teeth at anterior margin (Figure 12). Each gnathochilarial palpus with a long lateral expansion; palp sensillae flexible at middle.

Trunk: Collum with barbate trichomes arranged in two large median areas (Figure 9) and a few lateral trichomes. Tergites II to XI with scale-shaped dorsal trichomes arranged in two transverse rows: submedian and posterior rows with each lateral end prolonged by barbate trichomes. Lateral barbate trichomes sometimes very long.

Legs: Legs short, last two pairs terminating in palettes rather than claws (Figures 16, 19). Long and very fine setae on trochanters, prefemora, tibiae and tarsi. Telotarsus without posterior lamellate process, bearing an anterior process with spinous projection; claw with two strongly pointed latero-anterior and posterior teeth (Figure 17). Female vulvae (termed ovipositors by Silvestri, 1923) elongate, subconical; coxal glands present in male.

Telson: Conical telson with a transversal row of a few scale-shaped trichomes and long barbate trichomes on distal part.

Condexenus biramipalpus sp.n.

Etymology
The specific name refers to the two expansions of each palpus.

Type material:
Three subadult specimens with 14 pairs of legs: holotype male and one paratype female deposited in the MNHN, Paris and one paratype male, deposited to National Museum of Namibia, Windhoek (SMWN). In Polyxenida the subadults show the characters of adults; for example, the subadult females of *Polyxenus lagurus* are reproductive.

Description
Subadults: Stage VIII

Measurements: Body length (without caudal penicil) 3 mm in holotype and paratype female, 2.40 mm in paratype male. Length of caudal penicil 0.70 mm; length of head trichomes 0.10 mm. Length tarsi II of first legs 120 µm in holotype, 97 µm in paratype male, 126 µm: in paratype female; those of 13th legs 166 µm in holotype, 136 µm in paratype male, 172 µm in paratype female.

Head: Nine ocelli on each side (Figure 9). Insertion of head trichomes (between ocelli and antennae) in four distinct areas (Figure 11). Antennal article VI with two apical thick sensilla basiconica, the posterior one shorter than the anterior, and with two (paratype female: Figure 5) or four (left antenna of holotype: Figure 7) others more basal; one posterior coeloconicum sensillum. Antennal article VII with 2 sensilla basiconica, posterior one the shortest; one coeloconicum sensillum posterior and one setiform sensillum between the two sensilla basiconica (Figures 4, 6). The two antennae of the paratype male and the right antenna of holotype are regenerated, hence these are not described. Three trichobothria of equal size with cylindrical funiculi (Figures 9, 10). The labral surface is covered by numerous flat papillae, with four to six posterior rows of smaller papillae in median part and 12 to 15 lamellate teeth at anterior margin (Figure 12). Clypeo-labrum with 5 to 8 setae along posterior margin. Each palpus with a long lateral expansion (*l.e*) and a short median expansion (*m.e*) (Figure 13). 24 to 29 sensilla on long expansion in males; 29 on left (Figure 13) and 32 on right expansion in female; 10 to 14 on short expansion (Figure 13); sensilla thinner from their middle and flexible at this level, except for five or six short antero-median sensilla. (median part of palpus and short expansion with a total about 25 sensilla).

Trunk: Collum (tergite I) with two median, separate, oval clusters of about 80 (holotype, Figure 9: *b.t*), 55 (paratype male) and 90 (paratype female) barbate trichomes and two isolated lateral barbate trichomes (Figure 9). Tergites II to X with submedian and posterior rows of scale-shaped trichomes (*sc*) directed caudal (Figure 1), the posterior one arranged along the posterior margin
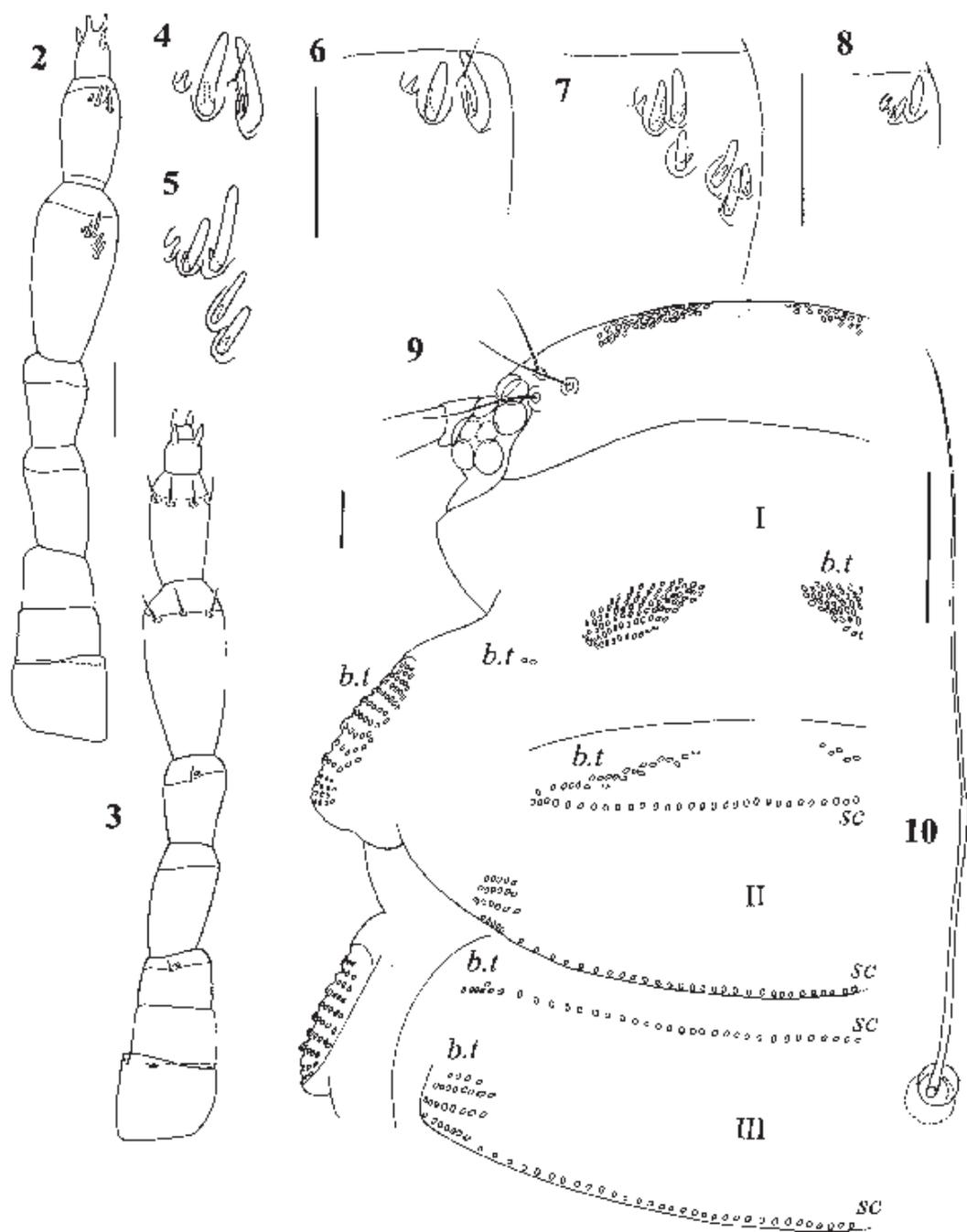
Figures 2-10. *Condexenus biramipalpus* n. sp. **2,3:** left antenna of paratype female, dorsal and ventral view; **4,5:** sensilla of articles VII and VI of previous antenna; **6,7:** sensilla of left antennal articles VII and VI of holotype; **8:** left antennal sensilla of article III of larva with 5 p.l.; **9:** head, insertions of trichomes on collum (I) and tergites II and III of left part of holotype; **10:** detail of left postero-external trichobothrium of holotype. Abbreviations: *b.t,* barbate trichomes; *sc,* scale. Scale bars: 2, 3, 9, 50 µm; others 25 µm.

of tergite (Figure 9); one area of aligned barbate trichomes (*b.t*) at end of each row (Figure 9), except on tergite II where the barbate trichomes form, on each side, two diagonal lines above the first scale row (Figure 9). In holotype, the number of scales by row is 32 and 40 on tergite II, 40 to 53 on tergites III to IX and 33 and 26 on tergite X.

Legs: Short, with 8 articles except on first and last (14th) pairs of legs; last pair without telotarsus, terminating in palettes (Figures 16, 19). One pair of appendage-buds (Figure 16: *e.b*) situated on lateral side of anal valves. Inside the external buds, the 15th pair of adult legs will develop and the adult will have its last two pairs (14th and 15th) of legs terminating in palettes.

Legs I to XIII with trochanter, prefemur and first tarsus each bearing one long and very fine seta; coxa leg I with one setae, coxa of leg II in males with 2 setae (Figure 15), other coxae without setae; tibial setae present on legs I to XIII in female, on I to XII in holotype and on I to IV in paratype male. Legs XIV only with two setae on trochanter (fig.16). Seta of second tarsus (Figure 18) longer than the claw (Figure 17). Telotarsus bearing anterior process (*a.p*) with spinous projection shorter than claw, without posterior lamellate process; claw with two subequal, strongly pointed latero-anterior and posterior teeth (Figure 17: *t*).
Female: subconical vulval sacs reaching as far as the fourth pair of legs and bearing numerous small setae, inserted in parallel circumferential rows, and fewer longer setae.
Male: all areas of penis with thin, ordinary, cuticular setae and a dozen longer setae (Figure 15). Coxal glands on coxae of legs X.

Telson: Conical telson with a transverse row of 14 (holotype), 8 (paratype male) and 19 (female) scale-shaped trichomes with each lateral end prolonged by barbate trichomes; long barbate trichomes on distal part (Figure 1).

Larvae stadium II
Material: One larva with 4 pairs of legs.

Measurements: Body length (without caudal penicil) 1 mm; tarsus II of 4th leg 90 µm.
Head: 5 ocelli. 3 subequal trichobothria. 5 antennal articles; article III with two sensilla basiconica – anterior short and thick, near smaller one – and one posterior coeloconicum sensillum inside a cavity (Figure 8). Article IV with same sensilla as in adults: two sensilla basiconica (posterior smaller than anterior), one setiform sensillum between them, and one coeloconicum sensillum. Clypeo-labrum with 6 setae along posterior margin. Labral surface covered by numerous flat papillae with six posterior rows of smaller papillae decreasing to three rows laterally. Each palpus with a long lateral expansion and a short median expansion.

Trunk: Collum with separate oval areas of 20 and 21 trichomes and two lateral trichomes. On tergites, the scales have been lost except one on tergite IV. One pair of external buds.

Larvae stadium III
Material: Four larvae with 5 pairs of legs.

Measurements: Body length (without caudal penicil) 1.10 mm in 3 larvae, 0.95 mm in 1 larva; tarsus II of 5th leg 108 to 114 µm.

Head: 7 ocelli. 3 subequal trichobothria. 5 antennal articles; antennal sensilla as in larva II. Clypeo-labrum with 6 to 7 setae along posterior margin. Labral surface covered by numerous flat papillae as in larva II. 11 lamellate teeth at anterior margin. Each palpus with a long lateral expansion and a short median expansion.

Trunk: Collum with separate oval areas of 28 to 31 trichomes and two lateral trichomes. One pair of external buds.

Telson: One row with 6 to 7 scales.

Larvae stadium IV
Material: One larva with 6 pairs of legs.

Measurements: Body length (without caudal penicil): 0.95 mm; tarsus II of 6th leg: 117 µm.
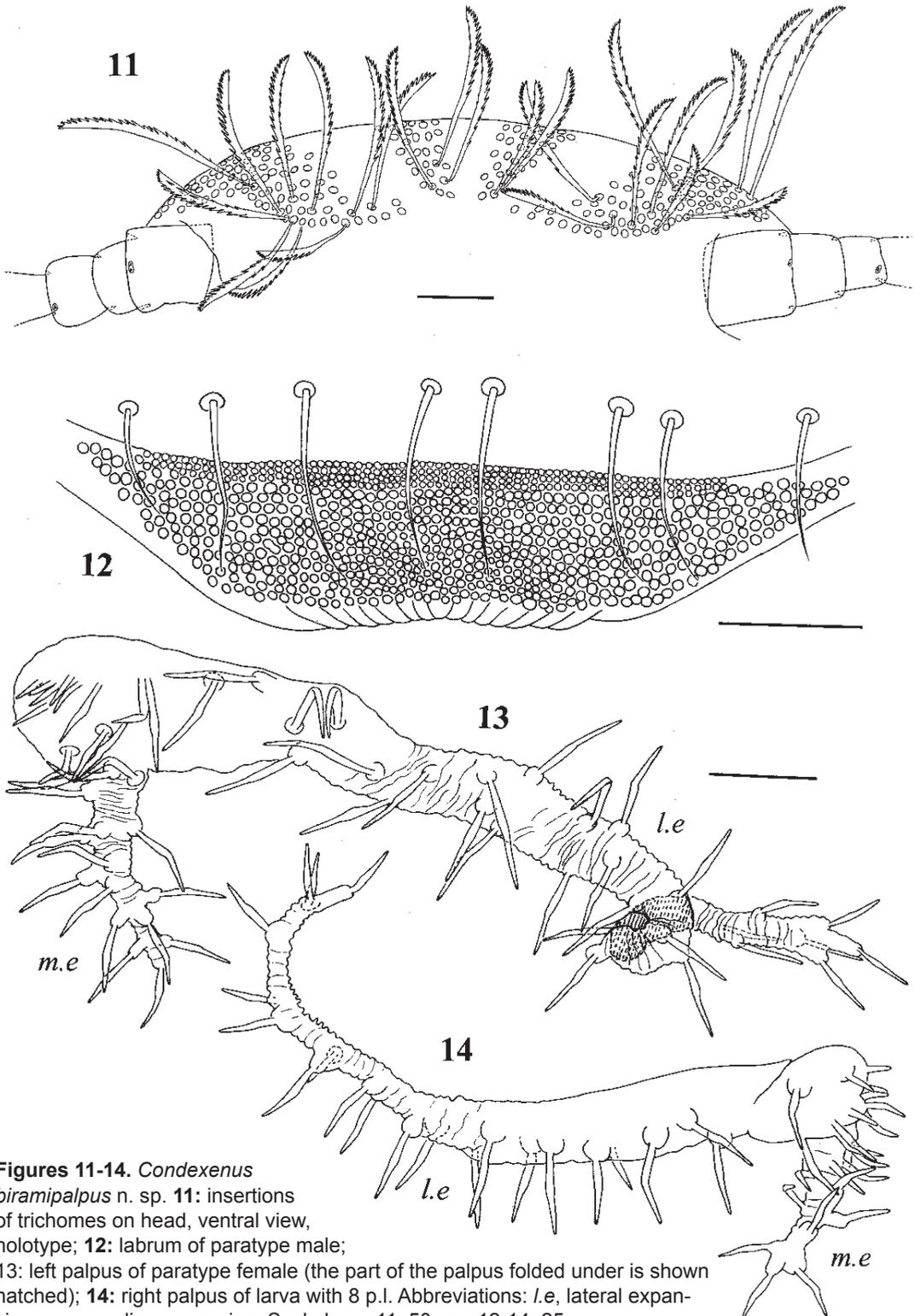
Figures 11-14. *Condexenus biramipalpus* n. sp. **11:** insertions of trichomes on head, ventral view, holotype; **12:** labrum of paratype male; 13: left palpus of paratype female (the part of the palpus folded under is shown hatched); **14:** right palpus of larva with 8 p.l. Abbreviations: *l.e*, lateral expansion; *m.e*, median expansion. Scale bars: 11, 50 µm; 12-14, 25 µm.

Head: 7 ocelli, 7 antennal articles; antennal sensilla, labrum and gnathochilarium as in larva III.

Trunk: Collum with separate oval areas of 32 trichomes and two lateral trichomes. Two pairs of external buds.

Telson: One row of 6 scales.

Larvae stadium V
Material: Eight larvae with 8 pairs of legs

Measurements: Body length (without caudal penicil) 1.20 to 1.45 mm; tarsus II of 8th leg 90 to 112 μm.

Head: 8 ocelli, 7 antennal articles; antennal sensilla as in larva IV. Clypeo-labrum with 6 to 7 setae along posterior margin. Labral surface covered by numerous flat papillae, with five or six posterior rows of smaller papillae in median part, decreasing to three rows laterally. 8 to 10 lamellate teeth at anterior margin. Each palpus with a long lateral expansion and a short median expansion (Figure 14). Two pairs of external buds.

Trunk: Collum with separate oval areas of 32 to 37 trichomes and two lateral trichomes.

Telson: One row of 4 to 6 scales.

Larvae stadium VI
Material: Two larvae with 10 pairs of legs

Measurements: Body length (without caudal penicil) 1.50 to 1.80 mm; tarsus II of 10th leg 115 μm.

Head: 8 ocelli. Probably 8 antennal articles (antennae broken); antennal sensilla as in larva II. Clypeo-labrum with 9 setae along posterior margin. Labral surface covered by numerous flat papillae, posteriorly with four or five rows of smaller papillae, decreasing to three rows laterally. 11 lamellate teeth at anterior margin. Each palpus with a long lateral expansion and a short median expansion.

Trunk: Collum with separate oval areas of 38 to 39 trichomes and two lateral trichomes. Two pairs of external buds.

Telson: One row of 6 or 7 scales.

Larvae stadium VII
Material: Two larvae males with 12 pairs of legs

Measurements: Body length (without caudal penicil) 2.10 mm; tarsus II of 12th leg 136-152 μm.

Head: 9 ocelli. Antennae broken, hence antennal sensilla not observed. Labral surface covered by numerous flat papillae, with five posterior rows of smaller papillae in median part and 13 lamellate teeth at anterior margin; clypeo-labrum with 7 setae along posterior margin.

Trunk: Collum with separate oval areas of 45 to 52 trichomes and two lateral trichomes. Coxal glands on legs X. Two pairs of external buds.

Telson: Telson with 8 or 9 scales.

Remarks on postembryonic development (Table 1)

From the stadium II onwards, the scales cover the tergites except the collum; the first larva of *Condexenus* is unknown, but it probably lacks scales, as in *Phryssonotus* (Condé 1971, Nguyen Duy-Jacquemin 1973). The larva III of *Condexenus* and *Phryssonotus* differs from those of Polyxenidea in having 5 antennal articles instead of 7. The larva V of *Condexenus* has only 7 antennal articles, whereas in all Polyxenoidea and in *Phryssonotus* from Australia (M. Short, pers. comm.), the larva V has 8 articles. It can be assumed that the larva VI of *C. biramipalpus* has 8 antennal articles (Table 1: 8?), in spite of the absence of antennae in larvae VI and VII. The stage of appearance the sensilla basiconica situated below the two apical sensilla (present from larva II onwards) is not known. However, the antennal development is evidently slower in
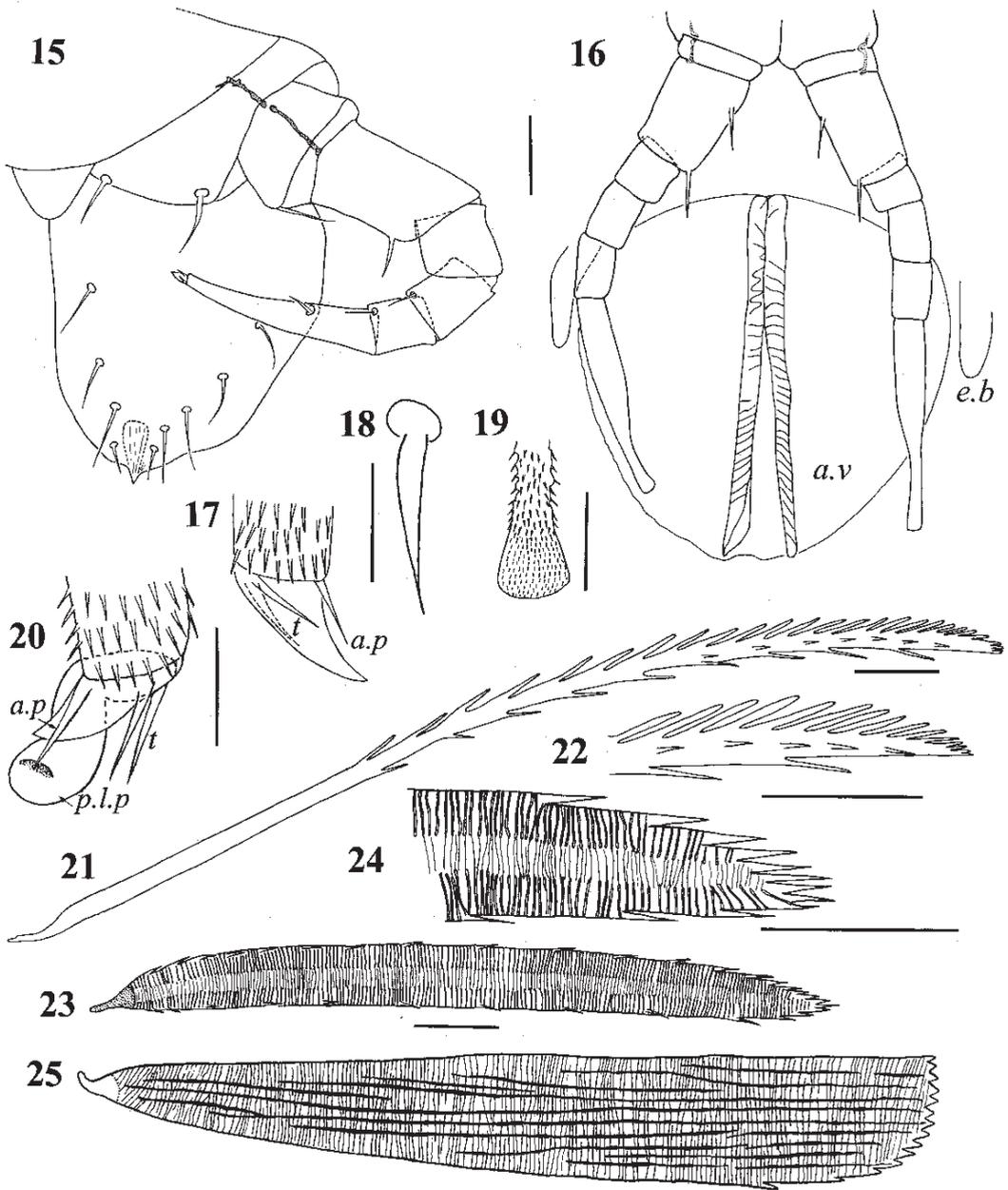
Figures 15-25. *Condexenus biramipalpus* n. sp. **15:** left leg II and penis of holotype; **16:** legs XIV and external buds of future legs XV of paratype male; **17:** telotarsus of right leg II and **18:** seta of left tarsus II of holotype; **19:** palette (end) of left tarsus XIV of paratype male; **20:** *Phryssonotus* sp. female with 16 p.l. from Zapallar Valparaiso Prov., Argentina, telotarsus left leg IX; **21:** *Condexenus biramipalpus* n. sp.: lateral barbate trichomes of a row of tergite VIII of holotype; **22:** end of an other barbate trichome; **23:** scale of posterior row of tergite VIII of holotype; **24:** detail of other scale of holotype; **25:** scale of tergite VIII of *Phryssonotus capensis* male with 12 p.l from Mtuzini, Natal. Abbreviations: *a.p*, anterior process; a.v, anal valves; *e.b*, external bud; *p.l.p*, posterior lamellate process; *t*, latero-anterior and posterior teeth. Scale bars:15, 16, 50 µm; 17 to 20, 10 µm; others 25 µm.

Lophoturus madecassus: Lophoproctidae
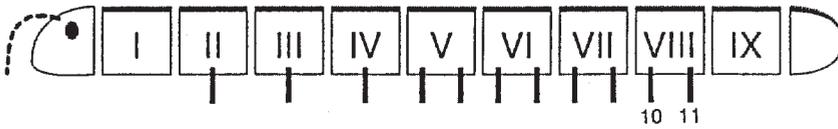
Lophoproctidae + Polyxenidae
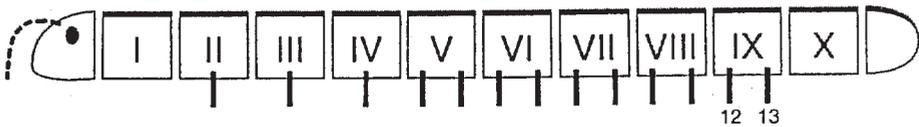
Condexenus biramipalpus: Synxenidae
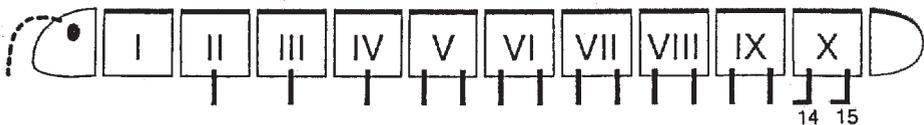
Phryssonotus: Synxenidae
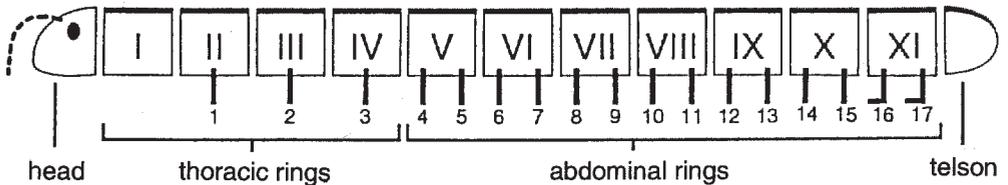
Figure 26. Comparison of segmentation in Polyxenida.

C. biramipalpus than other Polyxenida.

DISCUSSION

In 1923, Silvestri defined the characters of genus *Synxenus* (valid name now *Phryssonotus*) and considered that the erection of a family was justified for this genus.

Comparison between *Condexenus* and *Phryssonotus*

Characters common to Condexenus and

Phryssonotus
- Numerous ocelli: 9 in *Condexenus*; 9 to 11 in *Phryssonotus*.
- Long lateral expansion of gnathochilarial palp.
- Two types of trichomes: barbate (Figures 21, 22) and scale-shaped (Figures 23, 25). Insertion of trichomes: head with barbate trichomes in 4 distinct areas, collum with barbate trichomes arranged in two large, oval, median areas and a few lateral trichomes. Tergites II to X with scale-shaped dorsal trichomes arranged in two

Table 1. Anamorphosis of *Condexenus biramipalpus*.

STADIUM	I	II	III	IV	V	VI	VII	VIII	IX
Leg pairs	3	4	5	6	8	10	12	14	15
Ocelli	5	5	7	7	8	8	9	9	9 ?
Antennal articles	5	5	5	7	7	8 ?	8	8	8

transverse rows: submedian and posterior rows with each lateral end prolonged by barbate trichomes. Conical telson with a transversal row of a few scale-shaped trichomes, with each lateral end prolonged by barbate trichomes and long barbate trichomes on distal part.
- Legs short, last two pairs terminating in palettes rather than claws.
- Female with subconical vulva sacs elongated (termed ovipositors by Silvestri, 1923).
Given all these shared characters, *Condexenus* undoubtedly belongs to the family Synxenidae

Differences between Condexenus and Phryssonotus
- 11 tergites, including collum and telson, in *Condexenus*; 12 tergites in *Phryssonotus*.
- 15 pairs of legs in *Condexenus*; 17 pairs of legs in *Phryssonotus*.
- Different structure of scale-shaped dorsal trichomes. It is noteworthy that there are no longitudinal stripes in *Condexenus* (Figures 23, 24, 25).
- Short median expansion of gnathochilarium is specific to *Condexenus*.
- 3 trichobothria of equal size in *Condexenus*; 2 subequal trichobothria and a smaller one in *Phryssonotus*.
- In *Condexenus*, the labral surface is covered by numerous flat papillae with four to six posterior rows of smaller papillae (Figure 12); in *Phryssonotus* the labral surface is covered by cuspidate papillae in addition to anterior rows of larger papillae.
- Telotarsus without posterior lamellate process in *Condexenus* (Figures 17, 20).
- The antennal article VI has two short and thick sensilla basiconica apically and two to four others

basally. Silvestri did not describe the antennal sensilla of *Phryssonotus*, but the specimens I have observed of this genus have thinner sensilla basiconica.

Position of the genus *Condexenus* in the Polyxenida

The description of *Condexenus biramipalpus* is based on 3 subadult specimens: 2 males and one female. All three have 14 pairs of legs and one pair of appendage-buds. Inside the external buds, the 15th pair of adult legs will develop; the adult has the last two pairs of legs terminating in palettes. By analogy with *Phryssonotus*, it is probable that *Condexenus* do not acquire a new tergite between the subadult and adult stages.

Table 2 shows the tergites and pairs of legs number in the different families of Polyxenida. One species of Lophoproctidae, *Lophoturus madecassus*, has only eleven pairs of legs and 10 tergites.

By the examining the trunk musculature of Diplopods, Manton (1961) and later Demange (1967) showed the original position of the legs in relation to tergites, sternites and pleurites. In *P. lagurus* Manton (1961) described a displacement of the anterior legs of each diplosegment, which lie below the pleurites and tergite of the preceding segment. In all Penicillata, at each moult from stage IV (with 6 pairs of legs) to the subadult stage, one posterior metamere of the diplosegment appears conjointly with an anterior metamere, a tergite and two paratergites of the next diplosegment (Nguyen Duy-Jacquemin 1969). During the moult

Table 2. Position of genus *Condexenus* (gen. n.) in Polyxenida.

SUPERFAMILY	FAMILY	GENUS Collum, telson included	Tergites number	Pairs of legs
POLYXENOIDEA	Lophoproctidae	5	10*	11*
			11	11
	Polyxenidae	21	11	13
	Hypogexenidae	1	Poorly known	
SYNXENOIDEA	Synxenidae	*Condexenus*	11	15
		Phryssonotus	12	17

* one species: *Lophoturus madecassus*.

from subadult to the adult stage, only the posterior metamere appears and thus only one pair of legs is added.

In adult Polyxenoidea, a new tergite and two paratergites are added (ring X in Polyxenidae and Lophoproctidae, except the species *Lophoturus madecassus*: ring IX), but not the anterior metamere (Figure 26). In adult *Phryssonotus*, no new tergites or paratergites are added and further development is not possible. This might also be true for *Condexenus*, but adults will be necessary to confirm whether this is the case. This supports the hypothesis of a trend towards a shortened postembryonic development in the evolution of Polyxenida (Condé 1969): Lophoproctidae are the most evolved and *Phryssonotus* the most primitive. Condexenus has 2 pairs of legs less than *Phryssonotus* and probably one diplosegment less. It therefore appears to occupy an intermediate position between *Phryssonotus* and the Polyxenoidea. On the other hand, the differentiation of the last two leg-pairs in Synxenidae into jumping legs might instead point to a secondary increase in the number of leg-pairs (Enghoff et al.1993) and the scales might be an adaptation to warm and dry biotopes. The fossil Polyxenidae and Synxenidae founded in Cretaceous ambers belong to recent genera, so it is still difficult to say anything about ancestral states of the characters. The comparison of the Upper Carboniferous/Lower Permian fossil *Arthropleura*

(Kraus 2005) with Recent Penicillata (*Polyxenus lagurus* and *Phryssonotus*), does not indicate which family is the oldest.

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The millipede tribe Sulciferini in Taiwan (Diplopoda: Polydesmida: Paradoxosomatidae)

Chao-Chun Chen, Sergei I. Golovatch & Hseuh-Wen Chang

Chen, C.-C., Golovatch, S. I. & Chang, H. -W. 2006. The millipede tribe Sulfericini in Taiwan (Diplopoda: Polydesmia: Paradoxosomatidae). Norw. J. Entomol. 53, 249-270.

Sulciferines are represented in Taiwan by five species in five genera, two of the species being endemic to the island. *Cawjeekelia* Golovatch, 1980 includes the endemic species *C. kanoi* (Takakuwa 1943), while the earlier records of the Japanese *C. nordenskioeldi* (Attems 1909) in Taiwan seem to be misidentifications. Both *Chondromorpha* Silvestri, 1897 and *Oxidus* Cook, 1911 are represented by the anthropochorous and widespread species *C. xanthotricha* (Attems 1898) and *O. gracilis* (C. L. Koch, 1847), respectively. *Kronopolites* Attems, 1914 encompasses the other endemic species, *K. formosanus* (Verhoeff 1939), resurrected from synonymy to the continental Chinese *K. swinhoei* (Pocock, 1895), which must be excluded from the fauna of Taiwan. *Orthomorphella* Hoffman, 1963 contains *O. pekuensis* (Karsch, 1881), a species widely distributed also in continental China, Korea and Japan, with *Orthomorpha flavomarginata* Gressitt, 1941 being its new junior synonym. All five species of Sulciferini occurring in Taiwan are keyed and mapped, with new faunistic records provided as well. Redescriptions of *Cawjeekelia kanoi* and *Kronopolites formosanus* are given to facilitate their recognition.

Keywords: millipedes, Diplopoda, Sulciferini, taxonomy, Taiwan

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INTRODUCTION

The diplopod tribe Sulciferini Attems, 1898 is defined by the gonopod showing a more or less coiled solenophore supporting a filiform solenomere and bearing one or two branches at base (Jeekel 1968, Golovatch 1995b). Sulciferines mainly occur in southeast and east Asia (Hoffman 1973), being only marginally represented in the remaining parts of the Oriental realm, as well as the Palaearctic and Ethiopian regions (Jeekel 1980). The tribe contains a few particularly widespread

species, such as the cosmopolitan *Oxidus gracilis* (C. L. Koch, 1847) and the pantropical *Chondromorpha xanthotricha* (Attems, 1898).

Jeekel (1988) included 21 genera in the tribe, removing three other genera placed there before: *Antichirogonus* Jeekel, 1980, *Polylobosoma* Jeekel, 1980 and *Armolites* Golovatch, 1984. In addition, he sank *Orientosoma* Golovatch, 1980 under *Cawjeekelia* Golovatch, 1980, and *Parchondromorpha* Golovatch, 1984 under *Parchondromorpha* Jeekel, 1980. Then Korsós &
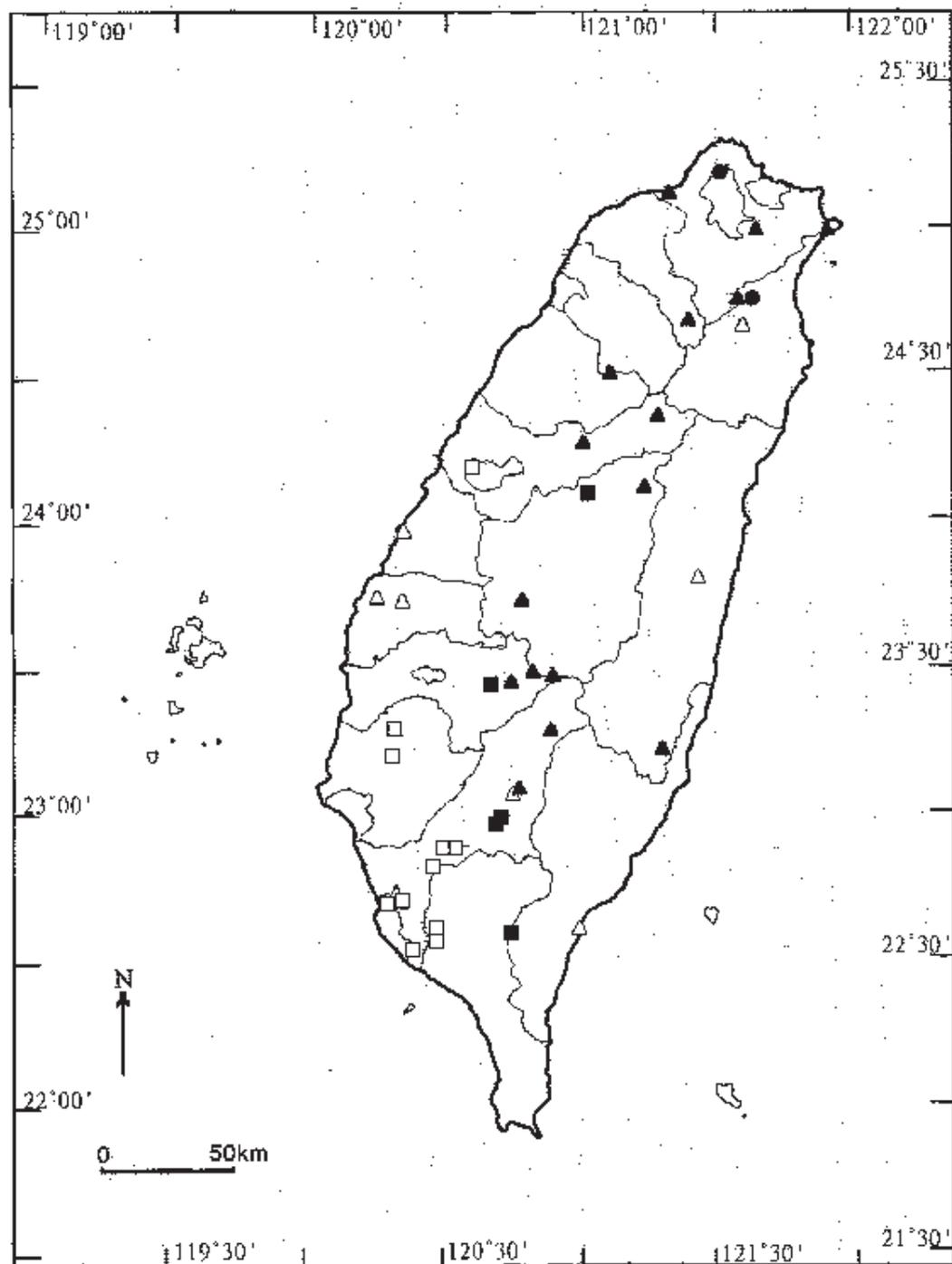
Map. Distribution of species of the tribe Sulciferini in Taiwan. Borderlines show borders between the counties.

☐ : *Cawjeekelia kanoi*
☐ : *Chondromorpha xanthotricha*
☐ : *Kronopolites formosanus*
☐ : *Orthomorphella pekuensis*
☐ : *Oxidus gracilis*

Golovatch (1989) proposed *Paratylopus* Korsós & Golovatch, 1989 as a new sulciferine genus, which Golovatch & Enghoff (1993) synonymized with *Tylopus* Jeekel, 1968. Finally, Shelley *et al*. (2000) assigned both *Antichirogonus* and *Polylobosoma* in the tribe again and added two more genera, *Enghoffosoma* Golovatch, 1993 and *Vietnamorpha* Golovatch, 1984. At present there are 25 accepted genera in the tribe.

Korsós (2004), in his recent review of the millipede fauna of Taiwan, has listed seven species of Sulciferini as occurring on the island. Some of these species were very poorly described in the 1950's to 1960's by Yu-Hsi Moltze Wang. Since most of his material, claimed to have been deposited in the Taiwan Museum, appears to be lost (Korsós & Lu 2005), collecting strict or nearly topotypic specimens has become mandatory (Chen *et al*. 2006). The present paper shows that only five species in five genera of Sulciferini actually inhabit Taiwan (Map 1).

The catalogue sections referring below to the widespread, apparently introduced genera and species are presented abridged, because such data are contained in Attems (1937), Jeekel (1968) and Hoffman (1980). In contrast, an as complete catalogue as possible is attempted for the presumably natural, autochthonous sulciferines of Taiwan.

MATERIAL AND METHODS

Abundant material (281 specimens) of Sulciferini has been taken and examined, representing the collections of five academic institutions in Taiwan: Department of Life Sciences, National Chung Hsing University (NCHUL), Department of Biological Sciences, National Sun Yat-Sen University (NSYSUB), Department of Life Science, National Taiwan Normal University (NTNUL), National Musem of Natural Science (NMNS) and Taiwan Forestry Research Institute (TFRI). Collections were made since 1988 all over Taiwan (Map) by hand-sorting from the soil, leaf litter and decomposed wood, the material being

preserved in 70% ethanol. External characters were examined, and drawings prepared, with a LEICA MZ 16 stereomicroscope, as well as with a HITACHI S2400 scanning electron microscope. Coloration of the specimens is being described below based on ethanol-preserved material, and occasionally on live specimens.

TAXONOMIC REVIEW

Genus *Cawjeekelia* Golovatch, 1980

The East Asian genus *Cawjeekelia* Golovatch, 1980, with the type-species *C. gloriosa* Golovatch, 1980, from Korea (Golovatch 1980), is known to be a senior synonym of *Orientosoma* Golovatch, 1980 (see Jeekel 1988). It currently includes seven species (Golovatch 1995a, b), not eight, as stated by Shelley *et al*. (2000). The distribution of the genus covers a vast area from the Maritime Province, Russian Far East in the north, to Hong Kong and Taiwan in the south. Two species have hitherto been recorded in Taiwan: *C. kanoi* (Takakuwa, 1943) and *C. nordenskioeldi* (Attems, 1909), both transferred to *Cawjeekelia* for the first time by Jeekel (1988).

C. kanoi was first described as *Kronopolites kanoi* Takakuwa, 1943, from Taiwan (Takakuwa 1943, Takakuwa 1954, Wang 1964). As the original description is very poor, a redescription, as well as new drawings and photographs prepared from fresh material are given below.

C. nordenskioeldi (Attems, 1909) was first described as *Strongylosoma nordenskiöldi* Attems, 1909 from material collected at Mizo, Kyushu, Japan; the locality is now called Mt. Kirishima, ca. 1400 m a.s.l., Miyazaki Prefecture, Japan. Later this species was reported from near Hot Spring, Tsuta, Aomori Prefecture, Japan (Chamberlin & Wang 1953).

The only record of *C. nordenskioeldi* in Taiwan was based on a single female taken at Hsin-Tien, northern Taiwan (Wang 1955). Korsós (2004), in his review, reiterated this record. However, we consider it as dubious not only because no reliable

identification could be possible based on female material alone, but also because *C. nordenskioeldi* has since never been recollected in any place of Taiwan, including Hsin-Tien. So we suggest to exclude *C. nordenskioeldi* from the Taiwanese millipede list, considering the species as being endemic to Japan.

Genus *Chondromorpha* Silvestri, 1897

The genus *Chondromorpha* Silvestri, 1897, with the type-species *C. severini* Silvestri, 1897 from India, encounters several junior synonyms: *Polydesmopeltis* Verhoeff, 1936, *Ceylonpeltis* Verhoeff, 1936, *Dasomus* Chamberlin, 1941 and *Xaymacia* Loomis, 1948 (see Attems 1937, Jeekel 1963). At present it encompasses eight species from India and Sri Lanka (Jeekel 1968, Hoffman 1980). One of them, *C. xanthotricha* (Attems, 1898), is pantropical, though recorded in Taiwan only recently (Chen & Chang 2002).

C. xanthotricha (Attems, 1898) was first described as *Prionopeltis xanthotricha* Attems, 1898, from Mauritius (Attems 1898). The species was first mentioned as new to Taiwan by Chen & Chang (2002), and later also repeated by Korsós (2004).

C. xanthotricha is a widespread, pantropical species: Neotropical Region: Suriname, Jamaica, Guadeloupe; Australian Region: North Mariannas (Guam), New Caledonia, Fiji, Samoa; Ethiopian Region: Mauritius, Seychelles; Oriental Region: Sri Lanka, Indonesia, Malaysia, the Philippines and Taiwan (Attems 1898, 1937, Wang 1961, 1964, Jeekel 1963, 1968, 1982, Golovatch & Korsós 1992, Golovatch 1996, Shelley *et al.* 1998, Shelley & Lehtinen 1998, Chen & Chang 2002, Korsós 2004). Its native area seems to be Sri Lanka and/or southern India, whence the species has been dispersed through human agency.

Genus *Kronopolites* Attems, 1914

The Asian genus *Kronopolites* Attems, 1914, with the type-species *Strongylosoma swinhoei* Pocock, 1895, from continental China (Pocock 1895), is known to be a senior synonym of *Kansupus* Verhoeff, 1934 and *Parakansupus* Verhoeff, 1939 (see Attems 1937, 1940, Hoffman 1963, 1980). At the moment, this genus includes six valid species ranging from central and southern continental China in the north (Pocock 1895, Hoffman 1963, 1980, Geoffroy & Golovatch 2004.) through Taiwan (Verhoeff 1939b, Attems 1940, Hoffman 1963, 1980, Wang 1963, Korsós 2004), Vietnam (Hoffman 1963, 1980, Enghoff et al. 2004) and Thailand (Jeekel 1982) to the Kashmir Himalaya (Golovatch & Martens 1996), India in the south (Golovatch 1983). Only one species, *K. formosanus* (Verhoeff, 1939), seems to occur in Taiwan.

K. formosanus (Verhoeff, 1939) was first described as *Kansupus (Parakansupus) formosanus* Verhoeff, 1939 from Taiwan, but was soon transferred to *Kronopolites* Attems, 1914 (see Attems 1940) and then synonymized with *K. ralphi* Wang, 1957, a species also described from Taiwan (see Hoffman 1963, Korsós 2004).

Recently, without any explanation, Wang & Mauriès (1996) sank *K. formosanus* under *K. swinhoei* (Pocock, 1895). Korsós (2004) stated that "Hoffman (1963) and Jeekel (1968) established the synonymies of *K. formosanus* Verhoeff, 1939 and *K. ralphi* Wang, 1957 with *K. swinhoei* (Pocock, 1895)". In fact, however, Hoffman (1963) separated *formosanus* from *swinhoei*, because the Taiwanese species was considerablely smaller than *swinhoei*, it was devoid of sternal cones and its solenophore showed a different structure. Jeekel (1968) followed Hoffman's opinion.

Therefore, we consider that *K. formosanus* (Verhoeff, 1939) must be resurrected from synonymy to *K. swinhoei* (Pocock, 1895), while the latter, continental Chinese species is to be ejected from the fauna of Taiwan. A redescription and new illustrations of *K. formosanus* prepared from fresh material are given below to substantiate this species' identity.

Genus *Orthomorphella* Hoffman, 1963

The monotypic genus *Orthomorphella* Hoffman, 1963, with the type-species *Polydesmus pekuensis* Karsch, 1881, is known to encounter only one synonym, i.e. the invalidly proposed

Orthomorphella Verhoeff, 1939 (see Hoffman 1963, 1980). Even though Jeekel (1968) sank it under *Chamberlinius* Wang, 1956, later both Hoffman (1973) and Jeekel (1988) revalidated *Orthomorphella*. This genus occurs in China, Korea and Taiwan (Takakuwa 1954, Wang 1955, 1963, 1964, Hoffman 1963, 1980), the sole record in Japan (Verhoeff 1931) being doubtful.

O. pekuensis (Karsch, 1881) was originally described as *Polydesmus (Paradesmus) pekuensis* Karsch, 1881 (see Karsch 1881), later synonymized with *Orthomorpha circofera* Verhoeff, 1931 and *O. circofera affinis* Verhoeff, 1936 (see Hoffman 1963, Jeekel 1968). The first record of this species in Taiwan is according to Wang (1955). Although Takakuwa (1954), based on Verhoeff's (1931) report from Japan, suggested that *O. circofera* could have been taken from near Tokio (Tokyo), he also mentioned "this collecting record can prove to be wrong, the correct locality lying in Korea".

Orthomorpha flavomarginata Gressitt, 1941 was described from Taiwan (Gressitt 1941). Because the original description was very poor and only based on a single female, Korsós (2004) removed this dubious species from his list of Taiwanese millipedes. We have been able to restudy the holotype (□) of *O. flavomarginata* (entry number 5616, California Academy of Sciences, San Francisco, USA). With its several features, i.e. the large size (length 30-35 mm, width 3.0-4.0 mm, these dimensions being among the largest paradoxososomatid species currently encountered in Taiwan), the often pitchy black live coloration (faded upon a long-term preservation in alcohol) and, above all, the shape and structure of the paraterga, pleurosternal carinae and telson, there can be no doubt that *Orthomorpha flavomarginata* Gressitt, 1941 is a junior subjective synonym of *Orthomorphella pekuensis* (Karsch, 1881), **new synonymy**. Below we provide some photographs taken from the holotype of *Orthomorpha flavomarginata* and from fresh material of *Orthomorphella pekuensis* to substantiate the above synonymy (Figures 41-48).

Genus *Oxidus* Cook, 1911

The east to southeast Asian genus *Oxidus* Cook, 1911, with the type-species *Fontaria gracilis* C. L. Koch, 1847, has only *Kalorthomorpha* Attems, 1914 as synonym (Hoffman 1980). This genus contains five species (Hoffman 1980, Enghoff et al. 2004), of which one is ubiquitous in distribution. This is *O. gracilis* (C. L. Koch, 1847), the only congener that occurs in Taiwan (Wang 1955, 1963).

O. gracilis (C. L. Koch, 1847), originally described as *Fontaria gracilis* C. L. Koch, 1847, is currently cosmopolitan, occurring nearly all over the world. Its synonymy list is rather long (Jeekel 1963, 1968), while the status of several of its presumed congeners still remains dubious. The first record from Taiwan belongs to Wang (1955).

List of genera and species

In summary, the following genera and species of Sulciferini (Class Diplopoda, Order Polydesmida, Family Paradoxosomatidae) are presently known from Taiwan:

Genus *Cawjeekelia* Golovatch, 1980.
    C. kanoi (Takakuwa, 1943), endemic to central and southern Taiwan.
Genus *Chondromorpha* Silvestri, 1897.
    C. xanthotricha (Attems, 1898), a pantropical species.
Genus *Kronopolites* Attems, 1914.
    K. formosanus (Verhoeff, 1939), endemic to northern Taiwan.
Genus *Orthomorphella* Hoffman, 1963.
    O. pekuensis (Karsch, 1881), Korea, China, and Taiwan. (= *O. flavomarginata* Gressitt, 1941, **new synonymy**).
Genus *Oxidus* Cook, 1911.
    O. gracilis (C. L. Koch, 1847), cosmopolitan.

DESCRIPTIVE AND FAUNISTIC PART

Genus *Cawjeekelia* Golovatch, 1980

Cawjeekelia Golovatch, 1980: 54 (type-species: *C. gloriosa* Golovatch, 1980); Jeekel 1988: 98, Golovatch 1995a: 89, 1995b: 75, Shelley et al. 2000: 91.
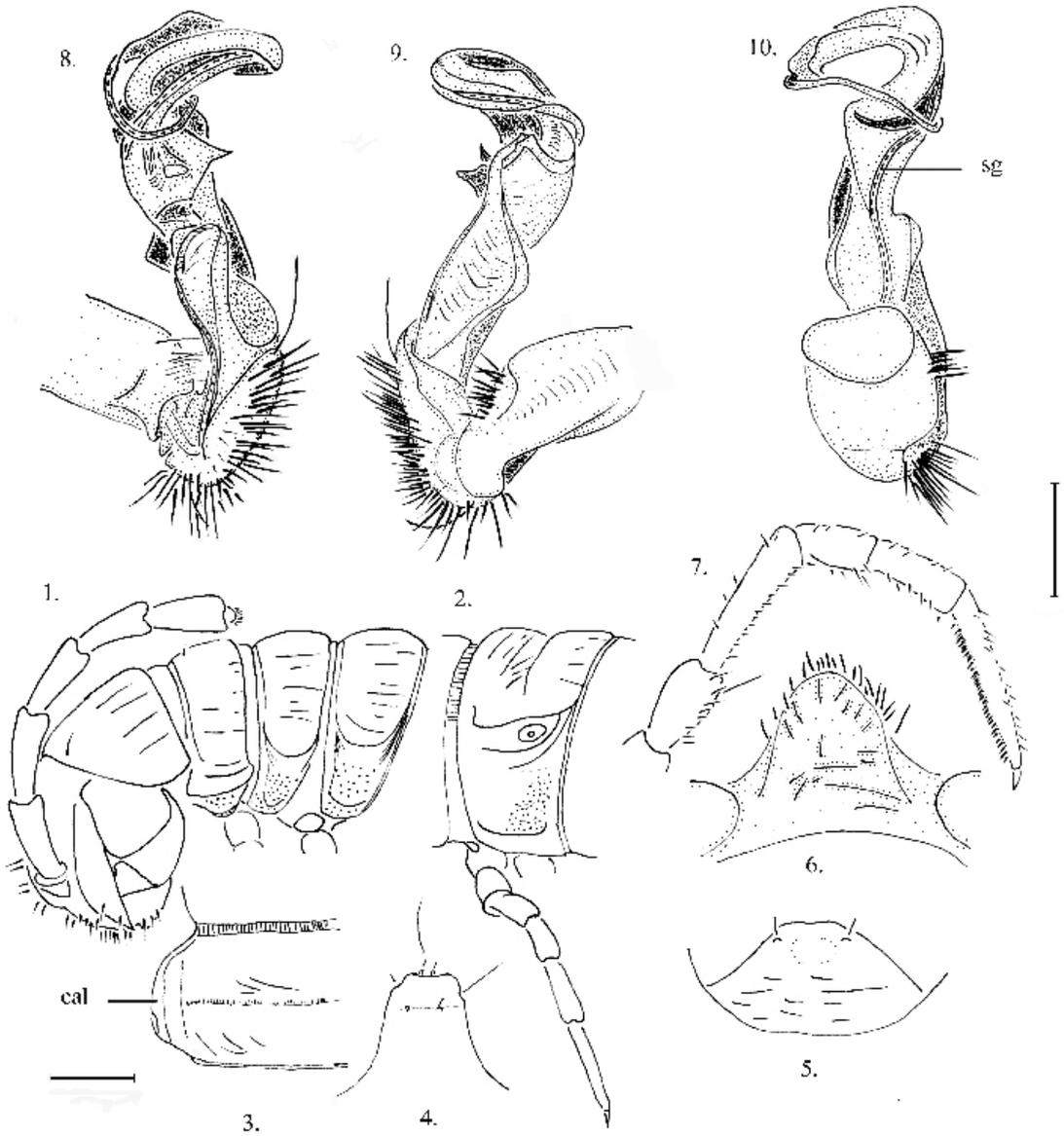
Figures 1–10. *Cawjeekelia kanoi*, male from NanFeng Mountain. (1) anterior body portion, lateral view. (2) segment 10, lateral view. (3) left half of metatergum 10, dorsal view. (4) epiproct, dorsal view. (5) hypoproct, ventral view. (6) sternal lobe between coxae 4, ventral view. (7) leg 11. (8–10) left gonopod, medial, lateral and dorsal views, respectively. Scale line = 0.5 mm for Figures 4-6, 8-10, 1 mm for figure 7; 1 mm for Figures 1-3. Designations: sg = seminal groove; cal = callus.

KEY TO TRIBE SULCIFERINI IN TAIWAN

Because each genus of Sulciferini in Taiwan appears to contain only one species, the following key applies both to the genera and the species.

1. Surface of collum and metaterga 2-19 strongly tuberculate, metaterga densely setose…………...*Chondromorpha (C. xanthotricha)*

- Surface smooth, without tubercles, metaterga sparsely setose at most 2

2. Distal part of gonopod with three branches, solenophore in situ directed laterad, away from the opposite gonopod (Figures 51, 52, three branches: sl, spro, and sph) ....*Cawjeekelia (C. kanoi)*

- Distal part of gonopod with four branches, solenophore *in situ* curved essentially mesad, towards the opposite gonopod (Figures 54, 63, 64, four branches: sl, spro, and processes A, B)...3

3. Body width <3.0 mm. Gonopod femorite short, obviously broadened distally (Figure 64)...*Oxidus (O. gracilis)*

- Body width 3.0-4.0 mm. Gonopod femorite long, not broadened distally.....................................4

4. Gonopod femorite obviously curved mesad (Figures 62, 63), live coloration usually shining black from head to anterior 1/2 part of epiproct ....…………….*Orthomorphella (O. pekuensis)*

- Gonopod femorite straight (Figures 18, 54, 56), live coloration pale brown alternating with brown (or brown alternating with dark brown)………………...........*Kronopolites (K. formosanus)*

Orientosoma Golovatch, 1980: 55 (type-species: *O. koreanum* Golovatch, 1980); Jeekel 1988: 98, Golovatch 1995a: 90, Shelley et al. 2000: 117.

Cawjeekelia kanoi (Takakuwa, 1943)
(Figures 1-10, 21-26, 49-53)
Kronopolites kanoi Takakuwa, 1943: 603, Fig. 1; 1954: 32, Figs. 24-26; Wang 1964: 69, Jeekel 1968: 69, Korsós 2004: 21.

"Kronopolites" kanoi Takakuwa, 1943: Jeekel 1968: 74, Korsós 2004: 21.
Cawjeekelia kanoi: Jeekel, 1988: 98; Golovatch 1995a: 90, Korsós 2004: 21.

Material examined
2 ☐, 1 ☐ (NCHUL), Taiwan (R. O. C.), Nantou County, RenAi County, HueiSun, forest, 1664 m a.s.l., 29 March 1998, leg. S. H. Wu. 1 ☐ (NSYSUB-DI 80.), JiaYi County, LongTou, ALiShan County, ALiShan, bamboo forest, 1307 m a.s.l., 21 April 2000, leg. J. L. Chao. 2 ☐ (NSYSU-DI 192-193), Kaohsiung County, MaoLin, ShanPing, ca. 700 m a.s.l., 30 June 2004, leg. C. L. Lin. 2 ☐, 1 ☐ (NTNUL-My 33-35), same locality, NanFeng Mountain, in tree trunk, 1722 m a.s.l., 28 January 1989, leg. S. H. Chen. 1 ☐ (NSYSUB-DI 81), Pingtong County, TaiWu County, DaWu Mountain, 2641-3092 m a.s.l., date unknown, leg. S. S. Dai.

Description
Length 31-34 (☐, n = 6) and 30-37 mm (☐, n = 4); width of metazonite 10 ca. 2.9-3.0 (☐) and 2.9-3.7 mm (☐).

Coloration in alcohol and live very dark brown to black-brown (black with naked eye); sternites
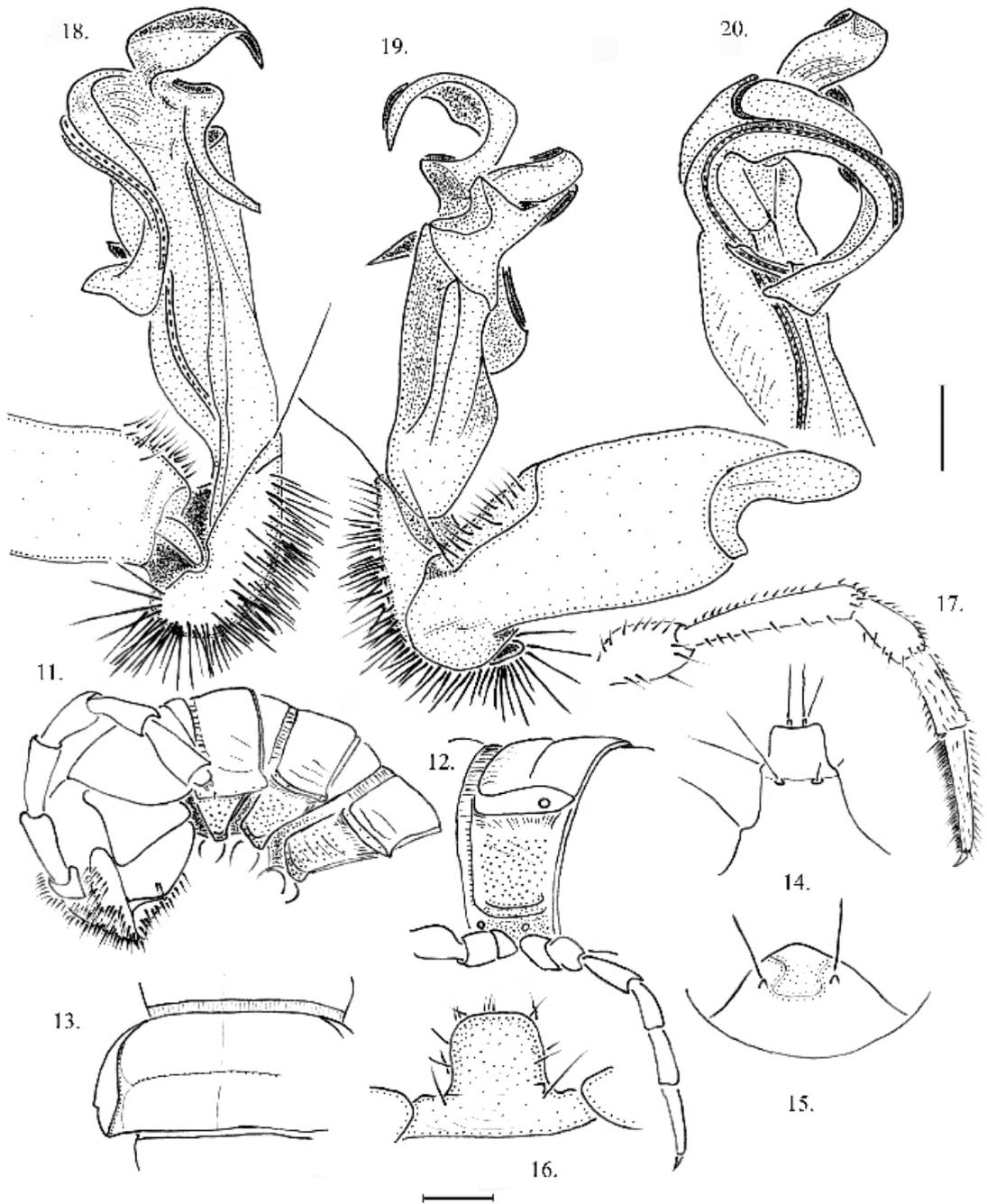
Figures 11–20. *Kronopolites formosanus*, male from FuShan botanic garden. (11) anterior body portion, lateral view. (12) segment 10, lateral view. (13) left half of metatergum 10, dorsal view. (14) epiproct, dorsal view. (15) hypoproct, ventral view. (16) sternal lobe between coxae 4, ventral view. (17) leg 15. (18–20) left gonopod, medial and lateral views, respectively, telopodite tip, dorsal view. Scale line = 0.25 mm for Figures 18-20, 1 mm for Figures 11-13; 0.3 mm for Figures 14-16, 0.5 mm for Figure 17.

brown to dark brown, basal segments of legs pale brown, increasingly blackish distally. Coloration is similar in both sexes.

Postcollar constriction faint, width of head = segment 2 = 4 ≥ collum = 3 < 5-13 in ☐, but head = segment 4 ≤ collum = 3 < 2 < 5-13 in ☐; further on toward telson trunk gradually and gently tapering both in width and height. Antennae of medium length, slender, reaching middle part of metatergum 3 to anterior part of metatergum 4 dorsally in ☐ (Figures 1, 21, 22), a little shorter in ☐, reaching posterior edge of metatergum 2 to anterior part of metatergum 3. Paraterga poorly developed (Figures 1-3, 21-24), calluses delimited by a sulcus both dorsally and ventrally only on pore-bearing segments, delimited only dorsally on poreless segments, calluses mostly like low ridges (poreless segments) or flat discs (pore-bearing segments), not surpassing caudal tergal contour (Figures 1, 22-24), never spiniform caudally. Axial line almost wanting (Figures 3, 24), only poorly visible in places. Transverse sulcus reduced and only traceable on segments 4 and 18, evident on segments 5-17 (Figures 2-3, 23-24), not reaching bases of paraterga, wanting on segment 19, lineiform, moderately deep, finely beaded at bottom (Figure 3). Surface generally shining and rather smooth, sometimes rugulose on metaterga; metazona below paraterga evidently and densely granulose. Limbus thin, caudal margin entire. Stricture between pro- and metaterga evidently but not strongly beaded, general appearance of body moniliform (☐) or submoniliform (☐). Tergal setae short, pattern 2+2 anteriorly on collum and also anteriorly on segment 2, onward abraded. Ozopores dorsolateral, lying on callus ca 1/3 metatergal length from caudal edge (Figures 2, 23). Pleurosternal carinae present, having the form of narrowly (segments 2-4) or more widely rounded (segments 5-7) ridges on pregonopodial segments (☐), or in the form of narrow ridges on segments 2–4 (☐), onward increasingly poorly developed, reduced to low bosses until segment 9 to 10 in ☐ (Figures 1-2, 22-23) or until segment 7 to 10 in ☐, thereafter virtually absent. Epiproct digitiform, subtruncate and faintly emarginate in dorsal view, flattened dorsoventrally, moderately

long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1:2.3 in ☐, slightly shorter in ☐; pre-apical papillae almost wanting to wanting, close to apex (Figures 4, 25). Hypoproct roundly subtriangular (in both sexes) to subtriangular (with a small central lobe at caudal edge only in ☐), 1+1 setae at caudal corners situated on well separated knobs, sides concave at base (Figures 5, 49).

Sternites moderately setose; not modified except for a linguiform, slightly emarginate to rather broad, setose lamina between ☐ coxae 4 (Figures 6, 50); each cross-impression with an evident transverse sulcus but with a poorly developed, shallow axial groove.

☐ legs 1 to anterior legs of segment 17 with tarsal brushes (Figures 7, 26), setation gradually thinning out toward telson. Legs long, ca. 2 times (☐) (Figures 2, 23) or ca. 1.2 times as long as midbody height (☐).

Gonopods (Figures 8-10, 51-53) simple. Coxite elongate, subcylindrical, strongly setose distoventrally; cannula normal. Telopodite strongly twisted; prefemoral part rather long, as usual densely setose; femorite (**fe**) slightly longer than prefemur, subequal in width all along its extent, with a small process (**spro**) on mesal side and a larger triangular process on lateral side (**bpro**), demarcated from postfemoral portion (**pof**) by a line on ventromesal side and by a clear oblique sulcus on dorsal face; postfemoral part large, distally with solenophore (**sph**) directed first laterad and then mesad, curving in ca.1.5 circle, very long, subequal in width along 2/3 its extent until, at ca. rear 1/3 length, suddenly becoming very slender; postfemoral part also with a short and thin process on ventral side; seminal groove running medially along femorite, then directed dorsad along remaining portion of femorite, finally again medially onto solenomere (**sl**) on mesal side of postfemoral part, **sl** broadened at base, flagelliform, long, completely supported/ sheathed by **sph** beginning ca. 1/3 distally of base (Figures 51-53, both solenomere and solenophore separated during SEM preparation).
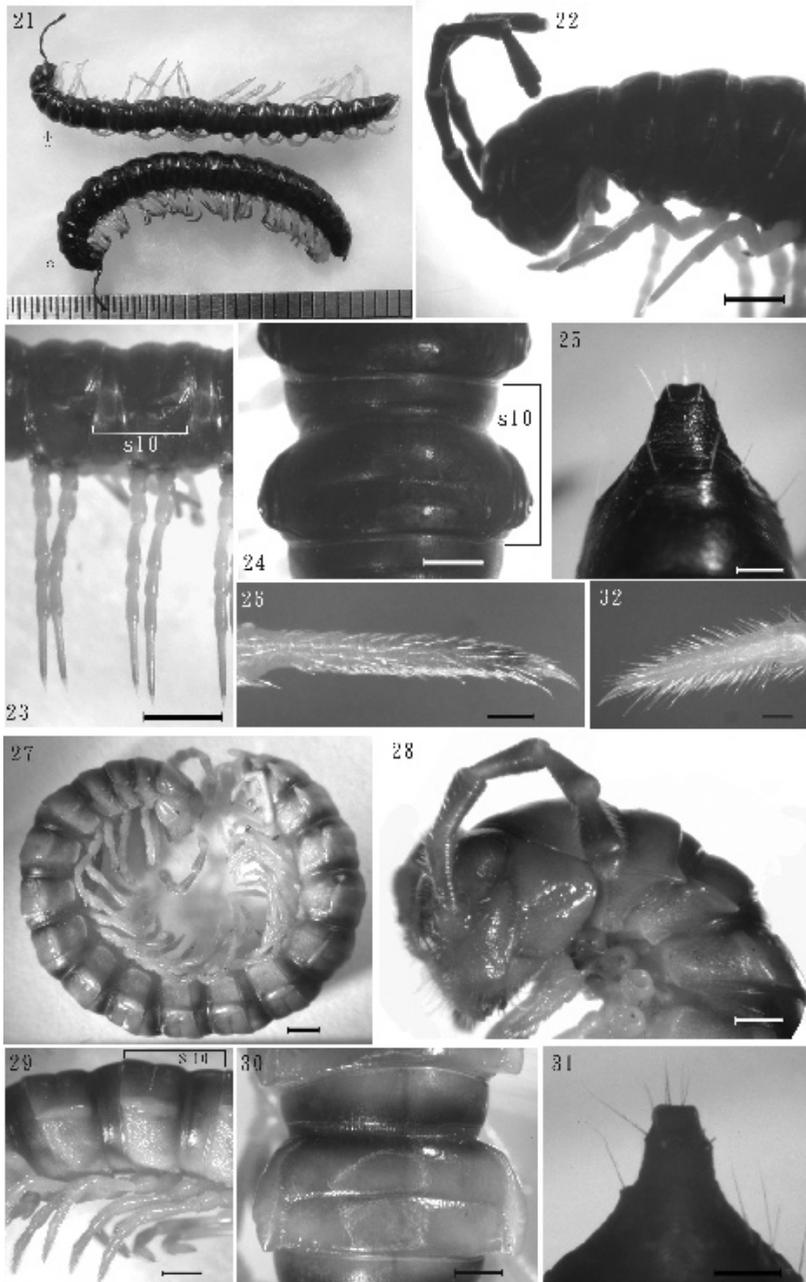
Figures 21-32. 21-26: *Cawjeekelia kanoi*, male from HueiSun forest. (21) entire body, dorsal view. (22) anterior body portion, lateral view. (23) s 10 = segment 10, lateral view. (24) The same, dorsal view. (25) epiproct, dorsal view. (26) tarsal brush of anterior leg of somite 10.
27-32: *Kronopolites formosanus*, male from FuShan botanic garden. (27) entire body, dorsal view. (28) anterior body portion, lateral view. (29) s 10 = segment 10, lateral view. (30) The same, dorsal view. (31) epiproct, dorsal view. (32) tarsal brush of anterior leg of somite 10.
Scale line = 0.2 mm for Figures 25-26, and 31-32; 0.5 mm for Figures 28 and 30; 0.8 mm for Figures 22, 24 and 29; 1.6 mm for Figure 23.

Remark
C. kanoi is endemic to the mountains (elevation ca. 700-3092 m a.s.l.) of central and southern Taiwan (Map 1).

Genus *Chondromorpha* Silvestri, 1897

Chondromorpha Silvestri, 1897: 356 (type-species: *C. severini* Silvestri, 1897); Attems 1937: 107; Wang 1961: 108; Jeekel 1963: 24; 1968: 82; Hoffman 1980: 169.

Chondromorpha xanthotricha (Attems, 1898)

(Figures 35-36, 58-61)
Prionopeltis xanthotrichus Attems, 1898: 359, pl. 5, Fig. 115.
Chondromorpha xanthotricha: Attems, 1937: 111, Fig. 146; Wang 1953: 3; 1961: 108 (misspelt as *C. xanthotrica*); 1964: 67 (misspelt as *C. xanthotrica*); Jeekel 1963: 24; 1968: 80; 1982: 238; Golovatch & Korsós 1992: 25; Golovatch 1996a: 131; Shelley & Lehtinen 1998: 88, Figs. 10-12; Chen & Chang 2002; Korsós 2004: 23).

Material examined
1 ☐ juv. (NMNS), Taiwan (R. O. C.), Taichung City, TungHai University, in decayed branches and leaves, below 100 m a.s.l., 22 November 2000, leg. H. L. Cyu. 1 (NSYSUB-DI 39), Tainan County, GuanTian, 12 September 2003, leg, C. L. Lin. 3 ☐, 1 (NSYSUB-DI 418-421), same County, LiouYing, GuangFu, leg. H. D. Zhu. 8 ☐, 9 (NSYSUB-DI 122-139), Kaohsiung County, MeiNong, under papers above soil, in decayed leaves and in soil in *Cocos* plantation, below 50 m a.s.l., 2 March 2002, leg. C. C. Chen & B. Y. Huang. 1 ☐ (NSYSUB-DI 147.), same County, RenWu, in soil in *Areca* garden, 80 m a.s.l., 13 April 2002, leg. B. Y. Huang. 1 ☐ (NSYSUB-DI 146), same county, CiShan, ShangHe, in soil in banana garden, 33 m a.s.l., 13 April 2002, same collector. 1 ☐ (NSYSUB-DI 148.), same locality, CiiWei, culvert of irrigation ditch, below 50 m a.s.l., 30 April 2002, leg. J. H. Chen. 1 ☐ (NSYSUB-DI 140), PingDong County, WanDan, SiunJhong, below 6 m a.s.l., 5 March 2002, leg. S. H. Lin. 5 ☐, 7 (NSYSUB-DI 141-145), same locality, ShePi, in soil near shrimp pool, below 16

m a.s.l., 16 March 2002, leg. C. C. Chen & S. H. Lin. 2 ☐ (NCKUB), Kaoshiung City, SiiaoGang Region, FengShan Reservoir, 23 m a.s.l., 2 May 2002, leg. M. H. Chuang. 1 ☐ (NSYSUB-DI 149), same city, ZuoYing Region, navy recruit training center, 16 m a.s.l., 10 October 2002, leg. J. N. Huang.

Remarks
Since solely lowland localities and disturbed habitats appear to support this species in Taiwan, its apparent anthropochory is unquestioned. Figures 35 and 36 are provided to show the degree of fading of alcohol-fixed material upon a long-term preservation as compared to fresh/live material.

Genus *Kronopolites* Attems, 1914

Kronopolites Attems, 1914: 187, 219 (type-species: *Strongylosoma swinhoei* Pocock, 1895); Attems, 1929: 272; 1936: 226; 1937: 49; Hoffman 1963: 579; Takakuwa 1954: 30; Jeekel 1968: 71; 1970: 225; Hoffman 1980: 169; Chang 1998: 580; Geoffroy & Golovatch 2004: 20.
Kansupus Verhoeff, 1934: 17 (type-species: *K. svenhedini* Verhoeff, 1934); Attems 1937: 49; Jeekel 1968, p. 71; Hoffman 1963: 579.
Parakansupus Verhoeff, 1939b: 273 (type-species: *Kansupus formosanus* Verhoeff, 1939); Jeekel 1968: 71; Hoffman 1963: 579.

Kronopolites formosanus (Verhoeff, 1939)

(Figures 11-20, 27-34, 54-57)
Kansupus (Parakansupus) formosanus Verhoeff, 1939b: 273, Figs. 1-3; Attems 1940: 541; Hoffman 1963: 585; Korsós 2004: 23.
Kronopolites formosanus: Attems, 1940: 541, Fig. 685; Chamberlin & Wang 1953: 5, Takakuwa 1954: 31, Fig. 23; Wang 1964: 69; Hoffman 1963: 585; Korsós 2004: 23).
Kronopolites ralphi Wang, 1957: 106, Fig. 3; Wang 1958: 342; Hoffman 1963: 585; Jeekel 1968: 71; Korsós 2004: 23.

Material examined
1 ☐, 2 ☐ (TFRI), Taiwan (R. O. C.), Taipei County, Ulai, FuShan botanic garden, 726 m a.s.l., 20-27 February 2001, leg. W. B. Huang. 2 ☐(TFRI),
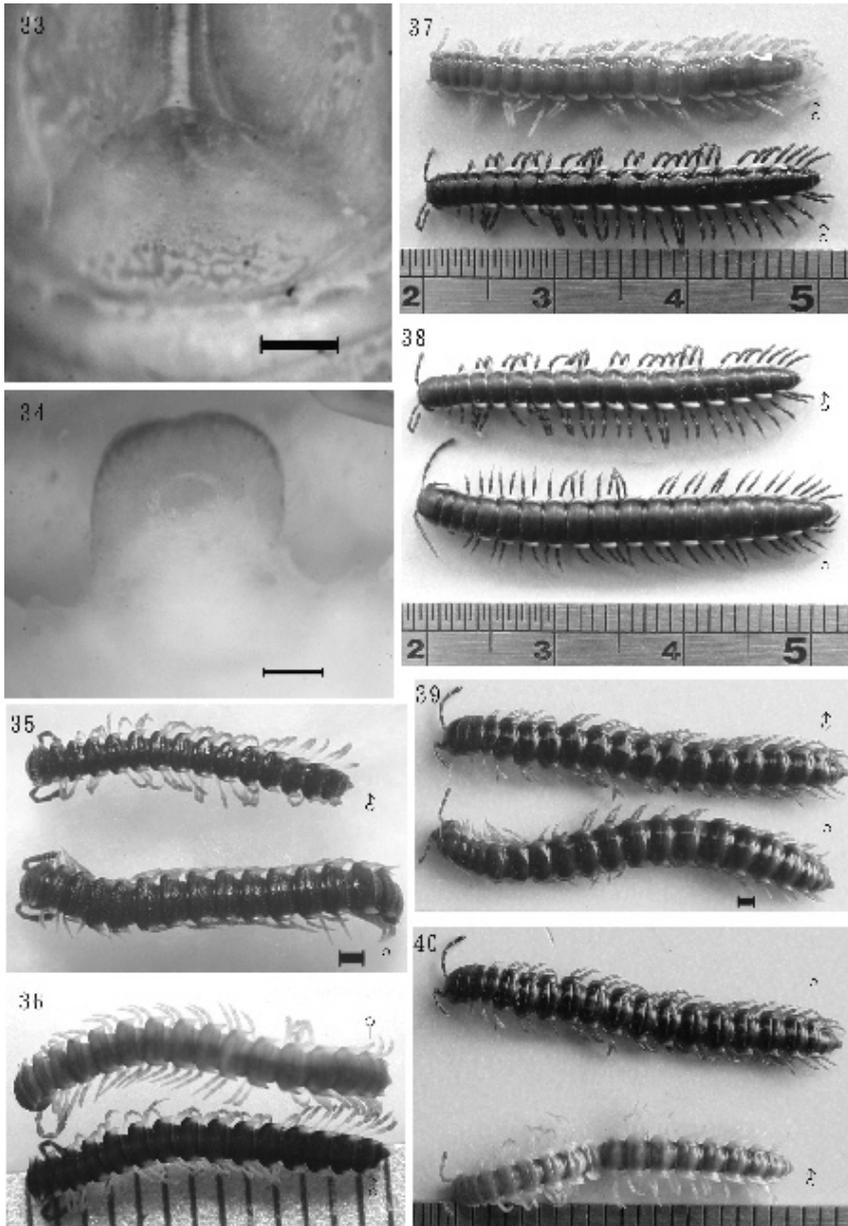
Figures 33-40. 33-34: *Kronopolites formosanus*, male from FuShan Botanical Garden. (33) hypoproct, ventral view. (34) sternal lobe between coxae 4, ventral view.
35-36: *Chondromorpha xanthotricha* (Attems, 1898), from ShePi, In order to show differences in coloration.
37-38: *Orthomorphella pekuensis*, male from WangGong (37) and TengJhih (38). Following a long-term preservation in alcohol, coloration is strongly faded compared to fresh material.
39-40: *Oxidus gracilis*, male from YangMingShan National Park (39), female from GuanU (40) and male from FengHuangGu. Following a very long preservation in alcohol, coloration is strongly faded compared to fresh material.
Scale line = 1 mm for Figures 33-34; 0.5 mm for Figures 35 and 39.

same locality, 23-30 March 2001, same collector. 2 □ (TFRI), same locality 23 April 2001, same collector. 1 □ (TFRI), same locality 18-25 May 2001, same collector. 3 □ (NSYSUB-DI 188-190), Taipei City, YangMingShan National Park, no. 101 Jiia County Road, near YuYouRen tomb, under decayed leaves, *ca* 750 m a.s.l., 31 March 2002, leg. S. Y. Wu.

Description
Length 23-27 (□, n = 4) and 30 mm (, n = 4); width of metazonite 10 ca. 2.5-3.0 (□) and 3.8-4.0 mm (□).

Coloration in alcohol almost entirely light yellow-brown to brown in both sexes, only antennae light yellow-brown to light brown; head, posterior parts of prozona and anterior edges of metazona near stricture brown to dark brown.

Postcollar constriction rather faint in □, particularly so in □, width of head = segment 3 > collum < segment 4 in □, or head < collum < segment 3 < segment 2 = 4 in □, following < 5 < 6 < 7 < 8 < 9 < 10 < 11 < 12 < 13 < 14 <15 <16 in both sexes or 16 =17 only in □; further on toward telson, trunk gradually and gently tapering both in width and height. Antennae of medium length, slender, reaching stricture of segment 3 dorsally in □ (Figures 11, 27-28), a little shorter in □, reaching posterior edge of segment 2 to stricture of segment 3. Paraterga (Figures 11-13, 27-30) moderately developed, much smaller on segment 19, always surpassing caudal tergal contour on segments 2-19 in □(sometimes except for segment 5), or on segments 2-4 and 10-19 in □, particularly so on posterior segments (Figures 11, 12, 27-29); calluses with three to four minute pits at lateral margin (Figure 11) on segments 2-4 in □ or 2 & 3 in □; callus with 1 setula at lateral margin on segment 2 (Figure 11) to segments 2, 6, 7, 10, 13, 15-19 in □, or fully abraded in □; calluses delimited by a sulcus both dorsally and ventrally in both sexes; calluses mostly like high ridges, spiniform caudally. Axial line (Figures 13, 30) very evident, particularly so in □, stretching from anterior edge of collum to anterior half of epiproct in □, sometimes visible on proterga,

always clear on metaterga (especially in rear 2/3 body) in □. Transverse sulcus (Figures 12-13, 29-30) clearly developed on somites 5-17, poorly traceable on segment 18, wanting on 19 in both sexes, shallow, particularly so in □, lineiform, much thinner in □, not beaded at bottom, reaching base of paraterga in both sexes. Surface generally shining and smooth, seldom transversely or longitudinally rugulose on different metaterga in □, seldom longitudinally rugulose on metaterga in □ (Figures 11-13); metazona below paraterga strongly granulose on segments 2-18 in both sexes (Figures 11-12, 28-29). Limbus thin, caudal margin entire. Stricture between pro- and metaterga evidently but not strongly beaded, not too deep so that general appearance of body submoniliform. Tergal setae short, almost fully abraded to a pattern of 6+6 anteriorly on collum (sometime setae also scattered over rear part of collum), completely abraded or still a few setae present as lying transversely anteriorly and posteriorly on metaterga 2-16, completely abraded or up to a few setae retained on metaterga 17-19 in □, or fully abraded or up to only 1-2 setae anteriorly on collum, onward abraded to only some retained on metatergum 19 in □. Ozopores lateral (Figures 12, 13, 29, 30), lying on callus ca 1/3 metatergal length from caudal edge (Figures 12, 29). Pleurosternal carinae (Figures 11, 12, 27-29) well-developed like wide rounded ridges on segments 2-17(18) in □, or on 2-16 (17) in □, with small caudal teeth on segments 2-7 (□) or on 3 (□), becoming a spine on segment 8 (only in □), surpassing rear contour on following segments, carinae like low bosses on 17(18), wanting on 18-19 in both sexes or on 19 only in □. Epiproct digitiform, subtruncate in dorsal view, flattened dorsoventrally, long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1 : 2 in □, slightly shorter in □; pre-apical papillae evident, removed far off apex (Figures 14, 31). Hypoproct subtriangular, 1+1 setae at caudal corners situated on well-separated knobs, sides slightly concave at base to almost straight (Figures 15, 33).

Sternites moderately setose, not modified except for a cuboid, slightly emarginate to even, broad, setose lamina between □ coxae 4 (Figures 16, 34);
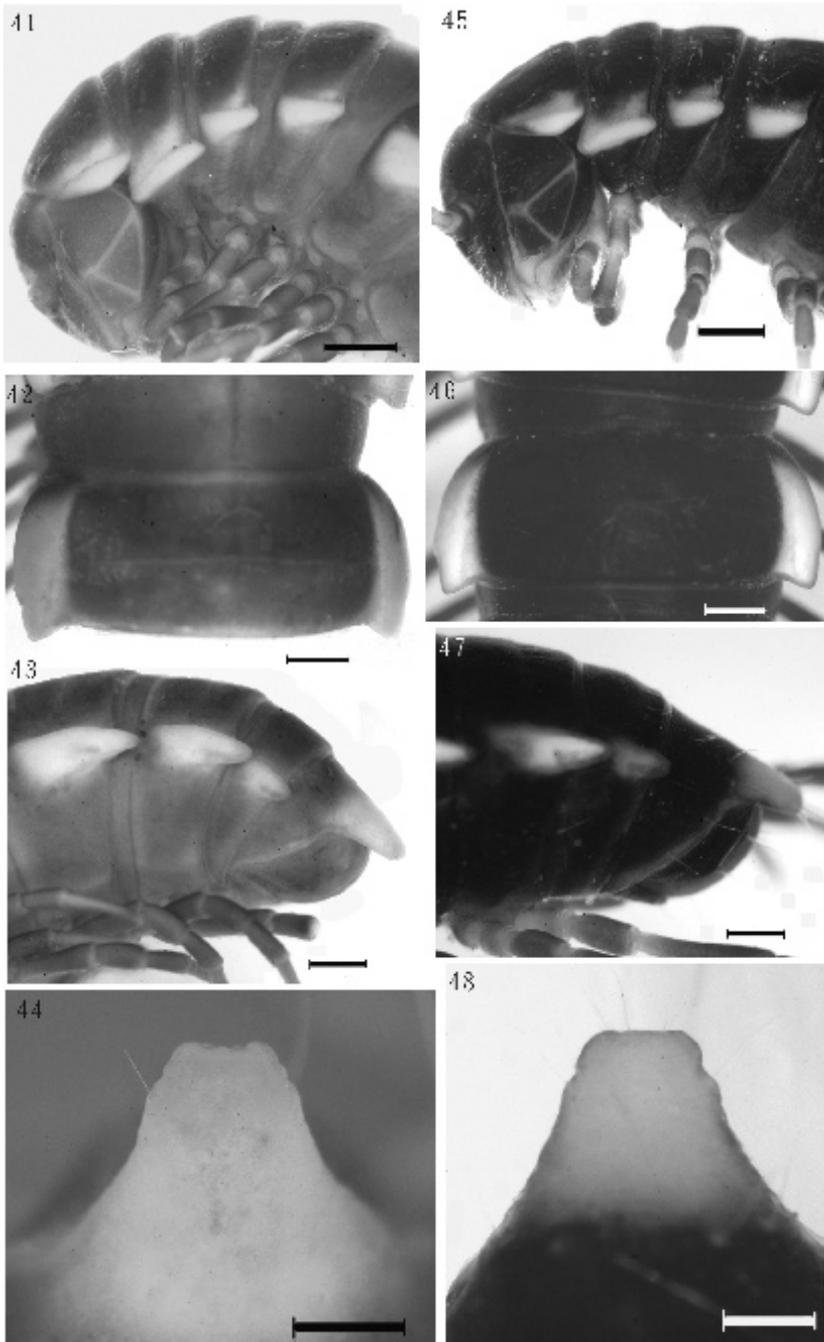
Figures 41-48. 41-44: *Orthomorpha flavomarginata*, female holotype (No. 5616, CAS) from central Taiwan. (41) anterior body portion, lateral view. (42) segment 10, dorsal view. (43) epiproct, lateral view. (44) epiproct, dorsal view.
45-48: *Orthomorphella pekuensis*, female from TengJhih. (45) anterior body portion, lateral view. (46) segment 10, dorsal view. (47) epiproct, lateral view. (48) epiproct, dorsal view. Scale line = 1 mm for Figures 41-48.

each cross-impression with an evident transverse sulcus but with a poorly developed, shallow axial groove.

☐ legs 1 to anterior legs of segment 17 with tarsal brushes (Figures 17, 32), setation gradually thinning out toward telson, relatively modest after posterior legpair of segment 17. Coxae with a spine distally on posterior legs of segment 8 to those of segment 15 in both sexes. Legs long and slender, ca. 1.5 times (☐) (Figures 12, 29) or ca. as long as height of segment 11 (☐).

Gonopods (Figures 18-20, 54-57) simple. Coxite elongate, subcylindrical, strongly setose distoventrally; cannula normal. Telopodites curved, in situ crossing each other; prefemoral part long, about half as long as femorite, and usually densely setose; femorite long, strong, subequal in width all along its extent except slightly narrowed at base, nearly straight, clearly set off from post-femoral part by a demarcation sulcus; postfemoral part with two mesal processes: a smaller basal process **B** with tip pointed downward to prefemoral part, and a larger, more distal process **A**, this latter first directed ventrad and then also distad of prefemoral part in ventral view; solenophore (**sph**) slender, slightly longer than or nearly as long as femorite, in situ curved essentially mesad (= in the direction of the opposite gonopod), with a distally strongly expanded membranous end (**me**), almost completely sheathing a filiform and longer solenomere (**sl**), leaving only end of **sl** exposed; seminal groove running mainly medially along femorite, then directed slightly dorsally in distal part of femorite, in postfemoral part and at base of **sl**, then following ventrad, finally changing its course laterad at end of **sl**.

Distribution
K. formosanus (Verhoeff, 1939) is endemic to northern Taiwan, occurring at elevations lower than 1000 m a.s.l.

Genus *Orthomorphella* Hoffman, 1963
Orthomorphella Verhoeff, 1939a: 117 (invalidly proposed without a type-species); Hoffman 1963: 587; 1980: 169.

Orthomorphella Hoffman, 1963: 587 (type-species: *Polydesmus pekuensis* Karch, 1881); Jeekel 1970: 229; Hoffman 1980: 169; Zhang et al. 1997: 513.

Orthomorphella pekuensis (Karsch, 1881)
(Figures 37-38, 41-48, 62-63)
Polydesmus (Paradesmus) pekuensis Karsch, 1881: 39, pl. 3, Fig. 10; Attems 1898: 336; 1937: 83; Hoffman 1963: 588; Korsós 2004: 24.
Polydesmus pekuensis Karsch, 1881; Jeekel 1970: 229.
Orthomorpha pekuensis: Attems, 1898: 336, pl. 4, Figs 81 and 82; Hoffman 1963: 588; Korsós 2004: 24.
Orthomorpha (Kalorthomorpha) pekuensis: Verhoeff, 1931: 448; Attems 1937: 83, fig 102; Takakuwa 1954: 39, fig 35; Hoffman 1963: 588.
Orthomorpha circofera Verhoeff, 1931: 448, pl. 8, Figs. 58-60: Hoffman 1963: 588; Jeekel 1968: 73; Korsós 2004: 24.
Orthomorphella pecuensis [sic]: Verhoeff, 1939a: 117; Hoffman 1963: 588.
Orthomorpha flavomarginata Gressitt, 1941: 58; Wang 1964: 69; Korsós 2004: 26. **New synonymy!**
Oxidus pekuensis: Chamberlin & Wang, 1953: 6; Wang 1955: 13; 1964: 69.
Oxidus circofera: Wang, 1957: 27, 1964: 69; Korsós 2004: 24.
Oxidus (K.) circofera: Wang, 1958: 342; 1963: 90; Korsós 2004: 24.
Oxidus (K.) pekuensis: Wang, 1963: 90.
Chamberlinius pekuensis: Jeekel, 1968: 73; Wang & Mauriès 1996: 87; Korsós 2004: 24.
Orthomorphella pekuensis: Hoffman, 1963: 588, Figs. 5-8; 1973: 378; Golovatch 1980: 54; 1981: 164; Jeekel 1988: 98; Zhang et al. 1997: 514; Mikhaljova et al. 2000; Korsós 2004: 24.

Material examined
20 ☐, 20 ☐ (NCHUL), Taiwan (R. O. C.), Changhua County, FangYuan, WangGong, land reclaimed from sea, date unknown, leg. S. H. Wu. 2 ☐, 2 ☐ (NSYSUB-DI 212-215), Yunlin County, MaiLiao, MaiLiao Bridge, 30 July 2004, leg. H. D. Zhu. 3 ☐, 5 ☐ (NSYSUB-DI 422-429), same
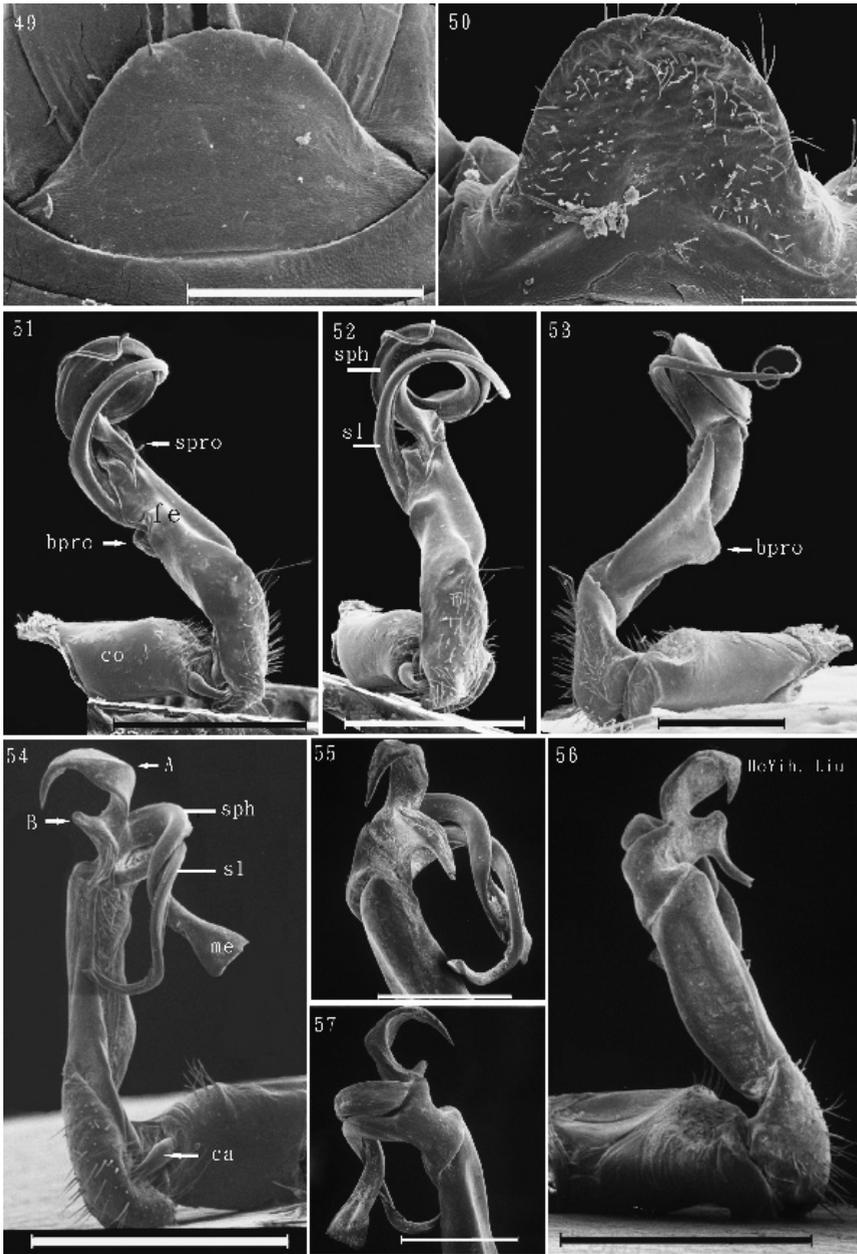
Figures 49-57. 49-53: *Cawjeekelia kanoi*, male from HueiSun forest. (49) hypoproct, ventral view. (50) sternal lobe between coxae 4, ventral view. (51-53): left gonopod, medial, subventro-medial and lateral views, respectively.
54-57: *Kronopolites formosanus*, male from WangGong, right gonopod. (54) entire, medial view. (55) telopodite tip, ventral view. (56) entire, lateral view. (57) telopodite tip, dorsal view. Scale line = 200 um for figure 50; 500 um for Figures 49, 55, 57; 1 mm for Figures 51-53, 54 and 56.
Designations: ca = cannula; co = coxite; bpro = a larger process of femorite; fe = femorite; pfe = prefemoral part; sl= solenomere; spro = a small process of femorite; sph = solenophore; A, B = two processes of postfemoral part; me = distally expanded membranous end of solenophore.

County, YuanChang, ChaoCuo, on ground, same date, same collector. 7 ☐, 13 ☐ (NSYSUB-DI 314-333), Kaohsiung County, TaoYuan, TengJhih, 1 452 m a.s.l., 2 July 2002, leg. H. W. Chang. 2 ☐ (NSYSUB-DI 40-41), Kaohsiung County, MeiNong, JhuZihNeng Power Plant, collection date unknown, leg. M. H. Shu. 1 ☐ (NSYSUB-DI 334), Ilan County, no. 7 provincial road, DaTong Station of Chinese Petroleum Corporation, near TaiYa Big Bridge, on wall of toilet, 163 m a.s.l., 19 August 2002, leg. J. N. Huang. 1 ☐ (NSYSUB-DI 196), Hualien County, ShouFeng, JhaoFeng Form, on the ground, 8 May 2005, leg. Y. K. Lin. 1 ☐, 1 ☐ (NSYSUB-DI 335-336), Taitung County, TaiMaLi, TaiMaLi, *Nephelium* garden, 44 m a.s.l., 26 January 2003, leg. S. S. Dai.

Remarks

This species occurs in Taiwan at different elevations in a variety of habitats, mostly disturbed or man-made though. It seems to have been introduced there from the mainland. In Korea and the adjacent parts of China, however, it is also one of the most common diplopods both in natural and anthropogenic environments (urban, parks, plantations etc.) (e.g. Mikhaljova *et al.*, 2000).

Genus *Oxidus* Cook, 1911

Oxidus Cook, 1911: 628; Jeekel 1970: 228; Hoffman 1980: 169; Chang 1998: 580; Shinohara & Tanabe 1999: 662.
Kalorthomorpha Attems, 1914: 191; Jeekel 1968: 71; Hoffman 1980: 169.

Oxidus gracilis (C. L. Koch, 1847)

(Figures 39-40, 64-65)
Fontaria gracilis Koch, 1847: 142; Koch 1863: 51, Fig 173; Cook 1911: 628; Chamberlin & Wang 1953: 7; Korsós 2004: 24.
Paradesmus gracilis: Cook, 1911: 631; Attems 1937: 82; Korsós 2004: 24.
Orthomorpha gracilis: Bollman, 1893: 197; Pocock 1895: 354; Attems 1898: 337, Figs. 89 and 90; 1914: 196; Saussure & Zehntner 1902: 84; Korsós 2004: 24.
Oxidus gracilis: Cook, 1911: 631; Attems 1937: 82; Chamberlin & Wang 1953: 7; Wang 1955: 13; 1958: 342; 1963: 90; 1964: 69; Golovatch

1981: 164; 1984; 54; Miyosi 1982: 741, 3 Figs.; Murakami 1993: 100; Wang & Zhang 1993: 848, Fig. 3; Golovatch & Enghoff 1993, 115, Figs. 12-14; Golovatch & Martens 1996: 170; Wang & Mauriès 1996: 86; Shelley & Lehtinen 1998: 81, Figs. 1-3; Korsós 2004: 24.
Orthomorpha (Kalorthomorpha) gracilis: Attems, 1937: 82, Fig 101; Takakuwa 1954: 37, Figs. 31 and 32.

Material examined

1 ☐ (NTNUL 73), Taiwan (R. O. C.), Taipei County ShTing County, 250~400 m a.s.l., 9 June 1988, leg. S. H. Chen. 1 ☐, 1 ☐ (NSYSUB-DI 376-377), same City, YangMingShan National Park, 20 September 2002, leg. H. D. Jhu. 6 ☐, 3 ☐ (NSYSUB-DI 367-375), Taoyuan County, FuSiing, HuaLing, ShangBaLing, 1343 m a.s.l, 17 August 2002, leg. C. C. Chen & J. N. Huang. 1 ☐ (NTNUL 71), Taipei County, ShihTing, 250~400 m a.s.l, 13 April 1996, leg. S. H. Chen. 1 ☐ (NCHUL), same County, GongLiao, YuanWangKeng (toward CaoLing old road), the beginning of Shuang Stream, 184-224 m a.sl., 9 May 1998, leg. S. H. Wu. 1 ☐ (TFRI), same County, Ulai, FuShan Garden, 726 m a.s.l., 1 November 2001, leg. W. B. Huang. 1 ☐ (NSYSUB-DI 379), same County, LinKou, close to coast, 120 m a.s.l, 15 April 2003, leg. S. I. Wu. 15 ☐, 12 ☐ (NSYSUB-DI 340-366), Hsinchu County, Ufong, GuanU ShanJuang (a hotel), ca. 2000 m a.s.l., 12 August 2002, leg. C. C. Chen, Y. H. Lin & J. N. Huang. 1 ☐, 1 ☐ (NTNUL 57-58), Nantou County, RenAi, YuanFong, on the UShe branch line of middle crossing road, under stones, 2 756 m a.sl., 31 August, 1988, leg. S. H. Chen r. 1 ☐, 1 ☐ (NTNUL 65-66), same County, ShinYi, Zjhong, 2335 m a.s.l., 1 July 1989, same collector. 1 ☐, 1 ☐ (NTNUL 63.-64.), same County, ShinYi, TaTaJiiaAnBu, 2,650 m a.s.l, 2 July 1989, same collector. 1 ☐ (NMNS), same County, LuGu, FengHuangGu, InTan, nature forests, 734 m a.s.l., 24 August-25 September 1995, leg. W. H. Chou. 1 ☐ (NMNS), same locality, 25 August -26 September year unknow, same collector. 33 ☐, 18 ☐ (NMNS), same locality, 9 August 1995, same collector. 1 ☐ (NMNS), same locality, 13 October 1995, same collector. 4 ☐, 3 ☐ (NMNS),
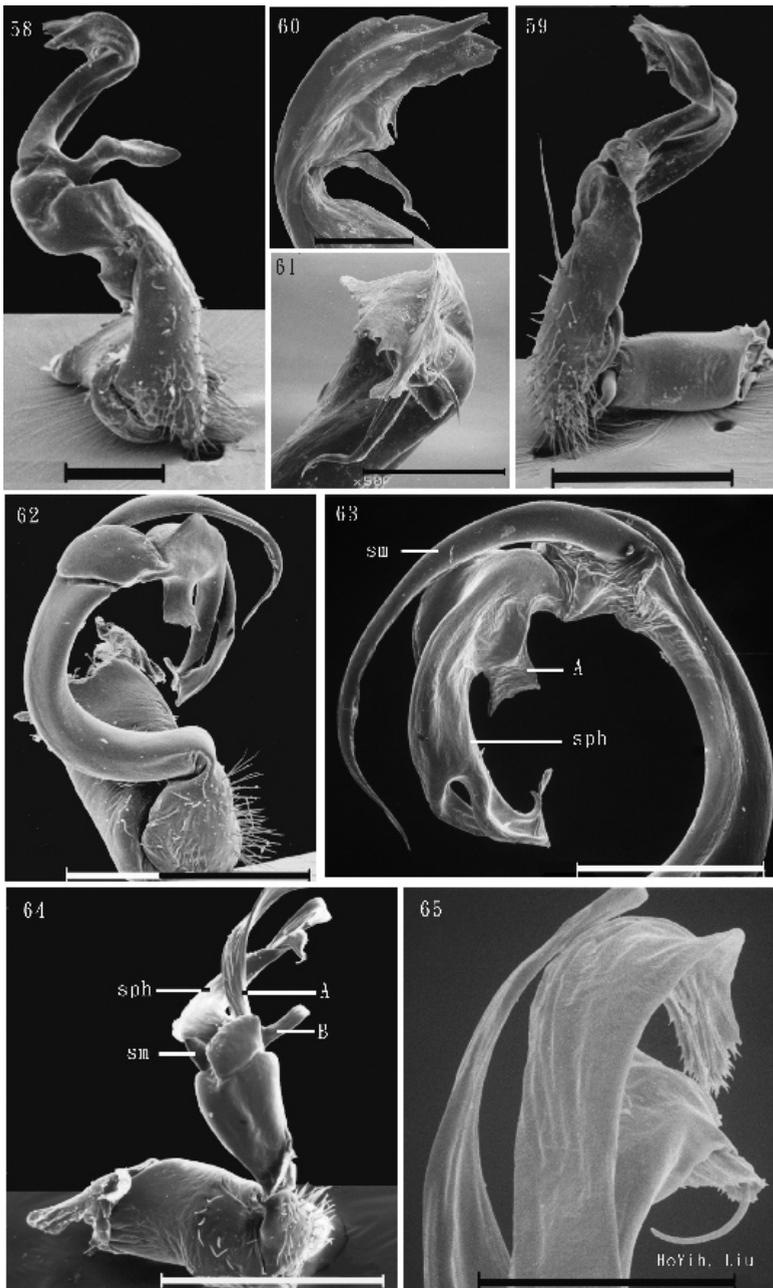
Figures 58-65. 58-61: *Chondromorpha xanthotricha*, male from WanDan, right gonopod. (58) entire, ventral view. (59) entire tip, medial view. (60) telopodite tip, dorsal view. (61) telopodite tip, lateral view. 62-63: *Orthomorphella pekuensis*, male from WangGong, right gonopod. (62) entire, ventral view. (63) distal telopodite, dorsal view
64-65: *Oxidus gracilis*, male from FengHuangGu. (64) right gonopod, entire, lateral view. (65) left gonopod, telopodite tip, medial view.
Scale line = 100 μm for figures 60, 61, 65; 500 μm for Figures 59, 63, 64; 0.3 mm for Figure 58; 1 mm for figure 62. Designation: A, B = two processes of postfemoral part

same locality, 29 May 1996, same collector. 1 ♂, 2 ♀ (NMNS), same locality, 31 May 1996, same collector. 6 ♂, 6 ♀ (NMNS), same locality, 24 August-25 September 1996, lawn behind administration building, same collector. 1 ♀ (NMNS), Taichung County, AnMaShan, decayed area, soil collection, 0~5 cm deep, 2000 m a.s.l., 15 August 1996, leg. R. F. Chao. 1 ♂ (NSYSUB-DI 337), same County, HePing, WuLing Farm, GaoShan river, in decayed branches and leaves, 1842-2327 m a.s.l, 14 July 2000, leg. S. H. Sie. 1 ♂, 4 ♀ (NTNUL 52-56), 1 ♂, 1 ♀ (NTNUL 67-68), Chia-I County, AliShan, ALiShan, 2 250 m a.s.l, 3 July 1989, leg. S. H. Chen. 1 ♂ (NSYSUB-DI 338), same locality, LongTou, bamboo forests, 2 250 m a.s.l, 21 April 2002, leg. J. L. Chao. 1♂ (NSYSUB-DI 339), Kaohsiung County, TaoYuan, TengJhih, ShihShan forest path, ca. 1600 m a.s.l., 1 August 2002, leg I. T. Chen. 1♂ (NSYSUB-DI 378), same locality, JhongJhihGuan, YueLing old road, in rotting wood, 2040 m a.s.l, 18 October 2002, leg. Y. H. Lin. 1 ♂, 1 ♀ (NTNUL 61-62), Hualien County, FuLi, 169-1,203 m a.s.l, 4 July 1988, leg. S. H. Chen.

Remarks

This cosmopolitan species of presumably East Asian origin occurs in Taiwan at very different elevations and in various habitats, ranging from (nearly) natural to strongly disturbed. It seems to have been introduced from the mainland China, where it is among the most common and abundant species (e.g. Geoffroy & Golovatch 2004).

The illustrations are provided to show that fading can be considerable during long-term conservation of the material in alcohol.

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Faunistical research on the chilopods of Hungarian Lower Mountains

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Dányi, L. 2006. Faunistic research on the chilopods of Hungarian Lower Mountains. Norw. J. Entomol. 53, 271-279.

In Hungary myriapodological research has always been connected with areas in the lower mountains, as it is there you can find diverse broad-leaved forests which offer microhabitats best fitting the needs of myriapods. This paper presents the results of a study on about 2700 specimens collected in the Hungarian Lower Mountains. It gives new species records from Kőszeg Mts., Sopron Mts., Mecsek Mts., Keszthely Mts., Bakony Mts., Vértes Mts., Gerecse Mts., Buda Mts., Börzsöny Mts., Mátra Mts., Bükk Mts. and Zemplén Mts., as well as the first description of the chilopod-fauna of the mountainous region of Medves. An overview on earlier researches in the Hungarian Lower Mountains is given along with the complete up-to-date species lists of each region. A faunistical evaluation is added regarding the occurrence data of each species and its chorotype.

Key words: Hungary, Chilopoda, Myriapoda, faunistic, distribution

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INTRODUCTION

Hungary is situated in the Southeast of Central Europe, in the Carpathian Basin. Its westernmost parts almost touch the Alps, in the Northeast, it is the proximity of the Carpathians that is characteristic, whereas the South is open to the Balkans. Considering this, we can rigthly expect an interesting chilopod fauna including species of different chorotypes.

A considerable part of Hungary is a plain at about 80-150 m above sea-level. Another part of the country is a slightly more elevated and more structured hilly country, whereas in the remaining, still considerable part we find „lower mountains". As the highest point of Hungary is only 1014 m high the „Lower Mountains" (hereafter abbreviated as „LM") are just about 400 to 1000 m above sea-level. These latter ones are the most structured surfaces in Hungary and this variability of the terrain is reflected in the variability of the

habitats and microhabitats. The majority of the forests in Hungary which are in a close-to-natural state is situated in these LM. The greater part of the lower, flatter areas is under agricultural cultivation and its forests rather consist of planted, alien species, such as *Robinia pseudoacacia* (black locust tree) and conifers and these areas are thus – from a myriapodologist´s point of view – far less attractive than the Mountains. For this reason, earlier myriapodological research took place mainly in the LM, whereas works on centipedes of the lower areas are much more rare (e.g. Korsós 1987, 1991, Loksa 1956, 1981, 1983).

PREVIOUS STUDIES

First insights into the chilopod fauna of the Hungarian LM were given by Robert Latzel's (1845-1919) fascinating work (Latzel 1880). However, Latzel gave only very rough locality

data, for example „South-Hungary", thus they cannot be really used for faunistical analysis at a finer scale. After Latzel we have to mention Ödön Tömösváry (1852-1884) and Jenő Daday (1855-1920), who (as well as Latzel) ment the old Hungary as it was at that time under the Austro-Hungarian Monarchy, which means that a lot of their data are from areas which are now far away from the present borders of the country. Tömösváry, however, has some useful data from the Zemplén Mountains (published by Chyzer 1886). Unfortunately, Daday´s (1889) determinations are not reliable, as Loksa (1955) has already noticed. This is supported here, too, thus Daday´s data is not regarded, except if re-examined.

After Daday it was Karl Wilhelm Verhoeff (1867-1945) and László Szalay (1887-1970) who published sporadic data on Hungarian chilopodes. Verhoeff (1901) described a new subspecies from the LM of the Mecsek (*Lithobius parietum mecsekensis* Verhoeff, 1901) whereas Szalay, curator of Myriapoda in the Hungarian Natural History Museum, gave quite a thorough list of species from the Kőszeg-Mountains and also published some new records from other mountains in Hungary (Szalay 1940a, 1940b, 1944, 1956). There was also György Ilosvay who published some records from the Bakony Mountains (Ilosvay 1982, 1983, 1985).

The last predecessors to mention, who researched on Hungarian LM, are Imre Loksa (1923-1992) and some of his students. Loksa, professor at the University of Budapest, collected and determined material from a wide range of Hungarian regions and published numerous works. He investigated for example the Keszthely Mountains (Loksa 1961b), the Bakony (Loksa 1961a, 1971), the Pilis (Loksa 1988, 1991) and the Bükk Mountains (Loksa 1968, 1979) more thoroughly, as well as Pannonian karst white oak low woods (Cerraso-Quercetum, Cotino-Quercetum Quercetum pubescenti) all around the country´s mountains (Loksa 1966). His name is connected with a chilopod-species, Lithobius *luteus Loksa*, 1947 which he described from Hungary (Loksa 1947).

Some of Imre Loksa's students who took part in ecological research in some of the LM and also explored the chilopod-fauna of a smaller region have to be mentioned separately. These investigations took place under the supervisorship of Loksa and as it was his knowledge that gave the background to the determinations, the data given in his students´ master thesis can be considered to be reliable. Júlia Pallag and Zsuzsa Szakál studied the fauna of the Mountains of Buda, whereas Enikő Kondás, Anikó Teglovics and Adrienn Kálnay did the Mountains of Visegrád. Zsuzsa Szilágyi explored the Börzsöny-mountain. Another one of Loksa´s students was Ágnes Sallai, who examined the Mountains of Buda, too (Sallai 1992).

The knowledge of the chilopod-fauna of the Hungarian LM, up to the time I started my work, is summarized in Table 1 („+" indicate the species known).

MATERIAL AND METHODS

This investigation includes 15 regions of the LM in the country (Figure 1) concentrating mostly on the less explored areas. The most typical and extensive habitat types are: rocky slopes (Brometalia erecti and Festucetalia valesiacae), which get quite hot and even dry out sometimes on the southern hill-sides; Pannonian karst white oak low woods (Orno-Cotinetalia) and oak woods (Quercetalia pubescentis), which also are rather dry; more closed, cooler and moister beech-forests (Fagetalia) and of course all the transitions (Simon 2000).

The basis of this work are my own collections, and those of colleagues, as well as undetermined material in the Hungarian Natural History Museum, the regional Natural History Museum of Bakony Mountains and the Museum of Mátra Mountains. The methods used for collecting by other collectors include pitfall traps, singling and sifting, whereas I used the latter two methods. To identify the animals the following works were of major help: Andersson (1979), Christian (1996), Eason (1964), Kaczmarek (1979), Koren (1986,
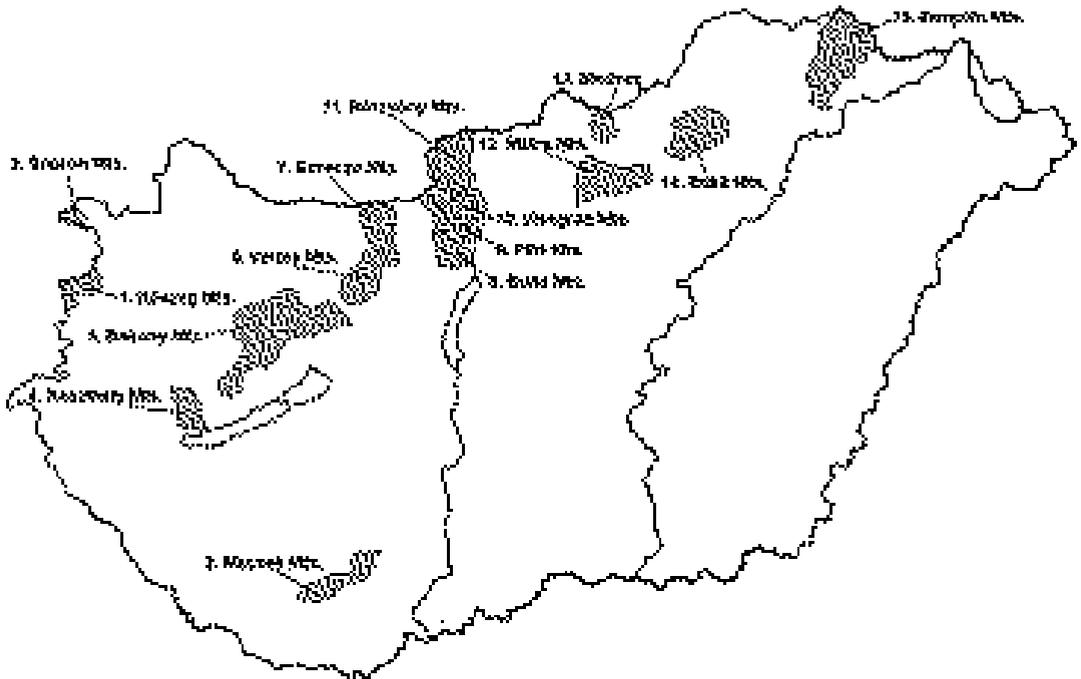
Figure 1. Map of Hungary showing the researched areas. Numbers are referring to Table 1.

1992), Loksa (1955), Matic (1966, 1972). The determined material is placed in the Myriapoda Collection of the Hungarian Natural History Museum.

RESULTS

About 2700 specimens of 37 species were studied from these mountainous regions of Hungary. One species, *Lithobius cyrtopus* Latzel, 1880 was new to the fauna of Hungary (Dányi & Korsós 2002). Table 1 shows the species lists of each region summarizing earlier and own results (,,+" indicates earlier species data, ,,+" shows new species data), adding the chorotype of each species according to Koren (1986, 1992) and Zapparoli (2002, 2003). By this, the number of centipede species known from the Hungarian LM rises to 49 representing 80,3 % of all known Hungarian species (61).

DISCUSSION

Most of the 12 Hungarian species missing from the LM are rare in Hungary and only known from few localitities (such as *Lithobius burzenlandicus* Verhoeff, 1931, *Harpolithobius anodus* (Latzel, 1880), *Henia bicarinata* (Meinert, 1870), *Pleurogeophilus mediterraneus* (Meinert, 1870)).

It is only *Lithobius curtipes* C. Koch, 1847, which occurs more frequently in the plains, however there is no support in the literature that it avoids mountainous regions anywhere else (Eason 1964, Matic 1966).

The composition of the centipede fauna according to chorotypes is the following: European or wider: 42,8% (21 species), Central European: 18,4% (9), South-European: 20,4% (10), Southeast-European: 4,1% (2), Mediterranean: 8,2% (4), Carpathian or Alpian-Carpathian: 6,1% (3).

Table 1. The species lists of each region summarizing earlier and own results (+ indicates earlier species data, **+** shows new species data), adding the chorotype of each species according to Koren (1986, 1992) and Zapparoli (2002, 2003). ACA= Alpian-Carpathian, CAR= Carpathian, CAE= Centralasiatic-European, CEU= Central European, EUR= European, MED= Mediterranean, SEE= Souteast-European, SEU= South-European, SIE= Sibiric-European, TUE= Turanic-European, WPA=W-Palearctic.
1. Kőszeg Mts.; 2. Sopron Mts.; 3. Mecsek Mts.; 4. Keszthely Mts.; 5. Bakony Mts.; 6. Vértes Mts.; 7. Gerecse Mts.; 8. Buda Mts.; 9. Pilis Mts.; 10. Visegrád Mts.; 11. Börzsöny Mts.; 12. Mátra Mts.; 13. Medves; 14. Bükk Mts.; 15. Zemplén Mts.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	chorotype
Schendyla carniolensis (Verhoeff, 1902)	+															MED
Schendyla montana (Attems, 1895)	+				+					+				+		SEU
Schendyla nemorensis (C.L. Koch, 1836)			+	+	+	+	+	+	+	+	+	+	+	+	+	EUR
Dignathodon microcephalus (Lucas, 1846)			+	+	+	+	+	+	+	+	+			+		MED
Henia illyrica (Meinert, 1870)	+		+	+	+	+	+	+	+	+	+		+	+		SEU
Strigamia acuminata (Leach, 1815)	+		+		+		+		+	+			+		+	EUR
Strigamia crassipes (C.L. Koch, 1835)				+					+				+			EUR
Strigamia transsilvanica (Verhoeff, 1928)	+		+		+	+				+	+	+		+	+	SEU
Geophilus carpophagus Leach, 1815					+							+				EUR
Geophilus electricus (Linneus, 1758)	+															WPA
Geophilus flavus (DeGeer, 1778)	+		+		+	+	+				+	+	+	+	+	SIE
Geophilus insculptus Attems, 1895	+		+	+	+	+	+	+	+			+	+			EUR
Geophilus linearis C.L. Koch, 1835					+											SEU
Geophilus proximus C.L. Koch, 1847						+		+	+					+		TUE
Clinopodes flavidus C.L. Koch, 1847	+		+	+	+	+	+	+	+	+	+	+	+	+	+	TUE
Pachymerium ferrugineum (C.L. Koch, 1835)	+		+	+	+	+									+	WPA
Cryptops anomalans Newport, 1844	+		+	+	+	+	+	+	+	+				+	+	SEU
Cryptops hortensis (Donovan, 1810)			+	+	+	+		+	+	+	+			+		CAE
Cryptops parisi Brölemann, 1920	+		+	+	+	+	+	+	+	+				+		SEU
Scolopendra cingulata Latreille, 1829					+											MED
Eupolybothrus transsylvanicus (Latzel, 1882)			+													SEU
Eupolybothrus tridentinus (Fanzago, 1874)	+		+	+	+	+			+	+				+		SEE
Lithobius aeruginosus L. Koch, 1862	+		+	+	+	+	+	+	+	+	+	+		+	+	EUR

Table 1. continued

Species	Distribution
Lithobius austriacus (Verhoeff, 1937)	CEU
Lithobius biunguiculatus Loksa, 1947	CAR
Lithobius crassipes L. Koch, 1862	WPA
Lithobius microps Meinert, 1868	EUR
Lithobius agilis C.L. Koch, 1847	CEU
Lithobius borealis Meinert, 1868	EUR
Lithobius cyrtopus Latzel, 1880	ACA
Lithobius dentatus C.L.Koch, 1844	CEU
Lithobius erythrocephalus C.L. Koch, 1847	EUR
Lithobius forficatus (Linnaeus, 1758)	EUR
Lithobius lapidicola Meinert, 1872	EUR
Lithobius lucifugus L. Koch, 1862	EUR
Lithobius luteus Loksa, 1947	CAR
Lithobius macilentus L. Koch, 1862	CEU
Lithobius melanops Newport, 1845	EUR
Lithobius mutabilis L. Koch, 1862	CEU
Lithobius muticus C.L. Koch, 1847	CEU
Lithobius nodulipes Latzel, 1880	CEU
Lithobius pelidnus (Haase, 1880)	EUR
Lithobius parietum Verhoeff, 1899	SEU
Lithobius piceus L. Koch, 1862	SEU
Lithobius stygius Latzel, 1880	SEE
Lithobius tenebrosus Meinert, 1872	CEU
Lithobius tricuspis Meinert, 1872	CEU
Lithobius validus (Meinert, 1872)	SEU
Scutigera coleoptrata (Linnaeus, 1758)	MED

European (or wider) and Central European species

There are a couple of species, which occur just about everywhere in Hungary and according to this, they were found in almost each of the examined 15 regions. Among these are *Lithobius erythrocephalus* C.L. Koch, 1847, *Lithobius forficatus* (Linnaeus, 1758), *Clinopodes flavidus* C.L. Koch, 1847, which are wide-spread throughout Europe, as well as *Lithobius muticus* C.L. Koch, 1847 and *Lithobius mutabilis* L. Koch, 1862, which are characterized by Zapparoli (2002) as being of Central European chorotype.

Another large part of the species is still quite common in the whole country, but there are a few mountains from which they are not yet known, although one can expect to find them also in those in the future, species like *Schendyla montana* (Attems, 1895), *Schendyla nemorensis* (C.L. Koch, 1836), *Geophilus flavus* (DeGeer, 1778), *Geophilus proximus* C.L. Koch, 1847, *Strigamia acuminata* (Leach, 1815), *Cryptops hortensis* (Donovan, 1810), *Lithobius aeruginosus* L. Koch, 1862, *Lithobius agilis* C.L. Koch, 1847, *Lithobius crassipes* L. Koch, 1862.

Another, bigger group consists of species which do occur all over Europe, but are quite rare, and of which we only have data from a few mountains: *Geophilus carpophagus* Leach, 1815, *Geophilus electricus* (Linneus, 1758), *Geophilus linearis* C.L. Koch, 1835, *Pachymerium ferrugineum* (C.L. Koch, 1835), *Strigamia crassipes* (C.L. Koch, 1835), *Schendyla carniolensis* (Verhoeff, 1902), *Lithobius lapidicola* Meinert, 1872, *Lithobius lucifugus* L. Koch, 1862, *Lithobius melanops* Newport, 1845, *Lithobius microps* Meinert, 1868, *Lithobius piceus* L. Koch, 1862, *Lithobius tenebrosus* Meinert, 1872, *Lithobius tricuspis* Meinert, 1872. Being rare, these single points of occurrence in the Hungarian LM certainly do not reflect their real distribution.

Among the typically Central European *Lithobius* species you can find some (*Lithobius borealis* Meinert, 1868, *Lithobius dentatus* C.L.Koch, 1844, *Lithobius macilentus* L. Koch, 1862, *Lithobius nodulipes* Latzel, 1880, *Lithobius pelidnus* (Haase, 1880), *Lithobius validus* (Meinert, 1872)) which show a peculiar pattern of distribution in Hungary. They seem to have quite distinct borders running from the North to the South through the country. *L. borealis*, mentioned already by Loksa as a „Western element", and *L. pelidnus*, have so far only been recorded at the western border of the country. We do not have any data of *L. macilentus, L. nodulipes* and *L validus* East of the Bakony Mountains, whereas *L. dentatus* seems to disappear completely East of the Danube, even though it can be found to the West of it. Characteristically, all 6 species prefer moister habitats within Hungary and are beech-forest and mixed beech-forest dwellers. As Országh (2001), Matic (1966), Stoev (1997) and Zalesskaja (1978) give records of the above species from Slovakia, the Ukraine, Romania and Bulgaria, it is probable that these borderlines running through Hungary do not show some really existing distributional limits and will move after future research.

The situation of *Lithobius austriacus* (Verhoeff, 1937) might be a bit different, as its distribution goes on to the Northeast through the Ukraine (Zalesskaja 1978) and continues to the West and to the South across Slovenia (according to Stoev 1997). Its area with an eastern "borderline" on the Eastern side of the Mátra Mountains will probably be extended further East thus connecting the Hungarian and the Romanian, Bulgarian or Ukrainian localities. However, as there are no occurrence data from further southeast as the Mecsek-Mátra-mountains-line it might be that this is a real border of its distributional area.

South-, Southeast European and Mediterranean elements

The two species of *Cryptops, Cryptops anomalans* Newport, 1844 and *Cryptops parisi* Brölemann, 1920 are more rare further North, and in some of the northernmost mountains of Hungary, they are not found so far. It is not very probable, that they are completely missing here, but more thorough research is needed to find them. The situation with *Dignathodon microcephalus* (Lucas, 1846) and *Henia illyrica* (Meinert, 1870) is similar. These

two species definitely prefer habitats which warm up easily and are thus quite dry.

In the case of the two Hungarian *Eupolybothrus* species, we probably see a part of the boundary of their actual distribution. *Eupolybothrus transsylvanicus* (Latzel, 1882) is in Hungary only known from a few stony, rather warm habitats, and it was found in similar places in the Mecsek Mountains, which is one of its northernmost occurrences. *Eupolybothrus tridentinus* (Fanzago, 1874) is present in a larger part of Hungary. Here it seems to prefer beech-forests. So far, it appears as if the river Danube draws a definite North and Northeast boundary to its distribution. As Országh (2001) does not give any records of this species from Slovakia, the northernmost populations in this part of Europe might live in the Hungarian mountains.

Two, basically Mediterranean species, Scolopendra cingulata Latreille, 1829 and *Scutigera coleoptrata* (Linnaeus, 1758), show few data from mountainous regions. S. cingulata was formerly only known from the Vértes Mountains, and in spring 2005 we also found it in the adjacent areas in the Bakony Mountain. These two Hungarian localities are far off and isolated from the main area. To explain this, Szalay (1956) suggested that they might be relicts from the Tertiary Period. (The only two species records from further North is from the Ukraine (Zalesskaja & Schileyko1992) and the environs of Vienna (Szalay 1956).) This is supported by the fact that while this species is common in every place around the Mediterranean Sea, in Hungary it definitely prefers the combination of quite warm rocky slopes and karst white oak low woods. *Scutigera coleoptrata* is known from some more, flatter areas in the country, but among all the mountains it was only found in the Mountains of Buda and Pilis, where anthropogenic influence can not be excluded.

Carpathian elements

L. luteus is known from the Romanian Carpathians, from Western Hungary (Loksa 1947, 1955, Matic

1966) and from Moravia (Czech Republic) (Tajovský 2001). On the basis of this occurrence data it can be assumed, that this species has a wider distribution in the Carpathians, if not even wider and that it probably is not yet detected in many places due to its rarity. This assumption is supported by recently discovered occurrences in the Hungarian LM (such as Sopron, Mecsek and Bükk Mts.). Thus the species´ chorotype can be characterized as Carpathian. The situation with *Lithobius biunguiculatus* Loksa, 1947 is similar, while *L. cyrtopus* can be characterized as an Alpian-Carpathian element showing a connection between the Zemplén Mountains and the nearby chain of the Carpathians.

From a biogeographical point of view it is certainly interesting to know about the occurrence of *Lithobius stygius infernus* described by Loksa (1948) from one of the caves in the Mountains of Buda. However, to evaluate this, an overall survey would be needed on the relations between all the members of the (sub)species groups living in caves in the Balkan. For this, we would need first to find the type material again, or, at least collect new specimens.

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Recent knowledge on the centipede fauna (Chilopoda) of south Aegean archipelago (Greece, Eastern Mediterranean)

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Simaiakis, S. & Mylonas, M. 2006. Recent knowledge on the centipede fauna (Chilopoda) of south Aegean archipelago (Greece, Eastern Mediterranean). Norw. J. Entomol. 53, 281-298.

The present knowledge on centipedes of south Aegean archipelago is described approaching the faunistic element of the major geographical compartments of the area and distribution of species. The examined material mainly derived from the well-explored islands of Kyklades and Dodekanisa and the rich centipede collection of the Natural History Museum of Crete. 71 species and subspecies belonging to 25 genera and 10 families are registered from the south Aegean islands; 33 taxa belong to Geophilomorpha, 27 to Lithobiomorpha, 10 to Scolopendromorpha and 1 to Scutigeromorpha. 56 species and subspecies are recorded from Dodekanisa, 43 from Crete and 38 from Kyklades. 19 species are referred for the first time from Kyklades, 18 from Dodekanisa and 1 from Crete. The analysis of the faunistic elements showed that 42% of the south Aegean centipedes have Mediterranean affinities (s.l.), 25% have European affinities (s.l.), 8% are Balkanic, 8% are south Aegean endemics, 6% have west Palearctic affinities, 6% have Turano Anatolian affinities, 3% have Turano Mediterranean affinities and 1% are Turano European.

Key-words: Insular Greece, Kyklades, Dodekanisa, Crete, Scutigeromorpha, Lithobiomorpha, Scolopendromorpha, Geophilomorpha.

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INTRODUCTION

Chilopoda

Centipedes (Chilopoda), are common and relatively familiar animals, which are found in soil and litter or under stones or bark (Lewis 1981). They are predators (carnivorous), living on other invertebrates and able to tackle relatively large and active prey (Eason 1964). Most species are easily found during the wet period of the year (spring, autumn), when temperature and humidity permit them to be active (Eason 1964). Centipedes are a rather difficult group to study from the systematic and faunistic point of view, while many species have been described in the past in a very concise way and on unstable characters (Zapparoli 2003). Identification problems arise from poor observations, inadequate description, lack of knowledge of the literature and descriptions based on juvenile specimens (Lewis 2003) and both, taxonomy and nomenclature have become chaotic (Zapparoli 2003).

Historical background

The centipede fauna of south Aegean islands is relatively well known, in contrast to other animal groups. Our current knowledge derives mainly from the studies of Lucas (1853), Karsch (1888), Cecconi (1895), Attems (1902), Verhoeff (1925), Chamberlin (1956), Kanellis (1959), Dobroruka (1977), Matic (1980), Matic & Stavropoulos (1988), Eason (1990), Matic & Stavropoulos

Figure 1. Sampling sites in the south Aegean Islands (collections by hand).

(1990a, b, 1993), Zapparoli (1993, 1994). Recently, Zapparoli (2002), based on the material collected from zoological trips of many naturalists from several research institutes, presented a modern catalogue of the centipede fauna of Greece. In this 29 species were recorded from Crete, 19 from Kyklades and 37 from Dodekanisa. Recent faunistic works concerning the centipede fauna of Crete and its satellite islets (Simaiakis et al. 2004) as well as the centipede fauna of south Aegean archipelago (Simaiakis et al. unpublished data) dramatically changed the knowledge on the centipedes of the mainland and insular Greece.

The Aegean archipelago

South Aegean archipelago appears to be an excellent geographical area for studying distributional patterns and faunistic relationships among different geographical subareas for a given animal group. Recent biogeographical and/or taxonomic works on the Aegean archipelago have dealt with beetles (Fattorini 2002, Chatzimanolis et al. 2003), butterflies (Dennis et al. 2000), centipedes (Simaiakis et al. 2004), land snails (Sfenthourakis et al. 1999, Welter-Schultes & Williams 1999), reptiles (Foufopoulos & Ives 1999), scorpions (Stathi & Mylonas 2000), spiders (Chatzaki et al. 2002, Chatzaki 2003) and terrestrial isopods (Sfenthourakis 1994, 1996, Sfenthourakis et al. 2004, Sfenthourakis & Giokas 1998).

The Aegean archipelago consists of more than 3000 islands, mostly continental in their origin (Trichas & Legakis 1987). Crete is one of the largest islands of the Mediterranean, with a surface of 8.261 km². The Kyklades complex, consisting of 21 main islands and hundred islets, lies on the center of the Aegean archipelago. The total surface of the Kyklades is approximately 2572 km². 75% of the area is mountainous and the rest consists of lowlands. Naxos is the
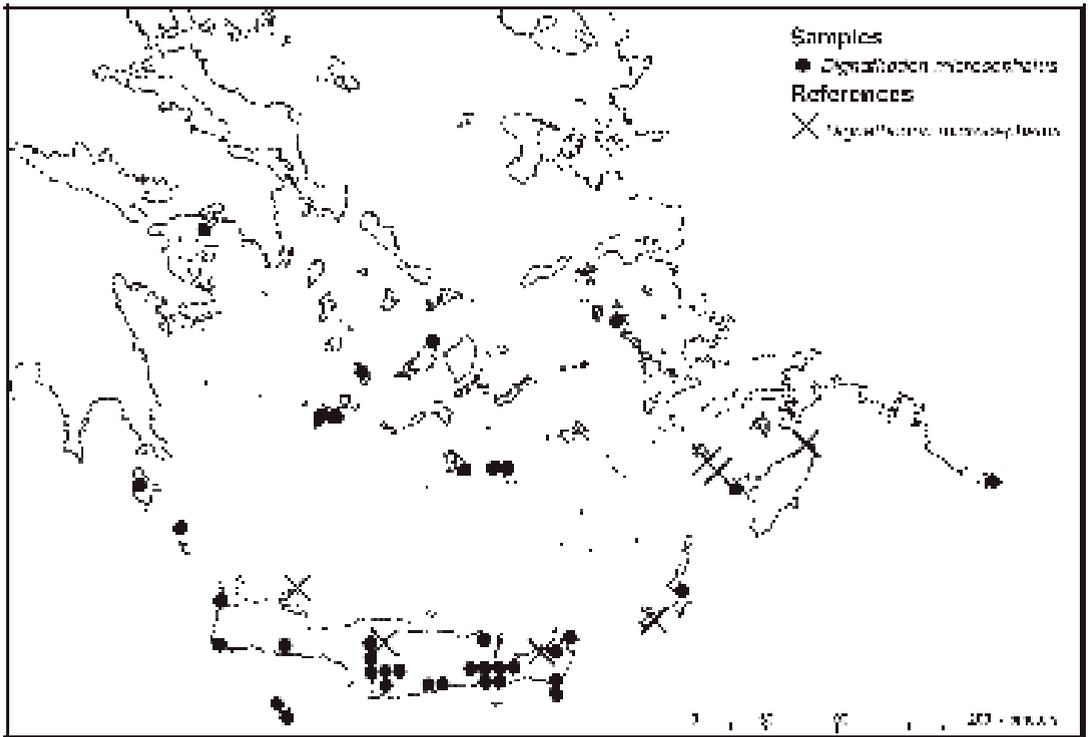
Figure 2. *Dignathodon microcephalus*, distribution on the south Aegean archipelago.

largest of the Kyklades in the Aegean Sea with a surface of 430 km². Dodekanisa is a complex located in the southeastern Aegean constituted by 18 large islands and many small islets. The surface of Dodekanisa is about 2705 km², 42% of total extent consists of lowlands, 26% is called submountainous and 32% mountainous. Rodos is the largest island of Dodekanisa, followed by Kos, Karpathos, Kalymnos, Astypalaia, Kasos, Tilos, Symi, Leros, Nisyros, Patmos, Kastelorizo, and Chalki.

Aim of the present investigation

In this paper we present a fully revised catalogue of the centipede fauna of the south Aegean archipelago based on the PhD research of the first author, on unpublished records in the collection of the Natural History Museum of Crete (NHMC) as well as on literature data. In total, we present data from 67 islands or islets of the south Aegean area. We present the faunistic element for each

geographical compartment as well as distributional maps for selected species.

The taxonomic status of several species groups: in *Bothriogaster, Pachymerium, Henia* and around *Lithobius piceus, L. peloponnesiacus and L. pusillus* needs be revised and information on habitat preferences of many species is still incomplete (Simaiakis et al., unpublished data).

MATERIAL AND METHODS

Within the framework of the PhD research of the first author (Natural History Museum of Crete – University of Crete), more than 3000 centipedes were collected by hand from 274 samplings stations during the wet period of two years field work (Figure 1). Centipedes were preserved in 95% alcohol. Identifications took place at the Natural History Museum of Crete (NHMC) and at
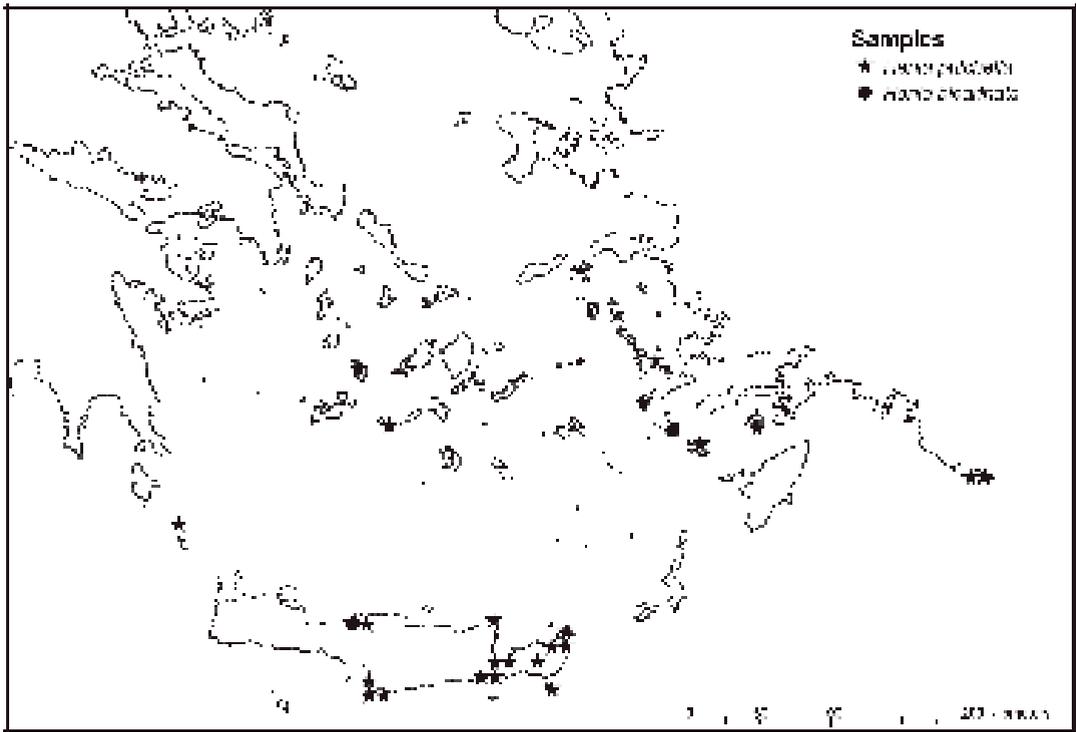
Figure 3. *Henia bicarinata & H. pulchella*, distribution on the south Aegean archipelago.

the Zoological Museum of Copenhagen (ZMUC). Apart from recent data, more than 3500 centipedes (deposited at the NHMC) collected from several sites (Crete, Kythira – Antikythira complex, Kastelorizo complex) were also examined. These samplings were carried out the period from April 1991 up to January 2004, and help us to improve the knowledge for many species.

For each species we give the distribution in the Aegean archipelago and the adjacent Anatolian peninsula, the chorotype and general remarks. Distribution maps of certain species were drawn with Arc View GIS version 3.1. and Corel Draw 10.

RESULTS

A list of the species studied in the south Aegean islands (Crete, Dodekanisa, Kyklades), the

chorotype and distribution of each species on mainland Greece and Turkey are presented in Table 1.

Information about the geographical distribution of all species has previously been published, and for the species of Crete mostly in Zapparoli (2002) and in Simaiakis et al. (2004). However, some important notes on several species are given below as remarks to Table 1.

Remarks to Table 1.
1. Dignathodon microcephalus (Lucas, 1846) (Figure 2). First record for Kyklades.
2. Dignathodon pachypus Verhoeff, 1943. First record for Dodekanisa and Greece.
3. Henia (Henia) athenarum Pocock, 1891. First record for Kyklades and Dodekanisa.
5. Henia (Henia) vesuviana Newport, 1845. First record for Dodekanisa and Greece.
6. Henia (Scotophilus) bicarinata Meinert,
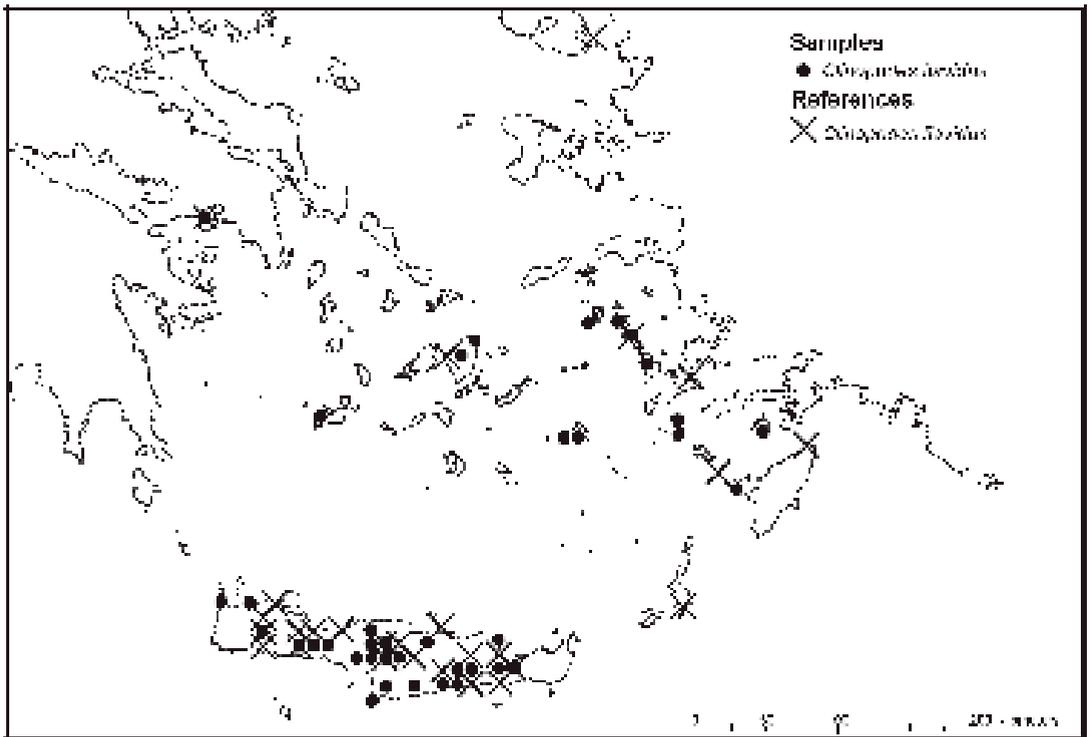
Figure 4. *Clinopodes flavidus*, distribution on the south Aegean archipelago.

1870 (Figure 3). The relationships between *H. bicarinata* and *H. pulchella* require further study. In the south Aegean and especially in Crete, a taxonomic distinction between them seems to be justified, but a sound assessment of the question requires a revision of the group in the whole Mediterranean area (Simaiakis et al. 2004).

7. *Henia (Scotophilus) pulchella* Meinert, 1870 (Figure 3).

8. *Clinopodes flavidus* C. L. Koch, 1847 (Figure 4).

10. *Geophilus conjungens* Verhoeff, 1898. First record for Kyklades.

12. *Geophilus fucorum* Brölemann, 1902. First record for Dodekanisa and Greece.

14. *Geophilus linearis* C. L. Koch, 1835 (Figure 5). First record for Kyklades, Dodekanisa and north Aegean.

15. *Geophilus naxius* Verhoeff, 1901 (Figure 5).

19. *Pachymerium ferrugineum insularum* Verhoeff, 1902. The true status of the forms treated here,

following tradition, as subspecies requires further study. In south Aegean a taxonomic distinction between them could be justified, but a sound assessment of the question will require a revision of the whole complex (Simaiakis et al. 2004).

25. *Bothriogaster signata thesei* Attems, 1902. According to Simaiakis et al. (2004), the true status of the forms treated here which, following tradition, are subspecies, requires further study. A taxonomic distinction between them could be justified, but a sound assessment of the question will require a revision of the genus in the whole Eastern Mediterranean area.

26. *Himantarium gabrielis* (Linné, 1767). First record for Kyklades.

29. *Haploschendyla europaea* (Attems, 1903) (Figure 6). First record for Kyklades and Dodekanisa.

31. *Nannophilus ariadnae* Attems, 1902 (Figure 6). First record for Kyklades.

32. *Nannophilus eximius* (Meinert, 1870). First

Table 1. Chorotype (s.l.) and distribution of the centipedes on the south Aegean archipelago and the adjacent regions. BAL: Balkan, EN: endemic, EUR: European, MED: Mediterranean, NEA: Neotropical, TUA: Turano Anatolian, TUE: Turano European, TUM: Turano Mediterranean, WPA: West Palearctic, CR: Crete, DO: Dodekanisa, KY: Kyklades, I Gr: Insular Greece, M Gr: Mainland Greece, Turk: Turkey, B: Balkan, CE: Central European, CNM: Central North Mediterranean, CSE: Central South European, CWP: Central West Palearctic, E: European, EM: East Mediterranean, EN: Endemic, M: Medietrranean, NE: North European, NEM: North East Mediterranean, NM: North Mediterranean, SA: South American, SB: South Balkan, SE: South European, SWA: South West Asiatic, SWP: South West Palearctic, WA: West Asiatic, WPA: West Palearctic.

	Chorotype									Distribution					
										in studied area			geographical		
	BAL	EN	EUR	MED	NEA	TUA	TUE	TUM	WPA	CR	DO	KY	I Gr	M Gr	Turk
Geophilomorpha															
Dignathodontidae Cook, 1895															
1 *Dignathodon microcephalus* (Lucas, 1846)	B			M						X	X	X	X	X	
2 *Dignathodon pachypus* Verhoeff, 1943				EM							**X**		X		
3 *Henia (Henia) athenarum* Pocock, 1891				NEM						X	X	X	X	X	X
4 *Henia (Henia) devia* C. L. Koch, 1847	B									X	X	X	X	X	
5 *Henia (Henia) vesuviana* Newport, 1845			E	NM							**X**		X	X	
6 *Henia (Scotophilus) bicarinata* Meinert, 1870			CE	M						X	X	X	X	X	X
7 *Henia (Scotophilus) pulchella* Meinert, 1870	B			CNM						X	X	X	X		X
Geophilidae Cook, 1895															
8 *Clinopodes flavidus* C. L. Koch, 1847			CSE				WA			X		X	X	X	X
9 *Geophilus carpophagus* Leach, 1815			E	M						X	X		X		X
10 *Geophilus conjungens* Verhoeff, 1898				NEM							X	X	X	X	X
11 *Geophilus flavus* De Geer, 1778			E								**X**		X	X	
12 *Geophilus fucorum* Brölemann, 1902				NM							**X**		X	X	
13 *Geophilus insculptus* Attems, 1895			E							**X**			X	X	
14 *Geophilus linearis* C. L. Koch, 1835			E	NM						X	X	X	X	X	X
15 *Geophilus naxius* Verhoeff, 1901				NEM						X	X	X	X	X	X
16 *Geophilus pygmaeus* Latzel, 1880	B		CE							**X**			X	X	
17 *Insigniporus sturanyi* Attems, 1903	B									**X**			X	X	
18 *Pachymerium ferrugineum ferrugineum* (C. L. Koch, 1835)									CWP	X	X	X	X	X	
19 *Pachymerium ferrugineum insularum* Verhoeff, 1902				NEM						X	X	X	X		

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Table 1. continued

#	Species			X 1	X 2	X 3	X 4	X 5	X 6	X 7	X 8	X 9	X 10
20	*Pachymerium syriacum* Attems, 1903	**EM**		X	X	X	X			X	X		X
21	*Pleurogeophilus mediterraneus* (Meinert, 1870)	SE	**M**		X	X	X			X	X	X	X
22	*Tuoba poseidonis* (Verhoeff, 1901)	M	**SWA**	X	X	X	X			X	X	X	
	Himantariidae Cook, 1895												
23	*Bothriogaster signata signata* Attems, 1926	B	EM **WA**		X	X	X		X	X	X	X	X
24	*Bothriogaster signata graeca* Verhoeff, 1901	**NEM**		X	X	X	X		X	X			
25	*Bothriogaster signata thesei* Attems, 1902	**EN**		**X**	X								
26	*Himantarium gabrielis* (Linné, 1767)	B	**M**		X		X			X	X	X	
27	*Stigmatogaster gracilis* (Meinert, 1870)	**M**			**X**	**X**	X			X			
	Linotaeniidae Cook, 1904												
28	*Strigamia acuminata* (Leach, 1814)	**E**	NEM	X			X			X			X
	Schendylidae Verhoeff, 1908												
29	*Haploschendyla europaea* (Attems, 1903)	**SB**		X	X	X	X			X	X		
30	*Hydroschendyla submarina* (Grube, 1872)	**NE**	NM		**X**					X	X	X	
31	*Nannophilus ariadnae* Attems, 1902	**SB**	**M**	X	X	X	X			X	X	X	
32	*Nannophilus eximius* (Meinert, 1870)	M		X	X	X				X	X	X	
33	*Schendyla nemorensis* C. L. Koch, 1836	**E**	M	X	X	X	X			X			
	Lithobiomorpha												
	Henicopidae Pocock, 1901												
34	*Rhodobius lagoi* Silvestri, 1933	**SA?**			**X**	X				X			
	Lithobiidae Newport, 1844												
35	*Eupolybothrus (Eupolybothrus) litoralis* (L. Koch, 1867)	B	**EM**	X	X	X				X	X	X	X
36	*Harpolithobius anodus* Latzel, 1880	SE	**NEM**		**X**	X				X	X	X	X
37	*Hessebius barbipes* (Porat, 1893)	EM **WA**			**X**	X				X	X	X	X
38	*Lithobius (Lithobius) agilis* C. L. Koch, 1847	**E**		**X**			X			X	X	X	
39	*Lithobius (Lithobius) carinatus* L. Koch, 1862	**EM**			X	X				X	X	X	X
40	*Lithobius (Lithobius) cretaicus* Matic, 1980	**EN**		**X**	X	X							
41	*Lithobius (Lithobius) creticus* Dobroruka, 1977	**EN**		**X**	X	X	X						

Table 1. continued

Species	Chorotype									Distribution in studied area			Distribution geographical		
	BAL	EN	EUR	MED	NEA	TUA	TUE	TUM	WPA	CR	DO	KY	I Gr	M Gr	Turk
42 *Lithobius (Lithobius) erythrocephalus* C. L. Koch, 1847			E				WA			X	X	X	X	X	X
43 *Lithobius (Lithobius) intermissus* (Chamberlin, 1952)				NEM							X	X	X		X
44 *Lithobius (Lithobius) lucifugus* L. Koch, 1862			E				WA			X	X	X		X	X
45 *Lithobius (Lithobius) nigripalpis* L. Koch, 1867				NEM						X	X	X	X	X	X
46 *Lithobius (Lithobius) piceus* L. Koch, 1862			E							**X**	**X**		X	X	
47 *Lithobius (Lithobius) pusillus* Latzel			SE								**X**		X		
48 *Lithobius (Lithobius) reductus* (Chamberlin, 1952)	B			NEM							**X**		X		X
49 *Lithobius (Lithobius) viriatus* Sseliwanoff, 1878				NEM						X	X	X	X	X	X
50 *Lithobius (Monotarsobius) aeruginosus* (L. Koch, 1862)			E	NEM		**WA**				X	X	X	X	X	X
51 *Lithobius (Monotarsobius) catascaphius* Verhoeff, 1901				NEM							X	X	X	X	X
52 *Lithobius (Monotarsobius) crassipes* (L. Koch, 1862)				NEM					**WPA**	X	X		X	X	X
53 *Lithobius (Monotarsobius) nudus* (Matic, 1976)	**SB**											**X**	X	X	
54 *Lithobius (Monotarsobius) peloponnesiacus* (Matic, 1976)	**SB**										**X**		X		
55 *Lithobius (Porobius) pamukkalensis* Matic, 1980				NEM						X	X	X	X		X
56 *Lithobius (Sigibius) micropodus* (Matic, 1980)			**SE**							X	X	X	X	X	X
57 *Lithobius (Sigibius) microps* Meinert, 1876			E							X	X	X	X	X	X
58 *Lithobius (Sigibius) tidissimus* (Chamberlin, 1952)				NEM							X	X	X	X	X
59 *Pleurolithobius orientis* (Chamberlin, 1952)				NEM							**X**		X	X	X
60 *Pleurolithobius patriarchalis* (Berlese, 1894)	B			EM						X	**X**		X	X	X

Table 1. continued

Scolopendromorpha

Cryptopidae Newport, 1894

No.	Taxon				SWP / CWP	WA	WA	EN	EM / M / SE						
61	*Cryptops anomalans* Newport, 1844									X	X	X	X	X	X
62	*Cryptops beroni* Matic & Stavropoulos, 1988	EN			**SWP**					**X**	X	X			
63	*Cryptops beshkovi* Matic & Stavropoulos, 1988	EN									**X**	X	X		X
64	*Cryptops hortensis* Leach, 1815				**CWP**					X	X	X	X	X	X
65	*Cryptops kosswigi* Chamberlin, 1952		EM							X	X	X	X		X
66	*Cryptops trisulcatus* Brölemann, 1902		M							X	X	X	X	X	X

Scolopendridae Newport, 1894

No.	Taxon					WA	WA	EN	EM / M / EM						
67	*Scolopendra canidens* Newport, 1844		EM	**WA**							X	X	X	X	X
68	*Scolopendra cingulata* Latreille, 1829		M			**WA**					X	X	X	X	X
69	*Scolopendra clavipes* C. L. Koch, 1847		**EM**								**X**	X	X	X	X
70	*Scolopendra cretica* Attems, 1911	EN							**X**	X	X	X			

Scutigeromorpha

Scutigeridae Gervais, 1837

No.	Taxon	SE	M												
71	*Scutigera coleoptrata* (Linné, 1758)	SE	**M**						X	X	X	X	X	X	

Figure 5. *Geophilus naxius & G. linearis*, distribution on the south Aegean archipelago.
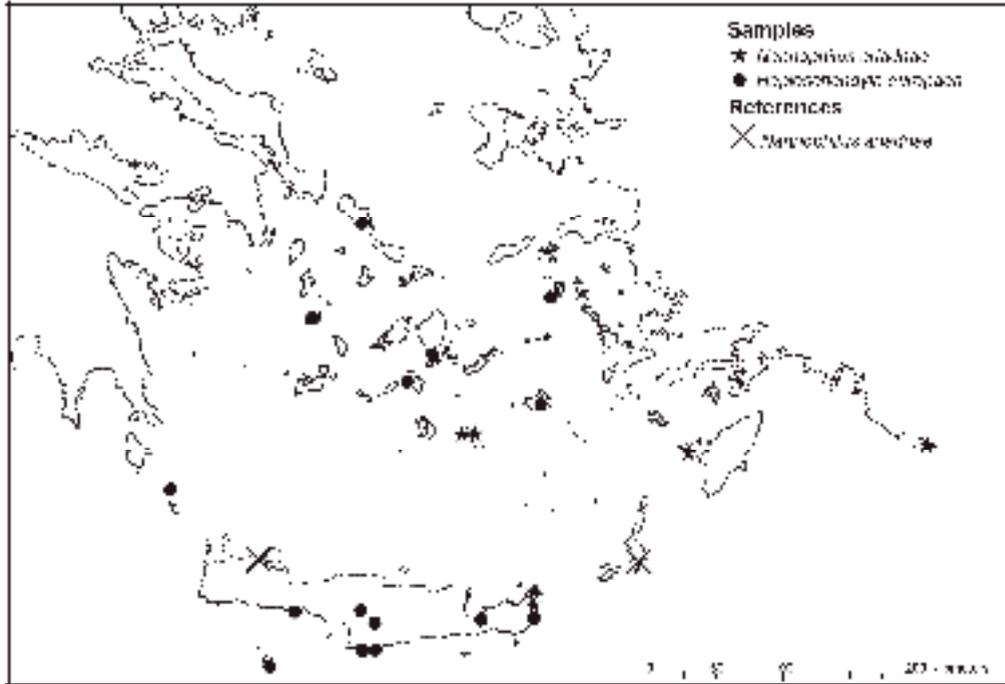
Figure 6. *Haploschendyla europaea & Nannophilus ariadnae*, distribution on the south Aegean archipelago.
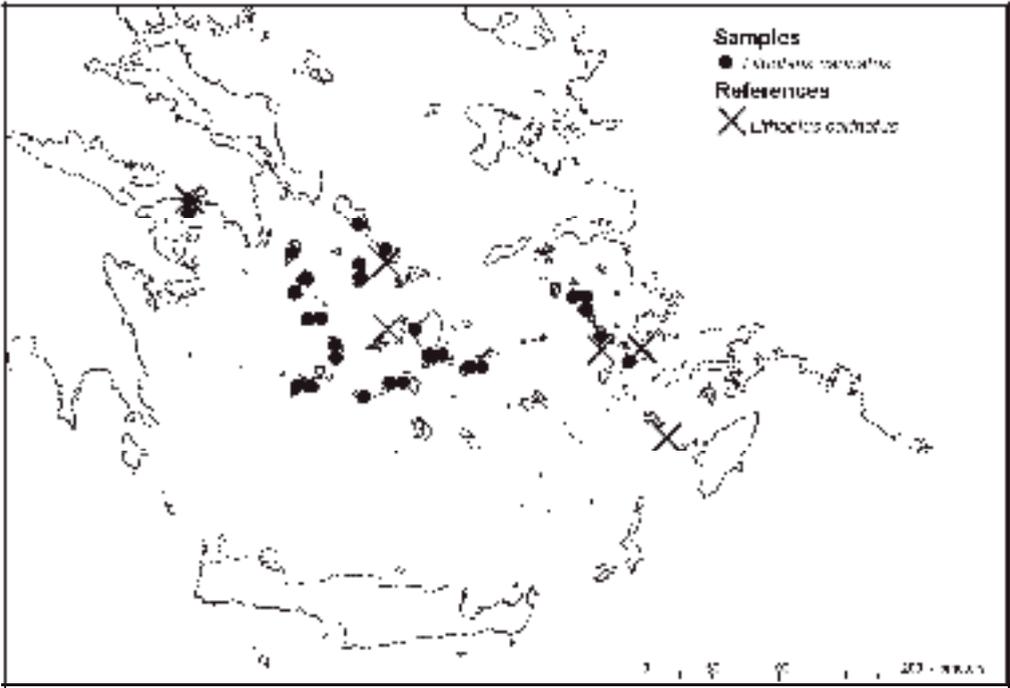
Figure 7. *Lithobius carinatus*, distribution on the south Aegean archipelago.
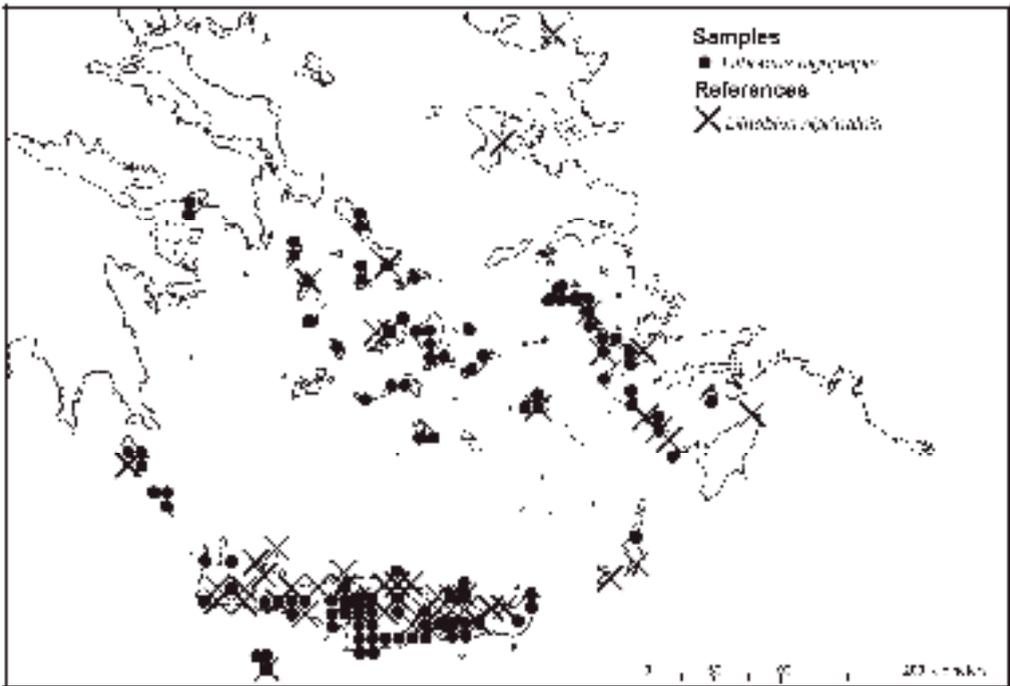
Figure 8. *Lithobius nigripalpis*, distribution on the south Aegean archipelago.
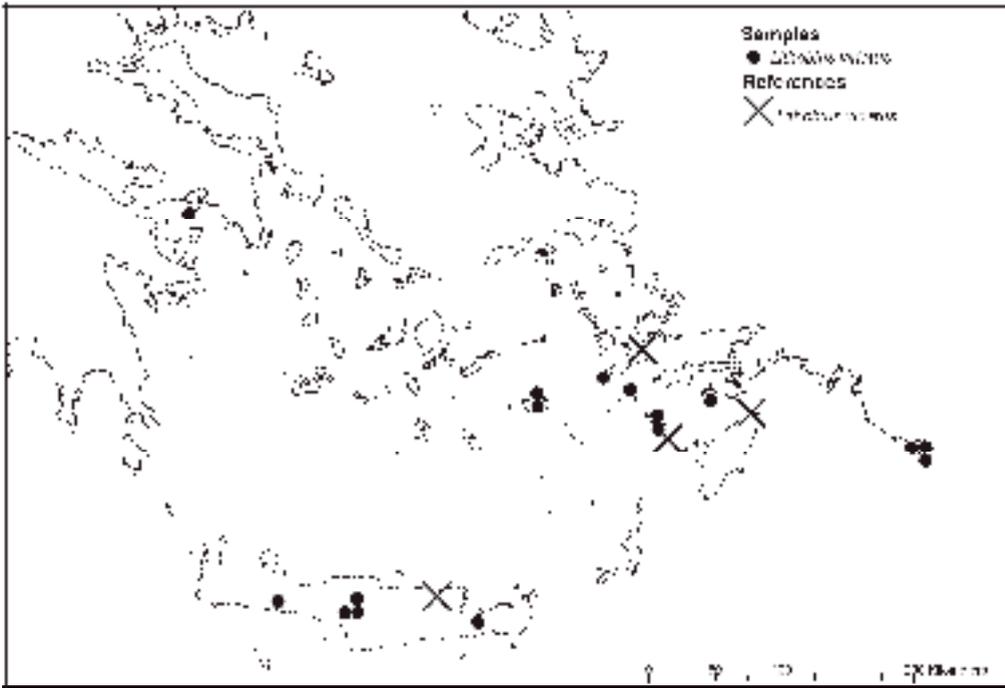
Figure 9. *Lithobius viriatus*, distribution on the south Aegean archipelago.
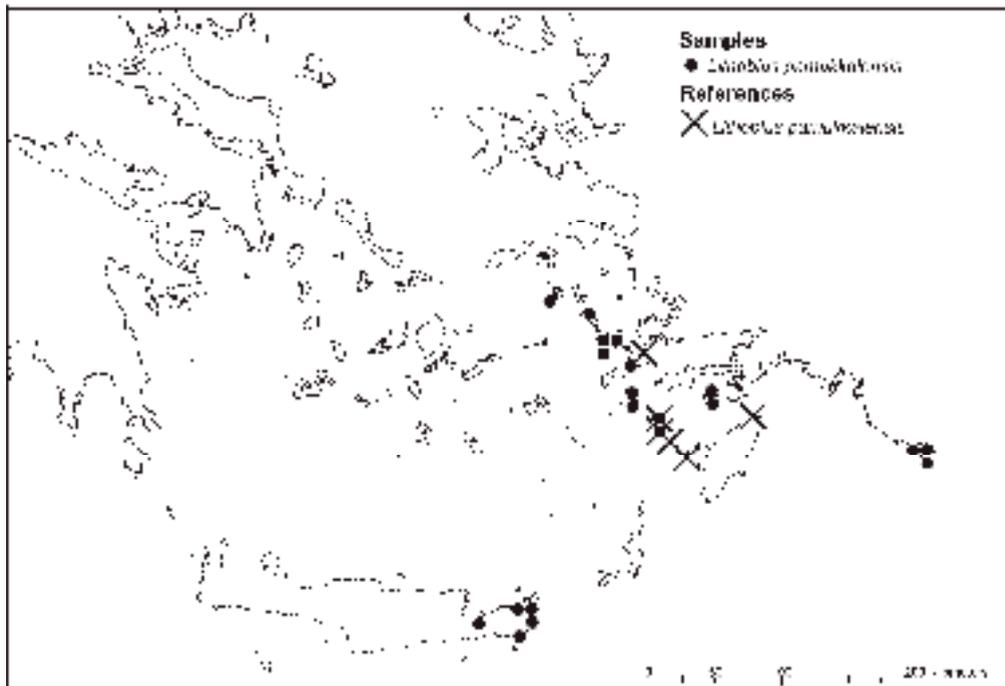
Figured 10. *Lithobius pamukkalensis*, distribution on the south Aegean archipelago.
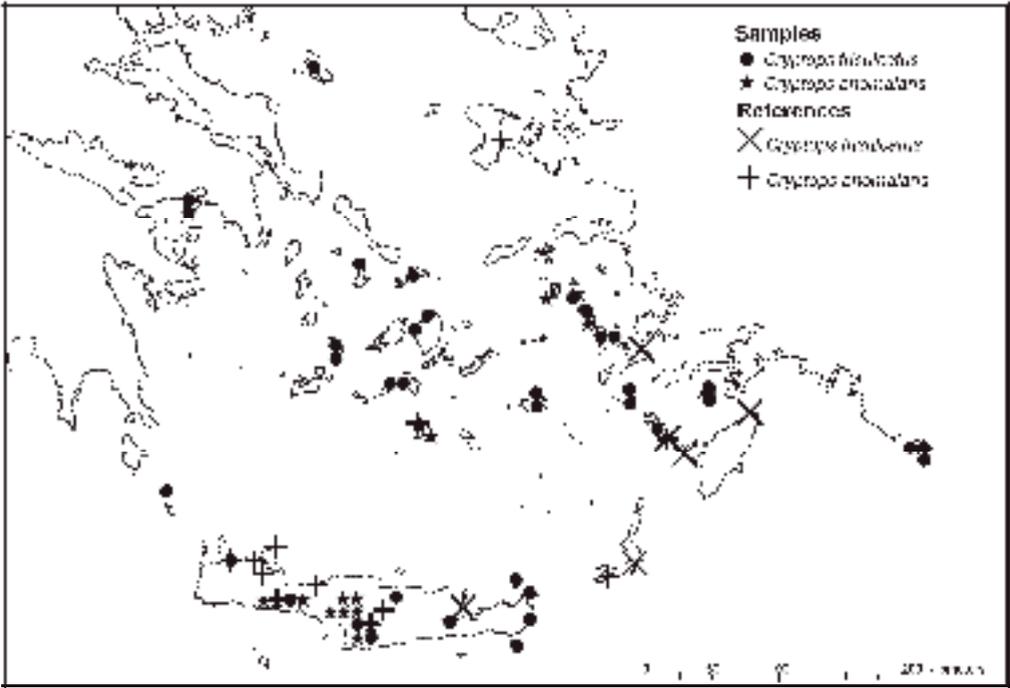
Figure 11. *Cryptops anomalans & C. trisulcatus species*, distribution on the south Aegean archipe-lago.
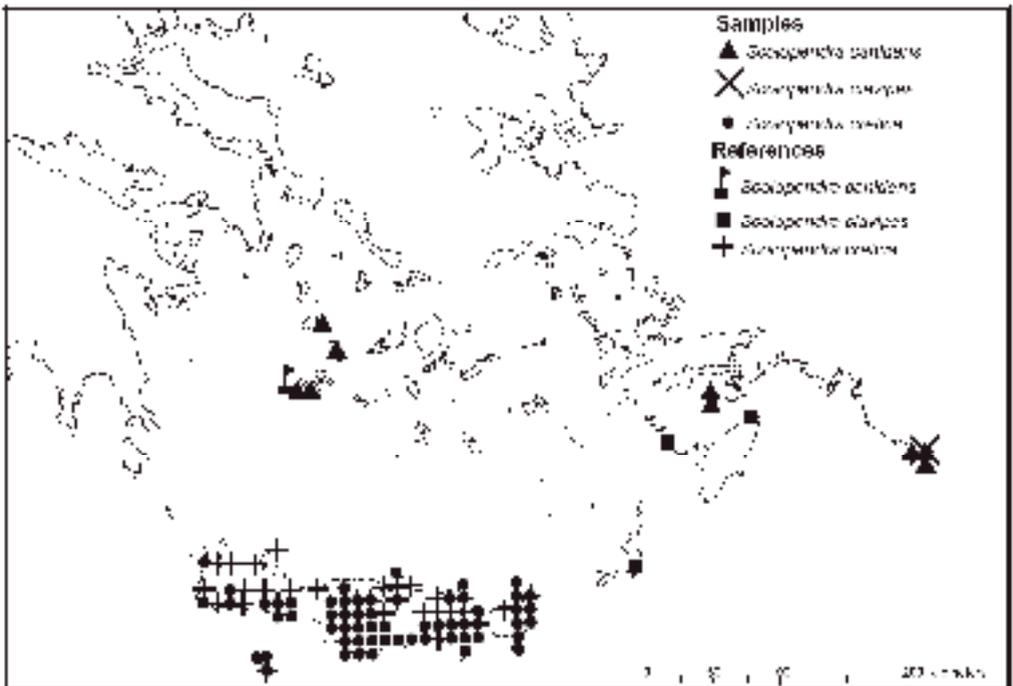
Figure 12. *Scolopendra canidens, S. cretica & S. clavipes*, distribution on the south Aegean archipelago.
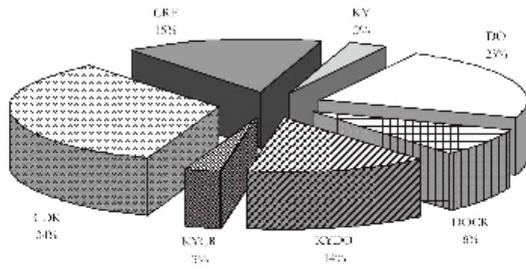
Figure 13. Distributinal patterns on the south Aegean archipelago. CRE: Cretan, DO: Dodekanisian, DO_CR: Dodekanisian – Cretan, KY: Kykladic, KY_CR: Kykladic - Cretan, KY_DO: Kykladic – Dodekanisian, CDK: Cretan - Dodekanisian - Kykladic (south Aegean).
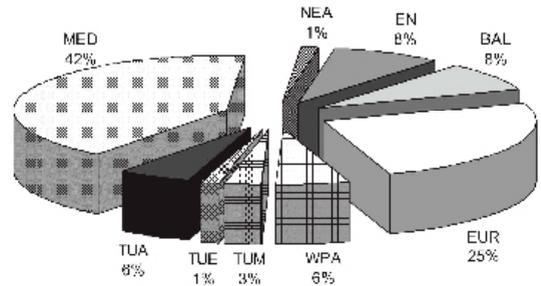
Figure 14. Chorotypes of the south Aegean centipede taxa. BAL: Balkan, EN: endemic, EUR: European, MED: Mediterranean, NEA: Neotropical, WPA: west Palearctic, TUA: Turano – Anatolian, TUE: Turano – European, TUM: Turano – Mediterranean.

record for Dodekanisa.

33. Schendyla nemorensis C. L. Koch, 1836. First record for Kyklades and Dodekanisa.

34. Rhodobius lagoi Silvestri, 1933. This species belongs to the subfamily Anopsobiinae Verhoeff, 1907, distributed in south America, south Africa, Australia, New Zealand and New Caledonia (Edgecombe: personal communication). The presence of *R. lagoi* in Rodos is certainly due to a human introduction (Zapparoli 2002).

36. Harpolithobius anodus Latzel, 1880. First record for Dodekanisa.

39. Lithobius (Lithobius) carinatus L. Koch, 1862 (Figure 7).

43. Lithobius (Lithobius) intermissus (Chamberlin, 1952). First record for Dodekanisa.

44. Lithobius (Lithobius) lucifugus L. Koch, 1862. First record for Kyklades.

45. Lithobius (Lithobius) nigripalpis L. Koch, 1867 (Figure 8).

47. Lithobius (Lithobius) pusillus Latzel, 1880. First record for Aegean Archipelago (Dodekanisa).

48. Lithobius (Lithobius) reductus (Chamberlin, 1952). First record for Aegean Archipelago (Dodekanisa), Greece and Europe.

49. Lithobius (Lithobius) viriatus Sseliwanoff, 1878 (Figure 9).

50. Lithobius (Monotarsobius) aeruginosus (L. Koch, 1862). First record for Dodekanisa.

51. Lithobius (Monotarsobius) catascaphius Verhoeff, 1901. First record for Aegean Archipelago (Kyklades, Dodekanisa) and Greece.

53. Lithobius (Monotarsobius) nudus (Matic, 1976). First record for Aegean Archipelago (Kyklades).

54. Lithobius (Monotarsobius) peloponnesiacus (Matic, 1976). First record for Aegean Archipelago (Dodekanisa).

55. Lithobius (Porobius) pamukkalensis Matic, 1980 (Figure 10).

57. Lithobius (Sigibius) microps Meinert, 1876. First record for Kyklades and Crete.

58. Lithobius (Sigibius) tidissimus (Chamberlin, 1952). First record for Kyklades.

61. Cryptops anomalans Newport, 1844 (Figure 11).

64. Cryptops hortensis Leach, 1815. First record for Kyklades.

66. Cryptops trisulcatus Brölemann, 1902 (Figure 11). First record for Kyklades.

67. Scolopendra canidens Newport, 1844 (Figure 12). First record for Dodekanisa.

69. Scolopendra clavipes C. L. Koch, 1847 (Figure 12).

70. Scolopendra cretica Attems, 1911 (Figure 12).

Table 2. The faunistic element of centipedes in the three main geographical regions (%). BAL: Balkan, EN: endemic, EUR: European, MED: Mediterranean, NEA: Neotropical, TUA: Turano-Anatolian, TUE: Turano-European, TUM: Turano-Mediterranean, WPA: West Palearctic.

	MED	EUR	TUM	TUE	TUA	WPA	NEA	BAL	EN
KYKLADES	49	16	5	3	8	8	-	11	-
DODEKANISA	50	21	4	2	7	7	2	5	2
CRETE	34	30	2	2	2	9	-	9	12

DISCUSSION

Seventy-one species and subspecies are by now registered, belonging to 10 families and 25 genera. *Dignathodon pachypus* and *Lithobius reductus* are recorded for the first time from Greece, while the latter, for the first time from Europe. Eight species (*D. pachypus, Harpolithobius anodus, Henia vesuviana, Lithobius catascaphius, L. nudus, L. peloponnesiacus, L. pusillus* and *L. reductus)* are reported for the first time from the south Aegean region.

Based on previous knowledge, 42 species were recorded from Crete (Simaiakis et al., 2004), 19 from Kyklades and 37 from Dodekanisa (Zapparoli 2002). Recently, *Lithobius microps* was added to the Cretan fauna, while 19 additional species have been added for the Kyklades and as many for the Dodekanisa. Dodekanisa has the richest fauna (56 taxa) followed by Crete (43 taxa) and Kyklades (38 taxa). Two families (Scutigeridae and Linotaeniidae) are represented by a single species, *Scutigera coleoptrata* and *Strigamia acuminata* respectively, whilst 15 of the 25 genera are represented in the area by one species only. The genus *Lithobius* is by far the most numerous, being represented by 21 species on south Aegean islands.

Almost half of the species (45 %) are also distributed on the adjacent continental areas (mainland Greece and Turkey).

34 % of the centipede fauna (24 taxa) is common to the three main geographical areas of the south Aegean archipelago (Crete, Kyklades, Dodekanisa), 23 % (16 taxa) were exclusively reported from Dodekanisa, 15 % (11 taxa) solely from Crete and its satellite islets and 3 % (2 taxa) only from Kyklades. It is also apparent that Kyklades and Dodekanisa have most of common species of the Aegean islands (14 % - 10 taxa), accompanied by the centipedes common to Dodekanisa and Crete (8 % - 6 taxa) and the common fauna of Kyklades and Crete (3 % - 2 taxa) (Figure 13).

The centipede fauna of the south Aegean archipelago has mainly Mediterranean (42%) (28 species and 2 subspecies) and European (25 %) (17 species) affinities (s. l.). Another 8 % belongs to the Balkan (6 species) element, 6 % are west Palearctic (4 species), while 6% have Turano–Anatolian affinities (4 species), 3 % Turano–Mediterranean (2 species), 1 % Turano–European (1 species) and 1 % Neotropical (1 species) (Figure 14). Endemic centipedes (8%) (Figure 14) have been registered in 2 islands, Crete (4 species and 1 subspecies) and Rodos (1 species).

Examining the chorotypes of the three main geographical regions (Crete, Kyklades, Dodekanisa) separately and analyzing the distributional pattern of each species we end up with the following conclusions. Of the 43 taxa examined from Crete, the Mediterranean and the European element are almost equally represented (34 % and 30 % respectively) (Table 2), unlike Kyklades and Dodekanisa, where the Mediterranean element predominates (49 % and 50 % respectively) (Table 2). On the other hand,

the percentage of the centipedes having European affinities on Kyklades and Dodekanisa (16 % and 21 % respectively) is significantly lower than the percentage among Cretan species (30 %) (Table 2). It is also remarkable that the endemic element is absent from Kyklades, whilst on Crete and Dodekanisa this element is represented by 12 % and 2 %, respectively (Table 2). As far as centipedes with Turanic affinities are concerned (Turano-Mediterranean, Turano-European and Turano-Anatolian), the Kyklades have the highest percentage (16%), the Dodekanisa has 13%, and Crete only 6% (Table 2). Furthermore, among the three major island areas the species with west Palearctic affinities show the same contribution, ranging from 7 % to 9 % (Table 2). The Balkan element is represented by 11 % on Kyklades island group, while 5 % and 9 % are known only from Dodekanisa and Crete, respectively.

Overall, the Mediterranean element decreases from western (Kyklades) to eastern areas of the Aegean archipelago (Dodekanisa) as well as from northern (Kyklades and Dodekanisa) to southern islands (Crete). The opposite pattern is presented by the species with European distribution. In detail, the European species are by far the most numerous on Crete (south Aegean), whilst on Kyklades and Dodekanisa the element is represented by fewer species. The complex geomorphology of Crete (Fassoulas 2000), the distinguished phytogeographical zones and the wide altitudinal range (from lowland plains to forests and subalpine phryganic areas) provide suitable areas for European species. Contrary to Crete, the significant insularity of the islands of Kyklades and Dodekanisa supports the presence of Mediterranean species. The significant percentage of endemics on Crete (12 %) is explained by the long isolation of the island since the Pliocene (Dermitzakis 1990a). In contrast, the low number of endemics on Dodekanisa (Rodos) and the absence of this element from Kyklades result from the recent geological relationships of Dodekanisa and Kyklades with Asia Minor and continental Greece, respectively (Dermitzakis 1990b, Anastasakis & Dermitzakis 1990).

Several species *(Harpolithobius barbipes, Hydroschendyla submarina, Lithobius pusillus, L. peloponnesiacus, Pleurolithobius orientis, P. patriarchalis, Pleurogeophilus medietrraneus and Scolopendra clavipes)*, whose geographical distribution is better known, range in the eastern part of south Aegean archipelago (Simaiakis et al. unpublished data). Moreover, *Lithobius pamukkalensis* and *L. pusillus* are spread in Dodekanisa, replacing L. carinatus in the southern islands (Simaiakis et al. unpublished data). The latter is known to range mainly in the Near and Middle East, while mainland Greece and the islands of Kyklades consist its western limit (Zapparoli 2003). *Himantarium gabrielis* is common in mainland Greece, ranging in Dodekanisa and northern Kyklades (Andros), whereas it is absent from the rest of Kyklades islands and Crete (Simaiakis et al. unpublished data). The most interesting distributional case is known to exist between *Lithobius nigripalpi*s and *L. viriatus. L. viriatus* seems to keep the former out of Dodekanisa and its satellite islands, whereas *L. nigripalpis* predominates on Crete and Kyklades (Simaiakis et al. unpublished data).

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New studies on myriapods (Chilopoda, Diplopoda) from Ibiza with a checklist for the Balearic Islands

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The paper presents the results of studies based on collections of Diplopoda and Chilopoda gathered on the island of Ibiza in the years 2004 and 2005. Approximately 270 specimens of 24 species were identified of which 19 species belong to the Chilopoda and five to the Diplopoda. Seventeen species were found for the first time on Ibiza, of which nine are new to the Balearic Islands. Two chilopods are new to science and their description is pending. Distributional and ecological notes of all species found are provided and habitat preferences are compared with data available from other authors.

Keywords: Balearic Islands, Ibiza, Myriapoda, faunistics, autecology

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INTRODUCTION

Ibiza (570 km²) is the third largest of the Balearic Islands. It is situated approximately 90 km east of the Spanish and 250 km north of the Algerian coastline (see Figure 1). Together with Formentera it forms the Pityusics, what means "islands of junipers". It has a hilly landscape with altitudes up to 470 m and vegetation mainly consisting of Mediterranean pine forests and sclerophyllous shrubs (Macchia). The flora and fauna includes many endemic species, e.g. the lizard *Podarcis pityusensis* (Boscá, 1883), the grasshopper *Euchorthippus angustulus* Ramme,

1931 and eleven species of endemic plants in the area of Ses Salines (Martínez Rica & Cirer Costa 1982, Gangwere & Llorente 1992, IUCN 1996). Ibiza's climate is typically Mediterranean with an average annual temperature of 21.5 °C maximum (August) and 14 °C minimum (January). The precipitation is higher from October to March and lower from June to September.

The colonization of the island by humans took place some 2600 years ago and at present it is populated by about 80 000 inhabitants. Being one of the popular tourist destinations in the last years the island is a subject of intensive anthropogenic

impact. The population density in the south and along the east coast is high, while it is low in the north and the northwest.

A limited number of publications deal with the myriapod fauna of the Balearic Islands, e.g. Koch (1881), Verhoeff (1924), Condé (1954, 1982), Negrea & Matic (1973), Căpuşe (1975), Mauriès & Vicente (1976), Serra (1983) and Enghoff & Vicente (2000). These faunistic publications focused mainly on the myriapod fauna of the Northern Balearic Islands, Majorca and Minorca. Verhoeff (1924) is the only author who published a paper specifically dedicated to the myriapod fauna of Ibiza. His study was based on material collected by Dr Söderlund in 1870 and 1871. The scope for renewed work on Ibiza's myriapods is thus obvious for faunistic reasons alone. Furthermore, the autecological knowledge of Ibiza's myriapods is unsatisfying and should be improved with this present work.

MATERIAL AND METHODS

Majority of the specimens were gathered by hand, sifting of leaf litter and pitfall trapping during March 2004 by Svenja Sammler and April 2005 by Karin Voigtländer. Collection was also conducted sporadically during autumn 2004 by Carsten H.G. Müller. Sampling took place mainly in the spring, since this is the most favourable season for collection of myriapods when the climate on the island is rather cool and humid with abundance of fresh vegetation. All collection sites (Figure 1) are listed below and for each site the exact GPS co-ordinates are given. All centipedes and most of the millipedes are preserved in 70% ethanol at the National Museum of Natural History Görlitz. Some millipedes are preserved at the Natural History Museum of Denmark (Zoological Museum), Copenhagen.

Collection sites
1. Cap des Rubio; 39° 04' 30" N, 1° 24' 10" E
   a) open-range Plateau, sporadic juniper
   b) pine growth, dense juniper scrubs

Figure 1. Collection sites on Ibiza belonging to the Balearic Islands, see large rectangle in the general map given in the lower left of the Figure (modified after Sommer et al. (2005)). Ibiza represents the bigger one of the so-called Pityusic Islands, see also smaller, arrow-pointed rectangle in the general map. **1**. Cap des Rubio. **2.** Penyal des Aquila. **3.** Portinatx. **4.** Mine Can Sopes. **5.** Can Codolar. **6.** Cala Nova. **7.** La Joya. **8.** Club Cala Llenya. **9.** Cala Olivera. **10.** Can Toni Jaumet. **11.** Coll des Rossellons. **12.** Ses Salines. **13.** Cala D'Hort. **14.** Cala Vadella.
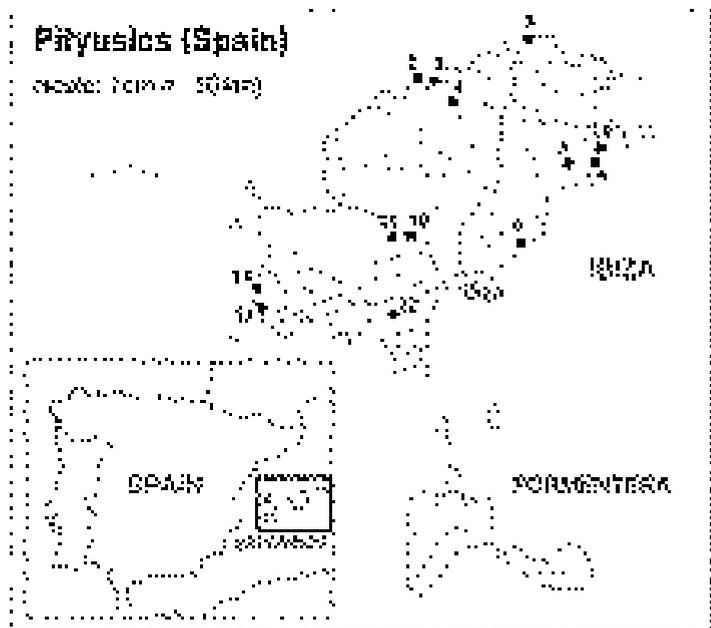
2. Penyal des Aquila; 39° 04' 40" N, 1° 25' 00" E; pine-trees and high bushes (Macchia alta)

3. Portinatx; 39° 96' 50" N, 1° 31' 30" E, pine-trees and high bushes (Macchia alta)

4. Mine Can Sopes; 39° 03' 00" N, 1° 27' 00" E, detrital rocks

5. Can Codolar, 39° 01' 30" N, 1° 33' 00" E
   a) dried yet moist riverbed bordered with pines, dense herb layer with predominantly *Oxalis pes-caprae*
   b) under decayed wood

6. Cala Nova; 39° 00' 40" N, 1° 35' 00" E; roadside nearby beach, low shrub vegetation (Macchia bassa)

7. La Joya; 39° 00' 50" N, 1° 35' 10" E; thicket of pines and heath

8. Club Cala Llenya; 39° 01' 10" N, 1° 35' 30" E
   a) pine population with much deadwood
   b) light pine growth, soil covered with lichens
   c) dried streambed
   d) dense pine growth
   e) meadow
   f) bungalow, wayside
   g) former sports ground, light pine growth

9. Cala Olivera; 38° 56' 10" N, 1° 30' 10" E; pine-trees and high bushes (Macchia alta)

10. Can Toni Jaumet; 38° 57' 00" N, 1° 24' 00" E; quarry with sporadic pines

11. Coll des Rossellons; 38° 56' 00" N, 1° 22' 00" E; slope, pine growth with rosemary thicket

12. Ses Salines; 38° 51' 50" N, 1° 21' 50" E; wayside, field for salt coagulation

13. Cala D'Hort; 38° 58' 30" N, 1° 13' 30" E; road of loam

14. Cala Vadella; 38° 54' 50" N, 1° 13' 40" E; meadow

RESULTS

Sites, number of specimens in brackets, distribution and ecological notes of all species found are provided below and habitat preference is compared with data available from previous authors.

Diplopoda

Polyxenida

Polyxenus lagurus (Linnaeus, 1758)
Sites: 7 (5), 8a (2), 8b (17), 8d (1)
Distribution: Europe and Central Sahara; Majorca: Enghoff & Vicente (2000); new to Ibiza
Ecological notes: On Ibiza *P. lagurus* was only found under bark of *Pinus halepensis* and *Juniperus oxycedrus*, which is not an unusual habitat for this species. Karamaouna (1990) reported to have found it under stones in similar Mediterranean coniferous forests in Greece.

Polydesmida

Brachydesmus proximus Latzel, 1889
Sites: 5a (7), 5b (1), 8e (1), 10 (2)
Distribution: Western Mediterranean; new to the Balearic Islands
Ecological notes: B. proximus prefers moist habitats. It is found on meadows under stones and in a dried yet moist riverbed.

Brachydesmus superus Latzel, 1884
Sites: 5a (1), 14 (2)
Distribution: Palearctic; Ibiza: Verhoeff (1924), Minorca: Demange (1961), Majorca: Enghoff & Vicente (2000)
Ecological notes: As the previous species, on Ibiza *B. superus* inhabits moist areas. It is found on meadows and in a dried yet moist riverbed under stones. Because of its high warmth-requirement, this species favours more synanthropic habitats in Middle Europe.
Remark: We are yet to identify the ecological differences between these two species of *Brachydesmus*.

Oranmorpha guerinii (Gervais, 1836)
Sites: 5a (58, many more individuals were seen), 8a (1), 8c (21), 8f (1)
Distribution: Southwest Europe, Macaronesia and Northwest Africa; new to the Balearic Islands
Ecological notes: It is worth mentioning the mass occurrence (more than 300 ind. /m^2) of *O. guerinii* in a dried yet moist riverbed. It was found there

mostly amongst leaf litter and occasionally buried in the ground.

Julida

Ommatoiulus inconspicuus (L. Koch, 1881)

Sites: 2 (1), 4 (1), 5a (6), 6 (3), 8a (5), 8f (2), 11 (2)

Distribution: Spanish mainland; Ibiza: Verhoeff (1924) as *Schizophyllum (Bothroiulus) ibizanum* Verhoeff, 1924, Cabrera: Jolivet (1953) as *Schizophyllum (Bothroiulus) ibizanum,* Majorca and Minorca: Koch (1881) as *Julus inconspicuus* L. Koch, 1881 and *J. nigritarsis* L. Koch, 1881 (see Enghoff & Vicente 200).

Ecological notes: O. inconspicuus is found under stones in an open habitat, under bark in forests of *Pinus halepensis* and under stones and amongst leaf litter in a dried yet moist riverbed.

Chilopoda

Geophilomorpha

Geophilus carpophagus Leach, 1815

Sites: 2 (2)

Distribution: widespread in Europe, Macaronesia, North Africa; Majorca: Negrea & Matic (1973); new to Ibiza

Ecological notes: G. carpophagus is known as euryoecious, mostly a woodland species (Minelli & Iovane 1987). On Ibiza it was found under stones in a forest of *Pinus halepensis*.

Geophilus truncorum Bergsöe et Meinert, 1866

Sites: 5b (1), 11 (1)

Distribution: widespread in Europe, Macaronesia and North Africa; Ibiza: Verhoeff (1924)

Ecological notes: In Middle Europe *G. truncorum* prefers woodlands and is often found under bark, decayed wood and leaf litter (Poser 1988, Vossel & Aßmann 1995, Leśniewska 2000). On Ibiza likewise we found it amongst leaf litter in a pine and under decayed wood in a dried yet moist riverbed.

Geophilus sp. nov.

Sites: 8a (1)

Ecological notes: This new species was found amongst leaf litter in a forest of *Pinus halepensis*.

Remarks: The material of this species was sent for identification to Prof. Alessandro Minelli and Dr Lucio Bonato (Padova, Italy) and they confirmed (in litt.) that it belongs to a new, yet undescribed species of *Geophilus*.

Tuoba hispanica (Meinert, 1870)

Sites: 1b (1), 5a (3), 5b (2), 7 (5), 9 (2)

Distribution: Spanish mainland; new to the Balearic Islands

Ecological notes: T. hispanica was found under stones and bark in a forest of *Pinus halepensis* and in a dried yet moist riverbed.

Remark: Minelli and Bonato (in litt.) wrote that *Geophilus hispanicus* Meinert, 1870 should be transferred to genus *Tuoba,* as the reasons for this taxonomic alteration will be explained elsewhere (Minelli & Bonato, in prep.).

Pachymerium ferrugineum insulanum Verhoeff, 1902

Sites: 1a (1), 3 (2), 8a (1), 9 (1)

Distribution: Eastern Mediterranean; Ibiza and Majorca: Verhoeff (1924), Majorca: Negrea & Matic (1973)

Ecological notes: The examined specimens belong to the *insulanum* subspecies which is characterized by a higher number of trunk segments (53-55 vs. 41-43 in the nominate one). Our material comes from coastal areas, which is in accordance with the habitat preferences of *P. f. insulanum* (cf. Verhoeff 1902, Simaiakis et al. 2004).

Henia vesuviana (Newport, 1845)

Sites: 1a (1), 3 (1), 5a (1), 5b (1), 8a (3)

Distribution: widespread in Europe, North Africa; Majorca: Verhoeff (1924), Negrea & Matic (1973); new to Ibiza

Ecological notes: H. vesuviana is known to prefer warmer temperatures (Ern 1960) and is a euryoecious species (Minelli & Iovane 1987). In Middle Europe, it occurs exclusively in towns (Voigtländer 1988, Schulte et al. 1989). We found it in open and dry habitats amongst leaf litter, in

forests of *Pinus halepensis* under stones and in a dried yet moist riverbed amongst deadwood and leaf litter.

Schendyla mediterranea Silvestri, 1897

Sites: 1b (1), 5a (3), 8a (2), 11 (2)

Distribution: Mediterranean; new to the Balearic Islands

Ecological notes: S. mediterranea was found in a forest of *Pinus halepensis* and in a dried yet moist riverbed. Minelli & Iovane (1987) found it under Mediterranean shrubs and trees, like *Arbutus unedo, Pistacia lenticus* and *Quercus ilex*.

Schendyla sp. nov.

Sites: 5b (1), 8a (5)

Ecological notes: This new species was found amongst leaf litter and under bark in a forest of *Pinus halepensis* and once under deadwood in a dried yet moist riverbed.

Remarks: The material of this species was sent for identification to Prof. Alessandro Minelli and Dr Lucio Bonato (Padova, Italy) and they confirmed (in litt.) that it belongs to a new, yet undescribed species of *Schendyla*.

Stigmatogaster dimidiatus (Meinert, 1870)

Sites: 1b (1), 7 (2), 8a (1), 9 (6), 11 (1)

Distribution: Western Mediterranean; occurrence on Majorca doubtful because of inexact data of sampling location (Minelli & Bonato 2004, Minelli pers. comm.); new to Ibiza

Ecological notes: S. dimidiatus was found under bark and stones in forest or thicket.

Stigmatogaster excavatus (Verhoeff, 1924)

Sites: 2 (1)

Distribution: Ibiza: Verhoeff (1924)

Ecological notes: S. excavatus was found only once under stone in a forest of *Pinus halepensis*.

Scolopendromorpha

Cryptops hispanus Brolemann, 1920

Sites: 5a (1), 8a (2), 8b (6), 11 (2), 13 (3)

Distribution: Continental Spain; new to the Balearic Islands

Ecological notes: C. hispanus was found mostly under stones in open habitats like Macchia and at roadsides. Matic (1960) recorded this species from caves in Spain.

Scolopendra oraniensis H. Lucas, 1846

Sites: 1a (1), 2 (1), 5a (6), 8a (1), 8b (1), 10 (3), 11 (3), 12 (1)

Distribution: Western Mediterranean; Ibiza, Formentera and Majorca: Verhoeff (1924), Ibiza: Müller & Meyer-Rochow (2006), Majorca: Negrea & Matic (1973) as *Scolopendra canidens oraniensis* H. Lucas, 1846

Ecological notes: As mentioned in the literature *S. oraniensis* is commonly found in all kinds of habitats, but most often under stones.

Lithobiomorpha

Lithobius crassipes L. Koch, 1862

Sites: 8a (2)

Distribution: Palearctic; new to the Balearic Islands

Ecological notes: In the literature *L. crassipes* is reported to be found in different habitats (Ern 1960, Minelli & Iovane 1987, Simaiakis et al. 2004). We found it under bark of *Pinus halepensis*.

Lithobius aff. dragani Negrea et Matic, 1973

Sites: 9 (1)

Distribution: Majorca: Negrea & Matic (1973); new to Ibiza

Ecological notes: Negrea & Matic (1973) found *L. dragani* between rocks of a cliff line. Similarly, on Ibiza, we found it close to the cliff line in a half open habitat under a stone.

Remark: We cannot be absolutely sure about the identity of this species since only one individual was examined. Despite that, our specimen agrees with the description of Negrea & Matic (1973).

Lithobius forficatus (Linnaeus, 1758)

Sites: 8a (1), 8f (1)

Distribution: Cosmopolitan; new to the Balearic Islands

Ecological notes: On Ibiza this euryoecious species was found in the house canalization and under a stone in a forest of *Pinus halepensis*.

Lithobius inermis L. Koch, 1856

Sites: 1a (1), 2 (1), 3 (1), 4 (1), 5a (4), 5b (1), 7 (1), 8a (2), 8g (2)

Distribution: Western Mediterranean; Majorca: Negrea & Matic (1973), Eason (1975), Minorca: Demange (1961) as *L. interruptus* Demange, 1961; new to Ibiza

Ecological notes: L. inermis was found in open and dry habitats under stones and amongst leaf litter, in forests of *Pinus halepensis* under stones and in a dried yet moist riverbed amongst wood and leaf litter. In contrast, Ern (1960) reported this species to be more hygrophilous and found it under stones and bark.

Lithobius microps oligospinus Demange, 1961

Sites: 1a (2), 1b (2), 3 (2), 8a (5), 8b (1), 12 (1)

Distribution: Minorca: Demange (1961) as *L. dubosqui oligospinus* Demange, 1961, Majorca: Negrea & Matic (1973) as *L. exarmatus mallorcanus* Negrea et Matic, 1973, Minorca: Serra (1983); new to Ibiza

Ecological notes: Demange (1961) found *L. m. oligospinus* amongst organic material. On Ibiza, we found it amongst leaf litter as well as under stones and bark.

Lithobius piceus tabacarui Negrea et Matic, 1973

Sites: 2 (2), 3 (1), 5b (3)

Distribution: Majorca: Negrea & Matic (1973), Eason (1975) as *L. p. incae* Eason, 1975, Serra (1983), Minorca: Demange (1961) as *L. p. verhoeffi* Demange, 1961; new to Ibiza

Ecological notes: Negrea & Matic (1973) found *L. p. tabacarui* in a cave amongst organic material and stones. On Ibiza we found it under stones in forests of *Pinus halepensis* and amongst deadwood in a dried yet moist riverbed.

Scutigeromorpha

Scutigera coleoptrata (Linnaeus, 1758)

Sites: 2 (1, more individuals were seen), 8a (2, more individuals were seen)

Distribution: indigenous species in the Mediterranean region; Majorca: Negrea & Matic (1973), Ibiza: Müller et al. (2003)

Ecological notes: S. coleoptrata is considered euryoecious species tending to a synanthropic mode of living (Minelli & Iovane 1987, Stoev 2004). On Ibiza it has been observed as a common species often seen under stone cairns covered by weathered pine-needles and under boulders of *Juniperus oxycedrus* in forests of *Pinus halepensis*.

DISCUSSION

Approximately 270 specimens of altogether 24 species were captured on the island of Ibiza. Nineteen species belong to the Chilopoda and five to the Diplopoda. Seventeen species are considered new for the fauna of Ibiza, while nine of them are reported for the first time on the Balearic Islands. Among the newly recorded species two are geophilomorph centipedes that are new to science. Their description is now in preparation by A. Minelli and L. Bonato.

To-date 48 myriapods, 21 millipedes and 27 centipedes, have been recorded on the Balearic Islands by previous authors (Table 1). Of them, only four millipedes and six centipedes had been registered on Ibiza. The present collection increases the number of Balearic millipedes to 23 and those of Ibiza to seven. Two of the species found in this investigation, *Brachydesmus superus* and *Ommatoiulus inconspicuus*, were already discovered on Ibiza (Verhoeff 1924), while *Polyxenus lagurus*, which is known from Majorca (Enghoff & Vicente 2000), was collected in La Joya and in Club Cala Llenya on Ibiza for the first time. Two species that are new to the Balearic Islands, *Oranmorpha guerinii and Brachydesmus proximus*, are both quite widespread in the Southwestern Mediterranean area and show synanthropic tendencies. In contrast, two species, *Glomeris ibiziana* Verhoeff, 1924 and *Stosatea soederlundi* (Verhoeff, 1924), both of which are provisionally regarded as Ibiza's endemics (Enghoff & Vicente 2000), were not collected during our recent sampling on the island. Concerning the Chilopoda,

Table 1: The distribution of myriapods (Diplopoda, Chilopoda) on individual Balearic Islands (Diplopoda modified after Enghoff &Vicente (2000)).
* new species for Ibiza
+? doubtful occurrence

Species	Majorca	Minorca	Ibiza	Cabrera	Formentera	Isla Pobre	References
Diplopoda							
POLYXENIDA							
Polyxenus lagurus (Linnaeus, 1758)	+		+*				Enghoff & Vicente (2000); present paper
Lophoproctus jeanneli Brolemann, 1910	+						Condé (1954)
Lophoproctus inferus Silvestri, 1903	+						Condé (1954)
Lophoproctus pagesi Condé, 1982	+						Condé (1982)
GLOMERIDA							
Glomeris ibizana Verhoeff, 1924			+				Verhoeff (1924)
CHORDEUMATIDA							
Ceratosphys sp. nov.		+					Enghoff & Vicente (2000)
POLYDESMIDA							
Oxidus gracilis (C. L. Koch, 1847)	+		+				Enghoff & Vicente (2000)
Stosatea soederlundi (Verhoeff, 1924)			+				Verhoeff (1924)
Stosatea (?) italica (Latzel, 1886)		+			+		Enghoff & Vicente (2000)
Brachydesmus proximus Latzel, 1889			+*				Present paper
Brachydesmus superus Latzel, 1884	+	+	+				Verhoeff (1924); Demange (1961); Enghoff & Vicente (2000); present paper
Polydesmus dismilus (Berlese, 1891)	+						Mauriès & Vicente (1976); Enghoff & Vicente (2000)
Polydesmus coriaceus Porat, 1871	+						Mauriès & Vicente (1976); Enghoff & Vicente (2000)
Oranmorpha guerinii (Gervais, 1836)			+*				Present paper
JULIDA							
Nopoiulus kochii (Gervais, 1847)		+					Enghoff & Vicente (2000)
Choneiulus sp.		+					Enghoff & Vicente (2000)
Orphanoiulus religiosus Silvestri, 1903	+						Mauriès & Vicente (1976); Enghoff & Vicente (2000)

Table 1: continued

Species	Majorca	Minorca	Ibiza	Cabrera	Formentera	Isla Pobre	References
Thalassisobates littoralis (Silvestri, 1903)		+					Demange (1961)
Pachyiulus varius (Fabricius, 1781)	+	+		+			Koch (1881); Brolemann (1901); Verhoeff (1923); Jolivet (1953); Enghoff & Vicente (2000)
Megaphyllum unilineatum (C. L. Koch, 1838)	+						Koch (1881)
Brachyiulus lusitanus Verhoeff, 1898	+						Enghoff & Vicente (2000)
Ophyiulus targionii Silvestri, 1898		+					Demange (1961)
Ommatoiulus inconspicuus (L. Koch, 1881)	+	+	+	+		+	Koch (1881); Verhoeff (1924); Jolivet (1953); Enghoff & Vicente (2000); present paper
Chilopoda GEOPHILOMORPHA							
Geophilus carpophagus Leach, 1815	+		+*				Negrea & Matic (1973); present paper
Geophilus tenellus L. Koch, 1881	+						L. Koch (1881)
Geophilus truncorum Bergsöe et Meinert, 1866			+				Verhoeff (1924); present paper
Geophilus sp. nov.			+*				Present paper
Tuoba hispanica (Meinert, 1870)			+*				Present paper
Tuoba poseidonis (Verhoeff, 1901)			+				Verhoeff (1924)
Pachymerium ferrugineum insulanum Verhoeff, 1902	+		+				Verhoeff (1924); Negrea & Matic (1973); present paper
Dignathodon microcephalus (Lucas, 1846)	+						Verhoeff (1924); Negrea & Matic (1973)
Henia vesuviana (Newport, 1845)	+		+*				Verhoeff (1924); Negrea & Matic (1973); present paper
Schendyla mediterranea Silvestri, 1897			+*				Present paper
Schendyla nemorensis (C.L. Koch, 1837)	+	+					Demange (1961); Negrea & Matic (1973)
Schendyla sp. nov.			+*				Present paper
Stigmatogaster dimidiatus (Meinert, 1870)	+?		+*				Minelli & Bonato (2004) + pers. comm.; present paper
Stigmatogaster excavatus (Verhoeff, 1924)			+				Verhoeff (1924); present paper
Stigmatogaster gracilis (Meinert, 1870)	+						Negrea & Matic (1973)

Table 1: continued

Species				References
Himantariella balearica Căpuşe (1975)	+			Căpuşe (1975)
Pachymerium dragani	+			Căpuşe (1975)
SCOLOPENDROMORPHA				
Cryptops hispanus Brolemann, 1920	+		+*	Present paper
Cryptops trisulcatus Brolemann, 1902	+			Negrea & Matic (1973)
Scolopendra oranienis Lucas, 1846	+	+		Verhoeff (1924); Negrea & Matic (1973); Müller & Meyer-Rochow (2006); present paper
LITHOBIOMORPHA				
Lithobius aeruginosus L. Koch, 1862	+			Negrea & Matic (1973)
Lithobius crassipes L. Koch, 1862	+		+*	Present paper
Lithobius dieuzeidei Brolemann, 1931	+			Negrea & Matic (1973)
Lithobius dragani Negrea & Matic, 1973	+		+?*	Negrea & Matic (1973); present paper
Lithobius fagei Demange, 1961	+	+		Demange (1961); Eason (1975); Serra (1983)
Lithobius forficatus (Linnaeus, 1758)	+		+*	Present paper
Lithobius georgescui Negrea & Matic, 1973	+			Negrea & Matic (1973)
Lithobius inermis L. Koch, 1856	+	+	+*	Demange (1961); Negrea & Matic (1973); Eason (1975); present paper
Lithobius microdon clarki Eason, 1975	+			Eason (1975)
Lithobius microps oligospinus Demange, 1961	+		+*	Demange (1961); Negrea & Matic (1973); Serra (1983); present paper
Lithobius peregrinus Latzel, 1880	+	+		Zapparoli (2004) + pers. comm.
Lithobius piceus tabacarui Negrea & Matic, 1973	+	+	+*	Demange (1961); Negrea & Matic (1973); Eason (1975); Serra (1983); present paper
Lithobius vivesi Serra, 1983	+			Serra (1983)
SCUTIGEROMORPHA				
Scutigera coleoptrata (Linnaeus, 1758)	+	+		Negrea & Matic (1973); Müller et al. (2003); present paper

the present collection increases the number of Balearic species to 34 and those of Ibiza to 20. Five of the species were discovered on Ibiza by Verhoeff (1924) and one by Müller et al. (2003), while seven species previously known from Majorca or Minorca were found on Ibiza for the first time (Table 1). Seven species are new to the Balearic Islands. One species, *Tuoba poseidonis* (Verhoeff, 1901), was not collected during our recent sampling on the island.

The possible explanation for the large amount of new recorded myriapods on Ibiza is the deficient collecting activity on the island in the last century. The collection of Dr. Söderlund, which was examined and published by Verhoeff (1924), had been gathered more than 130 years ago. It is possible that mankind intentionally or otherwise have introduced new species to the island during this interval. Enghoff & Vicente (2000) reported that many, if not most species of Diplopoda having been artificially introduced on the Balearic Islands.

Sixteen species presently appear to be endemic to the Balearic Islands (*Lophoproctus pagesi, Glomeris ibiziana, Statosea soederlundi, Himantariella balearica, Stigmatogaster excavatus, Schendyla* sp. nov.*, Geophilus tenellus, Geophilus sp. nov., Pachymerium dragani, Lithobius fagei, L. dragani, L. piceus tabacarui, L. georgecui, L. microps oligospinus, L. microdon clarki* and *L. vivesi*). Five of them, *Glomeris ibiziana, Statosea soederlundi, Stigmatogaster excavatus* and the two new species, are known only from Ibiza.

Three of all species previously recorded on Ibiza were not found during our collections. Multiple species were either sighted occasionally or once. Based on these facts, it is safe to assume that the list of Ibiza's myriapods is not yet complete. More species are expected to be found in future collections. Besides, the autecology of many hitherto listed species remains unsatisfactorily.

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Habitat preferences and seasonal distribution of developmental stadia in *Lamyctes emarginatus* (Newport, 1844) (*L. fulvicornis* Meinert, 1868) and comparisons with some *Lithobius* species (Chilopoda, Lithobiomorpha)

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Andersson, G. 2006. Habitat preferences and seasonal distribution of developmental stadia in *Lamyctes emarginatus* (Newport, 1844) *(L. fulvicornis* Meinert, 1868) and comparisons with some *Lithobius* species (Chilopoda, Lithobiomorpha). Norw. J. Entomol. 53, 311-320.

This study is based on part of a large collection of centipedes in the Göteborg Natural History Museum. The material of *Lamyctes emarginatus* (Newport, 1844) used consists of 578 specimens from 317 localities in Sweden. Percentages for the distribution of the localities for *L. emarginatus* in different habitat types is presented as well as standardized percentages which take the proportion of habitats in the investigation into consideration. In Sweden the main habitats for the species are shores of lakes and open disturbed areas.

The seasonal distribution of the different developmental stadia collected is presented. Adults of *L. emarginatus* are mostly found in late summer and autumn, larvae and juveniles in spring and early summer. A comparison is made with five *Lithobius* species (*Lithobius erythrocephalus, L. borealis, L. curtipes, L. microps* and *L. crassipes*). These species show quite another picture. Adults are even found in the spring and findings of larvae and juveniles are spread out over the year. A comparison is made with the same five *Lithobius* species concerning the total number of specimens collected per locality investigated during the different months. July and August are the best months to find *L. emarginatus* in Sweden. The five *Lithobius* species show quite different patterns.

Several facts indicate a life cycle of one year for *L. emarginatus*: the findings of larvae almost only in spring or late autumn, the very few adults found in spring, the rapid growth of the larvae and juveniles and the low minimum number of postlarval stadia.

It is uncertain if *L. emarginatus* hibernates as eggs only or if larvae, hatched in the late autumn, will survive the winter and continue development the following spring.

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INTRODUCTION

In most parts of the world the species concerned has been known as *Lamyctes fulvicornis* Meinert, 1868. For a long time the Australian species *L. emarginatus* (Newport, 1844) has been suspected to be conspecific with *L. fulvicornis* (Johns 1976 and pers. comm., Eason 1985, Mesibov 1994, H. Enghoff pers. comm.) but the matter was not investigated in detail and not formally published until 1996 by Eason. According to Eason (1996) the correct name of the species should be *Lamyctes emarginatus*.

L. emarginatus is an almost cosmopolitan species but it is not found in the tropics (Eason 1985). It is most widespread in the Paleartic region and is the only centipede species so far found outdoors in Greenland (Böcher & Enghoff 1984). The species is parthenogenetic in most of its distribution area. Males are found in the Macaronesian Islands (Eason 1985), Tasmania (Mesibov pers.

Table 1. Number of investigated localities distributed on different habitats. Data from Norrland (Andersson 1985), Dalsland (von Proschwitz 1991) and Halland (Waldén 1969b).

Habitat type	Number of investigated localities				Localities with
	Norrland	Dalsland	Halland	Totally	L. emarginatus
Coniferous and mixed forests	488	388	32	908	5
Deciduous forests	153	151	305	609	8
Pastures and meadows	105	98	91	294	12
Shores, wetlands	74	92	101	267	55
Man-made habitats	77	72	83	232	23
Totals	897	801	612	2310	103

comm.), New Zealand (Archey 1937) and Hawaii (Zapparoli & Shelley 2000, Edgecombe pers. comm.).

The aim of this article is to use comprehensive material from a Swedish survey to throw light on the biology of *L. emarginatus* particularly concerning its habitat preferences, which are slightly different in various parts of the world, as well as the seasonal distribution of the different developmental stadia and its life cycle.

MATERIAL AND METHODS

The present study is mainly based on a large collection of centipedes from the Göteborg Natural History Museum. The material was collected mostly by H. Lohmander and H. W. Waldén in a specific survey: A *faunistic and ecological survey of certain terrestrial invertebrate groups in Sweden* (Waldén 1969a). The collecting method was sifting of litter completed by hand collection. The survey comprises material of Mollusca, Diplopoda, Chilopoda and Isopoda from approximately 28 000 investigated localities. Centipedes were found in about half of these localities. Data concerning the localities and from material so far identified have been loaded into a data base (von Proschwitz & Andersson 1997). There are still a lot of unidentified samples of centipedes. This study only deals with material from 15 provinces, from Halland in the south to Lappland in the north
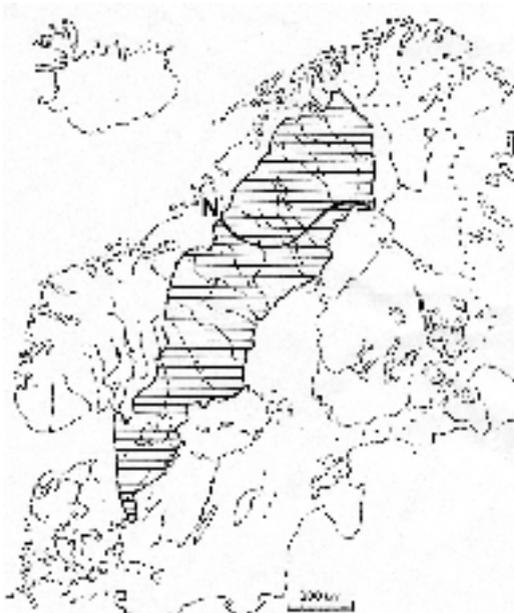
Figure 1. The area covered in this investigation. N = the northern limit for *Lamyctes emarginatus* in Sweden.

(Figure 1), from which all samples have been identified, partly by Lohmander, partly by the author. In these provinces 13 681 localities were investigated. Centipedes were found in 6 189 of these localities and *L. emarginatus* appeared in 317 localities. A total of 578 specimens of this species were collected.

In Sweden *L. emarginatus* is also found outside the area covered in this study. It is registered from all Swedish provinces except Södermanland (from which province many samples of the survey still are unidentified) and Lappland. The northern limit for the species in Sweden is marked in Figure 1.

The habitat data in the data base is in the form of a written description of the habitat but there are no standardized classifications regarding main habitat types (von Proschwitz & Andersson 1997). For the analysis of *L. emarginatus* the 317 localities for this species were classified concerning habitat in the same manner as the investigated localities from Norrland (the northern part of Sweden) used in Andersson (1985). But as most of the 13 681 investigated localities are yet to be classified in a standardized manner it is not possible to get exact figures for the proportion of different habitats investigated for the complete material. The proportion of different habitats is only available for some parts of the material which has been analysed and published. This is shown in Table 1, where habitat data concerning investigated localities for Norrland (Andersson 1985), the province of Dalsland (von Proschwitz 1991) and the province of Halland (Waldén 1969b) are put together. In these three regions *L. emarginatus* was found in 103 localities. Only these data could be used to calculate standardized percentages, which take the collecting efforts for each habitat group into consideration. Such standardized values are calculated in the manner described by Barber & Keay (1988).

Standardized percentage for a habitat =
$(L_{em}/L_{tot})/\sum$all habitats$(L_{em}/L_{tot})*100$
L_{em} = Number of localities from Norrland, Dalsland and Halland with *L. emarginatus* in the habitat

Table 2. Number of specimens of the different developmental stadia of *Lamyctes emarginatus* collected. Abbreviations for the stadia follow Andersson (1978).

Stadium	Number of specimens	
LIII	5	} larvae
LIV	35	
PL1	29	} juveniles
PL2-PL3	137	
PL4-PL5	372	adults

L_{tot} = Number of investigated localities from Norrland, Dalsland and Halland in the habitat

It was necessary to group some habitats together as there was not exactly the same habitat classification used in the three sources.

For comparison concerning seasonal distribution data from the survey for five *Lithobius* species were used (number of specimens in parenthesis): *Lithobius crassipes* L. Koch, 1862 (562), *L. borealis* Meinert, 1868 (1061), *L. microps* Meinert, 1868 (966), *L. curtipes* C. L. Koch, 1847 (5756) and *L. erythrocephalus* C. L. Koch, 1847 (5130). The trend lines in the diagrams are calculated in Excel, using the polynom regression with the formula:
$$y = b + c_1x + c_2x^2 + c_3x^3 + \ldots + c_6x^6.$$

RESULTS

The number of specimens of the different developmental stadia are shown in Table 2. No specimens of the three first larval stadia (L0, LI and LII) were found in the material.

The distribution of the localities for *L. emarginatus* in different habitat types is presented for the whole material in Figure 2. The most common habitat is unquestionably shores of lakes. The percentages in Figure 2 do not take the proportion of habitats investigated into consideration. In Figure 3, standardized percentages are presented

Figure 2. Percentages for the distribution of the localities for *Lamyctes emarginatus* in different habitat types.
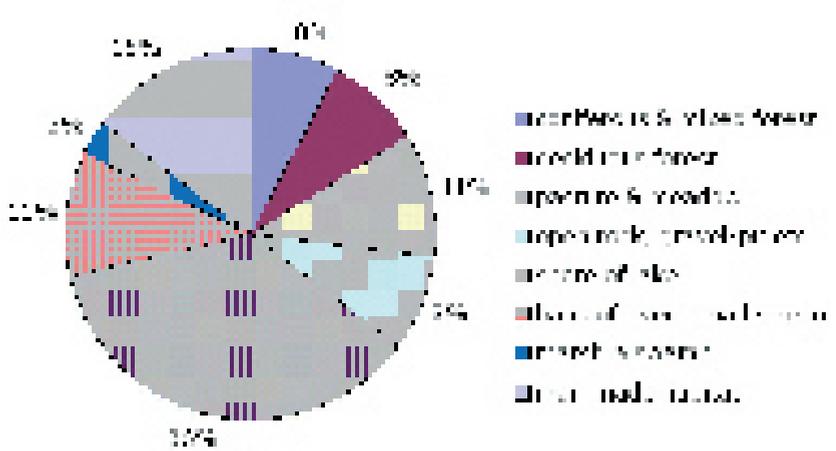
Figure 3. Standardized percentages (see Methods!) for the distribution of the localities for *Lamyctes emarginatus* in different habitat types. Only the materials from Halland, Dalsland and Norrland are used (see Table 1!).
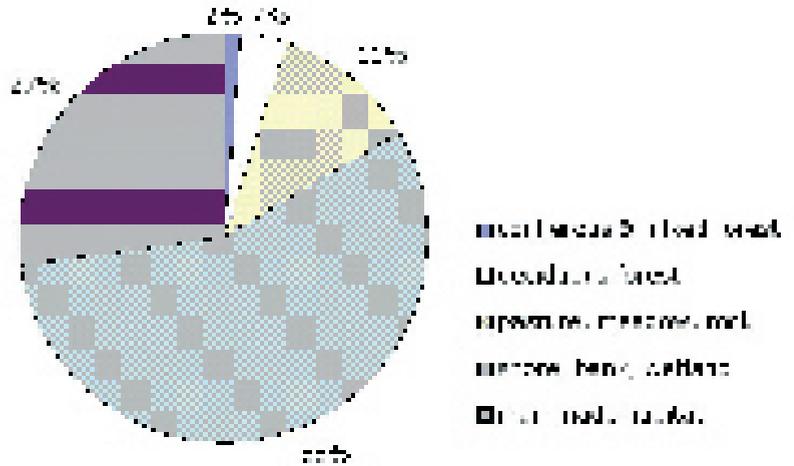
Figure 4. The seasonal distribution of the different developmental stadia of *Lamyctes emarginatus*.
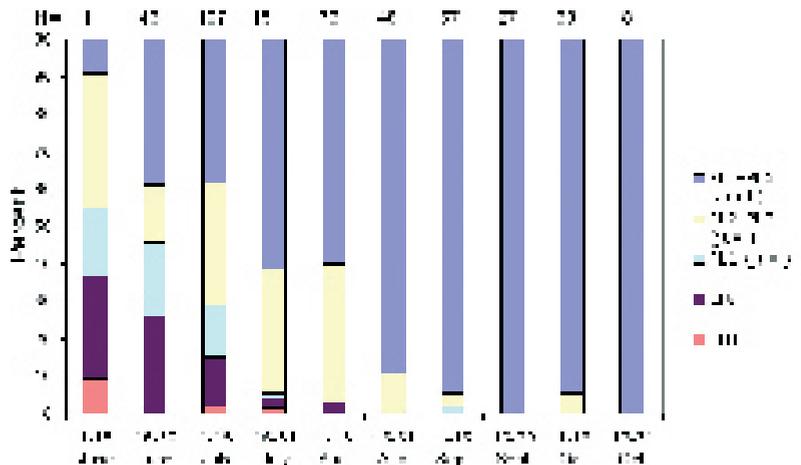
as described above. The 103 localities with the species from the three regions, where all localities were habitat classified, were the only ones which could be used. The differences between the two diagrams are an increase in percentage for shore,

bank and wetland, a pronounced increase for man-made habitats and a pronounced decrease for all forests in the standardized diagram. More than half the localities where the species is found are lake shores, river banks, marshes or swamps,
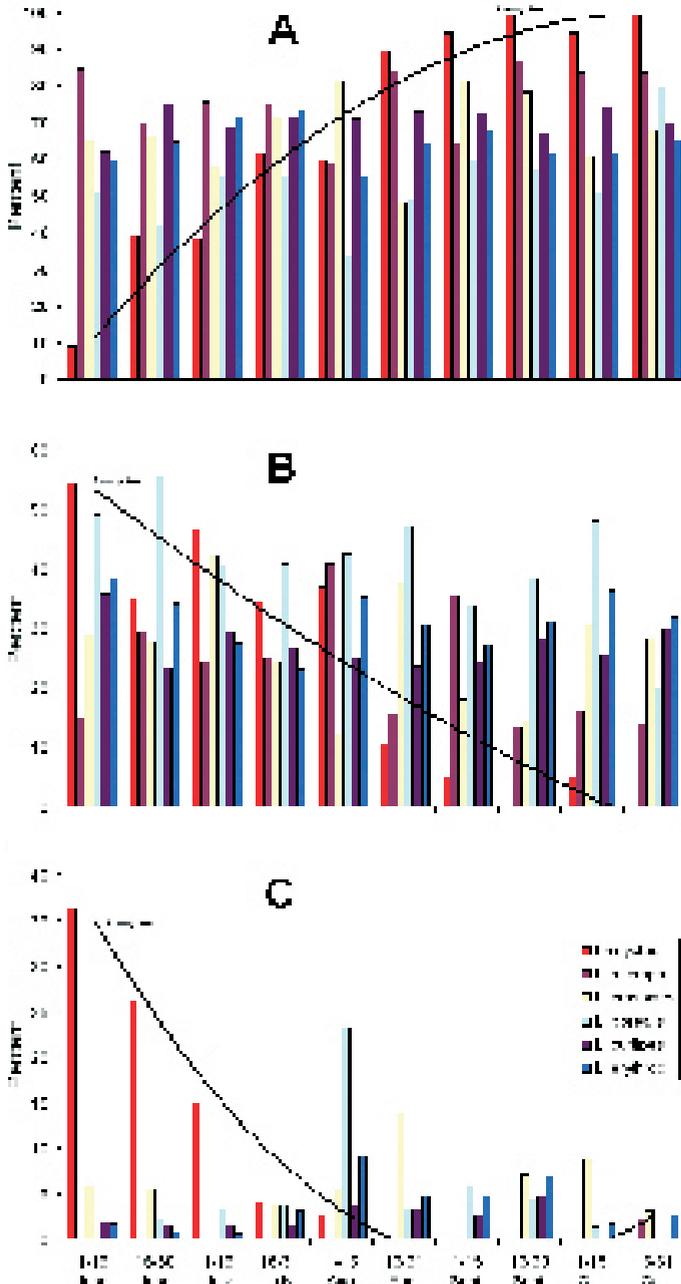
Figure 5. The seasonal distribution of *Lamyctes emarginatus* compared with five *Lithobius* species (*Lithobius crassipes, L. borealis, L. microps, L. curtipes* and *L. erythrocephalus*). A: Adults in percent of all specimens of the species found in the time period. B: Juveniles in percent of all specimens of the species found in the time period. C: Larvae in percent of all specimens of the species found in the time period.

Table 3. Number of larvae of different stadia found in cultures where adult females were reared to give offspring.

Stadium	Time period						
	10 Sept	15-21 Nov	8-15 Dec	22-29 Dec	2-12 Jan	19-26 Jan	23 Feb
L0	-	2	-	-	-	-	1
LI	-	4	3	2	1	-	-
LII	-	4	3	5	7	1	-
LIII	1	2	2	1	1	2	-
LIV	-	1	-	1	-	-	-

showing a preference for shores. The second most common habitat is man-made habitats. Most of the localities in the group pasture, meadow and rock are also influenced by man (59 %). Very few localities are from coniferus or deciduous forests.

The seasonal distribution of the different developmental stadia collected is presented in Figure 4. There is a clear dominance of larvae and juveniles in June and the first half of July. From August and onwards only 2 LIV and 1 PL1 are found. Only a few adults are found before the middle of June but in September and October almost all specimens found are adults.

A comparison is made with the five *Lithobius* species *L. crassipes, L. borealis, L. microps, L. curtipes* and *L. erythrocephalus*. The material is divided into three groups: larvae, juveniles and adults. The percentage of adults of all specimens of the species found in the time period is calculated (Figure 5A). The same is done for juveniles (Figure 5B) and larvae (Figure5C). For *L. emarginatus* there is a decrease of larvae from spring to autumn, in contrast to the five *Lithobius* species, where the percentage of larvae is almost constant during the whole period. (The high value for larvae of *L. borealis* in the first half of August depends on a special collecting effort, made by the author in Dalsland). A clear decrease from spring to autumn is apparent even for juveniles of *L. emarginatus*. For the *Lithobius* species there is a tendency towards decrease in autumn only for *L. borealis* and *L. microps*. Adults of *L. emarginatus*

show a clear increase from June to October while only two of the *Lithobius* species, *L. borealis* and *L. microps*, indicate a tendency of increase during the autumn.

Figure 6 shows a comparison of *L. emarginatus* with the five *Lithobius* species where the number of specimens of all stadia are grouped together. For the different time periods the number of specimens collected per locality investigated is calculated. The figures are presented as percent of all specimens collected of the species. Thus the figures for common and rare species will obtain the same magnitude. There are less *L. emarginatus* in June than of the *Lithobius* species, but from July to October no such difference is found. A trend line for *L. emarginatus* shows an increase to a peak in August. Most of the *Lithobius* species show the opposite – more specimens are found in spring and autumn than in summer. *L. borealis* shows just a little change during the year – a small decrease in the autumn. *L. curtipes* shows a more distinct decrease from spring to autumn.

DISCUSSION

Habitat preferences

The habitat preferences of *L. emarginatus* in Sweden are in good correspondence with what is found in other parts of the world. Open and disturbed areas with sparse vegetation are highly dominant among the localities where *L. emarginatus* is found in Sweden. A great deal of these localities are associated with lake shores and

Table 4. Data for Figure 7. P = percentage of all specimens collected of the species (including stadia PL2 to adults). h-l = mean value of head-length in mm.

	PL1		LIV		LIII		LII	
	P(%)	h-l	P(%)	h-l	P(%)	h-l	P(%)	h-l
Lithobius forficatus	12,3	0,785	4,6	0,698	2,5	0,601	1,2	0,538
L. melanops	8,3	0,597	0,5	0,520	0,0	0,470	0,0	0,417
L. macilentus	12,5	0,674	3,4	0,601	0,8	0,515	1,5	0,460
L. borealis	5,6	0,549	2,4	0,482	0,8	0,437	1,9	0,394
L. erythrocephalus	7,5	0,608	1,6	0,543	0,8	0,488	0,6	0,435
L. tenebrosus	1,9	0,567	1,6	0,512	1,9	0,455	1,9	0,416
L. calcaratus	6,4	0,696	2,3	0,618	0,6	0,549	0,1	0,494
L. crassipes	3,4	0,461	3,9	0,420	1,6	0,371	0,0	0,340
L. curtipes	4,9	0,554	1,2	0,503	0,6	0,464	0,2	0,426
L. microps	0,8	0,404	0,1	0,368	0,1	0,334	0,0	0,303
Lamyctes emarginatus	5,0	0,634	6,1	0,520	0,9	0,416	0,0	0,374

river banks (Figures 2 and 3). This is in agreement with the results of investigations of floodplains with inundation periods on the European continent (Zulka 1992, Zerm 1997), where *L. emarginatus* is one of the most commonly found centipedes. Man-made habitats are the second most common habitat in Sweden for the species. In New Zealand the species is most frequent in gardens and agricultural areas (Johns 1976) and in Rome (Italy) the species is only found in artificial habitats (Zapparoli 1992). On the British Isles there is a wide variety of habitats recorded for the species (Barber & Keay 1988, Barber 1992) but no marked preference for shores or banks. Eason (1964) remarks that the reputation for favouring banks of streams is probably undeserved. Even in the Swedish material the species is collected in a variety of habitats including both coniferous and deciduous forests but to a much lesser extent. The few localities in the group forest habitats are mostly described to include some wet microhabitat (small stream etc.) or some open area (small meadow or rock with lichens).

Seasonal distribution
Many publications stress the character of *L. emarginatus* as an autumn species (Lohmander 1945, 1947, Barber & Keay 1988, Barber 1992).

This means that it is very rarely found in other periods than late summer and autumn. This is also the case in the present study but only as far as adult specimens are concerned. Larvae and juveniles of the species are commonly found in June and July. If all stadia are taken into account, July and August are the best months to find *L. emarginatus* in Sweden (Figure 6). The five *Lithobius* species investigated for comparison show quite another picture (Figure 5). There is no clear difference in percentage of adults between the months, and findings of larvae and juveniles are also evenly spread out.

The Swedish data are in agreement with the findings of Zerm (1997), that *L. emarginatus* has a normal lifespan of one year and probably hibernates as eggs. However the adult specimens found in June suggest that a few adults may survive the winter or that the post-embryonic development for some specimens may start in the autumn.

The only adult found in early June was one specimen collected in Ångermanland 1 June without habitat data (not part of the main investigation mentioned above). It could be a greenhouse collection. The specimens from late June were collected 20 June - 30 June in different

localities (shore of a lake 20 June, no habitat data 22 June, in a greenhouse 23 June and 26 June, in a market garden 27 June, in pastures and meadows, open rocks and mixed forest 28 June and 30 June).

All these specimens could have reached the adult stadium from eggs layed in the autumn, but it is not clear if hatching takes place in the spring only. Zerm (1997) found that the species hibernates as eggs, but also found LII and LIII as late as 16 November.

In my earlier work with laboratory rearing of adult specimens for production of larvae (Andersson 1978), larvae of L. emarginatus were found in the cultures from September to February (Table 3). The cultures were started primarily to get larvae for descriptions (Andersson 1984) and were held at room temperature. The females were captured from 8 August to 18 October. It is uncertain if larvae which hatch during late autumn can survive winter outdoors and continue development the following spring, but findings of adult specimens as early as late June do indicate this. In the laboratory the mean duration of the development from hatching to adult for L. emarginatus was 84 days (Andersson 1990).

Eason (1970) suggests that larvae IV and juvenile specimens migrate to relatively deep soil layer, which can make finding them difficult. Larvae hatched in the autumn may act like this thereby avoiding capture at the surface, for instance in pitfall traps. The above mentioned larvae which were found by Zerm 16 November were from soil extraction, not from pitfall traps like the majority of the material (Zerm 1997).

Does L. emarginatus act differently compared to other Lithobiomorpha and in this way avoid capture? Or is it just a matter of size – a smaller animal is harder to find? To elucidate this the numbers of collected specimens of the smallest stadia (LII, LIII, LIV and PL1) for L. emarginatus and ten Lithobius species were plotted against the mean head-length of each stadium. Head-length is a good measurement of size and data was available from an investigation of post-embryonic development (Andersson 1978). The data is shown in Table 4 and the resulting regression line in Figure 7. As can be expected the proportion of larvae and small juveniles found is less for the smaller species and stadia. The four stadia of L. emarginatus in Figure 7 are marked with arrows. Three stadia are very close to the line and the fourth (LIV) is far above the line, which means that L. emarginatus LIV are percentually captured more often compared to some Lithobius specimens of the same size. There is nothing in the Swedish material suggesting that juvenile stadia of L. emarginatus should behave differently than juveniles of Lithobius species.

Several facts speak for a life cycle of one year, contrary to the Lithobius species:

Figure 6. Number of specimens collected per locality investigated in percent of all specimens collected of the species for *Lamyctes emarginatus, Lithobius crassipes, L.borealis, L. microps, L. curtipes* and *L. erythrocephalus*.
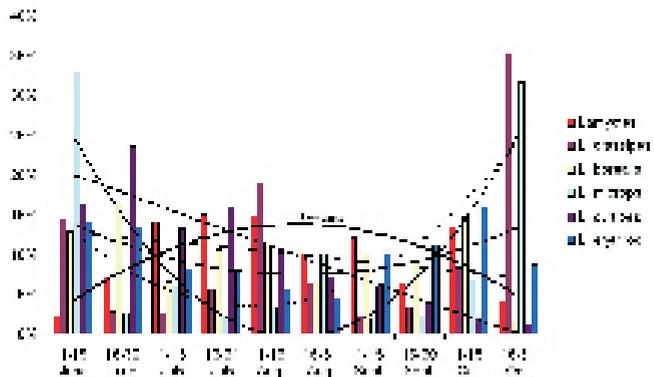
– findings of larvae almost only in spring or late autumn
– very few adults found in spring
– rapid growth of the larvae and juveniles compared with *Lithobius* species. *L. emarginatus* has a mean of 38 days from L0 to PL1 compared with a mean of 55-150 days for seven *Lithobius* species (Andersson 1990, Figure 2)
– low minimum number of postlarval stadia (5) compared with *Lithobius* species (6-9) (Andersson 1981, Table 3)

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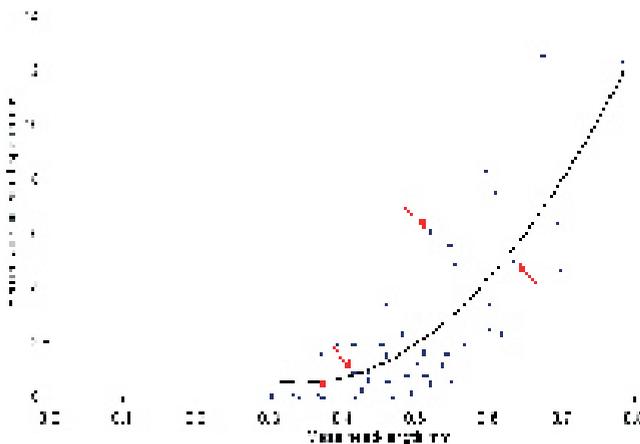
Figure 7. Correlation between percentage collected specimens of a developmental stadium and the mean size of the stadium for ten *Lithobius* species and *Lamyctes emarginatus*. As a measurement of size mean of head-length is used. For species and values see Table 4. The four stadia of *L. emarginatus* are marked with arrows.

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The South African savanna millipede (Diplopoda) fauna: taxonomic diversity, endemism, spatial and temporal effects on conservation assessments

M. L. Hamer, R. H. Slotow & S. Lovell

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The savanna biome covers almost half the land surface of southern Africa, and is considered to be homogenous, with high tree species richness, but low levels of beta and gamma diversity. Savanna has been neglected in terms of biodiversity research, and millipedes are especially under-sampled in this biome. Recent intensive surveys in the Mkhuze / Phinda reserves of KwaZulu-Natal, and collecting at other savanna sampling sites have provided data which are used here to answer several questions related to (1) the conservation value of the savanna millipede fauna, and (2) the effects of spatial and temporal scales on value assessments. Five of the seven orders, 10 of the 14 families and 21 of the 58 genera in South Africa are represented in savanna, with 76 species (16.6% of the fauna) restricted to this biome. The dominant order in savanna is the Spirostreptida, which comprises 53% of the fauna. Levels of endemism are high, with 50% of species in savanna known only from a 10km or less area, which is only a slightly lower proportion than for forest. Spatial scales are an important consideration for categorizing the distribution of savanna millipedes. Species may be widespread across the region, but restricted to a few sites at a local scale, so a species may have a large area of occurrence, but a small area of occupancy. This is not related to body size or mobility. Temporal changes do occur between seasons and different years, which means that measurement of millipede diversity at a site at any one time is unlikely to give an accurate indication of the abundance (rarity) or species richness of that site. Temporal variation therefore needs to be considered when comparing or prioritizing sites, or during monitoring programmes. Additional research into beta and gamma diversity for savanna millipedes is required to determine the scale at which conservation needs to be implemented for the fauna, and efforts to strategically sample additional savanna sites are required. This preliminary assessment of the savanna millipede fauna has indicated that unlike the vegetation, it does have high conservation value in terms of taxonomic diversity and richness as well as endemism.

Keywords: taxon richness, Diplopoda, savanna, endemism, spatial scale, temporal variation

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INTRODUCTION

There are several global, regional and national programmes to assess the conservation status of the components of biodiversity, to prioritize species, ecosystems and regions for conservation attention, and to monitor the state of biodiversity (Millenium Ecosystem Assessment, Balmford et al. 2005, Loh et al. 2005). These programmes require data on species richness, abundance, distributions, and changes in these over time. There are no universally agreed upon criteria or tools to assess conservation status, or for monitoring changes, but this field of research

is currently receiving attention (for example Balmford et al. 2005, Buckland et al. 2005). Generally, the conservation status of a region is measured as the number of species or species richness, the level of endemism and the level of threat (Myers et al. 2000). The conservation value of species is usually based on one or more of the following: 1. level of threat, which is related to the distribution and abundance, and past or predicted changes in these in response to human activities, 2. endemism and 3. phylogenetic uniqueness. For invertebrates, however, species data sets are incomplete. Many species have not yet been described (Stork 1999), the distribution of most described species is poorly known, and vast areas remain unsurveyed. Invertebrates form a major component of biodiversity and play crucial roles in the maintenance of ecosystems and the survival of more obvious taxa (Horwitz et al. 1999), and their inclusion in biodiversity conservation programmes is therefore important for these to be effective.

South Africa recently developed legislation to protect its biodiversity (Department of Environmental Affairs & Tourism 2004), a National Biodiversity Strategy and Action Plan has been developed (Department of Environmental Affairs & Tourism 2005), and a National Spatial Conservation Assessment carried out (Driver et al. 2005). The implementation of these documents requires biodiversity data. A major complication for interpreting biodiversity data is the complexity associated with scale, especially for small animals such as invertebrates. For every species that has been examined by appropriate quantitative methods, the distribution and abundance have been shown to be variable at a hierarchy of spatial and temporal scales (Underwood & Chapman 1996). The scaling hierarchy will therefore affect the determination of the conservation value of a species, and the definition of the scale at which habitats need to be conserved for a particular species or fauna. In addition, understanding temporal changes in abundance that occur in the absence of direct human disturbance is important in interpretation of data collected in monitoring programmes.

The savanna biome is characterized by a grassy ground layer and a distinct upper layer of woody plants (Low & Rebelo 1996). The tree layer usually consists of a discontinuous canopy of two to 10 meters, which overlies a grassy layer one half to two meters tall, and there may be an intermediate layer of small trees or shrubs. Savanna is one of the world's major biomes and covers approximately half the land surface of Africa, 46% of the area of southern Africa, and a third of the land surface of South Africa. Savanna, however, has received the least ecological study in southern Africa and most research has focused on the large mammal fauna which is diverse and abundant in this biome, as well as the tree-grass interaction, fire and production ecology (Cowling et al. 1997). Because of the large mammals, savanna is critical for the ecotourism industry, but it also provides grazing, building materials and fuel for rural communities. Increasing human populations in southern African savanna regions has led to an increased demand for natural resources. Increased development in the form of large agricultural schemes and mining, as well as alien invasive plants all contribute an ongoing and accelerating loss of savanna habitat and its associated biodiversity. In terms of biodiversity, however, savanna is not considered to be a priority. Although the plant species richness and the number of different vegetation types in savanna are higher than for other biomes, the beta and gamma diversity are low (Cowling et al. 1989).

The millipede fauna of South Africa is considered to be relatively well known as a result of the major contributions of Attems (1928, 1934), the Lund University Expedition as published by Schubart (1956, 1958, 1966), Kraus (1960, 1966) and Lawrence (1953, 1958, 1962, 1963, 1966). However, most of the Lund expedition survey sites and those sampled by R.F. Lawrence were in South African forests, although both did include some sites in the Kruger National Park. Recent surveys of millipedes in several different savanna areas produced sufficient data to provide some understanding of faunal patterns for ground-dwelling, flightless invertebrates in this biome.
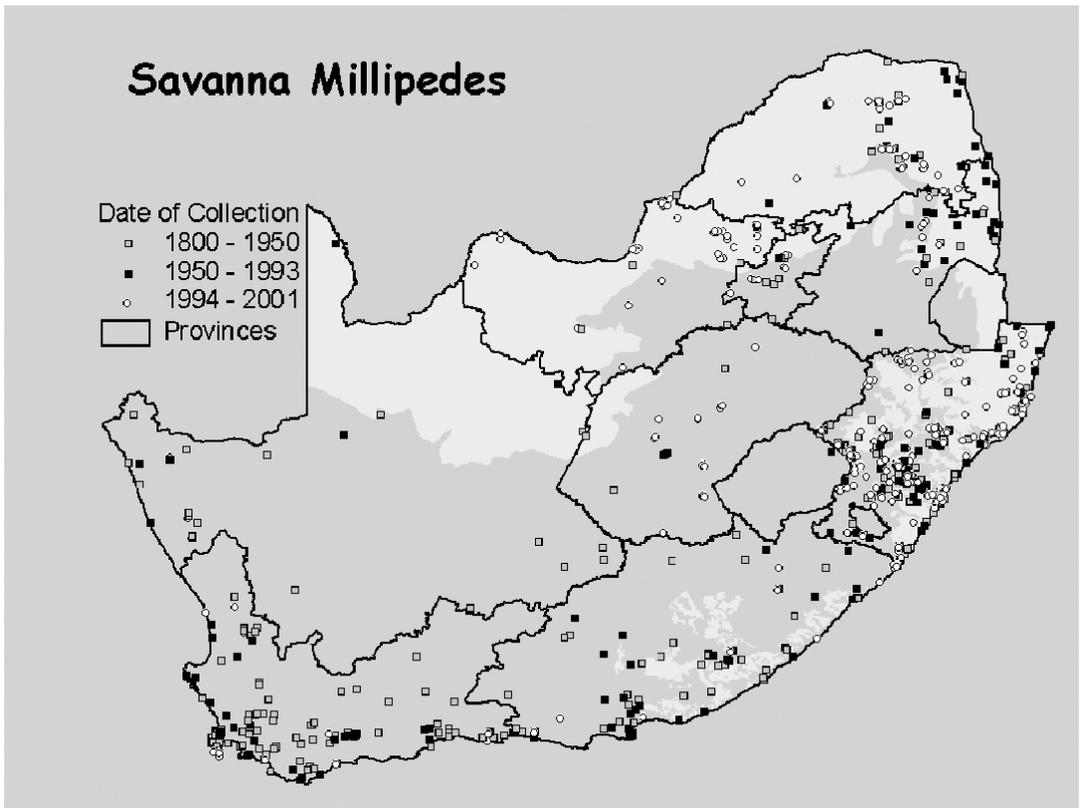
Figure 1. Map of South Africa showing millipede sampling localities relative to the distribution of savanna. Savanna represented by blue shading.

Savanna is relatively uniform in terms of vegetation, it covers a large area and is continuous, and the tree and shrub species are generally widely distributed in Africa. The climate is relatively dry, with heavily seasonal rainfall, and high mean temperatures. In terms of invertebrates, the following predictions are made:

1. Species richness should be high, because savanna has the highest plant species richness (Cowling et al. 1989) and invertebrate richness is usually related to diversity patterns for vegetation (Myers et al. 2000, Dangerfield & Telford 1992).
2. However, this richness should be concentrated in certain drought-tolerant higher taxa only, and taxa considered to be forest specialists should be absent.
3. Levels of endemism amongst savanna species

should be low, and most species should be distributed throughout the African savanna.
4. Spatial scales should not influence distribution patterns / conservation value of individual species because of the continuous nature and relative homogeneity of savanna. 5. Temporal changes in abundance and in species richness within and between years should be low, because millipede species inhabiting savanna should be tolerant of dry conditions and drought periods.

This paper examines these predictions for the millipede fauna of South Africa. Where appropriate, contrast between the savanna and the forest fauna is made because forest in South Africa is highly fragmented, and so would be predicted to have high diversity, as well as high levels of narrow endemics for less mobile taxa such as
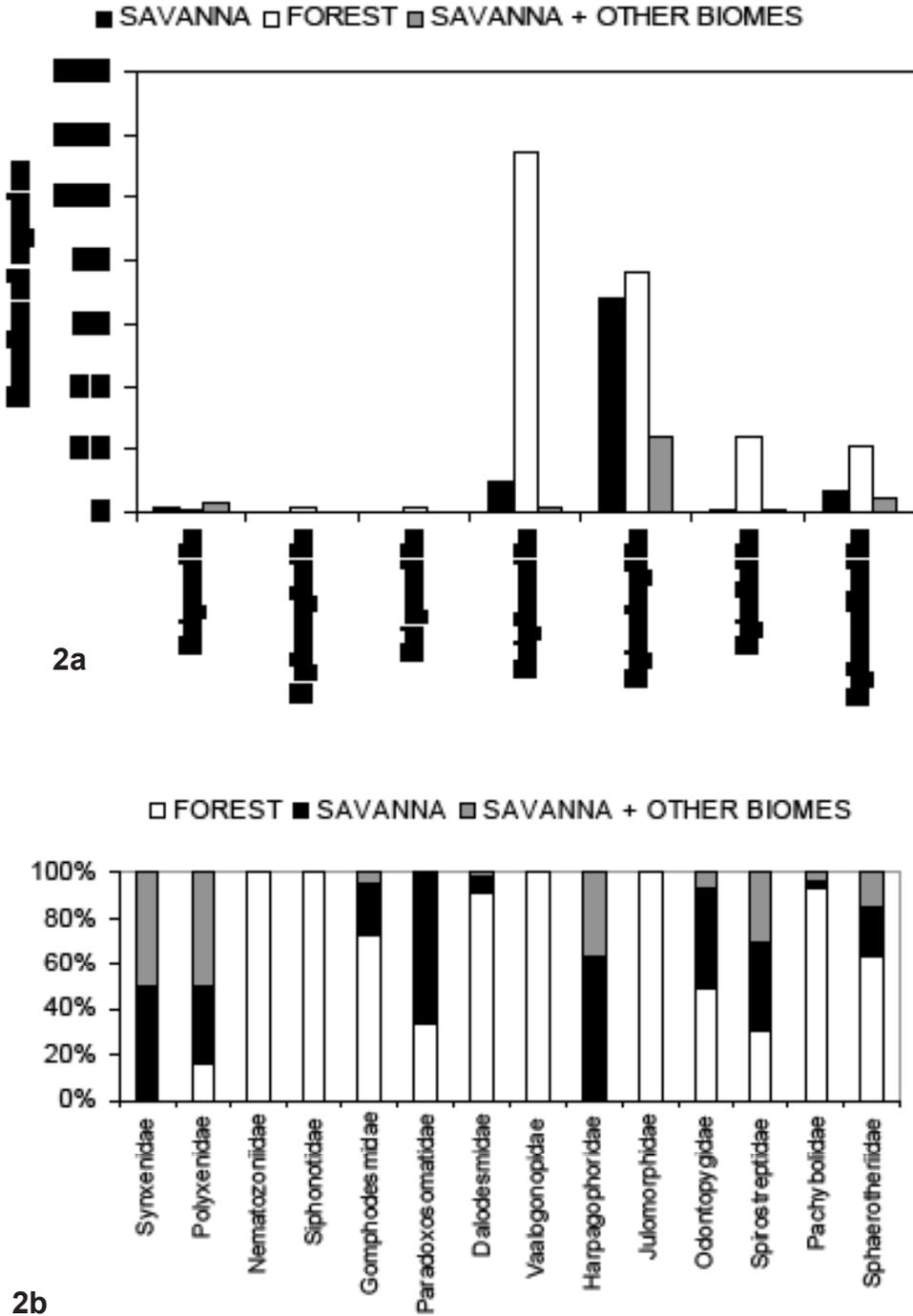
Figure 2. Millipede orders and families represented in South Africa. Number of species in different orders **(a)** and percentage of species in different families **(b)** in savanna only, savanna shared with other biomes (grassland, forest, thicket, and Karoo) and forest.

millipedes. In addition, the extent of sampling in savanna in South Africa is assessed.

MATERIALS AND METHODS

Species data for this study were compiled from a database of southern African millipedes, which includes all records from the literature, and all specimens from museum collections in South Africa. Only those species from South Africa, and only records where locality information provided is adequate to determine the vegetation type, and for which identification to species level were available, were included in the analyses. This provided a total of 1919 records.

In addition, a comprehensive survey of Mkhuze and Phinda Game Reserves in KwaZulu-Natal, South Africa was carried out between 2002 and 2005 in the summer months (November, January and March), and this provided 2499 records from 43 one hectare sites covering 11 different savanna vegetation communities. The sampling sites were spread across the reserves at locations where detailed vegetation surveys and soil analysis had been carried out and sites were selected to represent a range of vegetation and soil types. Twenty sites were re-sampled in different months during the summer season, including early summer (November), mid-summer (January) and late summer (March) and across years, giving a total of 77 sampling events of the 43 sites. Three sites were sampled each year, from 2002 to 2005 (three years), and for each year in at least two of the summer months.

This survey comprised quantified sampling which consisted of using a hand trowel to completely search the upper 5-15 cm of soil and litter, depending on the hardness of the substratum, and under any fallen logs or rocks of a two meter wide and 10 meter long quadrate divided into two meter blocks. This searching required 30 to 60 minutes per two by two meter block, and all millipedes were collected for recording. In addition, a 20 by 20 m plot was searched for a total of one hour with likely habitats such as around the base of trees,

under logs and rocks and in places where leaf litter or wood fragments had accumulated. Again, all individuals found were collected for recording. Two plots and two quadrates were sampled for each one hectare site. The quadrates allow estimation of millipede density, and all density figures presented in results are either mean values for the 10 two by two meter blocks sampled in the two quadrates, or totals for the 40 m2 covered by the two quadrates. Species richness for a site was determined by combining data from quadrates and plots. Reference specimens were collected, but all replicate specimens were released after recording to minimize the impact on the fauna. When the same site was sampled repeatedly at different times, the quadrates and plots were positioned so that the same area was not resampled, but the vegetation community was kept consistent.

Reference specimens of all species were identified by the first author. Those species which are undescribed were allocated to the appropriate genus and referred by the genus name and a morphospecies number. Undescribed species were included in the analyses for temporal changes in diversity. All material will be deposited in the Natal Museum, Pietermaritzburg, South Africa, at the end of the study.

RESULTS

Extent of millipede sampling in savanna
In terms of millipede survey in South Africa, savanna has been neglected compared to forest, with 968 forest and 392 savanna records. Recent collecting has covered previously neglected parts of the savanna in South Africa, but large gaps still exist (Figure 1).

Taxonomic diversity of savanna millipedes
The 76 species that are restricted to savanna comprise 16.6 % of the South African fauna (458 species in total), while forest species make up 52.6 % (241 species) of the fauna. The savanna species are spread across five of the seven orders represented in South Africa, and only the small,
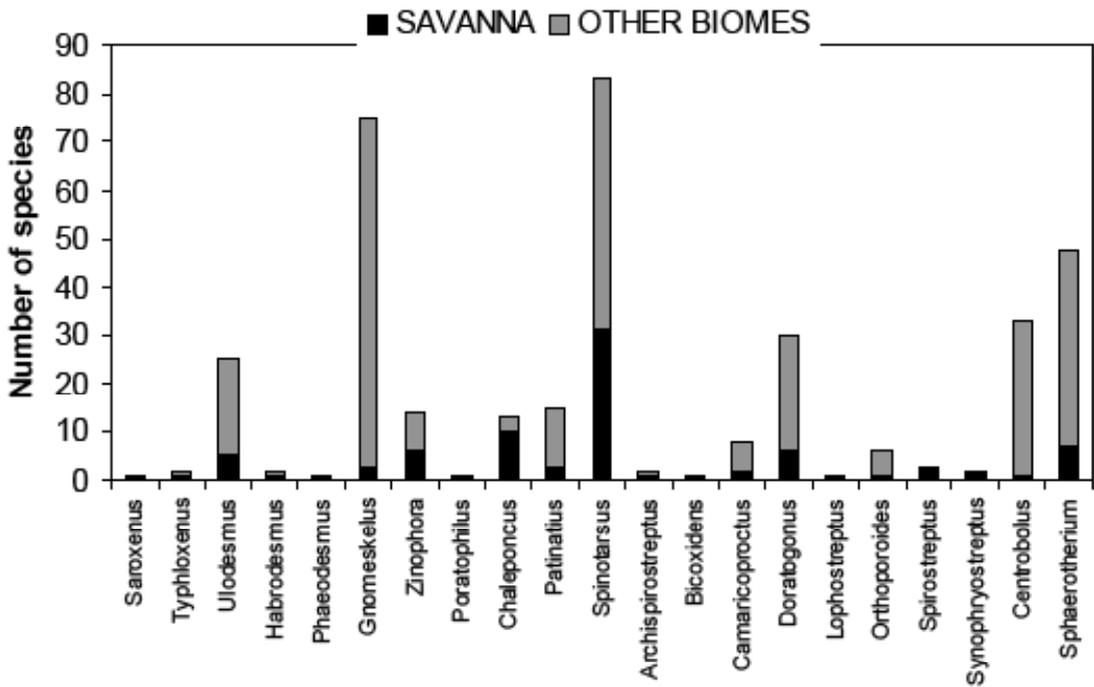
Figure 3. Richness of savanna millipedes in South African genera, relative to the total number of species in each genus. Only those genera for which savanna species are represented are included.

obscure and species-poor Siphonophorida and Polyzoniida are absent (Figure 2a). Species richness within the orders considered typical of forest, the Sphaerotheriida and Polyxenida, is lower in savanna than in forest, and no orders are dominated by savanna species. A relatively small number (35) of species within orders are shared between savanna and other biomes (Figure 2a); most shared species are spirostreptids that occur in savanna and forest, and savanna and grassland.

Ten of the 14 families (Figure 2b), and 21 of the 58 genera in South Africa are represented in savanna (Figure 3). Families that are absent in savanna are those belonging to the siphonophorids and polyzoniids, as well as the polydesmid family Vaalogonopidae and the spirostreptid Julomorphidae. The small polydesmid family Paradoxosomatidae, and the spirostreptid Harpagophoridae have the highest proportion of species in savanna relative to forest (2 vs 1 and 7 vs 0 species respectively) (Figure 2b).

The composition of the fauna at both order and family levels differs between forests and savanna, with the Spirostreptida making up 53 % of the savanna fauna, the majority of these belonging to the Odontopygidae, and all other families contributing less than 10 % to the total number of species. The Polydesmida, particularly the Dalodesmidae make up most (40 %) of the forest diversity (Figure 2b).

Of the 21 genera represented in savanna, the following are confined to savanna, at least in South Africa: *Saroxenus, Phaeodesmus, Poratophilus, Bicoxidens, Lophostreptus, Synophryosteptus a*nd *Spirostreptus*. However, all of these genera, except *Spirostreptus* (three species), and *Synophryostreptus* (two species) are represented by a single species in South Africa. Only one South African genus that has more than three species in South Africa has more than 50% of species confined to savanna. This is the odontopygid *Chaleponcus*, for which 10 of the 13
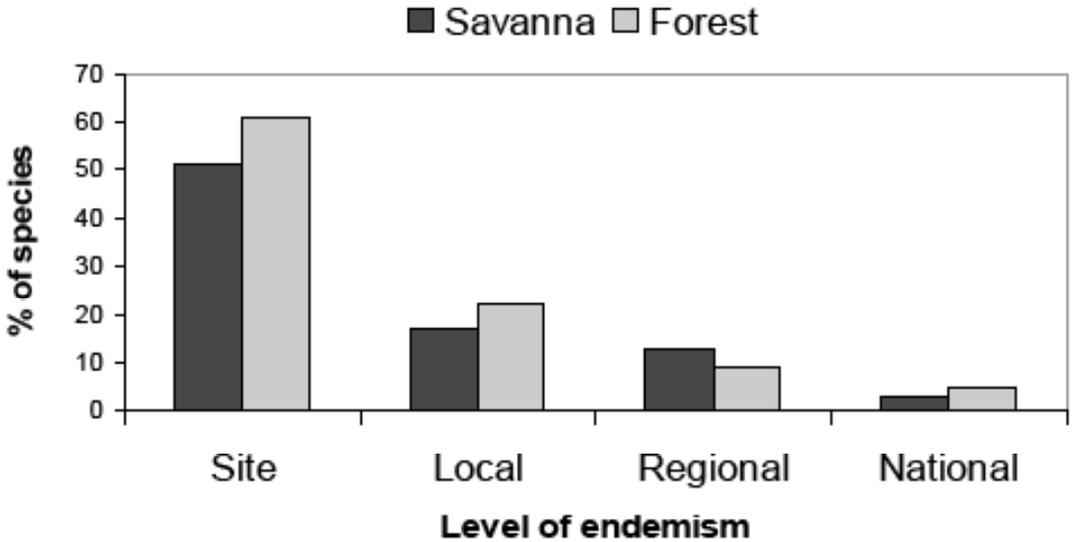
Figure 4. Percentage of species with different levels of endemism for forest and savanna biomes. The percentage given is that of the number of species as a percentage of the total number of species exclusive to savanna or forest. Site endemic = only one locality, and those including more than one locality but with <10 km separating the two furthest localities; local endemics = all species with between 11 and 70 km separating the two furthest localities; regional endemics = all species with between 11 and 150 km separating the two furthest localities and South African endemics = species restricted to South Africa (Hamer & Slotow 2000).

known species (77 %) are restricted to savanna. *Bicoxidens* is predominantly a Zimbabwean genus and *Lophostreptus* and *Synophryostreptus* also occur north of South Africa; these genera are probably also confined to savanna.

That the millipede fauna of South African savanna is far from completely known is shown by the intense sampling at Mkhuze / Phinda Game Reserves. Prior to the 2002-2005 survey, only two species were known from the reserves. The 28 species known now have changed the status of Mkhuze / Phinda from one of the lowest quarter degree grid blocks (Hamer & Slotow 2002) to one of the highest in terms of species richness. Of the 28 species sampled, at least 50 % are undescribed. These undescribed species belong to the following genera: *Sphaerotherium* (two species), *Ulodemus* (one species), *Camaricoproctus* (one species), *Chaleponcus* (three species), *Spinotarsus* (six species), unknown odontopygid genus (one species).

Levels of endemism
of savanna millipedes

Forty-five site endemics (those species recorded only from one locality, or from more than one locality, but with less than 10 km separating the two furthest localities (Hamer & Slotow 2002)) are limited to savanna. While the actual number of site endemics in forests is three times that in savanna, the proportion of species that are limited to a small area (site and local endemics (between 11 and 70 km separating the two furthest localities)) is similar in both biomes (Figure 4).

Spatial scale and conservation value:
examples of species from
Mkhuze Game Reserve

The conservation status of species differs at different spatial scales. Examples of four species, all found within the Mkhuze / Phinda Game Reserve area, are used to illustrate patterns (Figure 5). *Doratogonus flavifilis* (Peters, 1855) is relatively widely distributed in the north-eastern
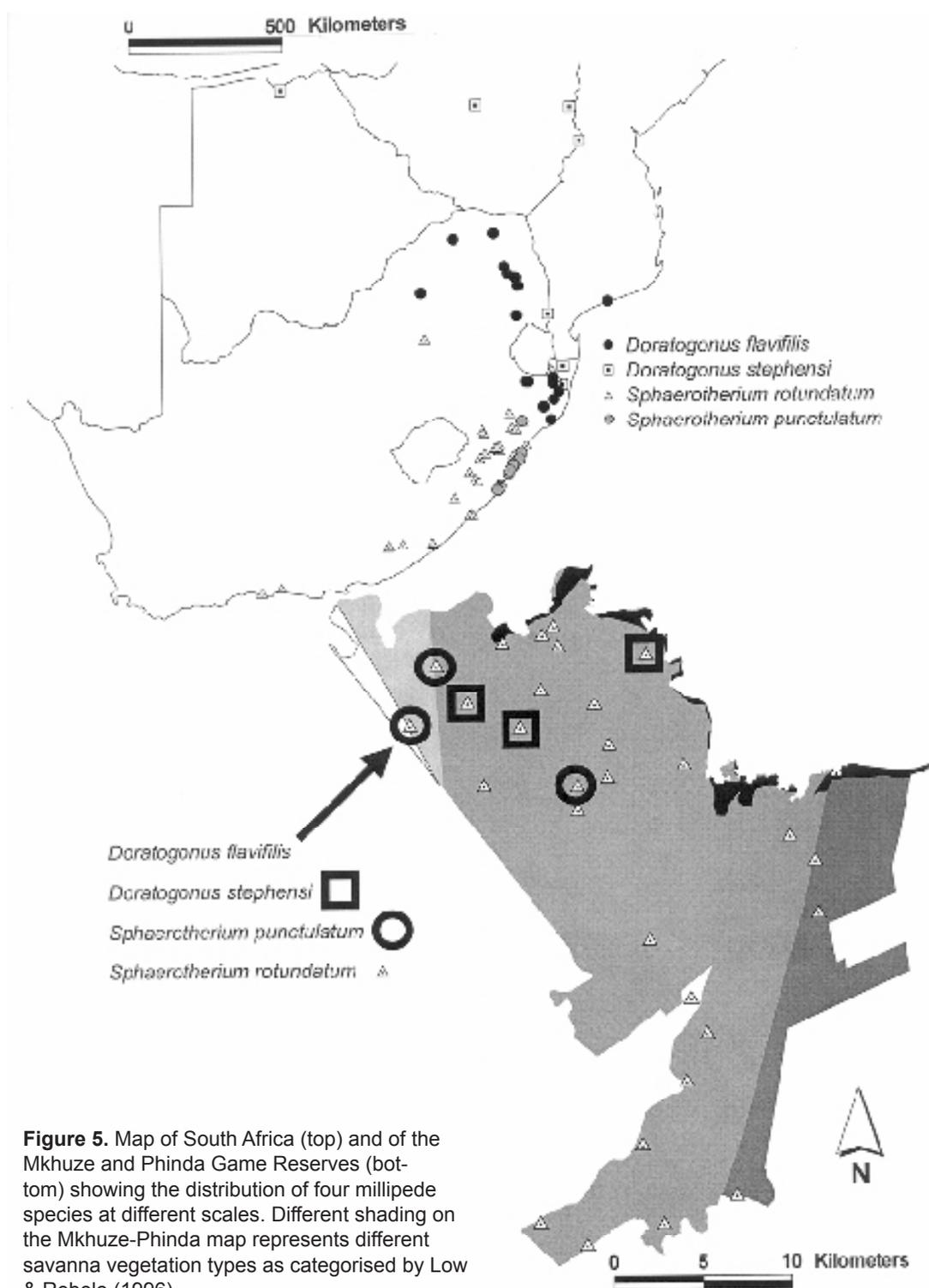
Figure 5. Map of South Africa (top) and of the Mkhuze and Phinda Game Reserves (bottom) showing the distribution of four millipede species at different scales. Different shading on the Mkhuze-Phinda map represents different savanna vegetation types as categorised by Low & Rebelo (1996).

part of southern Africa, from the Umfolozi River in the south to the Limpopo River in the north but it does not occur continuously throughout the region (Figure 5). At Mkhuze / Phinda Game Reserves this species was collected at only one sites, where abundance was relatively low. In IUCN Red Listing terms (IUCN 2001) the species has a large area of occurrence, but a small area of occupancy. *Doratogonus stephensi* Hamer, 2000 shows a similar pattern of distribution and occurrence (Figure 5). Both these *Doratogonus* species are large-bodied, more than 10cm in length, with *D. stephensi* reaching 20cm, and they would be expected to be mobile, and not particularly habitat restricted.

Two *Sphaerotherium* species illustrate contrasting patterns of distribution. The smaller bodied *S. rotundatum* Brandt, 1833 occurs virtually throughout Mkhuze and Phinda , but is mostly limited in distribution to the more mesic east coast region (Figure 5). This species has a large area of occupancy, but a moderate area of occurrence. The larger-bodied *S. punctulatum* Brandt, 1841 has been recorded from Malawi, and along the coast of South Africa (large area of occurrence), but is known from only three sites within Mkhuze and Phinda (small area of occupancy) (Figure 5), and at only one of these it was abundant (approximately one individuals / 2 m^2).

These four examples illustrate that millipede distributions are not directly linked to the distribution of the biome, but that other factors, which operate at a smaller scale than broad vegetation type, limit distribution. Both local and broad scale distributions need to be considered when categorizing a species as widespread or localized and the threat status related to this. The need for caution when extrapolating distribution from isolated points and for modeling distributions is also highlighted by these patterns.

Temporal changes in savanna millipede abundance and community structure

Repeated sampling in different months representing early, mid- and late summer and through three years at the same sites in Mkhuze Game Reserve showed distinct temporal changes in abundance and diversity (Figure 6). Some species, such as *S. rotundatum* had a low abundance (1 or fewer individuals / 2 m^2), and this was generally maintained throughout the three years of sampling. In other species, however, abundance declined substantially through the sampling period. This was most evident in *Spinotarsus* but only at some sites (for example M22 and M61). Co-incidentally to the decline in identified *Spinotarsus* species, the density of unidentified immature *Spinotarsus* increased at these sites. Some species (*Z. laminata* and *Spinotarsus* sp. 4) disappeared and were not sampled in one period, but they were sampled again later. Other species, for example *Doratogonus castaneus* (Attems, 1928), and *D. stephensi*, however, appeared to disappear from the sites after 2002 (Figure 6).

The extent of change in species richness through the three years differed between sites. At M36 species richness changed a maximum of 20 %, while at site M22 the maximum change was 33 % and at M61 species richness declined 75 % from four down to one species. Peaks in species richness did not coincide with any one month or year but rather differed according to site (Figure 6).

DISCUSSION

The perception exists that savanna is homogenous, arid, and unlikely to be inhabited by a rich fauna of moisture dependant invertebrates such as millipedes. This is illustrated by the low number of millipede records from before 1994 in South Africa (Figure 1), when collectors focused on forest habitats where the abundance and richness are high and relatively easy to sample. A recent focus on savanna millipedes has provided new data, but there are still large collecting gaps. Given the rapid rate of development and habitat alteration in South African savanna, and time and funding constraints, it is unlikely that this biome will be comprehensively surveyed in the near future. It is therefore more sensible to develop an understanding of general principles of millipede diversity which can be used to generate
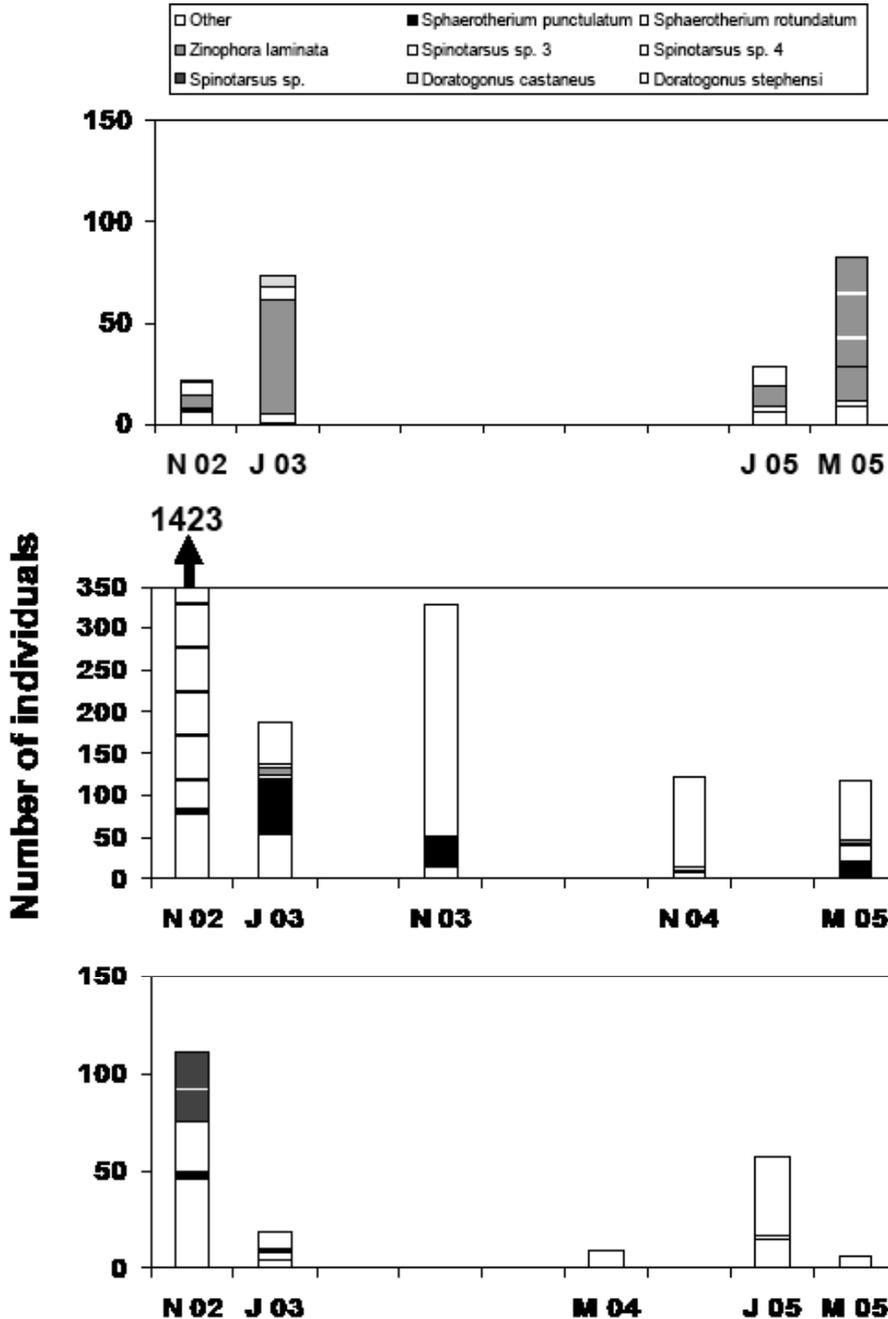
Figure 6. Species richness and abundance at three sites over a three year period in Mkhuze Game Reserve. The sites represented from top to bottom are M36 (*Acacia nigrescens* / fine leaf low open woodland), M22 (*Combretum apiculatum* open woodland, broadleaf savanna) and M61 (*Terminalia sericea* open woodland). The total number of individuals in the two 2x10 m quadrates and the two 20x20 m plots combined is presented. The sampling date is presented on the x-axis as the month and the year in which Sampling period is indicated along X axis as N=November, J=January, M=March; 02=2002, 03=2003, 04=2004, 05=2005.

generalizations and focused research questions for application in conservation planning.

The savanna millipede fauna has high conservation value, since 16.6 % of South African species are confined to the biome, and the higher taxon diversity is also rich. Millipede species richness in savanna is relatively high, but according to existing data, it is less than 50% of the forest fauna. The scale of the difference is more extreme when the actual area of the two biomes is considered. Forest apparently covers less than 0.5 % of the total land area of southern Africa (Midgley et al. 1997) while savanna covers 46 % of the area of the subcontinent. The high number of forest millipede species is a reality, and is probably a result of the fragmented and isolated nature of South African forests, the age of this biome, the change in forest extent associated with past climatic extremes and the persistence of refugia (see Lawes 1990 for description of forest history in South Africa), and the more suitable nature of the habitat for ground-dwelling, moisture dependant detritivores. The history of savanna is unclear but during glacial maxima it is possible that savanna retreated from South Africa. This might also explain the absence of genera that are restricted to, and have radiated in savanna in South Africa. The total number of tree species in forests is much lower than in savanna (Geldenhuys & MacDevette 1989), but because of the small size of forests, the total species density is higher. This shows that there is little direct relationship between overall plant species richness and millipede richness, but that species density may be more important. However, the low number of savanna millipede species may be a gross underestimation associated with a lack of sampling effort. The increase in species in the Mkhuze area from two to 28, of which 14 are undescribed illustrates the extent of the lack of knowledge, but it also indicates the potential dangers of using data that are far from complete, for taxa that are poorly understood.

The taxonomic diversity of the savanna fauna is not unexpected in its makeup. The spirostreptids are the most diverse order in savanna, as was predicted based on the work of Dangerfield

& Telford (1991, 1993, 1996) and Druce et al. (2004b). However, perhaps as a result of the greater number of records from forest, the proportion of spirostreptid species restricted to forest was higher than for savanna. There are also no known genera that have radiated in, and are confined to savanna in South Africa, while many monotypic or diverse genera are confined to forest. This reduces the conservation value in terms of phylogenetic diversity of the savanna millipede fauna.

Small-bodied, higher taxa typical of forests are absent, or are represented by few species in savanna. However, sphaerotheriids and polydesmids do occur in savanna. Lawrence (1984) stated that the former order avoids semi-arid regions, and the latter order is confined to the forest floor of indigenous bush or to small localities where the soil is rich in humus. Dangerfield & Telford (1992, 1993, 1996) made no mention of taxa other than spirostreptids in their sampling of savanna in Zimbabwe and Botswana, but whether this indicates absence is unknown. Detailed quantified sampling provided an insight into the exact nature of habitats occupied by "forest" millipedes in savanna. *S. rotundatum* was common in most habitats sampled in Mkhuze Game Reserve, even those lacking humus or moisture. An unidentified gomphodesmid belonging to the genus Ulodemus was confined to the most arid, open, rocky parts of the reserve, and the dalodesmid *Gnomeskelus tenuipes* Lawrence, 1953 also occurred in dry habitats. *Gnomeskelus, Ulodesmus* and *Sphaerotherium* were also recorded from savanna in the Limpopo Province of South Africa (Druce et al. 2004b). These and the larger-bodied spirostreptids must have strategies for surviving the dry winter months, and the often prolonged droughts in the area. There has been no work examining these strategies in detail, but it is assumed that millipedes are able to burrow into deep soil (Dangerfield & Telford 1996), often at the base of trees, where there may be some moisture.

Our study did show changes in density and species presence over time, which may be associated with

dry periods, or they could be linked to life cycles, or natural rarity of some species resulting in them not being sampled at all times. Contrary to the observations of Dangerfield & Telford (1996), there was a large amount of evidence of high mortality for some of the large spirostreptids in the form millipede rings on the substrate. Again, however, whether this mortality is related to normal life span or is a result of dry periods is uncertain. For the *Spinotarsus* species sampled, their decline over time often did coincide with an increase in the abundance of unidentifiable, juvenile *Spinotarsus* specimens (Figure 6), which could indicate a natural cycle and distinct cohorts.

Dangerfield & Telford (1996) stated that the spirostreptids (Odontopygidae, Harpagophoridae and Spirostreptidae) showed distinct patterns of surface activity during the summer rainfall season from October to April in Zimbabwean savanna, and in the semi-arid *Acacia* savanna in Botswana savanna millipede activity was initially linked to rain, but later in the summer season (February, March) rains had no effect on activity. Similarly in the current study, March generally had the lowest abundance and richness even if it had rained before or during sampling. The rainfall season in Mkhuze is also between October to April, but rains during the three years of sampling for this study were unpredictable. The first rains were delayed each year, making November the driest month. Richness and abundance were, in spite of this, generally highest in November (Figure 6). Dangerfield & Telford (1996) also stated that there were between site differences in surface activity, and this was also observed by Druce et al. (2004a). Temporal changes in savanna millipede richness and abundance do occur and their causes in savanna millipedes are obviously complex and require more investigation. This is important because a particular site or area could appear to have low conservation value based on ground-dwelling invertebrate richness and abundance, but this may be related to natural processes and patterns of population and community ecology, or the result of localized drought.

The high proportion of narrow endemics in South African savanna may be a result of inadequate sampling, and future surveys could provide additional and more widespread localities for species currently considered site or local endemics. However, experience has shown that while this might be true, additional sampling usually results in the discovery of new species restricted to the site. In additional, the fact that large-bodied species such as *D. stephensi* and *D. flavifilis* must be limited in terms of distribution by some environmental factors, as shown in Figure 5, suggests that even in a relatively homogenous biome, it is possible to have range-restricted species.

An important aspect of diversity and conservation value is beta and gamma diversity, or species turnover with distance. This is linked to the number of site and local endemics, and the restricted distribution of several species (Figures 4 and 5) which suggests that turnover should be high. This aspect of diversity is beyond the scope of this paper, and will be addressed elsewhere.

In conclusion, the South African millipede fauna is not as diverse as that in forest, but it still does have high conservation value in terms of species richness covering all major orders, and levels of endemism. Caution is required in assessing the conservation status of millipede species or sites in terms of millipede richness because of the effects on these of spatial and temporal scales. Data, however, are incomplete, and crucial questions linked to more contemporary approaches to biodiversity conservation such as long term temporal changes through different climatic extremes, and species richness turnover at different scales remain to be answered.

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Diurnal epigeic activity of myriapods (Chilopoda, Diplopoda)

Ivan H. Tuf, Jana Tufová, Eva Jeřábková & Pavel Dedek

Diurnal epigeic activities of myriapods in a floodplain forest and a neighbouring deforested area, was studied in late spring and early in autumn of 2004, by pitfall trapping. One hundred traps were checked every three hours. In total, 7 species of centipedes and 11 species of millipedes were trapped. Only *Lithobius mutabilis, Glomeris connexa, Unciger foetidus,* and *Unciger transsilvanicus* were dominant. The whole millipede community and all its dominant species, and the centipede *Lithobius forficatus* showed significant patterns of diurnal activity. The millipedes, both the whole community and *U. transsilvanicus* and *Polyzonium germanicum*, were significantly affected in their activity by temperature of soil surface too.

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INTRODUCTION

Soil is inhabited by a huge number of invertebrate species, the so called soil fauna. For some of them, the soil represents a refuge. Out of the soil the environment is less suitable; there is too much light, and the humidity and temperature are more instable. For these reasons many species of soil fauna show specific pattern of epigeic activity – they are more active during periods with more favourable conditions, i.e. during spring and autumn in annual rhythm and/or during night in diurnal rhythm.

Circadian rhythms are widespread in the animal kingdom. Rhythms of epigeic activity is not only shown by surface animals, reacting to changes in light conditions, but also by troglobiotic species from constant dark environment (Koilraj et al. 2000). Generally, myriapods show mainly epigeic activity at night with various exceptions (Lewis 1981, Hopkin & Read 1992), for example dusk (dawn & twilight) activity (Bano &

Krishnamoorthy 1979). This rhythm is controlled by internal physiological factors (timers), but it can differ in length in relation to environmental conditions. For instance, the centipede *Scolopendra* sp. with strictly night activity (in natural light regime) rapidly lost this rhythm in LL (constant light) conditions (Cloudsley-Thompson & Crawford 1970). In another experiment, with varying DL (dark-light) periods, it was shown that the length of the activity cycle (from peak to peak) is correlated to the length of the light period. This cycle was shorter in DD conditions (24 hours of dark), than in 12:12 DL or LL conditions for the millipede *Syngalobolus* sp. (Koilraj et al. 1999). In comparison, millipedes showed less activity during the light periods than centipedes (Dondale et al. 1972).

Beside light stimulus, other environmental conditions like temperature or humidity were tested for their influence on diurnal rhythms of myriapods. For millipedes, Cloudsley-Thompson (1951) described the decrease of temperature

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Table 1. Diurnal epigeic activity of myriapods during late spring (May–June). Catches of individuals by 60 traps during 18 days in individual time-parts of day (3:00 means that animals were catched from 0:00 to 3:00), greyed columns mark dark period.

	forest								clear-cut							
	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00
Lithobius agilis L.Koch, 1847	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2
Lithobius curtipes C.L.Koch, 1847	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lithobius forficatus Linnaeus, 1758	2	1	2	-	1	-	-	2	17	8	-	5	-	-	2	14
Lithobius microps Meinert, 1868	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lithobius mutabilis L.Koch, 1862	14	23	8	9	4	4	3	18	35	23	21	15	5	12	17	47
Strigamia acuminata (Leach, 1814)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strigamia transsilvanica (Verhoeff, 1928)	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chilopoda	**17**	**25**	**10**	**9**	**5**	**4**	**3**	**20**	**53**	**30**	**21**	**20**	**5**	**12**	**18**	**62**
Glomeris connexa C.L.Koch, 1847	11	3	-	2	1	-	3	19	45	20	5	3	2	-	21	54
Brachydesmus superus Latzel, 1884	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Polydesmus denticulatus C.L.Koch, 1847	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
Haplogona oculodistincta (Verhoeff, 1893)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melogona voigti (Verhoeff, 1899)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ochogona caroli (Rothenbuehler, 1900)	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Enantiulus nanus (Latzel, 1884)	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Leptoiulus proximus (Němec, 1896)	4	3	1	2	-	1	-	9	3	-	2	2	-	-	2	-
Unciger foetidus (C.L.Koch, 1838)	2	3	7	-	1	1	1	4	3	3	3	2	2	-	2	6
Unciger transsilvanicus (Verhoeff, 1899)	2	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Polyzonium germanicum Brandt, 1831	1	2	2	3	-	2	2	2	-	-	-	-	-	-	-	-
Diplopoda	**20**	**13**	**10**	**7**	**2**	**4**	**6**	**36**	**53**	**24**	**9**	**6**	**5**	**-**	**24**	**60**
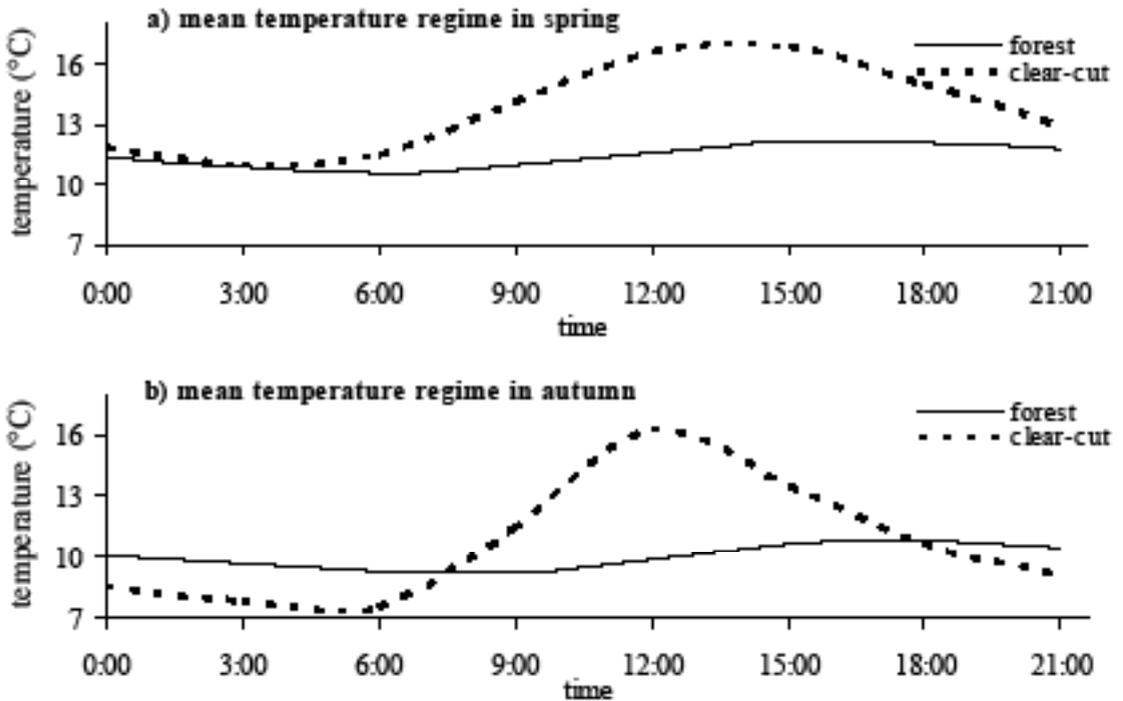
Figure 1. Mean day-temperature regime on the localities during the study period: a) in late spring (May-June 2005), b) in early autumn (September-October 2005).

in night as the starter of locomotory activity. Similarly, Banerjee (1967) found correlations (coefficient higher than 0.5) between temperature of air and activity of all studied millipedes, but the correlation of activity and humidity was relatively low.

Diurnal activity of centipedes and millipedes, as a part of an epigeic macrofauna, was studied in a floodplain forest and a nearby deforested (clear cut) area, during spring and autumn 2004.

MATERIAL AND METHODS

The study area was located in the Litovelské Pomoraví Protected Landscape Area, a natural landscape around the meandered Morava River (Central Moravia, Czech Republic) with floodplain forests and meadows. The localities under comparison were an old floodplain forest

(*Querco-Ulmetum*) and a nearby deforested area (49°65´N, 17°20´E, altitude 210 m a.s.l.). The herbal layer of the floodplain forest was created by *Anemone nemorosa, Polygonatum* spp*., Lathyrus vernus* and *Maianthenum bifolium.* The dominant moss was *Eurhynchium hians*. In November 1998, the litter biomass (dry weight) was 622 g/m². The alluvial soil was loamy-sandy to loamy at the locality, with pH 4.8-5. The annual precipitation was around 520 mm and mean annual temperature was 9.1 °C. Part of this forest was cut in November 2002 and replanted in March 2003 with oak, elm and lime tree (ratio 8 : 1 : 1) using heavy forest machines. Before that, the remaining wood residue was chipped and scattered throughout the whole area. Epigeic invertebrates were caught using pitfall traps (plastic pots) without fixative solution. 60 traps were arranged in the forest and 40 traps in the deforested area. The traps were placed in line with a spacing of three meters.

Table 2. Diurnal epigeic activity of myriapods early in autumn (September–October). Catches of individuals by 60 traps during 18 days in individual time-parts of day (3:00 means that animals were catched from 0:00 to 3:00), greyed columns mark dark period.

	forest								clear-cut							
	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00	3:00	6:00	9:00	12:00	15:00	18:00	21:00	24:00
Lithobius agilis L.Koch, 1847	1	1	-	-	-	-	2	-	-	-	-	1	-	-	-	-
Lithobius curtipes C.L.Koch, 1847	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Lithobius forficatus Linnaeus, 1758	3	2	1	-	-	-	3	2	6	1	1	-	-	-	2	6
Lithobius microps Meinert, 1868	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lithobius mutabilis L.Koch, 1862	9	16	15	5	3	3	20	19	6	5	6	1	2	-	6	5
Strigamia acuminata (Leach, 1814)	2	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-
Strigamia transsilvanica (Verhoeff, 1928)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Chilopoda	**14**	**20**	**17**	**5**	**3**	**3**	**27**	**21**	**11**	**6**	**7**	**2**	**-**	**2**	**8**	**10**
Glomeris connexa C.L.Koch, 1847	2	2	1	1	-	-	3	3	6	1	-	-	-	-	2	8
Brachydesmus superus Latzel, 1884	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polydesmus denticulatus C.L.Koch, 1847	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Haplogona oculodistincta (Verhoeff, 1893)	-	1	1	-	1	1	-	1	-	-	-	1	-	-	-	1
Melogona voigti (Verhoeff, 1899)	-	-	-	-	-	1	2	2	-	-	-	-	-	-	-	-
Ochogona caroli (Rothenbuehler, 1900)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Enantiulus nanus (Latzel, 1884)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptoiulus proximus (Němec, 1896)	1	2	-	-	-	-	1	2	-	-	-	-	-	-	-	-
Unciger foetidus (C.L.Koch, 1838)	14	14	3	-	-	1	14	17	2	6	2	-	-	1	5	5
Unciger transsilvanicus (Verhoeff, 1899)	27	17	5	1	-	-	11	23	3	3	1	-	1	1	2	5
Polyzonium germanicum Brandt, 1831	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Diplopoda	**44**	**35**	**10**	**2**	**1**	**2**	**32**	**48**	**11**	**10**	**3**	**3**	**1**	**2**	**9**	**18**
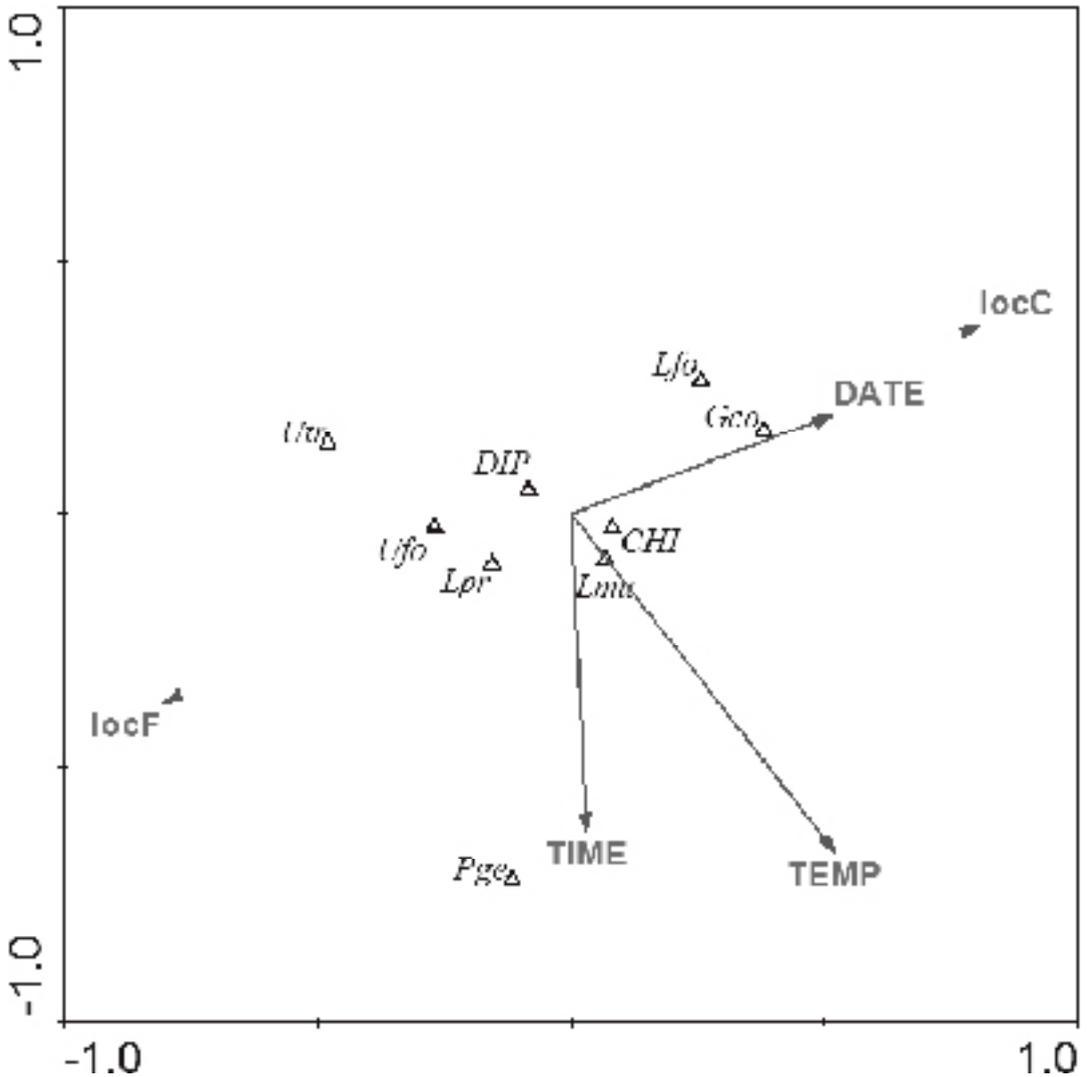
Figure 2: CCA ordination plot showing epigeic activity of dominant myriapod species (catched more than 10 specimens) in relation to locality (locF-forest, locF-clear-cut), day-time (TIME), season (DATE), and TEMPERATURE. Abbreviations: CHI – Chilopoda, Lfo – *L. forficatus*, Lmu – *L. mutabilis*, DIP – Diplopoda, Gco – *G. connexa*, Lpr – *L. proximus*, Ufo – *U. foetidus*, Utr – *U. transsilvanicus*, Pge – *P. germanicum*. (Plot: F = 2.65, p = 0.0052, number of permutation (Monte Carlo) = 5000; Conditional effects: clear-cut: F = 10.9, p = 0.000, DATE: F = 4.54, p = 0.000, TIME: F = 2.65, p = 0.005, TEMPERATURE: F = 5.35, p = 0.000).

The investigation was carried out in late spring (20 May – 7 June, 18 days) and early autumn (23 September – 18 November, 25 days) of 2004. Traps were checked every three hours (i.e. at 3, 6, 9, 12, 15, 18, 21 and 24 hours). The temperature of the soil surface was measured at collecting hours at both localities by the use of data-loggers, Minikin TH. A canonical correspondence analysis and generalised additive models for evaluating the results were created in the programme CANOCO for Windows 4.5© (ter Braak & Šmilauer 1998). Graphs were created in CanoDraw for Windows 4.0©.

The soil macrofauna of isopods, spiders, harvestmen, centipedes, millipedes, bugs and ground beetles was sorted out. Here only the myriapods are treated.
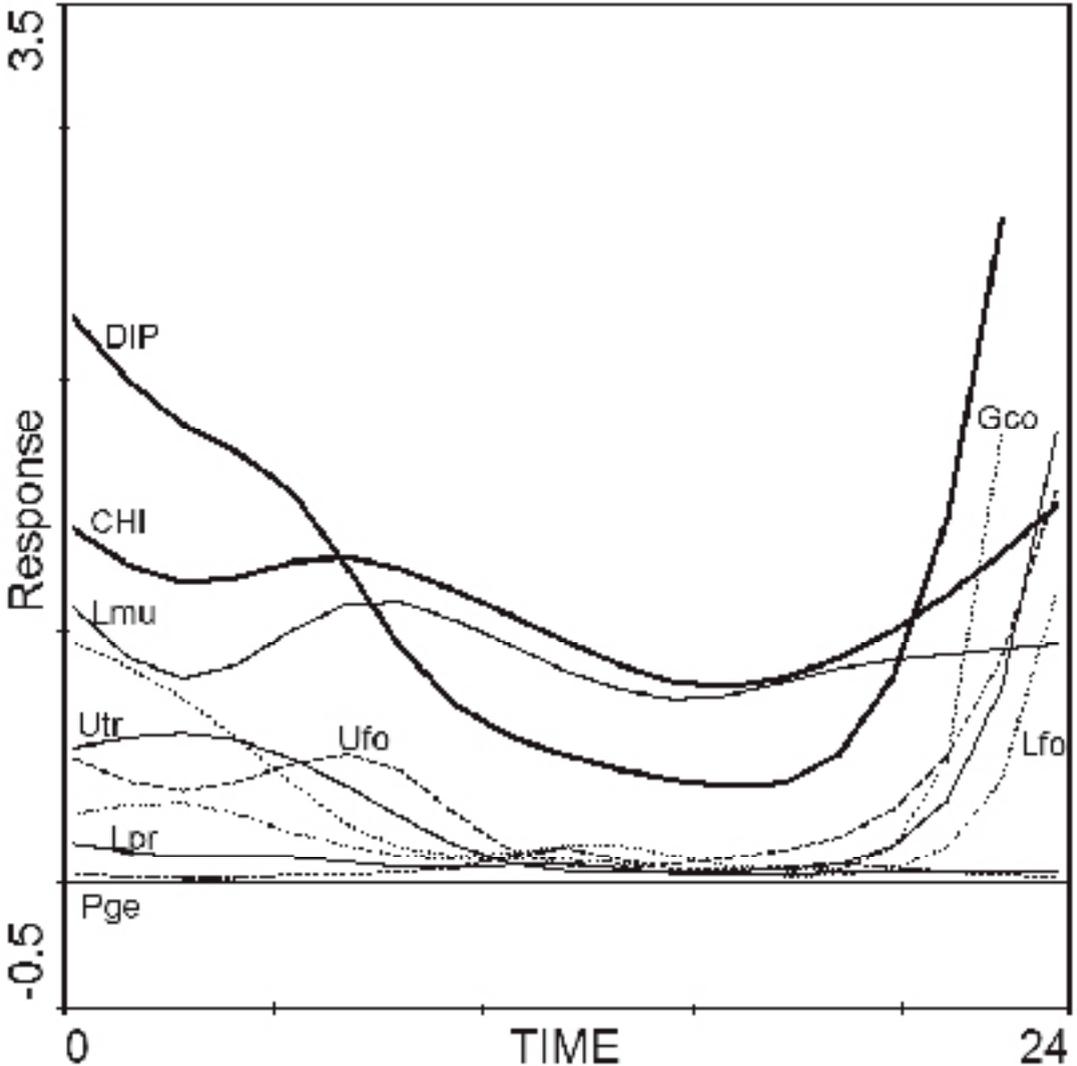
Figure 3. Response of epigeic activity of dominant myriapod species to day-time (GAM). For significance of model for individual species see Table 3. Abbreviations see Figure 1.

RESULTS

Almost 12.000 specimens of the epigeic macrofauna were trapped. Myriapoda represented 8 % of the total catch. Seven species of centipedes (Chilopoda) and 11 species of millipedes (Diplopoda) were recorded totally. Dominant species were the centipede *Lithobius mutabilis,* and the millipedes *Glomeris connexa, Unciger foetidus,* and *Unciger transsilvanicus*.

Although the epigeic macrofauna as a total did not show differences between night and day time, the highest epigeic activity of the myriapods was during night, from 18 to 6 o'clock approximately. This pattern of diurnal activity was the same for centipedes as well as millipedes, for the forest as well as the clear-cut area and for spring as well as autumn (compare Tables 1 and 2). Almost all species showed this pattern except *Polyzonium germanicum*, which was active during the whole day without any evident peak in activity (Table 1). In spring, *Leptoiulus proximus* and *U. foetidus* showed tendency to be active during the light-period too.

Beside this main pattern, there were observed differences between localities and seasons. Higher epigeic activity was evident during spring on the clear-cut area, while higher epigeic activity was showed during autumn in the forest. This difference was probably due to different temperature regime. During late spring, the temperature was higher in the clear-cut area than in the forest during whole day. On the other hand the nights were warmer in forest in the autumn (Figure 1). This aroused high epigeic activity of *L. mutabilis, Lithobius forficatus,* and *G. connexa* in the clear-cut area during spring. In the Canonical Correspond Analysis, all tested factors (locality, day-time, date and temperature) were significant. A similar effect of season (DATE) and locality (clear-cut area) is evident from CCA too (Figure 2). Models for individual, dominant species showed that day-time is an important factor influencing epigeic activity of *L. forcifatus, G. connexa,* both species of the genus *Unciger*, and the entire millipede community (Figure 3, Table 3). *L. forficatus* and *U. transsilvanicus* were the most active species at 3 A.M., whereas *U. foetidus* had a peak of activity later, at 6.30 A.M. *G. connexa* and the entire millipede community were most active around midnight.

Beside this, another model showed that knowledge of temperature is a useful predicting tool for epigeic activity of *U. transsilvanicus, P. germanicum* and the entire millipede community (Figure 4, Table 4). From that model it is evident that *P. germanicum* was more active

Table 3. Significance of day-time factor to prediction of epigeic activity of dominant myriapod species (GAM).

Species/Group	Deviance	F	p
L. forficatus	75.86	2.64	**0.016819**
L. mutabilis	452.48	1.04	0.398784
Chilopoda	618.28	1.17	0.320182
G. connexa	383.22	5.89	**0.000008**
L. proximus	40.41	1.07	0.380031
U. foetidus	169.49	3.03	**0.007005**
U. transsilvanicus	224.35	3.84	**0.001097**
P. germanicum	16.78	1.82	0.095785
Diplopoda	744.03	11.68	**< 1.0e-6**

in higher temperature and *U. transsilvanicus* in lower temperatures. Other species showed peak of epigeic activity somewhere between these species. This model created unimodal curves for several species. Only *L. mutabilis* and *G. connexa* had a peak around 14 °C. *U. foetidus* was the most active at temperatures of 5 °C or lower.

DISCUSSION

Almost all the studied species showed epigeic activity during night and the dusk period, several species also showed a low activity during full light (*L. mutabilis, G. connexa, Haplogona oculodistincta, U. foetidus* and *L. proximus* in late spring) and one species was active during whole day without evident peak (*P. germanicum*). The higher activity of myriapods during dark period
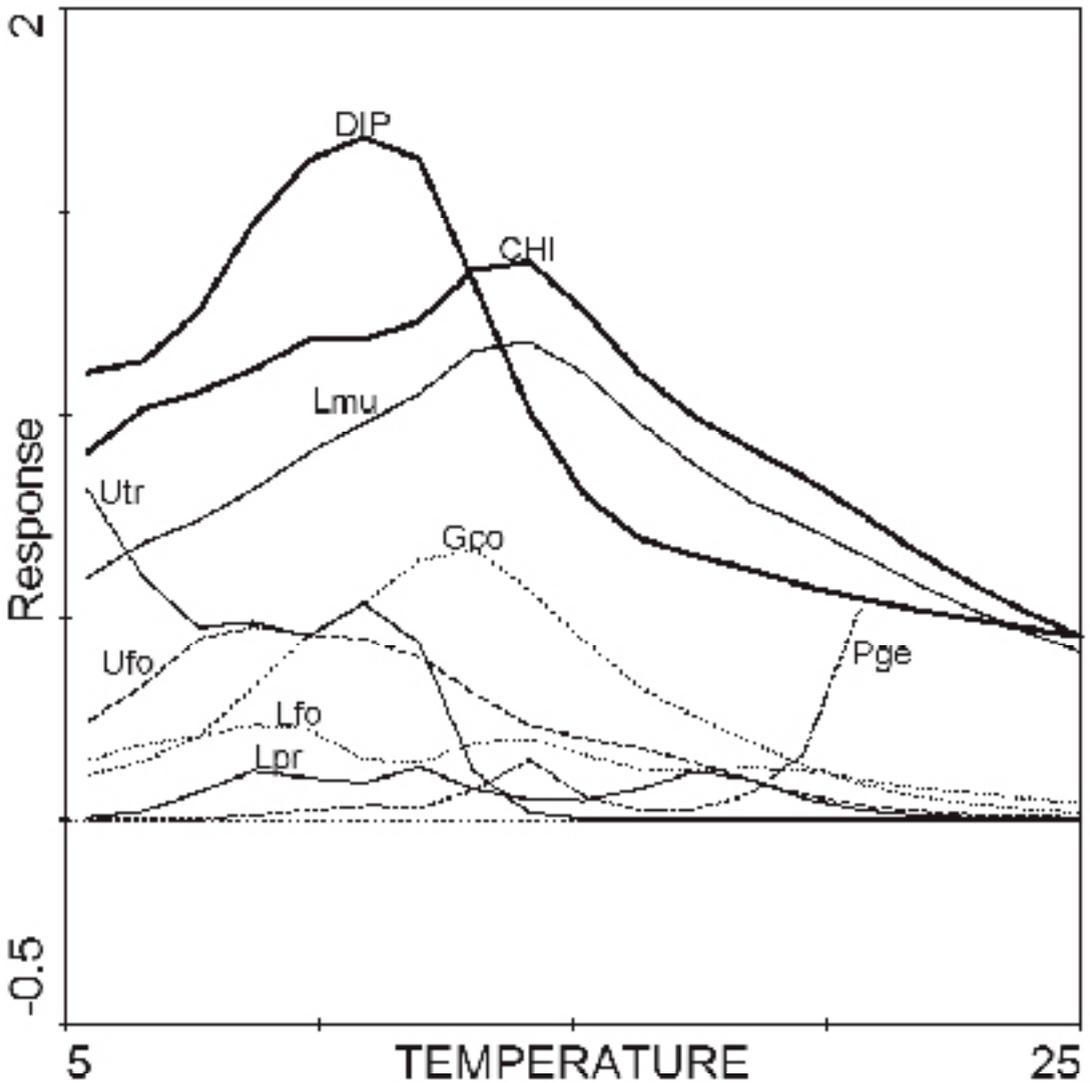
Figure 4. Response of epigeic activity of dominant myriapod species to temperature (GAM). For significance of model for individual species see Table 4. Abbreviations see Figure 1.

has been found by many researchers (Cloudsley-Thompson 1951, Banerjee 1969, Dondale et al. 1972, Koilraj et al. 1999, 2000). Dondale et al. (1972) showed that millipedes are stricter in their night activity than centipedes. Similarly, in our observation, time was a significant predictor of activity for the millipede community only. Time was a significant predictor for the three most abundant species of millipedes. As to the centipedes, the pattern of activity for *L. forficatus* was significantly affected by day-time. It wasn't possible find this relation for the most dominant species, *L. mutabilis*.

Prolongation of period of activity of some millipedes in summer has been described by several authors (Banerjee 1969, Dondale et al. 1972), and is probably caused by their higher resistance to desiccation in the summer months (Perttunen 1953). This can be the mechanism that enabled an activity of *G. connexa, H. oculodostincta, U. foetidus* and *L. proximus* in late spring 2004 with relatively warm weather. This is in accordance with our experiences from the field. We repeatedly found several specimens of *Glomeris* on paths or similar exposed surfaces in the direct sunlight on hot summer days. We also found a significant correlation between temperature and epigeic activity of *U. transsilvanicus, P. germanicum* and the total millipede community. Both these species

of millipedes had unimodal curve of dependence of temperature and activity with a peak on the edge of the temperature span. *U. transsilvanicus* seems to be more active at lower temperatures whereas *P. germanicum* shows activities at higher temperatures (Figure 4). Although Banerjee (1967) found a relatively good correlation between temperature and activity in millipedes, this can be caused by differences in development. *P. germanicum* is spring active (from end of March), with egg laying during May-June (Lokschina 1969). *U. transsilvanicus*, has its main peak of epigeic activity in September, and a smaller one in April (Ožanová 2001). Since our project only covered parts of the year the patterns of activity for these species here shown, can be biased.

Generally, the millipedes showed a higher affinity to the dark phase of the day than did centipedes. This is in accordance with previous researches in this field. For some species, temperature can influence epigeic activity too.

Table 4. Significance of temperature factor to prediction of epigeic activity of dominant myriapod species (GAM).

Species/Group	Deviance	F	p
L. forficatus	78.13	0.834	0.457669
L. mutabilis	450.80	1.26	0.273524
Chilopoda	622.46	0.766	0.404730
G. connexa	410.38	1.56	0.157943
L. proximus	40.58	0.820	0.446732
U. foetidus	173.79	1.49	0.183428
U. transsilvanicus	222.55	4.34	**0.000330**
P. germanicum	16.12	4.31	**0.000360**
Diplopoda	854.30	2.46	**0.024764**

time. We would also like to acknowledge our colleagues Adam Véle and Emil Tkadlec for their help with the statistical analyses.

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Studies on millipede assemblages (Myriapoda, Diplopoda) as influenced by habitat qualities of afforested mine sites

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Voigtländer, K. & Balkenhol, B. 2006. Studies on millipede assemblages (Myriapoda, Diplopoda) as influenced by habitat qualities of afforested mine sites. Norw. J. Entomol. 53, 345-360.

Post-mining areas are suitable for studies on the development of fauna in the form of an immense outdoor experiment. In the present study, colonization by millipedes was studied by pitfall-traps in the German brown-coal open-cast mining districts Cottbus (Brandenburg, Lower Lusatia) and Berzdorf (Saxony, Upper Lusatia). The investigations took place in sites with different substrata, melioration and (re-) cultivation techniques. Eleven forests with different vegetation on mine sites, as well as five forests on undisturbed soil were investigated. Millipede colonization, species inventory, activity-based abundance, and dominance were used as evaluation criteria. Faunistic similarities were evaluated using the Wainstein-index. The colonization process was mainly influenced by soil quality of the spoil heap. Loamy soils accelerated the development of millipede assemblages. Introducing industrial ash (Koyne, Lower Lusatia) had a negative effect. Sites afforested with "hard leaf" deciduous (*Quercus*) or coniferous trees (*Pinus*) showed more millipede species on humic soils (Pleistocene in Berzdorf) than those on sandy, humus-poor soils (Tertiary in Cottbus). No differences were found between influences of indigenous *Quercus petraea* forests and of neophytic *Quercus rubra* forests on the number of millipede species, activity density or dominance structure of millipede assemblages.
Millipede species richness and activity density increased with site age in correspondence with the soil development only on loamy mine sites (Pleistocene Berzdorf district). In contrast, on the sandy mine sites of the Tertiary open cast districts (Cottbus), millipede assemblages did not show differences corresponding to site age, but were generally poor in species, like those of investigated pine forests on undisturbed sandy soils. In nutrient-poor mine sites with absence or poor presence of earthworms, millipedes became very important by taking over the function of litter decomposition. The study shows that the development of millipede assemblages gives a sound indication of the soil biological activity of wooded sites.

Keywords: *Quercus rubra*, neophyte, post-mining area, oak forests, deciduous forests, pine forests

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INTRODUCTION

For more than 50 years large areas in mid and eastern Germany were used for open-cast mining of lignite leaving behind many square kilometers of spoil heaps. The waste substrate is initially free from soil organisms and biogenic soil structures. Reclaimed land is the starting point for self-sustaining, naturally developing ecosystems and offers the possibility for studies on colonization processes in a large "outdoor experiment" (Dunger 1968, 1998, Bradshaw & Hüttl 2001, Bell 2001). In the ideal situation, this can occur by natural succession with human influence being restricted to process protection (Felinks & Wiegleb 1998). Normally however, man does not allow free succession, but applies a complex management program. The main aim of reclamation is the

creation of sustainable fertility, indicated by an increase in species richness, sequential interaction with soil development and soil fertility (Brüning et al. 1965, Bradshaw & Chadwick 1980, Bairlein et al. 1989). Detailed knowledge of the development of the soil fauna helps to evaluate the results of reclamation.

Soil organisms have been used as indicators of the developmental stages of soils and of humus conditions. Quantitative methods (e.g. density, activity abundance, biomass, decomposition rates) have enabled the establishment of a reference series for the Berzdorf mining district in Upper Lusatia (Dunger 2004, Dunger & Voigtländer 2002, 2005) that can be compared with other spoil heaps. Continuing this method, comparisons of specific mine sites with sites on indigenous soils were made as well using millipedes as a test group.

In particular, this report focuses on the diplopod fauna of red oak (*Quercus rubra*) afforested sites. This tree species represents a non-indigenous element within the German flora but is often used for plantations on nutrient-poor soils. Investigations on the influence of this tree species on the soil animal assemblages (e.g. of millipedes) has not previously been done. The differences in structural parameters of the diplopod fauna between such neophytic forests and those with indigenous tree species (*Quercus petraea*) were studied here.

STUDY PERIOD AND SITES

Berzdorf mining district (Upper Lusatia)
In the "Upper Lusatian lignite mining district" near Berzdorf investigations by the State Museum of Natural History Görlitz (Dunger 1968, Dunger et al. 2001) ran during several investigation periods (yearly studies in 1960-65, 1976-77, 1984-86, 1996-99). Three sites afforested with deciduous trees (*Alnus, Populus* and *Robinia*) and one site with *Pinus sylvestris* were evaluated here.

Table 1 lists the mine sites investigated with periods of observation and important characteristics. Site designation follows the principle: district – tree type – age of afforestation, numbers in parentheses: unforested sites.

In Berzdorf (berz-dec-10; 34; 46 and berz-pin-10; 34; 46), "real time series" were studied over at least 40 years. At berz-pin there was a special situation: after afforestation with coniferous trees, a stepwise change to a mixed forest occurred after approximately 30 years by the natural growth of deciduous trees (especially *Acer pseudoplatanus*).

In combination, shorter "false time series" (chronosequences with up to three-years-observation) took place in berz-dec-02, berz-dec-04 and berz-dec-22. The latter site was strongly influenced by water and wind erosion so it was more open for a longer period.

Cottbus mining district (Lower Lusatia)
In the Lower Lusatian lignite mining district near Cottbus six mine sites afforested with *Quercus rubra* and *Pinus* between two and 52 years old were studied (Table 1).

The *Q. rubra* afforestation süd-rot-02 was covered with a sown grass layer which built up a thick matt of grass roots. All the other *Q. rubra* forests were characterized by a poorly developed herb layer (Table 2). The litter layer of forest sites varied in depth between 3-4 cm in April and 2 cm in August. All sites on the spoil heaps were characterized by intensive rooted organic layer and no bioturbation.

As a comparison with the forests, two unforested mine sites (koy-cal-50, koy-het-50) were also investigated.

Sites on native soils
In the Neiße Valley between Ostritz and Hirschfelde (Upper Lusatia) the soil fauna of a natural Arunco-Aceretum on loamy soils was investigated in 1962 and 1988 (Dunger et al. 1972, Voigtländer & Dunger 1992).

Table 1. Characterisation of the investigation sites. Soil dates after Dunger (1968), Dunger et al. (2001), BTU Cottbus. Site designation follows the principle: district – tree type – age of afforestation (marked bold). Numbers in parentheses: unforested sites.

süd-rot-02 – Schlabendorf-Süd, „Roteiche" red oak *Quercus rubra*, 2 years old
nor-rot-20 – Schlabendorf-Nord, „Roteiche" red oak *Quercus rubra*, 20 years old
koy-rot-20, 29 – Koyne, „Roteiche" red oak *Quercus rubra*, two sites 20 and 29 years old
koy-het-(50) – Koyne, heterogeneous, unforested
koy-cal-(50) – Koyne, Calamagrostis, unforested
ple-rot-40 – Plessa, Roteiche" red oak *Quercus rubra*, 40 years old
alt-rot-40 – Altsorgefeld, Roteiche" red oak *Quercus rubra*, 40 years old
alt-tra-gew – Altsorgefeld, "Traubeneiche" *Quercus petraea*, „gewachsen" native soil
alt-tra-25 – Altsorgefeld, "Traubeneiche" *Quercus petraea*, 25 years old
dom-rot-37 – Domsdorf, "Roteiche" red oak *Quercus rubra*, 37 years old
dom-pin-37 – Domsdorf, *Pinus sylvestris*, 37 years old
berz-dec-02, 04, 22 – Berzdorf, deciduous wood, **three sites** 2, 4 and 22 years old
berz-dec-11, 34, 46 – Berzdorf, deciduous wood, one site 11, 34 and 46 years old
berz-pin-10, 14, 34, 46 – Berzdorf, *Pinus sylvestris*, one site 10, 14, 34 and 46 years old
nv-dec-gew – Neiße valley, deciduous wood, "gewachsen" native soil and wood
dh-pin-35 – Dübener Heide, *Pinus sylvestris*, 35 years old

site designation	district	years after afforestation	soil	afforestation / vegetation	investigation period
Sites at Lower Lusatia					
süd-rot-02	Schlabendorf-Süd	2	unchanged sandy to loamy heaping substrate	*Quercus rubra, sown* of *Festuca* and *Poa angustifolia*	2001-2003
nor-rot-20	Schlabendorf-Nord	20	as koy-rot-20, but without melioration by ash	*Quercus rubra*	2001-2003
koy-rot-20	Koyne	20	sandy to loamy Tertiary substrate, high content of lignite and pyrite, meliorated by power station ash, 2 cm humus layer, "Kippregosol"		
koy-rot-29	Koyne	29	as koy-rot-20	*Quercus rubra*	2001-2003
koy-het-(50)	Koyne	not afforested	as koy-rot-20	*Quercus rubra*	2001-2003
koy-cal-(50)	Koyne	not afforested	as koy-rot-20	Koelerio-Corynephoretum *Calamagrostis epigejos-association*	2001-2003
ple-rot-40	Plessa	40	sandy to loamy Tertiary substrate and silt, intensive rooted humus layer	*Quercus rubra*	2001-2003

Table 1. Continued

site designation	district	years after afforestation	soil	afforestation / vegetation	investigation period
alt-rot-40	Altsorgefeld	40	native sandy brown soil, mor-like moder humus with poor humus layer	*Quercus rubra*	2001-2003
alt-tra-gew	Altsorgefeld	very old	native sandy brown soil, peat-like intensive rooted raw humus (5 cm)	*Quercus petraea* dominated mixed forest	2001-2003
alt-tra-25	Altsorgefeld	25	native sandy brown soil, 8 cm humus layer	*Quercus petraea*	2001-2003
dom-rot-37	Domsdorf	37	as koy-rot-20, without ectohumus	*Quercus rubra*, small amount of *Tilia cordata*	1997-1998
dom-pin-37	Domsdorf	37	as koy-rot-20, moder humus (5 cm)	*Pinus sylvestris*	1997-1998
Sites at Upper Lusatia					
berz-dec-02	Berzdorf	2	loamy, mainly Pleistocene substrate, low to medium content of lignite and pyrite, no soil cover, melioration: fertilisation, liming	*Alnus, Populus, Betula, Acer*	1962
berz-dec-04	Berzdorf	4	as berz-dec-02	*Alnus, Populus, Robinia,Lupinus*	1962
berz-dec-22	Berzdorf	22	as berz-dec-02	strongly eroded slope in the border area of berz-dec-10 to 46; *Alnus, Populus*	1976
berz-dec-10, 34, 46	Berzdorf	10, 34, 46,	as berz-dec-02	*Alnus, Populus, Robinia*	1962-1998
berz-pin-10, 14, 34, 46	Berzdorf	10, 14, 34, 46	as berz-dec-02	*Pinus sylvestris* becoming mixed forest by natural growth of deciduous trees	1962-1998
nv-dec-gew	Neiße Valley	-	native loess-loamy soil with well developed humus layer	Arunco-Aceretum	1962, 1988
dh-pin-35	Dübener Heide (Bitterfeld)	appr. 35	native podzol-brown soil, moder-like raw humus (6 cm)	*Pinus sylvestris*	1977, 1978

Table 2. Coverage percentage of vegetation cover at the investigation sites. For explanation of site abbreviations see Table 1.

	dh-pin-35	nv-dec-gew	berz-pin-46	berz-pin-34	berz-pin-10	berz-dec-46	berz-dec-34	berz-dec-22	berz-dec-10	berz-dec-04	berz-dec-02	dom-pin37	dom-rot-37	alt-tra-gew	alt-tra-25	alt-rot-40	ple-rot-40	koy-rot-29	koy-rot-20	nor-rot-20	sud-rot-02	koy-het-(50)	koy-cal-(50)
tree stratum	90	60	60	60	0	70	70	30	0	0	0			77	78	78	80	81	83	84	0	15	0
shrub layer	0	35	40	50	70	10	50	0	100	35	0	no data	no data	6	0	11	0	0	0	4	0.8	23	8
herbaceous plant layer consists of	90	90	80	80	5	90	85	45	85	60	0			7	20	5	2	2	0	4	54.3	5	67.6
herbs	-	-	-	-	-	-	-	-	-	-	-			0	17	0	0	0	0	0	0.3	2	7
grasses	-	-	-	-	-	-	-	-	-	-	-			3	2	0	0	0	0	3	54	2	60
woody plants juv.	-	-	-	-	-	-	-	-	-	-	-			5	1	5	2	2	0	1	0	1	0.6

Near Altsorgefeld (Lower Lusatia), three sites on native sandy brown soil, afforested with *Quercus rubra* and *Quercus petraea*, were studied. Alt-rot-40 had a large amount of dead wood on the ground.

A young pine forest near Bitterfeld/Leipzig (Middle Germany) on Pleistocene sandy soil was investigated in 1977/78 and was selected for comparison with the conifer forests on the spoil heaps.

METHODS

Diplopod populations were studied using pitfall traps. Due to the long investigation period and different projects there were variations in the methods used.

At Berzdorf mine sites there were nine traps per site, each filled with 4 % formalin and operated in 1961, 1962 and 1965 for the whole year and in 1985, 1986, 1997 and 1998 for four to eight occasions in spring and autumn. They were emptied every two weeks.

In Cottbus (mine sites and sites on native soils) six traps per site were used, each filled with ethylene glycol and operating from July to October in 2001 and March 2002 to July 2003. The traps were emptied every two weeks during the vegetation period and every four weeks during the winter months. To get well-fixed material for microscopic investigations, one trap filled with 4 % formalin was set in parallel. As a secondary effect, the influence of conservation fluid on activity abundance could be observed.

In the Neiße Valley data were obtained from a spring and autumn series in 1988 and over the whole year 1989. 10 pitfall traps (with 4 % formalin) were used.

In the pine forest of Dübener Heide, eight pitfall traps per site were filled with 4 % formalin and operated from April to October in 1977 and 1978. They were emptied every two weeks.

Additional information concerning soil fauna was gained from area-samples, macro-cores, and soil core samples.

Because the differences in trapping methods, investigation periods and loss of some traps, the numbers of trapped individuals needed to be standardized. Therefore, the numbers were expressed as individuals per trap per week. Dominance was calculated according to Engelmann (1978). Faunistical similarities of the assemblages were evaluated using the Wainstein-similarity-index. UPGMA was used as a clustering method.

RESULTS

Species number and activity abundance
From the 19 sites investigated a total of 3560 individuals were collected.

At the mine sites in Lower Lusatia (Cottbus mining district) one to five species per site were recorded. Most of the species were found in the oldest *Q. rubra* forests ple-rot-40 and alt-rot-40 (Figure 1). Only one or two species were recorded from open, young afforested and ash-meliorated sites. The first immigration of a millipede species, *Polydesmus inconstans* Latzel, 1884, was recorded from the youngest afforested site süd-rot-02 at an age of two years.

Species number increased from zero to eight with increasing afforestation age in deciduous as well as pine afforestations in the Berzdorf mining district. Figure 1 shows only five species at site berz-dec-46, captured by pitfall trapping. Including all other investigation methods (area-samples, macro-cores, and soil core samples), nine species were found. The natural Arunco-Aceretum in the Neiße valley has a normal to rich diversity with 15 species, whereas only three or four species inhabit the studied *Quercus* (alt-
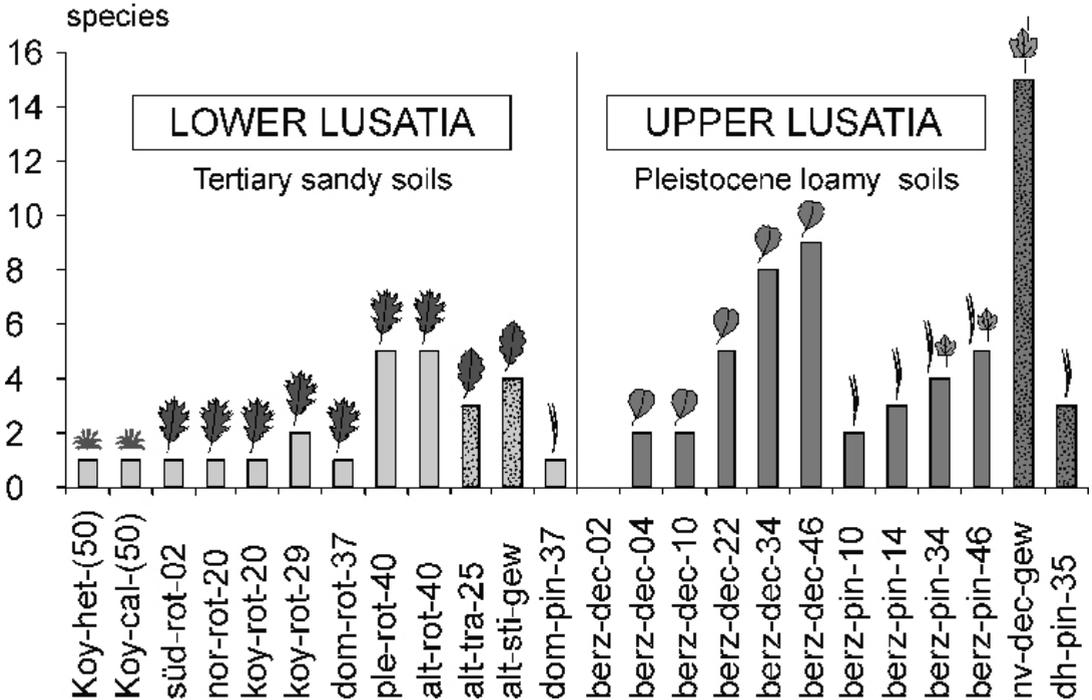
Figure 1. Species numbers from investigation sites in Lower and Upper Lusatia and Middle Germany. For explanation of site abbreviations see Table 1

tra-25, alt-tra-gew) and *Pinus* forests (dh-pin-35) on native, but poor sandy soils.

The influence of nutrient quality became especially evident in older and native sites: *Quercus*- and other deciduous forest show more species than pine forests with poorly degradable needle litter. Differences between indigenous *Quercus petraea* and neophytic *Quercus rubra* forests were not found, whereas forests with "soft" deciduous leaf litter (such as *Alnus* or *Populus*) were inhabited by more species than *Quercus* forests with "hard" leaf litter.

The activity abundance of millipedes also depends on nutrient quality (Figure 2). The older deciduous forest sites at Berzdorf exhibit the highest densities, followed by oak forests (independent of the *Quercus* species) and pine forests.

The activity abundance showed a clear difference between Lower and Upper Lusatia. High activity abundances were reached in the older

afforestations with deciduous trees in Berzdorf. In these four sites the abundance is clearly correlated with the age of afforestation in both afforestation types. The activity is much lower in pine forests than in deciduous forests of this area but much more than in pine forests of Lower Lusatia. No influence of age and forest type or soil could be seen in the Cottbus district with sandy soils.

The site berz-dec-46 showed the highest activity abundance (2.4 ind./trap/week) much higher than the native deciduous wood in the Neiße valley. This results from the extremely high abundance of *Glomeris hexasticha* Brandt, 1833, which was recorded for the first time in Berzdorf after 46/47 years.

The activity abundance of millipedes seems to depend also on the conservation fluid used in traps as shown by different trapping types as used in the Cottbus region (see Methods). On the average, the numbers of millipedes trapped in ethylene glycol
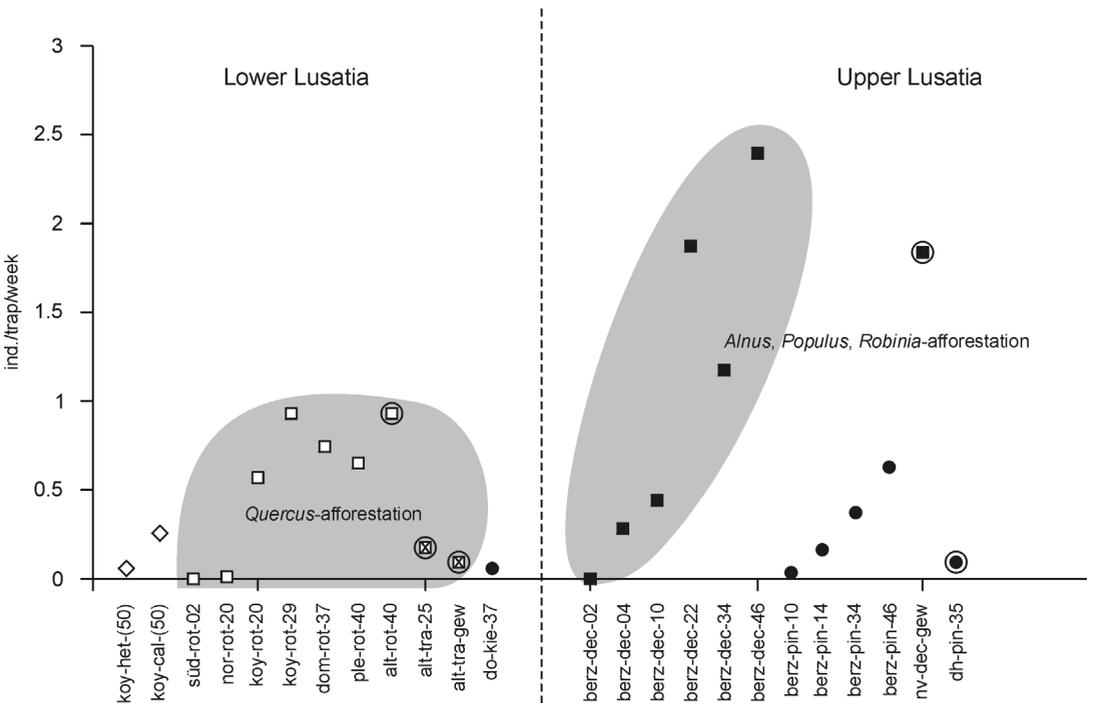
Figure 2. Activity abundance (ind./trap/week) at the mine sites in the brown-coal mining district near Cottbus (Lower Lusatia) in comparison with a mine site near Berzdorf (Upper Lusatia). For explanation of site abbreviations see Table 1

Table 3. Species dominance at the investigation sites in Lower and Upper Lusatia and Middle Germany. Dominance classes according to Engelmann (1978), black – eudominant, dark gray – dominant, light gray – subdominant, white – resident and sub resident. For explanation of site abbreviations see Table 1.

Species	dh-pin-35	nv-dec-gew	berz-pin-46	berz-pin-34	berz-pin-14	berz-pin-11	berz-dec-46	berz-dec-34	berz-dec-22	berz-dec-10	berz-dec-04	bberzbereberz-dec-02	domdom-pin37	dom-rot-37	alt-tra-gew	alt-tra-25	alt-rot-40	ple-rot-40	koy-rot-29	koy-rot-20	nor-rot-20	süd-rot-02	koy-cal-(50)	koy-het-(50)
C. rawlinsii Leach, 1815		0.5						1.1	6.7	13.5	96.6							4.0					100	100
J. scandinavius Latzel, 1884	89.9	18.1	44.1	16.7	33.3	71.4	17.8	8.5	11.0						45.0	90.1	84.0	78.8	99.7	100				
P. denticulatus C.L. Koch, 1847		1.1													42.5	1.4	12.8	0.3	0.3					
P. fuscus (Am Stein, 1857)	6.7	0.2						1.1							10.0	8.5	2.6	0.3						
N. kochii (Gervais, 1847)								20.2	3.3															
P. inconstans Latzel, 1884		0.7		6.7	33.3	28.6		12.8	56.7	86.5	3.4				2.5									
B. superus Latzel, 1884									23.3													100		
O. sabulosus (Linné, 1758)													100	100				16.5			100			
N. variecorne (C.L. Koch, 1847)																	0.3							
P. germanicum Brandt, 1831		0.2	5.9	23.3			4.3	19.2									0.3							
P. complanatus (Linné, 1761)		4.8																						
G. hexasticha Brandt, 1833		0.2	45.6				65.6																	
G. connexa C.L. Koch, 1847					3.3																			

Table 3. Continued

Species											
U. foetidus (C.L. Koch, 1838)	18.1	3.1						53.3	1.5	5.9	
M. voigti (Verhoeff, 1899)	18.1	9.3							2.9	0.3	
S. stigmatosum (Eichwald, 1830)										52.7	
M. bosniense (Verhoeff, 1897)										0.7	
C. caroli Rothenbühler, 1900										3.6	
M. germanicum (Verhoeff, 1892)										8.1	
M. projectum kochi (Verhoeff, 1907)										0.2	
L. proximus (Němec, 1896)											3.4

Legend:
- < 1.0 %
- 1.0 - 3.1 %
- 3.2 - 9.9 %
- 10 - 31.9 %
- >32%

(0.37 ind./trap/week) is a decimal power higher than in formalin (0.03 ind./trap/week).

Species spectrum and dominance structure

The current investigations recorded a total of 21 millipede species. The species spectrum differs clearly between the Upper and Lower Lusatian sites (Table 3). Six species, *Nopoiulus kochii* (Gervais, 1847), *Brachydesmus superus* Latzel, 1884, *Glomeris hexasticha, GLomeris connexa* C.L. Koch, 1847, *Unciger foetidus* (C.L. Koch, 1838) and *Melogona voigti* (Verhoeff, 1899) occurred only on investigated mine sites in Upper Lusatia and six (mostly woodland) species were only found at Neiße valley. Two species, *Ommatoiulus sabulosus* (Linné, 1758) (a "sand animal") and *Nemasoma variecorne* (C.L. Koch, 1847) were found only in Lower Lusatia.

The dominance structure of coenoses in unforested sites with two to 37 year old trees is similar in Lower Lusatia, but differs clearly to that at Upper Lusatian sites (Table 3). With the exception of the young *Q. rubra* sites (süd-rot-02 and nor-rot-20), where *Polydesmus inconstans* or *Ommatoiulus sabulosus* were the only species found, *Julus scandinavius* Latzel, 1884 dominated the species spectrum completely. At koy-het-50, koy-cal-50 and koy-rot-20, it was the only species found. In Upper Lusatian sites this species plays an important role only in berz-pin-46, after *G. hexasticha*.

In Berzdorf as well as in Cottbus mine sites, there was a well balanced dominance structure, related to the age of deciduous afforestation. However, no influence of native/technical soils and *Q. petraea/ rubra* on the dominance structure could be established. The dominance structure at Berzdorf sites with "soft" deciduous forests is much more balanced, than in "hard" needle or oak forests.

Similarity of the diplopod assemblages

To assess both qualitatively and quantitatively the faunistic similarities of the coenoses, the Wainstein Index was used. This index uses not

only the species similarity, but also the species dominance (dominance similarity) of sites.

The similarities are arranged in three cluster complexes (Figure 3): 1) "Upper Lusatia-complex", 2) "Lower Lusatia-complex" and 3) a group of outsiders (dom-rot-37, dom-pin-37 and nor-rot-20), which show limited similarity, because they have only *O. sabulosus*.

Within the "Upper Lusatia-complex" the oldest afforestations and the native site nv-dec-gew were separated from the younger afforested sites. In this "younger Upper Lusatia-complex", the similarity of süd-rot-02 (Lower Lusatia-complex!) with the relatively young berz-dec-10 site is remarkable. This is caused by the high dominance of *P. inconstans* at these sites.

The "Lower Lusatia-complex" is divided in forest sites (including dh-pin-35 site) and open sites.

Within the Cottbus forest sites it is impossible to build up groups related to the age of the forests or the age of the substrate. The open sites koy-

rot-20, koy-cal 50 and koy het-50 are poor in being inhabited by *J. scandinavius* only.

DISCUSSION

Millipedes colonizing mine sites

Recultivated areas should offer conditions allowing immigration, settlement and the build up of stable populations. For soil animals such as millipedes the determining conditions are humidity, a moderate soil acidity and availability of suitable food (Dunger 2004). The immigration rate depends on the surroundings as well as on the migratory capacity of the species. However, only some species can tolerate the extreme conditions at the beginning of reclamation. For further development the colonization and succession process is influenced by continuously changing additional factors such as increase in plant cover, animal and micro-organism settlement, stabilization of the nutritional regime and water balance with increasing development of (first) an
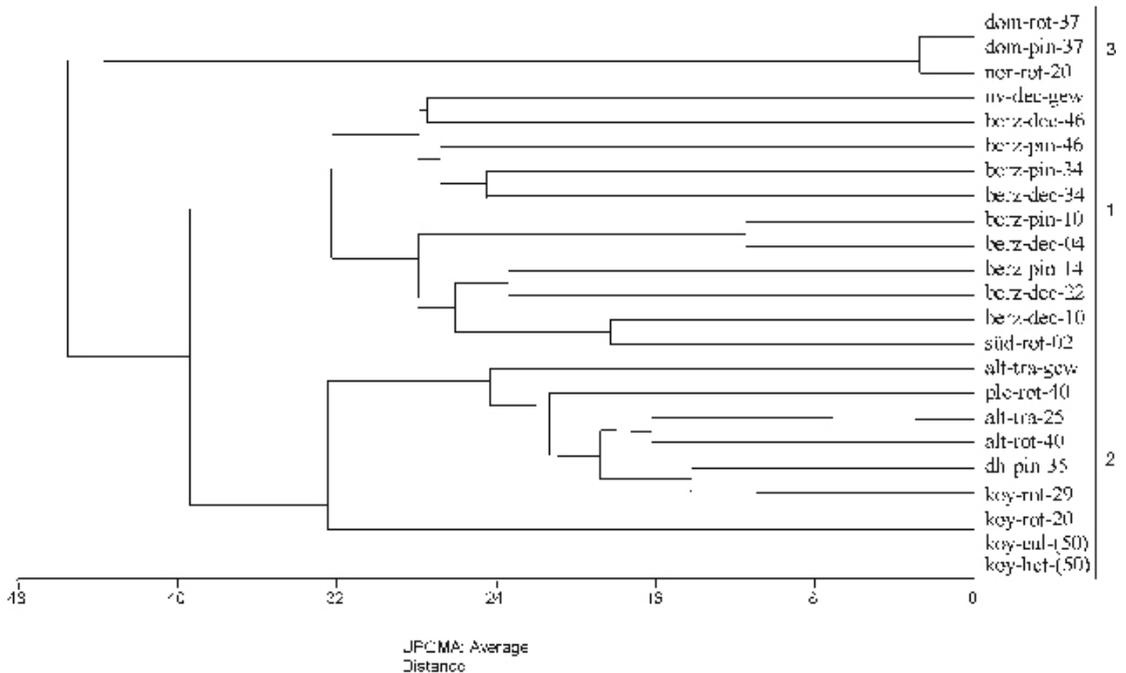
Figure 3. Biocoenotical similarity of the diplopod coenoses according Wainstein. Clustering method: UPGMA. Fir explanation of site abbreviations see Table 1

ectohumus layer and (secondly) the enrichment of endohumus in the A-horizon (Dunger et al. 2004). In many studies it has been shown for different groups of the soil fauna that the improvement of conditions with increasing age of the spoil sites causes an increase in abundance as well as in species diversity (Dunger 1968, Dunger & Voigtländer 1990, Kobel-Lamparski & Lamparski 1995, Tajovský 2001 and in print, Balkenhol et al. 2002).

Reliance on basic food, especially on litter quality

Although most millipedes are non-specialized feeders, leaf litter and dead wood are their main nutrient resources (Schmidt 1952, Dunger 1958, 1962). Grass is exceptionally accepted as their sole food source (Voigtländer 1987). This effectively restricts the settlement at sites such as koy-cal-50 where hardly any herbs other than the reedgrass, *C. epigejos*, occurs. Only *J. scandinavius* has built up stable populations here. Evidence of permanent settlement could be found at these sites in the form of young juveniles. In contrast, the very damaged and nearly vegetation-free site koy-het-50 probably recruited its *J. scandinavius* population only by immigration from surrounding woodland. There is every reason to believe this theory, because we found only adults.

The preference of millipedes to decomposing material is not only correlated with the leaf species but also with the chemical composition (e.g. nitrogen, carbohydrate), moisture, etc. which varies during the decomposition process (Sakwa 1974). Therefore preference for a particular leaf species is also a function of time. Because of their toughness and high tannin content, leaves of different oak species have not been the preferred food as recorded from feeding tests and hence are eaten only after leaching for one or more years at the earliest (Schmidt 1952, Dunger 1958, 1962, Voigtländer 1987). Hence it is not surprising that differences scarcely exist between the old *Quercus rubra* forest sites and those with *Q. petraea*, but very clear differences can be seen between oak and soft deciduous leaf litter.

Pine needle litter is a very unsuitable food for millipedes and most other saprophagous soil animals. They spurn it because of hardness and chemical content. This accounts for the poor diversity and activity density.

Importance of soil quality

The colonization process studied at Lower Lusatian sites (Cottbus) is very slow compared with that in Upper Lusatia (Berzdorf) or in Bohemia (Sokolov) (Dunger & Voigtländer 1990, Tajovský 2001). The 40-year-old *Q. rubra* forests have only five species whereas afforestation with soft leaved trees reaches this diversity after 10 to 20 years in Berzdorf and Sokolov. The epigeic activity increased only little more with the development of a thin humus layer in the oldest *Q. rubra* Lower Lusatian forest. Nevertheless, the activity density on normally acid Tertiary substrate never reached that of the Pleistocene soil (with higher pH-degrees) at the Upper Lusatian sites (Figure 2), nor that of the native sandy soil sites at Altsorgefeld. In general, these results are comparable with that of springtails, proturans and particularly earthworms (Dunger et al. 1997b).

At the other hand, pine forests are generally poor in millipedes because of the acid soil conditions, bad humus quality (raw humus) and bad nutrient quality (see above). As a rule, a species diversity of not more than eight (mostly three dominant) species and an activity on average of 0.05 ind./ trap/ week can be reached (Voigtländer1995 a, b; Weigmann et al. 1989; Wytwer 1992, 2000). Therefore, millipedes are not generally suitable indicators of the quality of coniferous sites.

Invasion capacity

Another major factor in the colonisation of new habitats and older successional stages is the presence of expanding populations in close proximity(Neumann1971,Kobel-Lamparski1989, Scheu 1996, Tajovský 1999, Dauber et al. 2005, Tajovský & Voženílková in print). Colonisation by millipedes takes place mainly through active locomotion (Dunger 1967, 1968, 1998, Dunger & Voigtländer 1990, Wanner et al. 1998). Wind has been suggested as a mechanism of dispersal only for small species or juveniles (Haacker 1968). Dispersal ability varies considerably

between species. Some species are more or less confined to their optimum habitat, e.g. *Enantiulus nanus* (Latzel, 1884) (Voigtländer 1987), whereas others have a marked tendency to wander, e.g. *O. sabulosus, Megaphyllum unilineatum* (C.L. Koch, 1838) and *Tachypodoiulus niger* (Leach, 1815) (Cloudsley-Thompson 1949, Helb 1975, Ćurčić & Makarov 1995, Korsós 1998, Ehrnsberger 2002, Voigtländer 2005).

The behaviour of *P. inconstans*, one of the first colonisers, demonstrates the influence of surroundings at the site süd-rot-02. The species was recorded in the second year after afforestation and this site is surrounded by older afforested sites from which the species could emigrate. In contrast, site berz-dec-02 (also in the second year after afforestation) was situated in amongst equally fresh spoil heaps. The immigration of *P. inconstans i*nto these larger unsettled areas required four years.

Many species have life-cycles and life strategies which allow them to invade new habitats in a very short time (Blower 1969). Parthenogenesis, short life-cycles as well as the phenomenon of periodomorphosis are aspects affecting the invasion ability of millipedes.

Colonisation ability in millipedes

Real pioneer species, those colonizing in the first years after recultivation only, do not exist within millipedes. However, we can distinguish between "early" and "later" colonizers.

Early colonizers

Craspedosoma rawlinsii Leach, 1815 and P. inconstans are known as the first species to immigrate and settle at vegetation free sites (Dunger 1968, Neumann 1971, Dunger & Voigtländer 1990, Dunger et al. 1997a). However, the absence of *C. rawlinsii* is inexplicable at young mine sites in Lower Lusatia (Cottbus). A similar pattern was recorded by Bode (1973) at mine sites in the district of Braunschweig. To understand this phenomenon it must be checked, whether *C. rawlinsii* is an inhabitant of the surroundings of these mine sites.

J. scandinavius occurs in association with the first vegetation cover rarely as soon as one or two years, however 5 to 10 years and during the grass and shrub stage is more usual (Dunger & Voigtländer 1990, Kobel-Lamparski & Lamparski 1995, Tajovský 1999, 2001, Topp et al. 1992, Topp 1998). This species appears at the afforested mine sites in Lower Lusatia (Cottbus) much later (20 years after afforestation) than in the other areas. The species also settles at the open sites where soil was heaped 50 years ago. *O. sabulosus* is a typical member of the fauna of sandy, dry and open sites (e.g. Verhoeff 1928, Haacker 1968, Voigtländer & Düker 2001) and belongs to the first group of colonizers of sites with a suitable heap substrate (Neumann 1971, Tajovský 1999). The species was found at the sites nor-rot-20, ple-rot 40, dom-rot 37 and neighbouring site dom-pin-37 in the Cottbus mining district (sandy soils) only. *O. sabulosus* is known as one of the most active swarming species (Kania & Tracz 2005, Voigtländer 2005). Such wanderings could be observed in 1997 and 2002 in the surrounding areas by the authors. Because of the absence of young juveniles and the low numbers of individuals found at the mine sites it can be considered that *O. sabulosus* possibly entered the study sites from adjacent dry sandy meadows.

Later colonizers

The blaniulid species *Proteroiulus fuscus* (Am Stein, 1857), *N. kochii* and *N. variecorne* usually live under bark, in dead wood and leaf litter with large amount of wood. Such conditions were found in the oldest *Q. rubra* mine sites and in the *Q. petraea* woodland (especially at alt-rot-40) in the Cottbus district and after more than 30 years at Berzdorf mine sites. These species are frequently highly aggregated (Gromysz- Kałkowska & Tracz 1977, Dunger & Voigtländer 1990). They show generally no tendency for high migrating or epigeic activity.

Polydesmus denticulatus is the species with the widest ecological tolerance within the genus *Polydesmus* but prefers cool and humid habitats (e.g. Blower 1985, Spelda 1999). This is consistent with finding the species at the first time

approximately 30 years after the recultivation of mine sites as well as in the *Q. petraea* forest.

CONCLUSIONS

The Tertiary mine sites in Lower Lusatia are nutrient-poor, acidic, almost without humus layer and with a high content of pyrites. The very low water-holding capacity of the soil frequently leading to plants dropping below the permanent wilting point is a typical feature of the spoil heaps of the Cottbus mining district area (Scherzer 2001, Düker 2003). At these sites the decomposition of organic matter and therefore nutrient cycling is impeded both by a reduced biotical production and bad conditions for macrosaprophages (Dunger et al. 1997b). Mine site afforestation with *Q. rubra*, in combination with site melioration using industrial ash, causes very bad conditions for earthworms (Dunger et al. 1997b). In such a situation, millipedes become important for at least a moderate level of litter decomposition and as bioindicators. However, even for this group there is often only one species (*J. scandinavius, O. sabulosus*) inhabiting soils with such impoverished conditions. Sites with a favourable combination of important regeneration factors, such as the Berzdorf mine sites, reach the pre-disturbed situation as early as 50 – 60 years (Dunger et al. 2001). Under more unfavourable conditions (as in Cottbus mining district), development often takes considerably longer (up to or exceeding 100 years) and/or leads to a poorer soil quality (Brüning et al. 1965, Dunger 1969, 1978, Keplin & Hüttl 1999, Wermbter 1999, Frouz et al. 2001, Topp et al. 2001).

A slower development rate at a reduced level is typical of the whole soil fauna at Lower Lusatian sites (Dunger 1978). There, the lumbricid fauna is particularly affected (Dunger et al. 1997b) and so the bioindication of mine site soil conditions may be better using millipedes.

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A soil population of *Glomeris marginata* (Villers, 1789) in a Mediterranean forest (Diplopoda: Glomerida)

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Serra, A., Mateos, E. & Miquel, C. 2006. A soil population of *Glomeris marginata* (Villers, 1789) in a Mediterranean forest (Diplopoda: Glomerida). Norw. J. Entomol. 53, 361-374.

A quantification of density and biomass of soil macroarthropods was conducted in a sclerophyllous forest of Mediterranean climate, consisting mainly of *Quercus ilex* and *Pinus halepensis*. Field sampling was performed during 24 consecutive months in an experimental plot (40 x 40 m) placed at 860 m of altitude in the Parc Natural de Sant Llorenç de Munt (Barcelona, Spain, UTM coordinates 31TDG1411). Three soil horizons were sampled: L/F, H, and A (leaf litter fall, humus, and the first five cm of the mineral layer respectively). A population of *Glomeris marginata* was found among the studied material. It presented a monthly mean density of 40.34 ± 5.79 ind.·m^{-2}, 61.1 % of them corresponding to adult individuals and 38.9 % to anamorphic larvae. The mean value of the sex ratio males: females was 1.33, although the mean monthly density value of males (14.12 ± 1.67 ind·m^{-2}) was not significatively higher than that of the females (10.51 ± 1.60 ind·m-2). Based on 105 individuals at different developmental stages, an estimate of individual biomass was performed. The biomass value (B) as fresh weight in mg was related to the width of the second segment in mm (T2) through B= $0.456 \cdot$ (T2)$^{3.189015}$ (R^2= 0.943, F=1719.4, p< 0.000). Based on this equation, the average individual of the studied population showed a biomass value of 47.9 ± 2.3 mg (fresh weight). The monthly mean population biomass was 1944.1 ± 237.1 mg·m^{-2}, 96.96 % of it corresponding to adult individuals (51.23% for females and 45.73% for males) and 3.03 % to anamorphic larvae. No significant differences were found between adult males and females. *G. marginata* occurred in all of the sampled soil horizons. Significant differences were found between monthly mean densities and biomasses in the different soil horizons. The mean density and biomass values in horizon H (26.65 ± 3.93 ind·m-2; 1300.2 ± 184.6 mg·m^{-2}) were significantly higher than those in A (9.79 ± 2.31 ind·m^{-2}; 379.5 ± 92.0 mg·m^{-2}) and L/F (3.91 ± 0.83 ind·m^{-2}; 264.4 ± 64.7 mg·m^{-2}). The mean density value found in A was significantly higher than that in L/F. The mean value of the Usher coefficient during the 24 months of the study also indicated a preference for horizon H. Horizontally, the values of the Morisita index showed that *G. marginata* forms aggregates in each one of the studied horizons.

Keywords: Diplopoda, ecology, population composition, density, spatial distribution, biomass

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INTRODUCTION

Glomeris marginata (Villers, 1789) is widely distributed across Europe. It is one of the most abundant saprophagous macroarthropods of the organic horizons of the soil, especially in Mediterranean sclerophyllous forests (Bertrand *et al*. 1987, David 1988, Bertrand & Lumaret 1992, David 1995, David *et al*. 1999). It has also been found abundantly in mesoxeric grasslands of Eastern Germany (Voigtländer & Dueker 2001). Several studies show that it is a key species in the processes of decomposition of organic matter due to its high rate of litter consumption (Bocock 1963,

Bertrand *et al*. 1987, David & Gillon 2002) and its relationship with microorganisms (Coûteaux et al. 2002) and earthworms (Bonkowski *et al*. 1998). The quantification of the effect of the activity of *G. marginata* on edaphic processes requires data on density and population biomass as well as on population composition, since different developmental stadia and also the two sexes may show different rates of consumption and assimilation of organic matter (David & Gillon 2002). In this study we present the temporal and spatial distribution of a population of *G. marginata* found in a Mediterranean forest soil. The large number of epimorphic individuals and the large amount of individuals in each larval stadium has allowed us to determine the population composition throughout the sampling period. A correlation algorithm has been determined to estimate an individual's biomass from a

morphometric parameter (width of the second tergite). This algorithm has yielded the biomass of an average individual of the population as well as the biomass of an average individual of each developmental stadium.

METHODOLOGY

Location
The study site is located in the Parc Natural de Sant Llorenç del Munt i Serra de l'Obac, 35 km north-west from Barcelona (Spain) (UTM coordinates 31TDG1411). The study was performed in a sclerophyllous forest consisting mainly of *Quercus ilex* L., 1753 and *Pinus halepensis* Miller, 1768; the most common bush species was *Arbutus unedo* L., 1753. Litter was of the leptomoder type, with a mean pH of 5.88
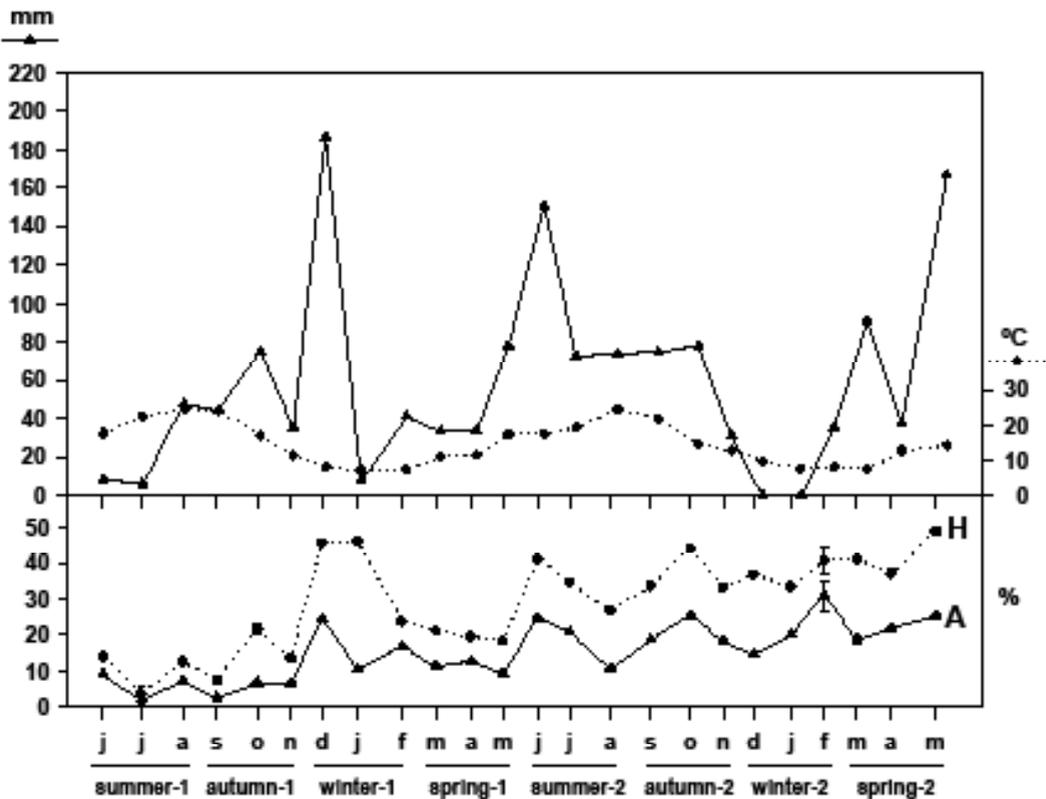
Figure 1. Above: Accumulated monthly rainfall (mm) and mean temperatures (ºC) recorded during the sampling period (data obtained from the climatology station of Terrassa (Barcelona, Spain). Below: Hydric content (%) in horizons H and A calculated as water percentage in weight.

(measured in 1:2.5 water). The experimental site is placed at 870 m above sea level.

Sampling

Samples were obtained in the field during 24 consecutive months from June 1991 to May 1993. In an experimental plot (40 x 40 m), three soil horizons were sampled: L/F, H, and A (leaf litter fall, humus and the first five cm of the mineral layer respectively). A cylindrical corer, 0.36 m in diameter (equivalent to 0.102 m²), was used as the sampling device. Each monthly sample included five sampling units randomly taken. The faunal components were obtained with Berlese-Tullgren devices.

Numerical methods

Data obtained during these 24 months were grouped in two periods, the first one (first year) corresponding to the first 12 months (June 1991 to May 1992) and the second one (second year) to the last 12 (June 1992 to May 1993). Mean population density (ind·m⁻²) and biomass (mg·m⁻²) values were calculated in each soil horizon for each month (n=5), for each weather season (n=15), for each one of the two years (n=12) and for the whole sampling period (n=24).

The differences in density and biomass values between samples were compared by means of parametric Anova, *t*-test, nonparametric Kruskal Wallis (KW) and Mann-Whitney U-test methods. *A posteriori* comparisons were carried out using Student-Newman-Keuls (SNK). Spearman's correlation coefficient was used to relate abiotic parameters (mean monthly air temperature, monthly accumulated rainfall and soil water content in H and A horizons) to population density parameters.

Usher index (Usher, 1975) was used to estimate the vertical distribution of the *G. marginata* population through the soil profile. Arbitrary depth values were designated for each horizon, being 3 for L/F, 2 for H and 1 for A. For each monthly value of this index, a confidence interval of 95% was calculated using bootstrap technique (resampling with replacement, 10^4 iterations with sample size of 5 in each point).

The Morisita dispersion index (Morisita 1962, cited in Elliott 1977) was used to estimate the horizontal distribution of the population.

Climatology

The climate of this region is typically Mediterranean. Figure 1 depicts the total rainfall and mean monthly temperatures recorded during the sampling period. Climatology varied between the first and second years. The second year showed a lower mean temperature, a more abundant rainfall and higher water content in the soil (Table 1) than the first one. It had an exceptionally rainy summer and a very dry winter, while the first year showed a typically Mediterranean climate, including a period of hydric stress in the summer.

RESULTS AND DISCUSSION

Biomass estimates

Fresh weight was obtained for 105 alive specimens of *G. marginata* of different ages and sizes after

Table 1. Mean temperature (ºC), accumulated rainfall (mm) and mean water content (%), for the first year, for the second year and for the 24 months period (Mean). s.e.=standard error.

	Temperature (ºC)	Accumulated rainfall (mm)	Water content horizon H % ± s.e.	Water content horizon A % ± s.e.
1st year	14.99 ± 1.87	596.70	20.68 ± 3.82	9.96 ± 1.76
2nd year	14.18 ± 1.63	812.10	37.65 ± 1.72	20.83 ± 1.54
Mean	14.58	704.40	29.16	15.39

Table 2. Mean monthly density value (ind·m-2) and standard error (s.e.) of *Glomeris marginata* for males and females, anamorphic stadia and total population in the first year (1st, n=12 month), in the second year (2nd, n=12 month) and in the whole sampling period (Mean, n=24 month) for each one of the sampled soil horizons (L/F, H, A) and for the whole of the soil profile (T).

		EPIMORPHIC		ANAMORPHIC				TOTAL
		Males	Females	Stadium II	Stadium III	Stadium IV	Stadium V	
		ind·m⁻² ± s.e	ind·m⁻² ± s.e	ind·m⁻² ± s.e	ind·m⁻² ± s.e	ind·m⁻² ± s.e	ind·m⁻² ± s.e	ind·m⁻² ± s.e
L/F	1st	1.19 ± 0.5	1.39 ± 0.62	0.16 ± 0.2	0.00	0.23 ± 0.2	0.17 ± 0.2	3.14 ± 1.2
	2nd	2.0 ± 0.8	1.18 ± 0.45	0.12 ± 0.1	0.40 ± 0.3	0.62 ± 0.3	0.36 ± 0.3	4.68 ± 1.2
	Mean	1.59 ± 0.5	1.29 ± 0.38	0.14 ± 0.1	0.20 ± 0.2	0.43 ± 0.2	0.26 ± 0.2	3.91 ± 0.8
H	1st	11.09 ± 1.7	7.59 ± 2.30	1.69 ± 1.1	1.84 ± 0.9	4.66 ± 1.5	1.25 ± 1.0	28.1 ± 4.8
	2nd	7.59 ± 1.9	7.05 ± 1.84	2.86 ± 2.2	4.32 ± 1.5	1.81 ± 0.9	1.54 ± 0.7	25.17 ± 6.3
	Mean	9.34 ± 1.3	7.32 ± 1.44	2.3 ± 1.2	3.08 ± 0.9	3.24 ± 0.9	1.40 ± 0.6	26.65 ± 3.9
A	1st	3.59 ± 0.9	2.44 ± 0.86	0.89 ± 0.5	0.70 ± 0.33	1.02 ± 0.4	0.35 ± 0.3	8.99 ± 2.1
	2nd	2.78 ± 1.2	1.37 ± 0.57	2.95 ± 2.3	2.23 ± 1.74	0.62 ± 0.3	0.63 ± 0.4	10.58 ± 4.2
	Mean	3.18 ± 0.7	1.91 ± 0.52	1.92 ± 1.2	1.47 ± 0.9	0.82 ± 0.3	0.49 ± 0.2	9.79 ± 2.3
T	1st	15.88 ± 2.1	11.43 ± 2.4	2.74 ± 2.3	2.54 ± 1.1	5.91 ± 1.9	1.77 ± 1.0	40.27 ± 6.1
	2nd	12.36 ± 2.6	9.6 ± 2.2	5.93 ± 4.5	6.95 ± 2.9	3.05 ± 1.3	2.53 ± 0.9	40.42 ± 10.2
	Mean	14.12 ± 1.7	10.5 ± 1.6	4.34 ± 2.3	4.75 ± 1.6	4.48 ± 1.2	2.15 ± 0.7	40.34 ± 5.8
%		35.00	26.05	10.76	11.77	11.11	5.33	100

having kept them fasting for 48 hours. Width of body segments 1, 2 and 5 was measured for each one of those 105 specimens and regression algorithms of these widths against fresh weight were calculated. The algorithm corresponding to the width of segment 2 (T2) showed the highest regression coefficient. Algorithms based on the widths of segments 1 and 5 were discarded.

Figure 2 shows the regression function between fresh weight of the individual and width of its second body segment. This function is $B = 0.456 \cdot (T2)^{3.189015}$ (n=105, $R^2 = 0.943$, F=1719.4, p< 0.000), where B is the biomass value (fresh weight) in mg and T2 is the width of the second segment in mm. All specimens collected during the study period were measured and their biomasses were inferred through that algorithm.

Population composition

Monthly mean density and biomass of the total population was 40.34 ind·m⁻² (Table 2) and 1944.1 mg·m⁻² (Table 3) respectively. Epimorphic stadia represent 61% of the density and 97% of the biomass, with mean monthly values of 24.6

ind·m^{-2} and 1885 mg·m^{-2}. Anamorphic stadia showed mean monthly values of 15.7 ind·m^{-2} and 59 mg·m^{-2}.

The sex ratio did not vary between the two years of sampling, achieving values of 1.37 and 1.29 respectively. Although it was a ratio above 1, the male population (14.1 ind·m^{-2}) did not show a density value significantly higher than that of the female population (10.5 ind·m-^{2}) along the two study years. These sex ratio values were not very different from those found by Heath *et al*. (1974) in *G. marginata* populations captured with pit-fall traps (sex ratio 1.25). This steadiness in the sex ratio value seems to be differentiating *G. marginata* from other species, such as *G. balcanica* where sex ratio values have been measured between 0.43 and 1.83 (Iatrou & Stamou 1991).

According to David & Gillon (2002), the higher the biomass of an individual is, the higher its rates of consumption and assimilation of organic matter are. These authors found that rates achieved by females were significantly higher that those achieved by males in experiments of consumption of *Quercus ilex* leaves. Similarly, different consumption and assimilation rates between individuals belonging to different developmental stadia could be expected. Because of that, models quantifying the degree of contribution of *G. marginata* to the processes of decomposition of edaphic organic matter must take into account the population composition in terms of developmental stadia or biomass ranks.

Distribution in time

For each one of the soil horizons, no significant differences were found in density (Figure 3) and biomass (Figure 4) values between months, seasons or years. Moreover, Spearman's rank correlation analyses between monthly mean density values in different horizons and abiotic parameters

fresh weight (mg)

$$B = 0.456 * T2^{3.189}$$

width T2 (mm)
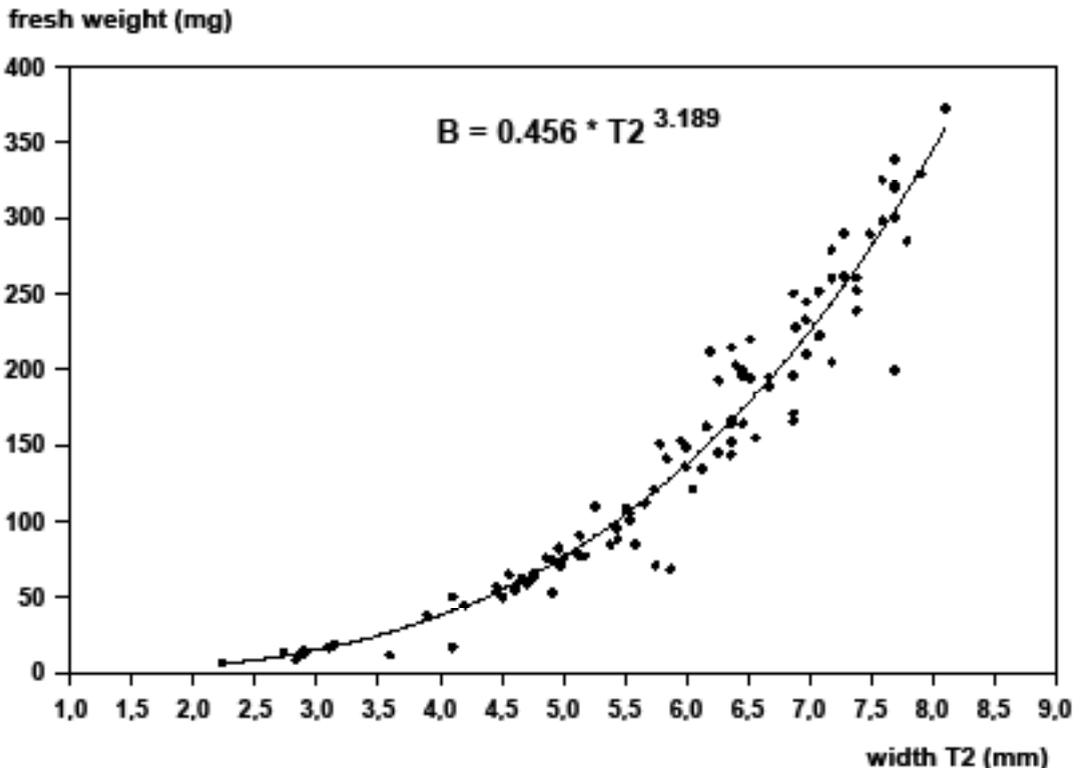
Figure 2. Regression function between individual fresh weight in milligrams and the width in millimetres of the second tergite (T2) of *Glomeris marginata*.
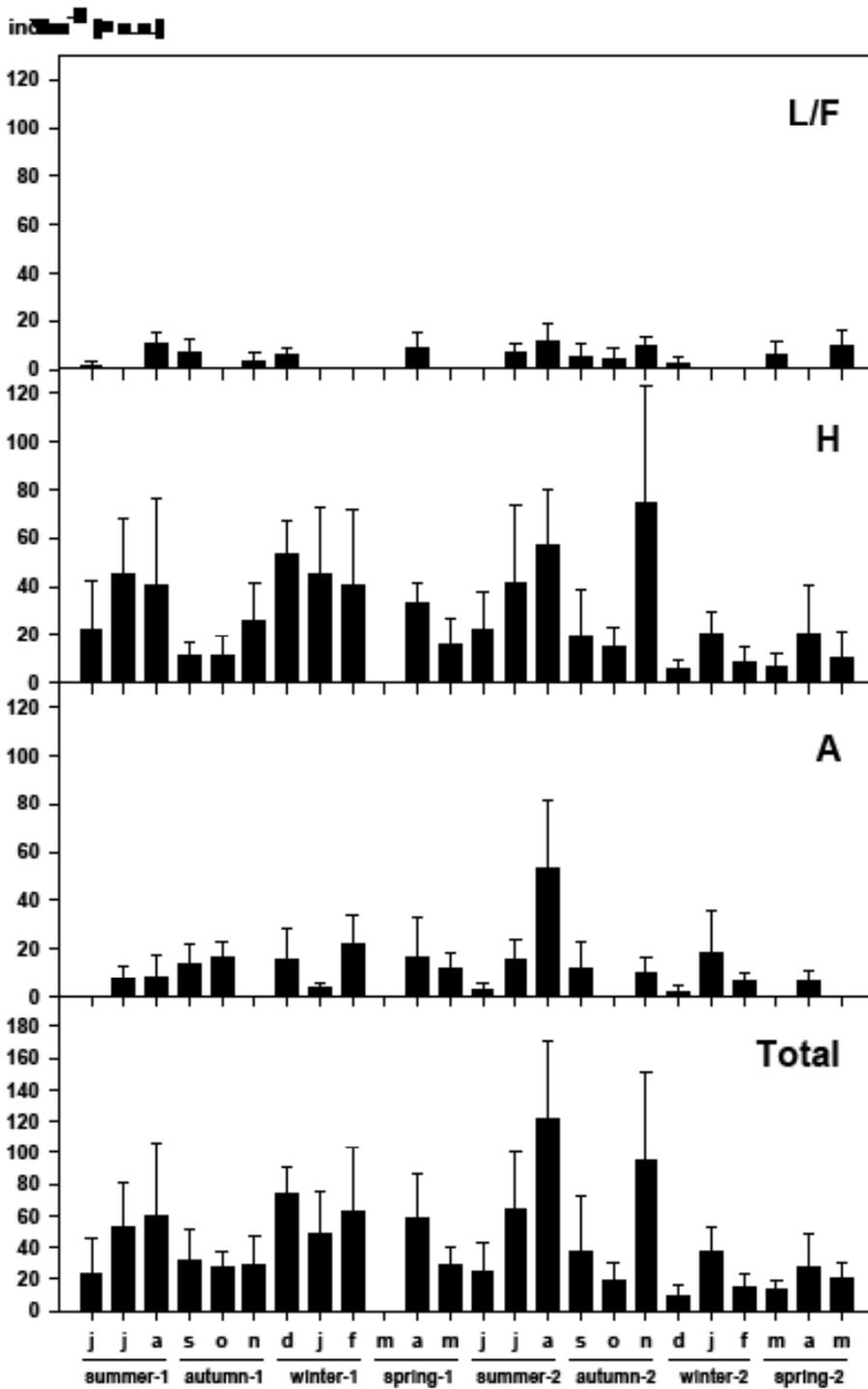
Figure 3. Mean monthly density values (and associated standard errors) showed by the whole of the *Glomeris marginata* population in each one of the soil horizons (L/F, H, A) and in the whole of the soil profile (Total).

Table 3. Mean monthly biomass value (mg·m⁻²) and standard error (s.e.) of *Glomeris marginata* for epimorphic stadia (males and females), anamorphic stadia (stadium II to stadium V) and total population in the first year (1st, n=12 month), in the second year (2nd, n=12 month) and for the whole sampling period (Mean, n=24 month) for each one of the sampled horizons (L/F, H, A) and for the whole of the soil profile (T).

		EPIMORPHIC			ANAMORPHIC			TOTAL
		Males $mg·m^{-2}$ ± s.e	Females $mg·m^{-2}$ ± s.e	Stadium II $mg·m^{-2}$ ± s.e	Stadium III $mg·m^{-2}$ ± s.e	Stadium IV $mg·m^{-2}$ ± s.e	Stadium V $mg·m^{-2}$ ± s.e	$mg·m^{-2}$ ± s.e
L/F	1st	51.2 ± 20.9	152.2 ± 80.4	0.1 ± 0.1	0.00	1.3 ± 1.3	1.6 ± 1.6	206.4 ± 92.2
	2nd	168.2 ± 72.7	146.9 ± 53.7	0.1 ± 0.1	0.8 ± 0.6	3.5 ± 1.9	2.9 ± 2.0	322.4 ± 91.6
	Mean	109.7 ± 38.9	149.5 ± 47.3	0.1 ± 0.1	0.4 ± 0.3	2.4 ± 1.2	2.2 ± 1.2	264.4 ± 64.7
H	1st	661.1 ± 91.0	645.6 ± 198.4	1.1 ± 0.6	3.3 ± 1.7	20.2 ± 6.3	16.7 ± 13.4	1348.5 ± 262.8
	2nd	493.6 ± 105.9	722.8 ± 164.4	2.5 ± 2.0	9.9 ± 3.4	12.2 ± 6.9	10.7 ± 4.1	1251.9 ± 270.1
	Mean	577.6 ± 70.5	684.2 ± 126.3	1.8 ± 1.0	6.6 ± 2.0	16.2 ± 4.6	13.7 ± 6.9	1300.2 ± 184.6
A	1st	208.6 ± 52.3	179.8 ± 75.1	0.6 ± 0.4	3.7 ± 2.7	3.8 ± 1.4	3.6 ± 2.7	400.1 ± 124.0
	2nd	194.9 ± 94.1	144.7 ± 64.5	2.4 ± 1.9	5.3 ± 4.3	3.0 ± 1.6	8.6 ± 4.7	358.9 ± 4.2
	Mean	201.7 ± 52.6	162.3 ± 48.6	1.5 ± 1.0	4.5 ± 2.5	3.4 ± 1.0	6.1 ± 2.7	379.5 ± 92.0
T	1st	921.4 ± 120.1	977.7 ± 258.3	1.8 ± 0.9	7.0 ± 3.0	25.3 ± 8.1	21.9 ± 13.5	1955.1 ± 344.4
	2nd	856.8 ± 147.3	1014.4 ± 201.4	5.1 ± 0.9	16.0 ± 7.0	18.7 ± 8.3	22.2 ± 7.6	1933.2 ± 341.4
	Mean	889.1 ± 93.2	996.0 ± 160.2	3.4 ± 2.0	11.5 ± 3.9	22.0 ± 5.7	22.1 ± 7.6	1944.1 ± 237.1
	%	45.73	51.23	0.17	0.59	1.13	1.14	100

(temperature, rainfall, water content in the soil) showed that no significant differences occurred between mean density values of the *G. marginata* population and any of these factors. This steadiness of population density and biomass values indicates that *Glomeris marginata* is a species that shows a high degree of independence from local climatic conditions.

Distribution in space

Significant differences between monthly mean densities (n=24, KW p=0.000, SNK p<0.05) and biomasses (n=24, KW p=0.000, SNK p<0.05) were found between the different soil levels. Mean values in level H (26.65 ind·m⁻² and 1300.2 mg·m⁻²) were significantly higher than those in A (9.79 ind·m⁻² and 379.5 mg·m⁻²) and L/F (3.91 ind·m⁻² and 264.4 mg·m⁻²). Mean values in A were significantly higher than those in L/F.

In most months, *G. marginata* occured across the whole of the soil profile, as shown by the 95% confidence intervals of the Usher index in Figure 5. During some months, basically the winter period of both years, the species tended to move towards the deepest horizon. Nevertheless, these fluctuations shown by the Usher index were not statistically significant and
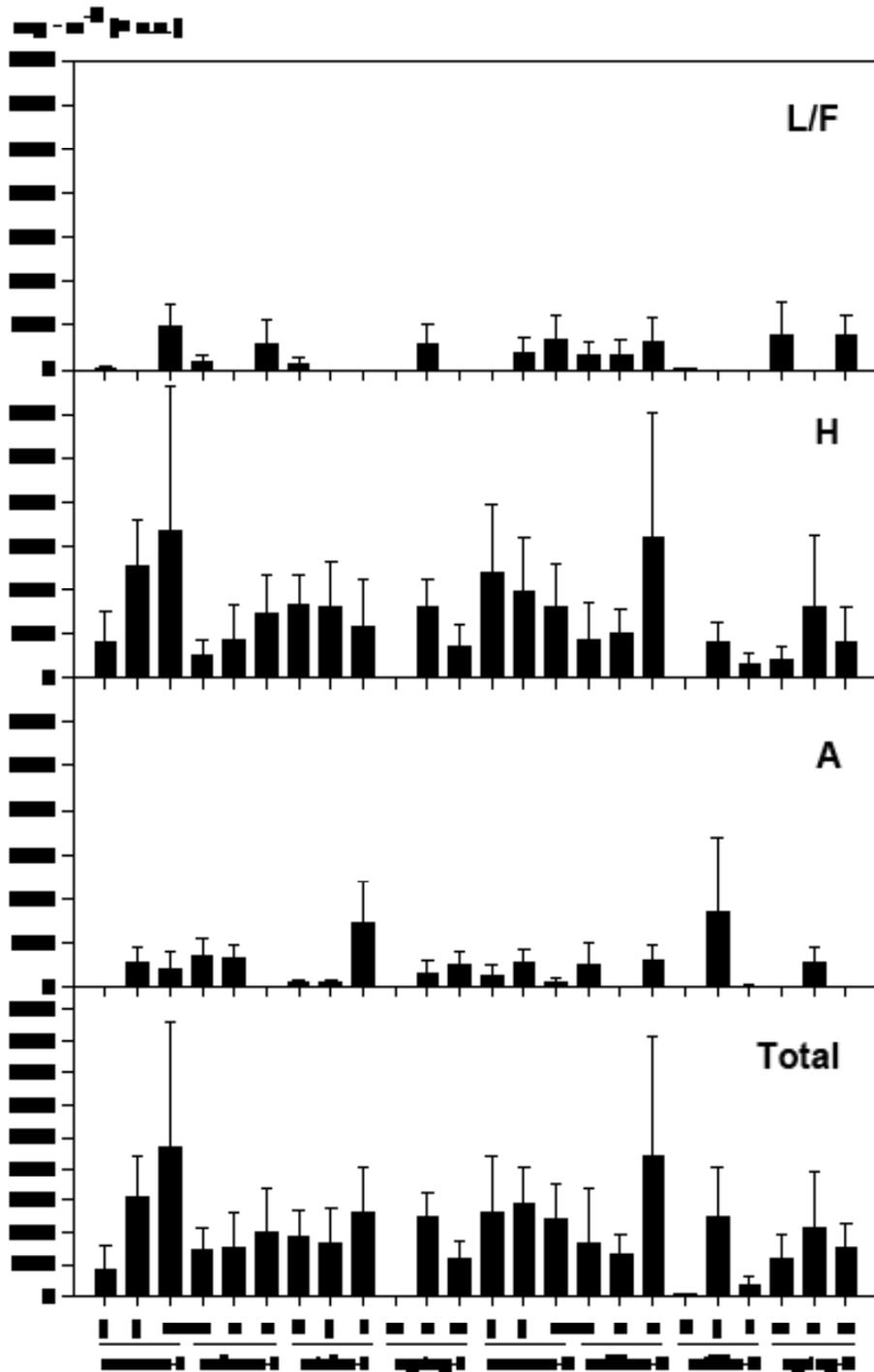
Figure 4. Mean monthly biomass values (and associated standard errors) showed by the whole of the *Glomeris marginata* population in each one of the soil horizons (L/F, H, A) and in the whole of the soil profile (Total).

they were not correlated with environmental parameters. Unlike other authors (Bocock & Heath 1967), we can not talk about vertical migrations along the soil profile during the annual cycle: the population was located preferably in horizon H, as some other studies pointed out before (Schubart 1934, Blower 1955).

Concerning horizontal distribution, Morisita index monthly values for each one of the horizons were always higher than one, which indicated that the species was distributed in patches. This kind of horizontal distribution is found in most edaphic arthropods, since it seems to favour their search for nourishment and protection or their reproductive activity (Blower 1969, Banerjee 1967).

Recruitment

Considering that stadium I of postembrionic development in *G. marginata* is found inside the egg, the time of recruitment corresponds to the apparition of individuals in stadium II. In the studied population, individuals in stadium II appeared all through the sampling period (Figure

6). Similarly, the whole set of anamorphic stadia occurred continuously during the two years of study (Figure 7).

According to Heath *et al.* (1974), although egg-laying in *G. marginata* mostly happens in April, May and June, females can lay eggs all through the year. Our results, with the appearance of individuals in stadium II along all seasons of the annual cycle, confirmed this capability.

Biomass of different developmental stadia

The value of individual mean biomass was obtained for each anamorphic and epimorphic stadium (Table 4). This value, estimated from the regression algorithm, can be considered as the standard individual biomass of each stadium and it allows a biomass to be assigned to an individual once its developmental stadium is known. The values of individual mean biomass of the whole anamorphic stadia (3.92 mg), of the epimorphic stadia (74.12 mg) and that of a type individual

Table 4. Mean individual biomass (mg±s.e.) of Glomeris marginata for each developmental stadium calculated using the regression algorithm B= 0.456· (T2)$^{3.189015}$. n=number of individuals in each stadium. Rank=minimum and maximum biomass values.

Stadium	Number of tergites	Number of pairs of legs	n	mg ± se	rank (mg)
Anamorphic					
I	8	3		---	---
II	8	8	42	0.77 ± 0.03	0.50 - 1.08
III	9	10	52	2.13 ± 0.07	1.27 - 3.24
IV	10	13	55	4.72 ± 0.18	1.81 - 8.05
V	11	15	26	10.89 ± 0.86	5.64 - 26.86
Mean anamorphic stadia biomass			175	3.92 ± 0.28	0.50 - 26.86
Epimorphic					
VI- XVI (□)	12	19	168	62.1± 2.5	10.3 - 185.5
(□)	12	17	125	90.3 ± 4.7	19.2 - 225.9
Mean epimorphic stadia biomass			293	74.12 ± 2.62	10.3 - 225.9
Mean individual biomass			468	47.87 ± 2.27	0.50 - 225.9

Table 5. Population density (ind·m^{-2}) and biomass (mg·m^{-2}) values obtained by different authors in different forests of temperate and Mediterranean climates. Values ≈ have been extrapolated from figures published by the author. Ref=References: 1= David (1988), 2 = David (1995), 3 = Bertrand & Lumaret (1992), 4 = Bertrand et al. (1987), 5 = David et al. (1999).

PLACE	FOREST	ind·m^{-2}	mg·m^{-2}	REF.
Temperate climate				
Massif d'Ingrannes Orléans, FRANCE	(*Quercus petraea* + *Q. robur*) (79%); *Fagus sylvatica* (19%)	51.84 16.05	676.2 276.8	1
"	(*Quercus petraea* + *Q. robur*) (72%); *Pinus sylvatica* (21%)	10.4	585	1
"	*Pinus sylvestris* (99%)	4.32	132	1
"	*Pinus sylvestris* (98%)	3.78	195.5	1
"	(*Quercus petraea* + *Q. robur*) (96%);	3.74 1.05	280 2.68	1
"	(*Quercus petraea* + *Q. robur*) (89%); *Carpinus betulus* (10%)	2.6	142.2	1
"	(*Quercus petraea* + *Q. robur*) (44%); *Pinus sylvatica* (38%)	1.9 1.6	411.6 166.8	1
"	*Pinus sylvestris* (86%); *Betula* (12%)	1.8	136.8	1
"	(*Quercus petraea* + *Q. robur*) (32%); *Fagus sylvatica* (36%); *Pinus sylvatica* (30%)	1.76	115.5	1
"	*Pinus sylvestris* (93%)	0.66	1.12	1
Mediterranian climate				
Puechabon Montpellier, FRANCE	Evergreen oak forest *Quercus ilex*	212	7800	2
Saint Gély du Fesc Montpellier, FRANCE	*Quercus coccifera*	124.1	3150	3
Puéchabon Montpellier, FRANCE	*Quercus ilex*	70.2	4000	3
Chêne vert Puéchabon Montpellier, FRANCE	*Quercus ilex* + *Q. pubescens*	50-100	7200-10800	4
Sant Llorenç del Munt Barcelona, SPAIN	*Quercus ilex, Arbutus unedo, Pinus halepensis*	40.34	1944.1	PRESENT ESTUDY
Mas de Cazarils Montpellier, FRANCE	Wooded sites *Quercus ilex* + *Q. pubescens*	≈ 33	---	5
"	Mixed semi-open sites herbs and dwarf shrubs	≈ 22	---	5
"	Semi-open sites shrubs and youg oaks	≈ 21	---	5
Saint Gély du Fesc Montpellier, FRANCE	*Quercus ilex* litterfrazing	20	222.5	3

of the *G. marginata* population (47.87 mg) were determined.

Although differences were not statistically significant, the value of individual mean biomass of males (62.1 mg) was considerably lower than that of the females (90.3 mg). Because of that, even though the value of male population density was higher than that of the female population, the value of male population biomass (889.1 mg·m^{-2}) was lower than that of the females (996 mg·m^{-2}). Nevertheless, those differences were not statistically significant either.

Epimorphic stadia (males and females) showed a wide range of individual biomass values: between 10 and 190 mg in males (Figure 8) and between 10 and 230 mg in females (Figure 9). Frequency distribution was biased towards lower biomass values, which showed that most males and females
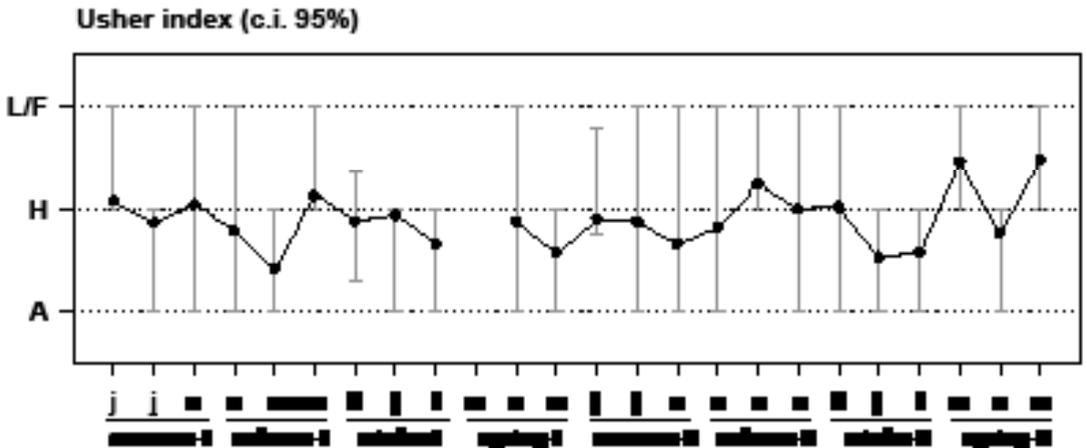
Figure 5. Vertical distribution of *Glomeris marginata* density calculated from the Usher index. Confidence intervals (95%) estimated using bootstrap technique.
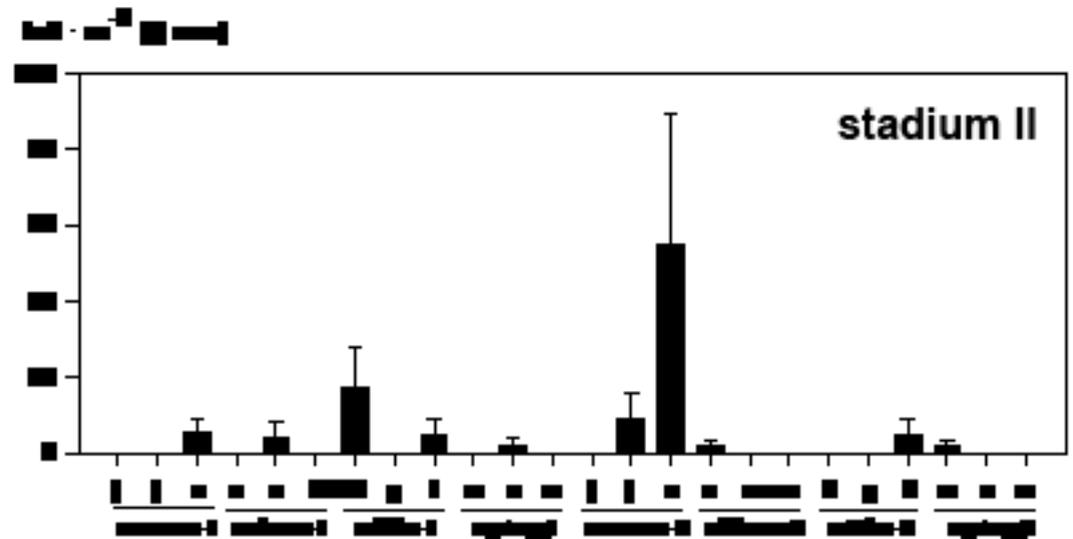
Figure 6. Mean monthly density values of *Glomeris marginata* specimens in anamorphic stadium II in the whole of the soil profile.

of the studied population were relatively small. From data obtained by Heath *et al*. (1974) with specimens from a mixed deciduous woodland in north-west England, male (56.1 mg) and female (172.3 mg) individual biomass values were estimated. The male value is similar to the one we calculated in our study population (62.1 mg), while that of the females is considerably higher than the one we obtained (90.3 mg). It must be

taken into account, though, that those specimens came from a very different habitat and that they were collected in spring only.

Comparison against other localities

Table 5 shows different density and biomass data obtained by different authors in Mediterranean (Bertrand *et al*. 1987, Bertrand & Lumaret 1992, David 1995, David *et al*. 1999) and Atlantic
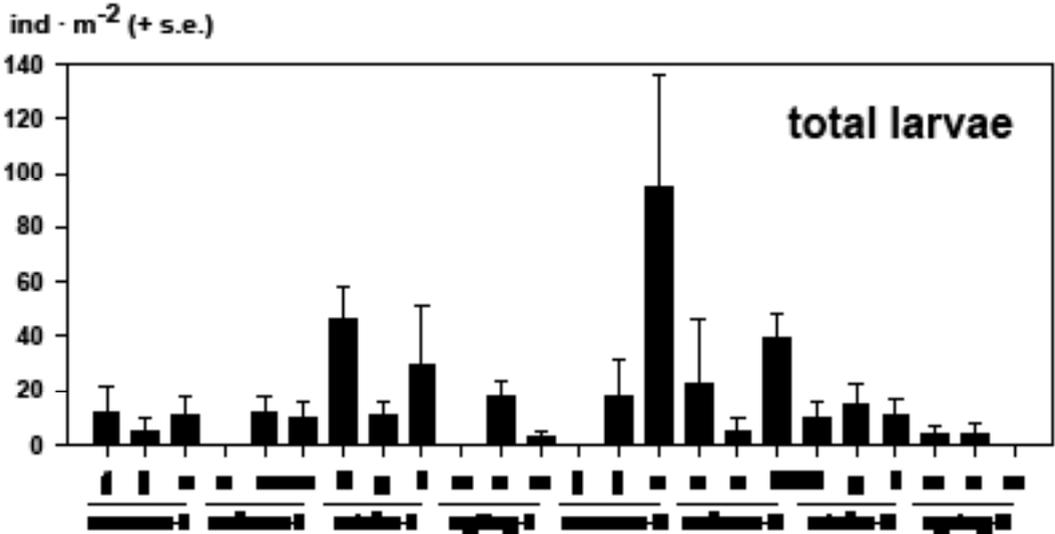
Figure 7. Mean monthly density values of all *Glomeris marginata* specimens in anamorphic stadia in the whole of the soil profile.
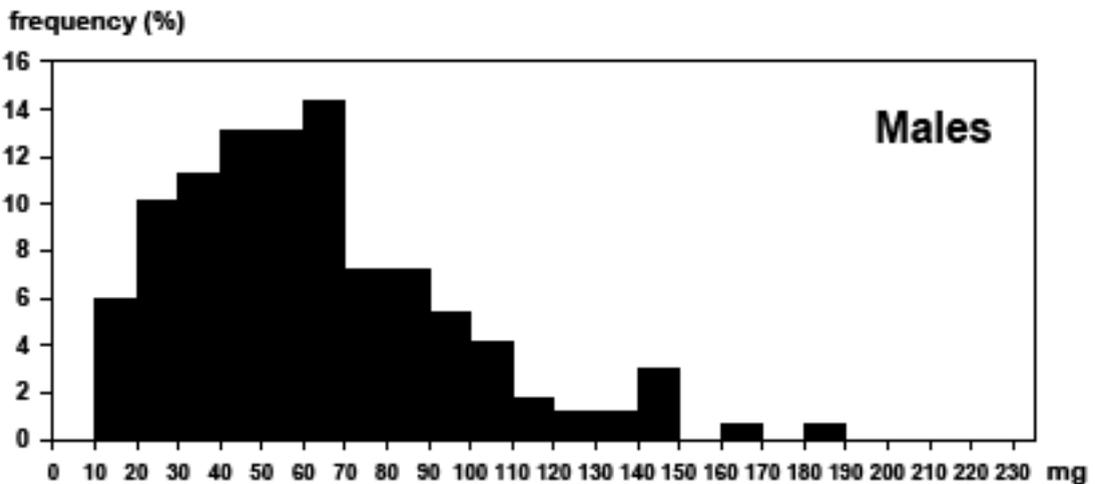
Figure 8. Frequency distribution of the male population of *Glomeris marginata* according to individual fresh weight ranges in milligrams.

(David 1988) ecosystems. Comparisons between different values in this table must be made with a certain caution due to the different sampling methods used, the different types of soil and edaphic horizons considered. Nevertheless, mean monthly density and biomass values obtained in our study (40.34 ind.m^{-2} and 1944.1 mg·m^{-2}) were relatively low when compared to other forests in the Mediterranean region.

In general, in Mediterranean forest soils, *G. marginata* shows higher values of population density and biomass (from 20 to 212 ind·m^{-2} and from 222.5 to 10800 mg·m^{-2}) than it does in temperate climate forests (from 0.66 to 51.84 ind·m^{-2} and from 1.12 to 676.2 mg·m^{-2}). These values highlight the capability of this species to face the strong changes that characterise Mediterranean climatology, allowing it to increase population densities and biomasses even in extreme situations (Haacker 1968, Stamou et al. 1984, Read & Martin, 1990, Iatrou & Stamou 1991, Dunger & Steinmetger 1981). This capability would explain the absence of significant correlations between density values of our population and temperature, rainfall and soil humidity, which results into the fact that changes in those parameters do not provoke relevant fluctuations in population density values. It is interesting pointing out that

Sustr (1996), studying different *Glomeris* species (*G. marginata, G. balcanica, G. hexasticha*), found that *G. marginata* is the best adapted one to the type of climate where it lives.

Table 5 shows also that, even though population biomass values are lower in temperate climates than they are in Mediterranean ones, individual mean biomass values tend to be higher in temperate climates. Nevertheless, we must consider that different studied populations may have a different population composition, which would affect individual biomass values.

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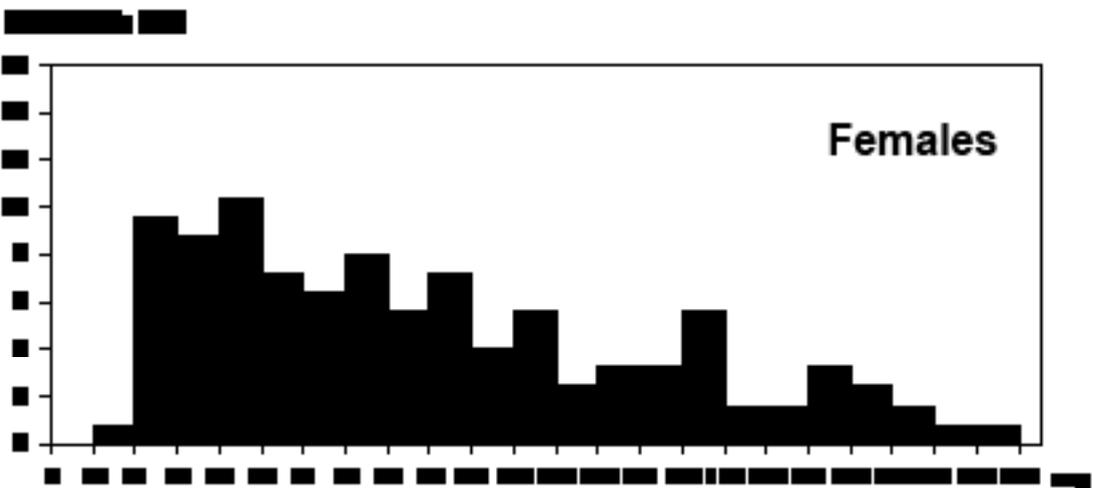
Figure 9. Frequency distribution of the female population of *Glomeris marginata* according to individual fresh weight ranges in milligrams.

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Myriapod records along the Sognefjord, Western Norway

Per Djursvoll, Tom Alvestad & Per Kristian Solevåg

Djursvoll, P., Alvestad, T. & Solevåg, P.K. 2006. Myriapod records along the Sognefjord, Western Norway. Norw. J. Entomol. 53, 375-385.

Localities along the Sognefjord in Western Norway were investigated in 2001 using pitfall traps. Myriapods were sampled and 11 millipedes, 5 centipedes and 1 symphylan species have been identified. Among these, 9 millipedes, 4 centipedes and 1 symphylan species are new to the county of Sogn og Fjordane. Records of Unciger *foetidus* (C.L. Koch), *Geophilus electricus* (Linnaeus) and *Lithobius melanops* Newport are noticeable. Localities with deciduous forest in the eastern/inner part of the fjord turned out to be most species rich.

Key-words: Myriapoda, Diplopoda, Chilopoda, Symphyla, pit-fall trap, Western Norway.

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INTRODUCTION

The knowledge of the myriapod fauna around the Sognefjord and further north in Norway is highly insufficient. Only scattered records are mentioned by Meidell (1972) and Scheller (1998). The geographical location, in the north of Europe (61° N), might be of interest in an attempt to investigate how far north the myriapods have established populations.

The Sognefjord is the longest fjord in Norway (Figure 1). It stretches 203 km from the western coast eastwards with steep mountains on both sides to the village of Skjolden. The fjord reaches a maximum depth of more than 1300 m. The height of the mountains gradually increases eastwards. Hard rocks (gneisses and granites) dominate in most areas of the fjord, resulting in a nutrient-poor soil. However, eastwards from Leikanger (loc. 16, 17 & 18) Precambrian and Cambrian - Silurian rocks are more common (Moe 1994). Here the soil is richer in accessible nutrients.

Extensive sampling using pitfall traps was carried out in forests along the Sognefjord in Western Norway during the months April to November 2001. The intention was to investigate the distribution of spiders and beetles along the fjord. The sampled material also included a large number of millipedes and centipedes. The field work was done by Tom Alvestad and Per Kristian Solevåg as part of their master's thesis (Alvestad 2006, Solevåg 2004).

The forests investigated are mostly pine forests and various deciduous forests, representing a wide variety of forest habitats. The moisture content on the forest floor varies between the forest types. The rich deciduous forest in western Norway with thermophilic tree species like *Ulmus glabra*, *Fraxinus excelsior, Corylus avellana* and *Quercus petraea*, is an extension of the deciduous forest belt in Europe, and many of these species have their northern limit in western Norway (Moen 1999). The forests have normally a high share of less thermophilic tree species like Alnus incana and *Prunus padus*, the two species often

being the most common trees in the area. The pine forests in the studied area are of different kinds, the dominant type being the *Calluna-Vaccinium* forest. Different kinds of heather species are also common, like *Vaccinium myrtillus* and *Empetrum nigrum*. Junipers (*Juniperus communis*) are quite common.

The westernmost areas are situated in the strong oceanic section with mild and wet winters. In the inner part of the fjord there is a transition zone between oceanic and continental climate with small amounts of rain and more continental temperatures during the year (cold winters and warm summers), all together making a climatic gradient from the outer to the inner part of the fjord.

The mean precipitation varies from 2500 mm p.a. in the outer areas to 400-500 mm p.a. in the inner

areas. Not far from the mouth of the fjord, the maximum annual precipitation is more than 4000 mm p.a., making it one of the wettest regions in Norway.

MATERIAL AND METHODS

The material was collected using pitfall traps in altogether 27 localities. The study area was mainly located along the northern side of the fjord (Figure 1). At each locality 8 pitfall traps were set out in a straight line, the distance between each trap ranged from 1.5 to 2 m.
Due to more than one trapping site in some localities, the actual number of series is 35, giving a total of 280 traps. The traps used were plastic cups, 9.5 cm high, 5 cm wide at the bottom and 7.5 cm at the top, half filled with 4 % formaldehyde solution to preserve the trapped animals. The
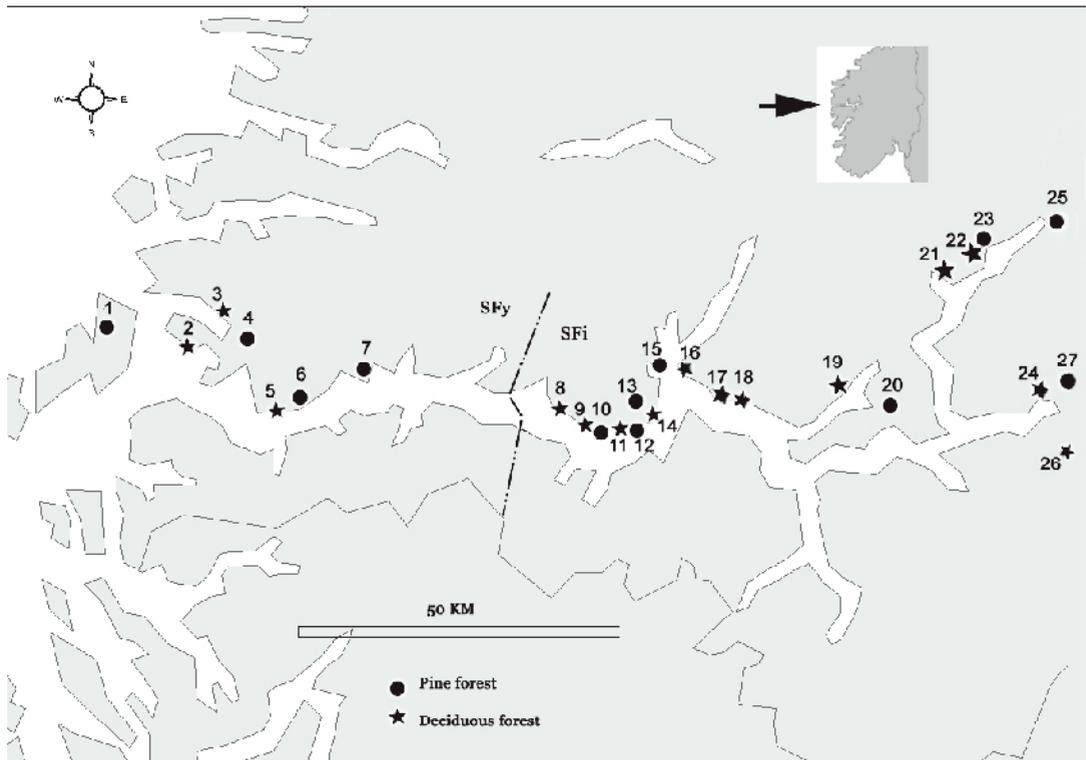
Figure 1. Map of the studied area and numbered localities along the Sognefjord. The border between SFy and SFi is marked.

pitfalls were covered by a metal roof, preventing vegetation and rain falling into the traps. The content of the traps was taken to the lab and transferred to 75% alcohol.

LOCALITIES

Below follow descriptions of the different localities, listed from the coast and inwards (e.g. from west to east) and with myriapod species added.

The dominating trees and some of the most abundant herbs in each locality are mentioned. The localities are placed in vegetation zones according to Moen (1999). The major parts of the study area are situated in the boreo-nemorale vegetation zone, but the inner parts lies in the south boreal vegetation zone.

Solund, Engvika (UTM: KN842860) **loc. 1**
Two trap series (1.1 and 1.2). Open pine forest dominated by *Hylocomium splendens, Calluna vulgaris* and *Vaccinium vitis-idáea. Juniperus communis*. There were some bare rocks in the area. Grazing sheep were observed. The area lies in the strong oceanic section of the boreo-nemoral zone.

Lithobius forficatus 3 April - 4 November 2001 (12 exx).

Hyllestad, Risnes (UTM: KN965872) **loc. 2**
One trap series. Dense *Corylus avellana* forest with scattered *Fraxinus excelsior* and *Prunus padus*. High diversity of herbs, among them: *Primula vulgaris, Anemone nemorosa, Ranunculus auricomus, Conopodium majus, Vicia sepium, Valeriana sambucifolia ssp. sambucifolia* and *Listera ovata*. The locality resembled no 21, but was more humid. Boreo-nemoral zone, strong oceanic section.

Lithobius forficatus 16 May - 7 August 2001 (4 exx), 7 August - 4 November 2001 (2 exx); *Polydesmus denticulatus* 16 May - 7 August 2001 (1 ♂, 3 ♀♀), 7 August - 4 November 2001 (2 ♀♀).

Hyllestad, Rønset (UTM: LN012902) **loc. 3**
Two trap series (2.1 and 2.2). A mixed deciduous forest dominated by *Corylus avellana, Prunus padus, Fraxinus excelsior* and some *Quercus petraea*. The locality was moist due to several small streams and shading from the trees, ground dominated by *Allium ursinum*. Other herbs like *Primula vulgaris* and *Anemone nemorosa* were abundant in the spring, also some *Lonicera periclymenum*. Trees more than 10 m high. Boreo-nemoral zone, strong oceanic section.

Lithobius forficatus 16 May - 7 August 2001 (2 exx), 7 August - 4 November 2001 (1 ex); *Nemasoma varicorne* 16 May - 7 August 2001 (1 ex); *Polydesmus denticulatus* 16 May - 7 August 2001 (10 exx), 7 August - 4 November 2001 (5 ♀♀).

Hyllestad, Staurdalen (UTM: LN035859) **loc. 4**
One trap series. A young open pine forest with some *Alnus incana* and *Fraxinus excelsior* trees. Ground dominated by grasses, *Calluna vulgaris* and *Vaccinium vitis-idaea*. Juniperus communis were abundant, partly shading the forest floor. The area lies in the south-boreal zone, strong oceanic section.

No myriapods were collected at this locality.

Høyanger, Værholm (UTM: LN102788) **loc. 5**
One trap series. An *Alnus incana* forest interspersed with *Sorbus aucuparia, Betula pendula* and *Corylus avellana*. The forest was wet and lush, with ground covered by dead leaves and twigs. A stream passed through the area. *Phegopteris connectilis, Oxalis acetosella* and *Trientalis europaea* present on the forest floor. Boreo-nemoral zone, strong oceanic section.

Polydesmus denticulatus 16 May - 7 August 2001 (3 ♂♂, 3 ♀♀).

Høyanger, Alværen (UTM: LN 149810) **loc. 6**
One trap series. *Myrtillus* type pine stand. Planted, even-aged pine forest with scattered *Pteridium*

aquilinum. Sorbus aucuparia, Anemone nemorosa and *Oxalis acetosella* also present. Boreo-nemoral zone, clear oceanic section.

No myriapods were collected at this locality.

Høyanger, Torvund (UTM: LN225838) **loc. 7**
One trap series. Open Calluna type pine stand with scattered *Pteridium aquilinum* and *Juníperus commúnis. Hylocomium splendens* was abundant on the forest floor. Boreo-nemoral zone, clear oceanic section.

Lithobius forficatus 7 August - 4 November 2001 (5 exx); *Proteroiulus fuscus* 7 August - 4 November 2001 (2 exx).

Balestrand, Nessane (UTM: LN5281) **loc. 8**
One trap series. Open mixed deciduous forest dominated by *Quercus petraea, Corylus avallana* and *Populus tremula*. The forest floor was covered with dense, lush grasses and *Rubus* sp. Boreo-nemoral zone, clear oceanic section

Lithobius forficatus 15 May - 7 August 2001 (6 exx), 7 August - 4 November 2001 (3 exx); *Cylindroiulus punctatus* 15 May - 7 August 2001 (2 exx), 7 August - 4 November 2001 (1 ex); *Polydesmus denticulatus* 15 May - 7 August 2001 (4 ♂♂, 5 ♀♀).

Balestrand, Tussvik (UTM: LN573794) **loc. 9**
One trap series. Mixed deciduous forest dominated by *Corylus avellana* and *Quercus petraea, Fraxinus excelsior, Populus tremula* and *Tilia cordata* also abundant. The forest floor was covered with dead leaves and twigs, Oxalis acetosella dominated in the herb layer, also some *Valeriana sambucifolia spp.sambucifolia*. The trees are 3-5 m high. Boreo-nemoral zone, clear oceanic section.

Lithobius forficatus 15 May - 7 August 2001 (12 exx), 7 August - 4 November 2001 (6 exx); *Proteroiulus fuscus* 15 May - 7 August 2001 (2 juv. exx).

Balestrand, Sæle (UTM: LN582784) **loc. 10**

Two trap series. Open pine forest, forest floor dominated by *Calluna vulgaris* and Hylocomium splendens. Some scattered birches (*Betula pendula*) and *Juniperus communis* also present. Herbs like *Succica pratensis, Melampyrum sp.* and *Viola sp.* were present. The trees were maximum 10 m high. Boreo-nemoral zone, clear oceanic section.

Lithobius forficatus 15 May - 7 August 2001 (13 ♂♂ 5 ♀♀), 7 August - 4 November 2001 (9 exx); *Cylindroiulus punctatus* 15 May - 7 August 2001 (2 ♀♀); *Polydesmus denticulatus* 15 May - 7 August 2001 (1 ex.), 7 August - 4 November 2001 (1 ♂); *Proteroiulus fuscus* 15 May - 7 August 2001 (2 exx).

Balestrand, Skardet (UTM: LN638788) **loc. 11**
One trap series. Dense and humid *Corylus avellana* forest with scattered specimens of *Alnus incana* and *Betula pendula*. The forest floor was covered with dead leaves and twigs; bare mould was visible in many places. Heavily grazed by sheeps. Several small streams irrigated the forest floor. Boreo-nemoral zone, clear oceanic section.

Lithobius forficatus 7 August - 3 November 2001 (3 exx); *Brachydesmus superus* 15 July - 7 August 2001 (1 juv. ♂); *Polydesmus denticulatus* 15 May - 7 August 2001 (14 ♂♂, 6 ♀♀).

Balestrand, Kvamsøy (UTM: LN6078) **loc. 12**
One trap series. Pine forest dominated by *Calluna vulgaris, Vaccinium vitis-idaea* and *Hylocomium splendens*. Some *Juniperus communis* and *Pteridium aquilinum* were also present. The canopy was open, making the forest floor warm and dry. Boreo-nemorale zone, weak oceanic section.

Lithobius forficatus 15 May - 7 August 2001 (1 ex), 7 August - 3 November 2001 (1 ex); *Cylindroiulus caeruleocinctus* 15 May - 7 August 2001 (1 ex); *Cylindroiulus punctatus* 4 April - 15 May 2001 (1 ex), 15 May - 7 August 2001 (1 ♂); *Proteroiulus fuscus* 15 May - 7 August 2001 (2 exx), 7 August - 3 November 2001 (1 ex).

Balestrand, Saurdalen (UTM: LN659818) **loc. 13.1**

One trap series. An open, old-grown pine forest. Ground vegetation dominated by *Vaccinium myrtillus* and *V. vitis-idaea*. An old forest with many trees covered with lichens. *Phegopteris connectilis* and *Blechnum spicant* present. South-boreal zone, weak oceanic section. Located 520 m a.s.l.

Lithobius forficatus 15 May - 7 August 2001 (1 ☐); *Proteroiulus fuscus* 15 May - 7 August 2001 (3 juv).

Balestrand, Saurdalen (UTM: LN663815) **loc. 13.2**

One trap series. Planted, even-aged spruce forest. Dense canopy. Ground vegetation absent. Forest floor covered with spruce needles. South-boreal zone, weak oceanic section. Located 330 m a.s.l.

Lithobius forficatus 15 May - 7 August 2001 (1 ☐), 7 August - 3 November 2001 (1 ex); *Nemasoma varicorne* 15 May - 7 August 2001 (3 exx); *Proteroiulus fuscus* 15 May - 7 August 2001 (1 ex); *Polydesmus denticulatus* 15 May - 7 August 2001 (1 ☐).

Balestrand, Saurdalen (UTM: LN667814) **loc. 13.3**

One trap series. *Vaccinium myrtillus* type pine stand with tall and thick trees. Canopy open. *Pteridium aquilinum* present. South-boreal zone, weak oceanic section. 250 m a.s.l.

Lithobius forficatus 15 May - 7 August 2001 (4 exx); *Nemasoma varicorne* 15 May - 7 August 2001 (1 ex); *Proteroiulus fuscus* 15 May - 7 August 2001 (1 ex); *Polydesmus denticulatus* 7 August - 3 November 2001 (1 ☐), 15 May 2001 - 7 August 2001 (16 exx).

Balestrand, Målsnes (UTM: LN669807) **loc. 14**

One trap series. Mixed deciduous forest dominated by *Quercus petraea* and *Fraxinus excelsior*. A stream was running next to the traps, making the forest floor rather moist. The ground vegetation was rich in species, with *Filipendula ulmaria* and

Geum urbanum dominating. Boreo-nemoral zone, weak oceanic section..

Lithobius forficatus 4 April - 15 May 2001 (14 exx), 15 May - 7 August 2001 (26 exx), 7 August - 3 November 2001 (14 exx), 4 April - 7 August 2001 (pitfall trap in hollow oak) (37 exx), 7 August - 3 November 2001 (pitfall trap in hollow oak) (23 exx); *Cylindroiulus sp*. 15.May - 7 August 2001 (2 ☐☐); *Polydesmus denticulatus* 15 May - 7 August 2001 (5 exx), 7 August - 3 November 2001 (3 mm, 1 ☐); *Proteroiulus fuscus* 15 May - 7 August 2001 (1 ex), 4 April - 7 August 2001 (pitfall trap in hollow oak) (50 exx.), 7 August - 3 November 2001 (pitfall trap in hollow oak) (7 exx).

Balestrand, Tjugum (UTM: LN678896) **loc. 15**

One trap series. Mixed, south faced deciduous forest with mostly *Quercus petraea* and *Corylus avellana*, also some *Prunus padus*. The forest floor covered with a thick layer of dead twigs and leaves. Dense foliage shaded the forest floor, few herbs. The locality lay next to agricultural areas. Boreo-nemoral zone, weak oceanic section.

Geophilus electricus 15 May - 7 August 2001 (1 ex), 7 August - 3 November 2001 (1 ex); *Lithobius forficatus* 15 May - 7 August 2001 (36 exx), 7 August - 3 November 2001 (1☐, 7 ☐☐); *Allajulus nitidus* 15 May - 7 August 2001 (9☐☐, 2 ☐☐), 7 August - 3 November 2001 (1☐, 4 ☐☐); *Brachydesmus superus* 15 May - 7 August 2001 (10 exx), 7 August - 3 November 2001 (1 ☐); *Nemasoma varicorne* 15 May - 7 August 2001 (1 ex); *Polydesmus denticulatus* 15 May - 7 August 2001 (22 exx); 7 August - 3 November 2001 (2 ☐☐, 1 juv.); *Polydesmus inconstans* 15 May - 7 August 2001 (1 ☐), 7 August - 3 November 2001 (1 ☐); *Scutigerella immaculata* 15 May - 7 August 2001 (10 exx); *Unciger foetidus* 15 May - 7 August 2001 (1 ☐).

Leikanger, Hella (UTM: LN720884) **loc. 16**

Two trap series. Warm and dry *Corylus avellana* forest, forest floor dominated by grasses and *Hylocomium splendens*. Other herbs were *Succica pratensis* and *Melampyrum sp*. Small specimens of *Quercus petraea* together with ferns (*Dryopterus*

sp) were also abundant. Boreo-nemoral zone, weak oceanic section.

Lithobius forficatus 15 May - 7 August 2001 (2 □□, 1 □), 4 April - 7 August 2001 (pitfall trap in hollow oak) (5 exx), 7 August - 3 November 2001 (pitfall trap in hollow oak) (5 exx); *Cylindroiulus latestriatus* 15 May - 7 August 2001 (1 □); *Cylindroiulus punctatus* 4 April - 15 May 2001 (1 □), 15 May - 7 August 2001 (5 □□, 1 □), 7 August - 3 November 2001 (1 □), 4 April - 7 August 2001 (pitfall trap in hollow oak) (3 exx); *Polydesmus denticulatus* 4 April - 6 May 2001 (9 exx), 15 May - 7 August 2001 (21 □□, 22 □□, 2 juv), 7 August - 3 November 2001 (3 □□, 3 □□, 2 juv), 4 April - 7 August 2001 (pitfall trap in hollow oak) (1 □). *Polydesmus sp.* 7 August - 3 November 2001 (1 juv), *Proteroiulus fuscus* 4 April - 7 August 2001 (15 exx, 7 juv. exx), 4 April - 7 August 2001 (pitfall trap in hollow oak) (51 exx), 7 August - 3 November 2001 (pitfall trap in hollow oak) (20 exx).

Leikanger, Grinde (UTM: LN7488) **loc. 17**
One trap series. *Corylus avellana* forest, more shaded and moist than loc. 16 due to denser foliage. The trees were maximum 4-5 m high. The forest floor was stony, with herbs growing between the stones. The herbs were mostly *Hylocomium splendens, Succica pratensis, Melampyrum sp.* and Vaccinium myrtillus. Also some *Viburnum opulus*. Boreo-nemoral zone, weak oceanic section.

Lithobius forficatus 4 April - 15.May 2001 (6 exx), 7 August - 3 November 2001 (1 ex.); *Allajulus nitidus* 4 April - 15 May 2001 (1 □, 1 □), 7 August - 3 November 2001 (6 exx); *Polydesmus denticulatus* 4 April - 15 May 2001 (1 □, 1 juv), 7 August - 3 November 2001 (2 □□, 1 □); *Proteroiulus fuscus* 4 April - 15 May 2001 (1 □).

Leikanger, Leikanger (UTM: LN80853) **loc. 18**
One trap series. Mixed deciduous forest consisting of *Betula pendula, Corylus avellana, Sorbus aucuparia, Quercus petraea, Ulmus glabra, Fraxinus excelsior* and *Salix caprea*. Dense canopy. Ground vegetation dominated by mosses,

grasses and dead twigs. Herbs like *Ranunculus ficaria, Taraxacum sp.* and *Silene dioica* present. Boreonemoral zone, weak oceanic section.

Lithobius forficatus 15 May - 7 August 2001 (6 exx), 7 August - 3 November 2001 (1 ex); *Allajulus nitidus* 15 May - 7 August 2001 (13 exx); 7 August - 3 November 2001 (17 exx); *Archiboreoiulus pallidus* 7 August - 3 November 2001 (1 □); *Cylindroiulus caeruleocinctus* 10 May - 7 September (3 □□, 1 □); 15 May - 7 August 2001 (5 □□, 2 □□), 7 August - 3 November 2001 (2 □□, 2 □□); *Cylindroiulus latestriatus* 15 May - 7 August 2001 (1 □); *Cylindroiulus punctatus* 15 May - 7 August 2001 (44 exx), 7 August - 3 November 2001 (13 exx); *Brachydesmus superus* 15 May - 7 August 2001 (16 exx), 7 August - 3 November 2001 (1 □, 1 □); *Polydesmus denticulatus* 10 May - 7 September (3 □□, 3 □□), 15 May - 7 August 2001 (54 exx), 7 August - 3 November 2001 (6 □□, 1 □); *Polydesmus inconstans* 15 May - 7 August 2001 (12 exx), 7 August - 3 November 2001 (11 □□, 1 □); *Polydesmus sp.* 7 August - 3 November 2001 (6 juv).

Sogndal, Stedjeberget (UTM: LN9788) **loc. 19**
One trap series. Dry, warm south-faced and dense *Tilia cordata* forest (4-5 meters high) interspersed with *Corylus avellana*. Some grasses, few herbs. The forest floor was dominated by naked stones, twigs and dead leaves and almost no mosses. The locality was hard to reach due to the location on the top of a steep scree. Some sun-exposed slopes with bare rocks were also present in the area, making it a very warm place when the sun was shining. The area lies in the south-boreal zone, weak oceanic section.

Lithobius forficatus 15 May - 7 August 2001 (1 □, 2 □□); *Lithobius melanops* 15 May - 7 August 2001 (2 □□, 1 □); *Nemasoma varicorne* 15 May - 7 August 2001 (1 □); *Polydesmus denticulatus* 15 May - 7 August 2001 (4 □□, 6 □□), 7 August - 3 November 2001 (2 □□, 1 □).

Sogndal, Vesterland (UTM: MN028874) **loc. 20**
One trap series. Young pine forest interspersed with some *Pícea abies* and *Juníperus communis*.

Forest floor dominated by *Vaccínium myrtíllus*. *V. vitis-idaea, Calluna vulgaris, Empetrum nigrum* and *Pterídium aquilínum* also present. South-boreal zone, weak oceanic/transition section.

Lithobius forficatus 14 May - 6 August 2001 (18 exx), 6 August - 3 November 2001 (3 exx); *Polydesmus denticulatus* 14 May - 6 August 2001 (14 exx), 16 August - 3 November 2001 (2 ♀♀, 1 juv♂); *Proteroiulus fuscus* 6 August - 3 November 2001 (3 exx).

Luster, Råum (UTM: MN10077) **loc. 21**
One trap series. *Corylus avellana* forest with some *Betula pendula*. Canopy relatively closed. Dense forest floor covered with different types of grasses and herbs like *Melampyrum sylvaticum, Campanula rotundifolia, Geum urbanum, Silene furcata* and *Víola sp.*. South-boreal zone, transition section.

Lithobius forficatus 15 May - 6 August 2001 (8 exx), 6 August - 3 November 2001 (3 exx); *Polydesmus denticulatus* 15 May - 6 August 2001 (189 exx), 6 August - 3 November 2001 (52 exx); *Polydesmus sp*. 15 May - 6 August 2001 (1 juv. ♂).

Luster, Luster (UTM: MP184136) **loc. 22**
One trap series. Mixed deciduous forest with *Ulmus glabra* and *Corylus avellana*. *Acer pseudoplatanus, Sorbus aucuparia, Viburnum opulus* and *Prunus padus* also present. Dense canopy shaded the forest floor, the latter covered with dead twigs. Except for some moss and grasses, ground vegetation was absent. Understorey of young tree seedlings. South-boreal zone, transition section.

Geophilus flavus 15 May - 6 August 2001 (1 ex); *Lithobius forficatus* 15 May - 6 August 2001 (9 exx), 6 August - 3 November 2001 (1 ex), 6 August - 3 November 2001 (pitfall trap in hollow oak) (4 exx); *Allajulus nitidus* 15 May - 6 August 2001 (1 ♀), 6 August - 3 November 2001 (1 ♀), 15 May - 6 August 2001 (pitfall trap in hollow oak) (3 ♀♀, 2 ♂♂); *Brachydesmus superus* 15 May - 6 August 2001 (3 exx.); *Nemasoma varicorne*

15 May - 6 August 2001 (pitfall trap in hollow oak) (1 ex); *Polydesmus denticulatus* 15 May - 6 August 2001 (1 ♂); *Polydesmus inconstans* 15 May - 6 August 2001 (6 ♀♀, 10 ♂♂); 6 August - 3 November 2001 (8 exx); 15 May - 6 August 2001 (pitfall trap in hollow oak) (4 ♀♀, 1 ♂, 4 juv); *Proteroiulus fuscus* 15 May - 6 August 2001 (33 exx), 6 August - 3 November 2001 (pitfall trap in hollow oak) (11 exx).

Luster, Bargarden (UTM: MP1913) **loc. 23**
One trap series. A warm and dry pine forest rich in nutrients due to calcium-rich bedrock. Herbs sparse, forest floor dominated by lichens and mosses. *Asplenium trichomanes ssp. quadrivalens* was very dense. Bare rocks were common. South-boreal zone, transition section.

Lithobius forficatus 14 May - 6 August 2001 (11 exx), 6 August - 3 November 2001 (4 exx); *Polydesmus inconstans* 14 May - 6 August 2001 (5 ♀♀, 2 ♂♂, 1 juv), 6 August - 3 November 2001 (1 ♂, 1 juv).

Årdal, Seimsdal (UTM: MN278913) **loc. 24**
Two trap series (24.1 and 24.2). 24.1 in a dense forest dominated by *Alnus incana* and *Prunus padus*, with forest floor covered by mosses and decaying organic material. The most common herb was *Oxalis acetosella*; also some *Rubus idaeus* bushes were present. 24.2 resembled the first one, but for growing *Ulmus glabra* and *Corylus avellana*. The ground was steeper and covered with a thick layer of dead twigs. South-boreal zone, transition section.

Lithobius forficatus 4 April - 14 May 2001 (7 exx), 14 May - 6 August 2001 (17 exx), 6 August - 2 November 2001 (4 exx); *Nemasoma varicorne* 5 April - 14 May 2001 (1 ♂); *Polydesmus denticulatus* 5 April - 14 May 2001 (1 ♂, 9 ♀♀, 7 juv); 14 May - 6 August 2001 (343 exx), 6 August - 2 November 2001 (58 exx); *Proteroiulus fuscus* 14 May - 6 August 2001 (1 ex); *Scutigerella immaculata* 14 May - 6 August 2001 (1 ex); *Scutigerella sp*. 6 August - 2 November 2001 (1 ex).

Luster, Fortun (UTM: MP301193) **loc. 25**

Table 1. List of myriapod species from the county of Sogn og Fjordane. X = new record, P = also found in the present study.

Species

Chilopoda

Lithobius forficatus (L., 1758)	P
Lithobius melanops Newport, 1845	X
Lithobius erythrocephalus C. L. Koch, 1847	X
Lithobius tenebrosus Meinert, 1872	X
Geophilus electricus (L., 1758)	X
Geophilus flavus (De Geer, 1778)	X
Geophilus proximus C. L. Koch , 1847	
Strigamia maritima (Leach, 1817)	

Diplopoda

Polyxenus lagurus (L., 1758)	
Brachydesmus superus Latzel, 1884	X
Polydesmus denticulatus C. L. Koch, 1847	P
Polydesmus inconstans Latzel, 1884	X
Nemasoma varicorne C. L. Koch, 1847	X
Proteroiulus fuscus (Am Stein, 1857)	X
Archiboreoiulus pallidus (Brade-Birks, 1920)	X
Unciger foetidus (C. L. Koch, 1838)	X
Allajulus nitidus (Verhoeff, 1891)	X
Cylindroiulus caeruleocinctus (Wood, 1864)	P
Cylindroiulus latestriatus (Curtis, 1845)	X
Cylindroiulus punctatus (Leach, 1814)	X

Symphyla

Scutigerella immaculata (Newport, 1845)	X

Pauropoda

Allopauropus cuenoti (Remy, 1931)	
Allopauropus vulgaris (Hansen, 1902)	

Two trap series (25.1 and 25.2). Open pine forest. Locality 25.1 with some *Juniperus communis*. Forest floor dominated by *Vaccínium myrtíllus*, *V. vitis-idaea* and *Calluna vulgaris*. *Alchemilla alpina* present. Boulders present. Middle-boreal zone, transition section.

Lithobius forficatus 15 May 2001 - 6 August 2001 (2 exx), 6 August 2001 - 3 November 2001 (1 ex); *Polydesmus denticulatus* 15 May 2001 - 6 August 2001 (11 exx), 6 August 2001 - 3 November 2001 (2 ♀♀).

Locality 25.2 with similar vegetation as 25.1, but with forest floor dominated more by grasses than heather. Middle-boreal zone, transition section. No myriapods were caught in this locality.

Lærdal, Husum.(UTM: MN346690) **loc. 26**
One trap series. The most continental deciduous forest in our study, dominated by *Ulmus glabra*, *Alnus incana* and *Prunus padus*. The forest floor was very dry due to its south-facing exposure and low precipitation. Ground flora with a high diversity; *Geum urbanum, Epilobium sp., Impatiens parviflora, Valeriana sambucifolia ssp. sambucifolia, Artemisia vulgaris, Verbascum nigrum, Filipendula ulmaria* and *Campanula rotundifolia*, altogether a dense, lush ground cover. Slopes with bare rocks were also present. The locality lies in the south-boreal zone, weak continental section.

Lithobius forficatus 14 May - 6 August 2001 (33 exx).

Årdal, Kammen (UTM: MN373990) **loc. 27**
One trap series. A dry pine forest, probably situated on a moraine from the last ice age. The soil is sandy. There were virtually no herbs on the forest floor, only mosses and lichens. The main component of the forest litter was pine needles, making the ground very acid. South/middle-boreal zone, transition section.

Lithobius forficatus 6 August - 2 November 2001 (28 exx.); *Lithobius erythrocephalus* 14 May - 6 August 2001 (1 ♂); *Polydesmus denticulatus*

14 May - 6 August 2001 (2 exx); 6 August - 2 November 2001 (1 □).

RESULTS AND DISCUSSION

In this investigation 11 millipede, 6 centipede and 1 symphylan species were found.

Nine millipede, 5 centipede and 1 symphylan species are new to the county of Sogn og Fjordane. This brings the total number of species known up to 12 millipede, 8 centipede, 1 symphylan and 2 pauropods (Table 1).

Considering the northern latitude, this study has included localities in the inner parts of Sognefjord with numerous myriapods. The study reflects the climatic gradient to the inner part where climate- and biotic conditions are more favorable. In Figure 1 we have marked the border between SFy and SFi accords to "The Strand-System" (Strand 1943) to separate the study area into an outer (SFy) and an inner (SFi) part. This separation is appropriate as it is in accordance with a climatic gradient.

As expected the SFi localities within deciduous forests and with cultural influence are most species rich, e.g. locality 15 (Balestrand, Tjugum), locality 18 (Leikanger) and locality 22 (Luster) (Figure 2).

Most of the species discovered are widespread elsewhere in Southern Norway. The most noticeably exceptions are *Unciger foetidus, Geophilus electricus* and *Lithobius melanops*.

Meidell (1968) reported U. foetidus new to Norway from the Bergen area. Since then only few records from eastern and western Norway are known. In the same publication he writes that Lohmander (1957) mentions East Central-Europe as the origin of its expansion toward the west and north. A synanthrophic distribution is therefore presumable in the Sognefjord. It is dependent on calcareous-rich habitats/soils. This record is the northernmost in Scandinavia, but not in Europe, as it is found on Iceland (Meidell, pers. comm.).

Lithobius melanops is mostly found under the bark of trees. It has an extensive costal, or along-fjord distribution on Iceland (Eason 1970) and the Faroe Islands (Meidell & Solhøy 1990). Anderson et al. (2005) regards *L. melanops* as fairly uncommon in all Nordic counties except Denmark and he explains the distribution as anthropochourous. Meidell (1972) has several records from the county of Hordaland, and it is likely that this species, although rare, has a wide distribution along the coast and in the fjords of western Norway.

Geophilus electricus is fairly uncommon and synanhropic according to Andersson et al. (2005). In addition to the record in Balestrand (loc.15), only few records in Norway are reported. The northernmost from the county of Møre og Romsdal.

We have to consider that the methods used here most likely obstructed finds of several species that presumably inhabit the region. In addition some of the species with few individuals represented could likely be more numerous if other sampling methods were used, e.g. collecting by hand. Not surprisingly, no pauropods were collected as they live more in the soil and needs more sophisticated methods for sampling. However, two pauropod species are reported by Scheller (1998). A total species list of myriapods on the county of Sogn og Fjordane is presented in Table 1.

The knowledge of the myriapod fauna in Norway is still limited, apart from some areas. Further investigations along our coast can provide material for interesting zoogeographical reflections.
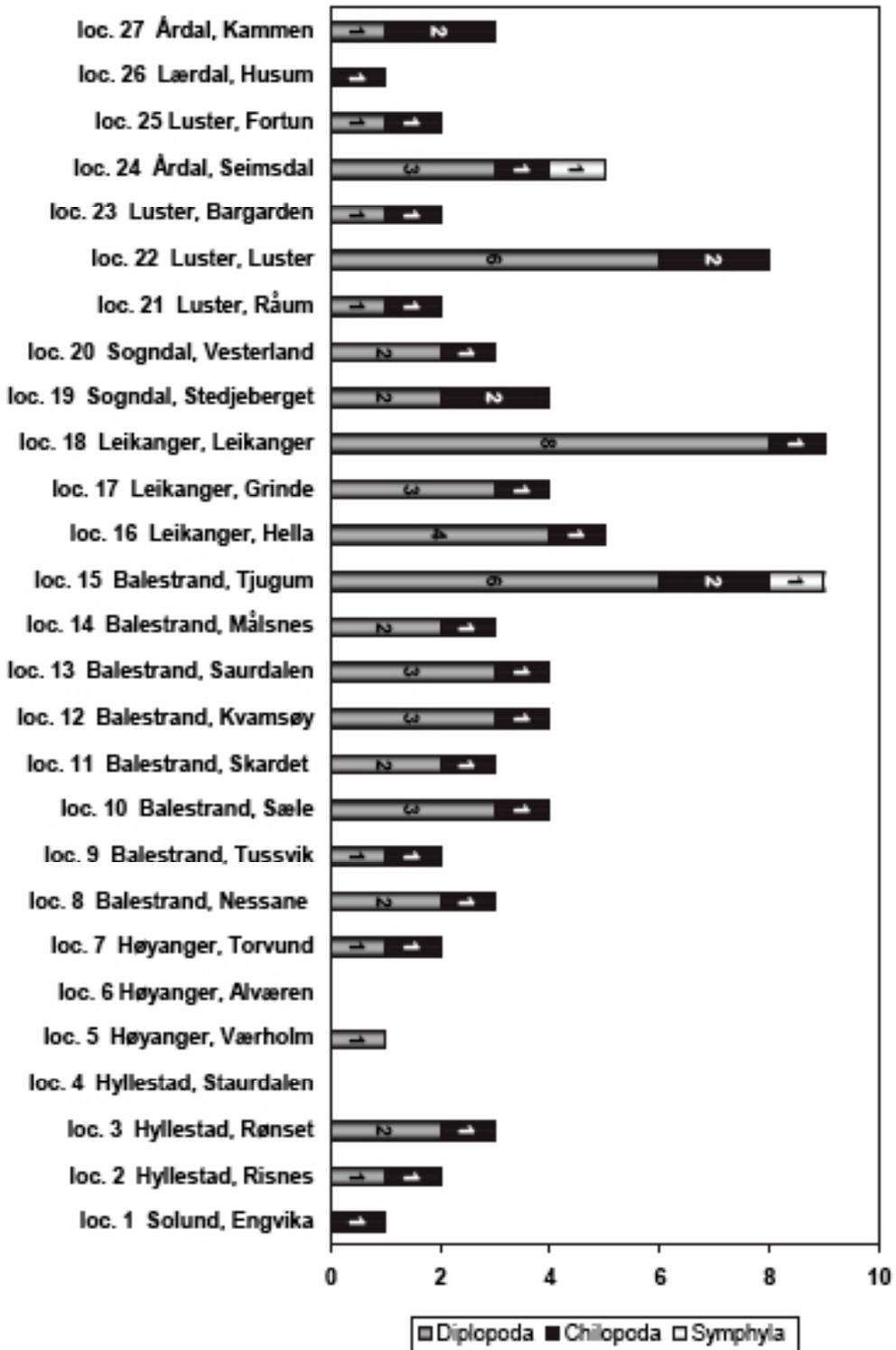
Figure 2. Number of species at each locality.

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Correspondence of dorsal and ventral parts in millipedes (Diplopoda). The summary of a free discussion

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The present article presents a summary of an open discussion at the 13th International Congress of Myriapodology held in Bergen 24 to 29 July 2005. In insects and most myriapods, the attribution of dorsal to ventral parts of segments poses no problems. In contrast, the correspondence between leg-pairs, sternites and tergites in millipeds (Diplopoda) is not obvious and has led to conflicting interpretations. Three different schemes which had been developed by morphological and embryological investigations were presented and discussed during the session. A possible solution to the problem has been proposed based in investigations on expression of segmentation genes. Obviously, there is an autonomy and a decoupling of dorsal and ventral segmentation processes in millipedes. Some other questions like the proposition of a stepwise subdivision of larger units into smaller metameres and the evolution of segmentation in general have been discussed cursorily.

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INTRODUCTION

In insects, the early segmentation processes on the ventral and the dorsal sides of the trunk seem to follow the same rules. The stripes of proteins expressed by the segment-polarity genes encircle the whole embryo without interruption. Thus, the dorsal part of a segment can easily be attributed to the corresponding ventral part.

In myriapods, there are multiple cases of heteronomy on the dorsal side. In many centipedes (Lithobiomorpha and Scolopendromorpha), long and short tergites alternate, with a typical "disturbance" (french: perturbation) between the 8th and 9th trunk segments which both bear large tergites. In Geophilomorpha, the segments are homonomous, but there are two tergites for each segment. In Scutigeromorpha, the short tergites have nearly vanished, and there is a very large tergite covering the 8th, 9th and 10th trunk segments which is probably a fusion product. Nevertheless, the attribution of tergal parts to their ventral counterparts has never been a problem either in old anatomical or embryological monographs or in recent develop-

mental investigations (Hughes & Kaufman 2002, Kettle et al. 2003).

In adult symphylids, there are always 12 pairs of legs (sometimes the first pair is reduced), but there are more dorsal scutes. In some species, we find 15 tergites, in others up to 24 (I do not mention the small intercalary tergites). As early as 1941, Tiegs revealed that in Hanseniella, which has 15 tergites, the trunk segments 4, 6 and 8 bear an extra tergite which enormously enhances the flexibility of the animal (Manton 1974). In most pauropods, there are less tergal shields than leg-pairs. But this is only true for the subgroup Tetramerocerata whereas the Hexamerocerata have the full number of tergites. Once again, Tiegs (1947) solved the problem as he showed that in some segments of *Pauropus*, the tergal shields simply do not differentiate. Speculations about diplosegmentation in pauropods are therefore futile.

In contrast to these easily explainable cases of heteronomy, millipedes (Diplopoda) have always been a problem. Careful anatomical analyses and embryological investigations have come to

different results concerning the concordance of sternites and tergites. With the exception of the first postembryological stadium, there are always more sternites and leg-pairs than tergal shields. In the middle and the hind trunk there is roughly double the number of leg-pairs than tergites. However, this does not hold true for the anterior part. Are two tergites fused to form one diplotergite? Are the most anterior segments cryptic diplosegments in which one pair of legs has been reduced or altered? Which leg-pair(s) belong to which tergite, both in forms with free sternites and in those with firmly fused rings? Some investigators sought to answer these questions by carrying out anatomical studies scrutinising the exoskeleton or analysing the sceletomuscular system and the nervous connections. Others believed the solution lay in embryological work seeking the correlation between ventral and dorsal parts on the early germ band. None of the propositions seemed to be completely convincing. Therefore, many myriapodologists hoped that the revelation and characterisation of genes affecting segmentation would solve the problem.

Several early attempts to visualise early segmentation by the application of antibodies which were cross-reactive in insects and crustaceans failed in millipedes. Finally, the working group in Cologne gathering around Wim Damen and Diethard Tautz was successful in isolating and characterising several segmentation genes in *Glomeris marginata* and to perform *in situ* hybridization to show the expression patterns (Janssen et al. 2004). Wim Damen accepted an invitation to the Myriapodological Congress in Bergen to bring these new results to the attention of the myriapodologists (see Janssen et al. 2006, this volume). In two other presentations (Nguyen Duy-Jacquemin 2006 and Short & Huynh 2006, both this volume) different segmentation schemes were presented for two different species of Penicillata. This, together with the discussion following Damen's talk provided the incentive to propose a free discussion on the topic on the evening of 28th July, 2005.

DIFFERENT SEGMENTATION SCHEMES

As a starting point, the two different segmentation schemes which had been presented by Monique Nguyen Duy-Jacquemin and by Megan Short in their contributions were drawn on the blackboard.

In the scheme proposed by Nguyen Duy-Jacquemin (2006), which will be called scheme 1, the collum is legless, the first pair of legs belongs to the next tergite (tergite II), the second pair of legs to tergite III, the 3rd pair to tergite IV. The first tergite to which two pairs of legs belong is tergite V, it is thus the first diplotergite. The last tergite to which two pairs of legs can be assigned is tergite IX, tergite X is legless and is followed by the telson. This is the scheme which has formerly been proposed by Manton (1956) and which is accepted by many myriapodologists.

In contrast, the scheme proposed by Short & Huynh (2006), which will be called scheme 2, attributes the legs to the tergites differently. In this scheme, the most anterior part of the trunk follows the same attribution of leg-pairs to tergites as in scheme 1: collum legless, first leg-pair to tergite II, second leg-pair to tergite III, and 3rd leg-pair to tergite IV. In contrast to scheme 1, tergite V has only one pair of legs (4th leg-pair), and tergite VI is the first diplotergite bearing two leg-pairs, namely leg-pairs 5 and 6. At the end of the trunk, the last-but-one tergite (IX) has two leg-pairs and the last tergite (X, in front of the telson) bears only one leg-pair.

Megan Short had devised this scheme 2 for the synxenid *Phryssonotus* but she adapted it in the discussion to *Polyxenus* in order to facilitate a comparison between the two schemes. This step of adjustment is not precarious as the early anamorphic stadia in *Phryssonotus* and *Polyxenus* agree in their number of leg-pairs and of tergites (see Enghoff et al. 1993). *Phryssonotus* has a stadium VII with 12 pairs of legs as the same stadium in *Polyxenus*. *Phryssonotus* adds three further stadia with an increment of leg-pairs (stadium VIII with 14, stadium IX with 16

and stadium X with 17 pairs of legs) whereas *Polyxenus* only has one additional stadium with 13 pairs of legs. There are subsequent moults, but they do not contribute to more leg-pairs.

Two interpretations are possible: the ancestral penicillate had 13 pairs of legs and acquired 4 additional leg-pairs through the intercalation of two additional moults; or the ancestral species was like a *Phryssonotus* with 17 leg-pairs, and *Polyxenus*-like species evolved by excalation of two anamorphic stadia. It seems plausible that the course of postembryonic development in *Phryssonotus* represents the ancestral type in Penicillata. However, this cannot be substantiated by a phylogenetic analysis. We can abandon this question as it has no relevance for our immediate problem.

It was reminded in the discussion that Dohle had proposed yet another scheme for millipedes (Dohle 1974). In this scheme (here called scheme 3), leg pair 1 belongs to the collum (which is regarded as a composite structure), leg-pairs 2 – 4 belong to the simple tergites II - IV, the segments with leg-pairs 5 and 6 form only one tergite V which is thus the first diplotergite.

Which facts and arguments speak in favour of the one or the other scheme, and which contradict them?

Scheme 1
Scheme 1 is supported by meticulous anatomical investigations in Polyxenus (Manton 1956, Nguyen Duy-Jacquemin 1969). Both the skeletomuscular system and the nervous system were analysed. However, as pointed out in the discussion, there is no really reliable marker as to what sternite belongs to which tergite. If we take the muscles attached to the sternite of the second leg-pair, we find muscle bundles connected to the collum (tergite I), others connected to tergite II and still others connected to tergite III. It is a matter of choice whether we take the one or the other muscle bundle as an indicator of the correspondence of ventral and dorsal parts. The same is true for the nerves stretching from the ventral to the dorsal side.

Another argument for scheme 1 is the actual body architecture of ring-forming millipedes. The scheme reflects the distribution of legs in Julida, Spirostreptida and Polydesmida (not in Spirobolida!). In these, leg-pair 3 is firmly attached to ring IV, leg-pairs 4 and 5 are attached to the ring-forming tergite V and so on. The last podous ring has two pairs of legs. The counterargument is that the ring-forming millipedes are the most derived ones within the Diplopoda. In Penicillata, Oniscomorpha, Colobognatha, and Nematophora, the sternites have no firm connection to the tergites or pleurotergites. If the phylogenetic analyses of Enghoff (1984) and Enghoff et al. (1993) are right, the assumption is inevitable that free sternites represent the original (=ancestral) condition in millipedes. Therefore, formation of rings is the derived condition. It is probable that through calcification, spiral coiling and fusion of tergites, pleurites and sternites into firm rings the original attribution of sternites and tergites has been shifted.

In a recent paper, Janssen et al. (2006) have pointed out that using the rings to attribute sternites/leg pairs to tergites may be misleading, and the authors have stressed the case of the spirobolids. In these, tergite II forms a ring with leg-pair 2 (!), III with 3, IV with 4 and V with 5. Tergite VI forms a ring with leg-pairs 6 and 7. Therefore, in spirobolids tergite V is associated with only one leg-pair (5), in the other ring-forming millipedes with two leg-pairs (4 and 5). In the model of Janssen et al., tergite V covers "about one and a half" ventral segments, and this may be the reason that it is either associated with only one leg-pair (5) in the spirobolids or with leg-pairs 4 and 5 in the other ring-formers (see www. frontiersinzoology.com)

Scheme 2
Scheme 2 is mainly based on the fact that several postembryonic stadia have an increase of one tergite and of two pairs of legs after each moult. In these stadia (stadia IV – VI in *Polyxenus* and stadia IV – VIII in *Phryssonotus*), the number of leg-pairs is even. In front of the telson, there is one tergite associated with two pairs of inarticulated leg-buds which will be fully differentiated

after the next moult. Only the first epimorphic stadium (stadium VIII in *Polyxenus* and stadium X in *Phryssonotus*) has an odd number of leg-pairs by addition of only one pair of legs. This scheme avoids the difficulty of scheme 1 that in most moults a two-step differentiation of each diplosegment has to be assumed: the anterior part of a diplosegment is fully differentiated and the posterior part is still rudimentary. It must be underlined that the different schemes do not differ in the basic observations (number of leg-pairs and of tergites in the different stadia) but only in the attribution of leg-pairs to tergites.

Scheme 3

Scheme 3 was devised on the ground of investigations into the formation of the germ band in *Glomeris*, but the early germ bands of *Polydesmu*s and of the julid *Ommatoiulus* have revealed to present the same characteristics. *Polyxenus* was also investigated, but was an unfavourable object for embryological analysis. The key observation was that the segments first become discernible on the ventral side of the embryo. The ventral segmental stripes then extend to the sides and form the so-called lateral plates (in German: Seitenplatten) which will give rise to the pleural and by dorsal migration to the dorsal parts of the developing embryo. There are cellular connections between the ventral embryonic segment and the lateral plates. These connections have been taken as indications of the connections between the ventral and dorsal parts of a segment.

A POSSIBLE SOLUTION: DECOUPLED DORSAL AND VENTRAL SEGMENTATION

It does not seem that millipedes lend themselves to simple solutions. The work of Janssen et al. (2004, 2006) on the expression patterns of several segmentation genes offers a new approach to the problem. The authors showed that the regulatory mechanism for the differentiation of the dorsal part of a segment must be different from the interactions responsible for the ventral part.

The expression patterns of genes active in ventral segmentation in millipedes are consistent with the regulatory loop which has been worked out for *Drosophila* and which is obviously conserved in many other arthropods, viz. spiders, crustaceans and also centipedes, as has been shown by Hughes & Kaufman (2002) and Kettle et al. (2003). (We left out in the discussion the further complication that the earliest segmental subdivision of the germ band, the parasegmentation, is shifted in comparison to the later embryonic segmentation). Wim Damen had explained in his lecture that in the ventral part of a millipede segment, transcripts of the *engrailed* (*en*) and *hedgehog* (*hh*) genes are concentrated at the posterior border of an embryonic segment. Immediately in front is a small stripe of Wingless protein which signals back to the cells posterior to maintain en and hh expression. Expression of the *cubitus-interruptus* (*ci*) gene is found in the anterior part of the ventral segment consistent with the fact that ci is required for expression of the wg gene. Surprisingly, Janssen et al. (2004) could not find expression of a *wingless*-related gene in the dorsal ectoderm. The segment-polarity genes *en* and *hh* were expressed in the middle of a lateral plate, ci posterior to it. Thus, dorsal segmentation is not in accordance with ventral segmentation, but is decoupled from it.

The alignment of dorsal and ventral parts is not a simple relation. Janssen et al. proposed that tergites do not exactly represent the sclerites of one or (in the case of diplotergites) two segments. Tergite III represents the dorsal sclerite of the posterior part of trunk segment 2 and the anterior part of trunk segment 3, tergite IV covers the posterior part of trunk segment 3 and the anterior part of trunk segment 4, tergite V is the sclerite covering the posterior part of trunk segment 4 and the complete trunk segment 5, tergite VI covers segments 6 and 7 (though 5 and 6 represent the first diplosegment, see also Janssen et al 2004, 2006, this volume). In this way, the basal bauplan of the Diplopoda can also be detected in their derived forms, the ring-forming millipedes.

The findings of Janssen et al. (2004) solve two issues which were part of a long-standing debate.

Firstly, the "diplotergites" are no fusion products of two equivalent subsequent tergites. If this were the case, then one would expect the expression of two *engrailed* and two *hedgehog* stripes in one tergite. However, only one stripe is expressed. Therefore, former speculations that pro- and metazonite represent two fused tergites, are being ruled out.

Secondly, the most anterior segments are not cryptic or reduced diplosegments. There are neither two *engrailed* stripes ventrally nor dorsally. Kraus (1990) observed in moulting polydesmids that anterior rings decompose into discrete plates similar to the more posterior ones. In the light of the recent findings, this does not mean that anterior segments are diplosegments, but that posterior tergites behave like single tergites. In Glomeris, Verhoeff speculated that the pectoral shield (Brustschild) is the fusion product of two diplotergites and thus a "quadruplotergite". In reality, it is a single dorsal sclerite.

Wim Damen suggested that there is an intrinsic counting mechanism for the increment of ventral and dorsal segmental parts which works to a certain extent independently in the ventral and dorsal parts. This idea is corroborated by the fact that in postembryonic development of different pentazonian species, the increment of tergites is always one per moult whereas the increment of ventral parts varies. One finds in the stadia of different species all sorts of odd and even numbers of leg-pairs, sometimes even differing on both sides (Enghoff et al. 1993). Wim added to this the remark that the "counting" of segments is of course not limited to millipedes. Most arthropods produce a well-defined number of segments. They thus have to know (count) when to stop producing segments.

Jean-Francois David raised the objection that the decoupling cannot be absolute. He expressed the opinion: "Decoupling yes, but not too much..." He had found a *Glomeris* with 1 extra tergite (13 in total) and 2 extra pairs of legs. This suggests that there may be only one counting process which adds 1 tergite and 2 leg-pairs as a unit.

The regulation (counting) process counts exactly as zoologists usually do: 1 tergite + 2 leg-pairs together. This counting process may be similar in *Glomeris* and in ring-forming species, and may be the distinctive feature of diplosegments in the Diplopoda.

It could be argued that the degree of independence of the ventral and dorsal counting processes varies within the Diplopoda. In ring-forming species the level of adjustment is very high so that a "law of anamorphosis" could be formulated. In others, it is very low and the degree of independence of dorsal and ventral segmentation is high. For instance, in *Brachycybe nodulosa*, individuals with 18 pleurotergites can have 25, 26, 27, 28 or 29 leg-pairs, and specimens with 28 leg-pairs can have 17, 18, 19, or 20 pleurotergites (Murakami 1962a, b, 1963, references in Enghoff et al. 1993). These cases have not yet received sufficient attention.

SOME OTHER QUESTIONS

Arkady Schileyko reminded the participants of the proposition which Minelli & Botroletto (1988) put forward with regard to the evolution of segmentation. The authors proposed that segmentation takes place by the stepwise subdivision of large units, eosegments, into smaller and smaller subunits. Schileyko found this explanation plausible and convincing. However, many recent insights are at odds with this explanation. Firstly, molecular and combined analyses of chilopod phylogeny come to the result that the subdivision of centipedes into Noto- and Pleurostigmophora is right which entails that epimorph development is to be regarded as derived. Anamorphosis, the gradual addition of new segments from a proliferation zone, is the ancestral mode of postembryonic development. Secondly, the investigations of segmentation gene expression show that a subdivision of larger segmental units into smaller ones does not take place in myriapods. Orthologues of the famous pair-rule genes which are expressed in every second segment in *Drosophila* are present in other arthropods (spiders, crustaceans, *Glomeris*)

but they do not seem to play the same role in segmentation as in *Drosophila* and several other insects.

Finally, Georg Mayer insisted that segmentation is not only a problem in millipedes and myriapods but in all arthropods including onychophorans. He alluded to the speculations developed by Budd (2001) that the arthropods must have originated from a one-segmented ancestor. The audience agreed that this is another question of great general interest but which cannot be solved in the present context. On top, wine and snacks had run out of stock.

DESIDERATA FOR FURTHER WORK

Everyone agreed that it is a great step forward that expression patterns of segment-polarity and Hox genes which have their homologues in other arthropods can now be analysed in millipedes. What are the immediate desiderata of myriapodologists? Head segmentation is a problem, but this problem is not confined to myriapods. The homologisation of head segments in spiders and insects is more problematic than in millipedes and insects. The formation of appendages in the antennal, mandibular and maxillary segments and their non-existence in the premandibular and post-maxillary segments can of course be confirmed. In particular, a possible homology of parts of the gnathal appendages and the exact contribution of the post-maxillary segment to the gnathochilarium and presumably to the collum would be much appreciated.

It would be a great revelation to see the same or another expression pattern of segmentation genes in a ring-forming millipede. Are the peculiar features of the regulatory mechanism of the dorsal part of *Glomeris* just a special character of the Oniscomorpha, or is it a general feature of all millipedes? We are always inclined to extend our findings in one object to many other groups. Sometimes we are right. The assumption that the segmentation process and the genes involved are very much conserved throughout the arthropods

has been revealed to be justified in many cases. But sometimes, unexpectedly, we are wrong. Who would have guessed that millipedes have a different regulatory loop for their dorsal parts which does not agree with that of centipedes, insects and spiders? But does it really concern all millipedes or just a special subgroup? If millipedes attracted as much attention as they deserved we would soon have the answer.

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Short communications

The following short notes are abstracts from presentations at The 13th International Congress of Myriapodology. The entire papers have been or will be published elsewhere.

First ultrastructural investigation of a salivary gland in Chilopoda: Maxilla I-gland of Scutigera coleoptrata

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In the head of Chilopoda three types of glands are distinguishable: epidermal glands, salivary glands, and vesicular glands (Hilken & Rosenberg 2006). Except epidermal glands, the other gland types are investigated only by light microscopy. Here, we present the first ultrastructural investigation of a salivary gland, the maxilla I-gland of *Scutigera coleoptrata*. This paired gland is located in the area of the first maxilla and extends up to the third trunk segment. The gland is of irregular shape and consists of a great number of acini. Each acinus releases its secretion into a small duct system of different order that converges into an unpaired main duct which leads into the hypopharynx.

Each acinus consists of a great number of glandular units. The units are composed of three cell types: a secretory cell, an intermediary cell and a canal cell. Distally, the pear shaped secretory cell is invaginated, forming an extracellular cavity, lined with microvilli, in which the secretion is released and collected. The intermediary cell forms a conducting canal and connects the secretion cell with the canal cell. In the lower part, the intermediary cell bears microvilli, whereas the upper part is lined with a smooth cuticle. The cuticle is in continuation to the cuticle of the canal cell.

Our investigation shows that the glandular units of the salivary maxilla I-gland are comparably structured as the glandular units of single epidermal glands and those of compound epidermal gland organs (Hilken et al. 2005). It is likely that in Chilopoda salivary glands and other exocrine glands share the same ground pattern. The comparative investigation of the different head glands provides new significant features useful for the reconstruction of phylogeny in Myriapoda.

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Ultrastructural organization of the anal organs in the so-called ano-genital capsule of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha)

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Rosenberg, J., Müller, C.H.G. & Hilken, G. 2006. Ultrastructural organization of the anal organs in the so-called ano-genital capsule of *Craterostigmus tasmanianus* Pocock, 1902 (Chilopoda, Craterostigmomorpha). Norw. J. Entomol 53, 397.

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In *Craterostigmus tasmanianus* Pocock, 1902, a unique bivalvular structure, the "ano-genital capsule" is present, projecting between the last 15th pair of leg (Rosenberg et al. 2006). The animal can open the capsule to the ventral side. The inner ventral surface of each valvula bears four pairs of triangular to rectangle pore fields, separated by broad cuticular bars. Each pore field contains several wide rounded to oval anal pores. The pore opening is surrounded by the single-layered epithelium of the anal organ which is described preliminary by Borucki & Rosenberg (1997). Now, the present study describes in detail the ultrastructure of the epithelium of the anal organ. It becomes evident that the main epithelium of each anal organ is organized as a transporting epithelium with its typical differentiation of the basal and apical cell membrane. The basal labyrinth comprises about 1/3 of the cell height. The apical complex, formed by infoldings of the apical cell membrane with its accompanied mitochondria is poorly developed. The apical infoldings lead down to the basal labyrinth. Elongated mitochondria are in close juxtaposition to the apical infoldings. These plasmalemma-mitochondrial-complexes are not as much developed as in coxal organs of other pleurostigmophoren chilopods (Rosenberg 1985). The specialized transporting epithelium is covered by an endocuticle and a spacious, undifferentiated subcuticle. The cuticle is covered by a distinct mucus layer, secreted by several exocrine glands, which surround each anal organ like a collar. The anal organs of each pore field are surrounded by a net-shaped cellular sheath with wide mesh openings. Numerous haemolymph vessels and tracheoles are found between neighbouring anal organs.

The general and ultrastructural organization of the anal organs of *Craterostigmus* is comparable to the coxal organs of other pleurostigmophoran chilopods. It is supposed the main function of the anal organs is the uptake of water vapour from the atmosphere.

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On the fine structure of epidermal glands in Chilopoda: structure and phylogenetic aspects

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Müller, C. H. G., Rosenberg, J. & Hilken, G. 2006. On the fine structure of epidermal glands in Chilopoda: structure and phylogenetic aspects. Norw. J. Entomol. 53, 399.

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In Chilopoda numerous isolated epidermal glands are distributed over the entire body within the single-layered epidermis. Despite of the recent work of Müller et al. (2003) on the interommatidial glands of *Scutigera coleoptrata* (Linnaeus, 1758), however, there is only poor knowledge of the ultrastructural organization of the epidermal glands of centipedes, especially of those located on the head capsule. In a comparative morphological approach (LM, TEM) we therfore examined different epidermal glands situated on the head of representatives of Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha and Geophilomorpha. We are now able to distinguish two different types of epidermal glands: directo- and flexo-canal epidermal glands. As the structure of the flexo-canal epidermal glands is not fully understood, we herewith present only the fine structural organization of the directo-canal epidermal glands.

The directo-canal epidermal glands are always formed as multicellular gland units. Each unit consists of three types of cells: 1-2 secretory cells, a single but small intermediary cell and 1-3 canal cells. The secretory cell(s) discharge their contents into an extracellular reservoir, which is not lined by a cuticular layer. Intermediary and canal cells form the conducting canal that passes through the cuticle and drains the secretion outside. Generally, the intermediary cell is lined only in its most distal part by a cuticle, whereas in its proximal part, the apex of this cell often forms a circular fringe of microvilli. In the area of the canal cells, the conducting canal is completely covered by a cuticle. The proximal canal cell shows deep infoldings of the apical cell membrane or a circular microvillar arrangement, whereas the distal canal cell is somewhat simpler in structure. According to our current state of knowledge, directo-canal epidermal glands display highest degree of complexity in the Scolopendromorpha, because three canal cells can be differentiated. The apex of the middle canal cell forms deep infoldings of the apical cell membrane. In this area, the cuticle of the widened conducting canal is pierced by several pores.

We can demonstrate that in Chilopoda the single-ducted epidermal glands share the same ground pattern which is different to epidermal glands of insects.

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A new classification of the class Chilopoda: Subclass Ovodispersa and Subclass Ovoconecta

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Prunescu, C.C. 2006. A new classification of the class Chilopoda: Subclass Ovodispersa and Subclass Ovoconecta. Norw. J. Entomol. 53, 401-402.

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In 1965 a phylogenetic tree of chilopods was presented for the first time (Prunescu 1965a). According to this phyletic tree, the primitive chilopod was reconstituted from the plesiomorphic characters selected from the orders Scutigeromorpha and Lithobiomorpha.

The structure of the genital system in the Order Craterostigmomorpha places this order very close to the Order Scolopendromorpha. This affirmation refers especially to the existence of a series of testicles arranged along the both sides of a unique deferent canal (Prunescu et al.1996). The relationships of these orders are confirmed by the morphology of the forcipular appendages and by an essential element of the reproduction biology: the brood care. By this character, the Order Craterostigmomorpha is placed in closed vicinity with the two orders with epimorphic development: Order Scolopendromorpha and Order Geophilomorpha.

The structure and organization of the respiratory system in the Order Craterostigmomorpha places this order at an extreme plesiomorphic level among the Pleurostigmophora Chilopoda. This affirmation refers to the pleural spiracles, the thin and numerous tracheae which never present anastomoses and the tracheal wall structure with simple taenidium (Prunescu 1965b, Hilken 1997).

The existence of two rudimentary Malpighian tubules supplementary to the functional pair of Malpighian tubules situates the Order Craterostigmomorpha at a plesiomorphic level similar to the Order Scutigeromorpha (Prunescu & Prunescu 1996, 2006). Some other features must be added: the 15 pediferous segments, the Tőmősvary organ and the persistence of one single anamorphic moulting.

In this situation, the Order Scutigeromorpha and the Order Craterostigmomorpha appear as sister groups because they concentrate more plesiomorphic traits than the Chilopoda orders which are grouped near every one of them. The five orders of Chilopoda are grouped in the following way:

1. Subclass. Ovodispersa
Ord. Scutigeromorpha
Ord. Lithobiomorpha

2. Subclass Ovoconecta
Ord. Craterostigmomorpha
Ord. Scolopendromorpha
Ord. Geophilomorpha

The name of the Subclass Ovodispersa refers to the eggs-laying way: every egg is deposed isolated from the others and without relation with the mother body. The name of the Subclass Ovoconecta refers to the eggs-laying way in
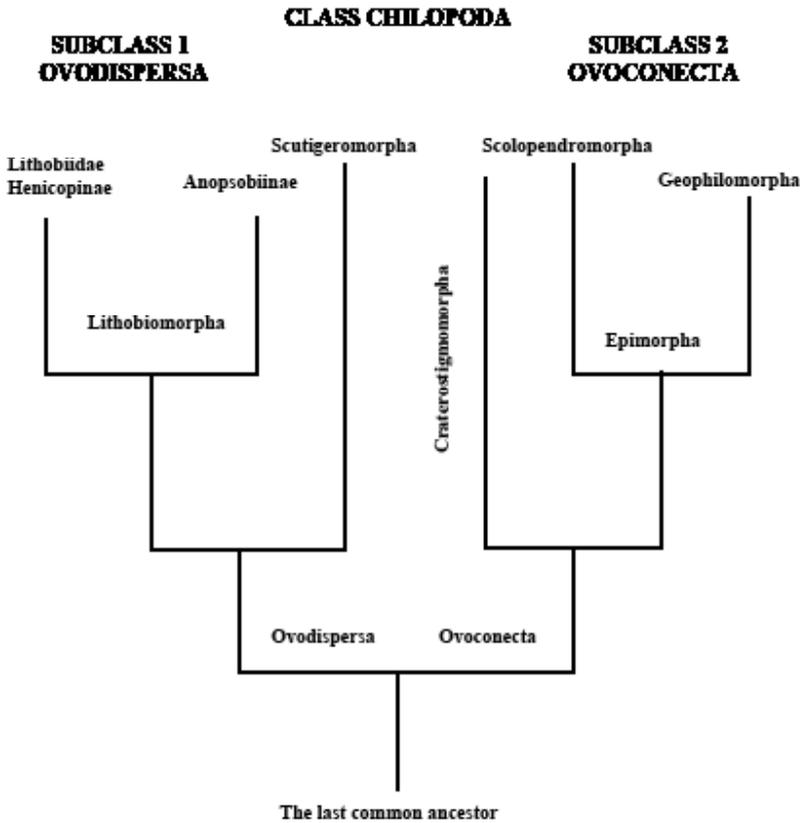
Figure 1. The new phylogenetic tree of the Class Chilopoda

a unique pile, which remains in contact with the female body and are brooded till after the eclosion.

Here is presented the new phylogenetic tree (Figure 1) corresponding to this new classification.

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Articles

The division of Norway in geographical regions – «The Strand-system».
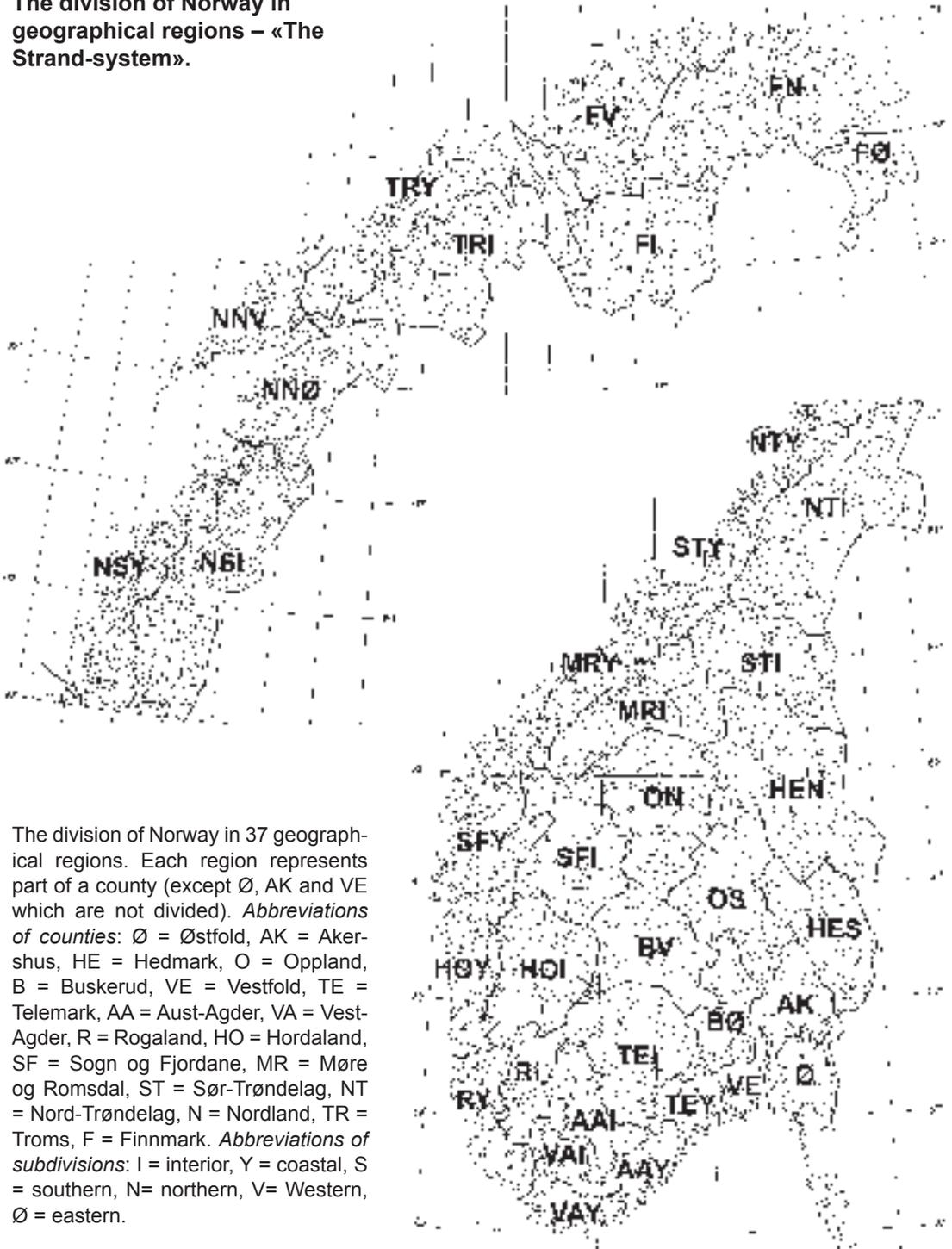
The division of Norway in 37 geographical regions. Each region represents part of a county (except Ø, AK and VE which are not divided). *Abbreviations of counties*: Ø = Østfold, AK = Akershus, HE = Hedmark, O = Oppland, B = Buskerud, VE = Vestfold, TE = Telemark, AA = Aust-Agder, VA = Vest-Agder, R = Rogaland, HO = Hordaland, SF = Sogn og Fjordane, MR = Møre og Romsdal, ST = Sør-Trøndelag, NT = Nord-Trøndelag, N = Nordland, TR = Troms, F = Finnmark. *Abbreviations of subdivisions*: I = interior, Y = coastal, S = southern, N= northern, V= Western, Ø = eastern.

The EIS-grid system of Norway

EIS-grid map of Norway based on
50x50 km squares.

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Chapter in book

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