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A study of the character 'palpal claw' in the spider subfamily Heteropodinae (Araneae: Sparassidae)

Изучение признака 'коготь пальпы' у пауков подсемейства Heteropodinae (Araneae: Sparassidae)

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ABSTRACT. The palpal claw is evaluated as a taxonomic character for 42 species of the spider family Sparassidae and investigated in 48 other spider families for comparative purposes. A pectinate claw appears to be synapomorphic for all Araneae. Elongated teeth and the egg-sac carrying behaviour of the Heteropodinae seem to represent a synapomorphy for this subfamily, thus results of former systematic analyses are supported. One of the Heteropodinae genera, *Sinopoda*, displays variable character states. According to ontogenetic patterns, shorter palpal claw teeth and the absence of egg-sac carrying behaviour may be secondarily reduced within this genus. Based on the idea of 'evolutionary efficiency', a functional correlation between the morphological character (elongated palpal claw teeth) and egg-sac carrying behaviour is hypothesized. The palpal claw with its sub-characters is considered to be of high analytical systematic significance, but may also give important hints for taxonomy and phylogenetics. Results from a zoogeographical approach suggest that the sister-groups of Heteropodinae lineages are to be found in Madagascar and east Africa and that Heteropodinae, as defined in the present sense, represents a polyphyletic group.

РЕЗЮМЕ. Коготь пальпы проанализирован как таксономический признак у 42 видов пауков семейства Sparassidae и также изучен для сравнения у 48 других семейств пауков. Гребневидный коготь, вероятно, синапоморфен для всех Araneae. Удлиненные зубцы и поведение, связанное с удерживанием яйцевого кокона, видимо, являются синапоморфными для подсемейства Heteropodinae, что поддерживает результаты более раннего систематического анализа. *Sinopoda*, один из родов Heteropodinae, демонстрирует изменчивые состояния признака. Исходя из онтогенетического паттерна, сделан вывод, что более короткие зубцы коготка и отсутствие поведения по удерживанию яйцевого кокона могут быть вторично утеряны в этом роде. Исходя из идеи 'эволюционной эффективности', предположено существование функциональной корреляции между морфологическим признаком (т.е. удлиненными зубцами когтя пальпы) и поведением по удерживанию яйцевого кокона. Показано, что коготь пальпы и его состояния имеют высокую аналитическую ценность в систематике, а также полезны для таксономии и филогенетики. Результаты зоогеографического анализа указывают на то, что сестринские группы родов Heteropodinae следует искать на Мадагаскаре и в Восточной Африке, и что Heteropodinae, в их современном объеме, являются полифилетической группой.

KEY WORDS: Sparassidae, Heteropodinae, palpal claw, character analysis, morphology, behaviour, systematics.
КЛЮЧЕВЫЕ СЛОВА: Sparassidae, Heteropodinae, коготь пальпы, анализ признаков, морфология, поведение, систематика.

Introduction

The palpal claw, as a taxonomic character for spiders, harvestmen and other chelicerates, has either not been included in former cladistic or phylogenetic analyses [Scharff & Coddington, 1997; Bosselaers & Jocque, 2000; Huber, 2000; Wang, 2002], or has been treated as one of many characters, without differential investigation of its morphology and functional relevance [e.g., Giribet *et al.*, 2002]. In the latter case, the character states considered were the absence or presence of the claw and whether it was prehensile or not. Only in a few papers has the claw itself been the subject of detailed analyses, e.g., the ontogeny and functional aspects of the claw (i.e., the course and types of muscles, tendons, etc.) [see Barrows, 1925], or the homology of certain characters [Camin *et al.*, 1958], which played an important role in scientific studies until the middle of the last century. By involving higher arachnid taxa, Dunlop [2002] provided a broader analysis of the claw, considering its phenotype, i.e., how many palpal and leg claws are present in the different arachnid groups.

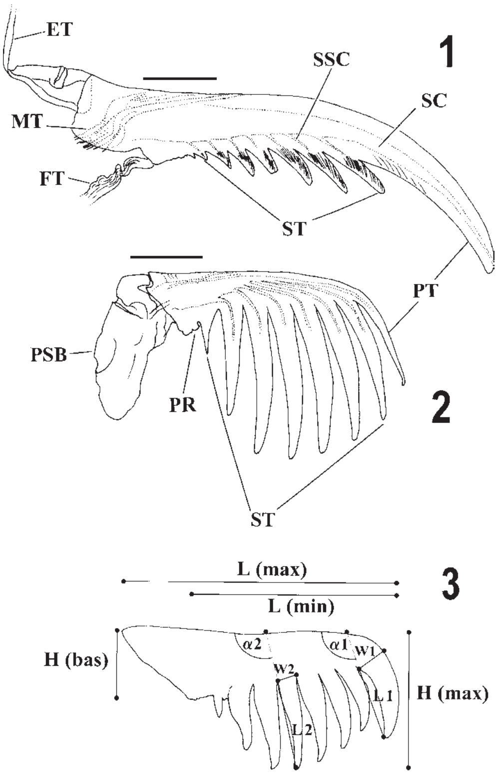
The subfamily Heteropodinae is characterized by a palpal claw with long and curved teeth [Jäger, 1998] and exclusively displays a special brood care behaviour, viz., females hold the discus-shaped egg-sac with their chelicerae, pedipalps and sometimes with the third pair of legs [Shinkai & Takano, 1984; pers. obs.]. Two species of the genus *Sinopoda* Jäger, 1999, namely *S. forcipata* (Karsch, 1881) and *S. hamata* (Fox, 1937), have palpal claw teeth that are shorter and straighter than in other species of Heteropodinae, but their egg-sac is fixed to the substrate and guarded rather than held [Shinkai & Tanako, 1984; Ono, pers. comm.; pers. obs.].

This study aims to tackle the following questions: (1) do all the *Sinopoda* species have shorter teeth on the palpal claws; (2) is short teeth a plesiomorphic or derived (i.e., a secondary reduction) state for *Sinopoda*; (3) is the egg-sac carrying behaviour correlated to long palpal claw teeth and, if yes, which of these evolved first; and (4) what is the analytical value of the morphological character 'palpal claw' for the taxonomy, systematics and phylogenetics of Heteropodinae?

Material and methods

For an outgroup comparison and polarizing characters in the subfamily Heteropodinae, 27 species of Heteropodinae, 15 species of other Sparassidae and members of 48 other spider families were examined. A list of the material examined is given in the Appendix. Preserved specimens were examined and kept in 70% alcohol. Palpal claws were examined with a Leica DM LS compound microscope with 50 to 1 000-fold magnification, according to the size of the particular claw. Illustrations were made using a camera lucida-attachment. All claws were drawn in an orthogonal view. Single palpal claws of alcohol-preserved *Heteropoda maxima* and egg-sac were used to test, whether the claws with the long teeth can practically interlock with the outer layers of the cocoon silk. Additionally, live specimens were observed in China, Laos, the laboratory in the Johannes Gutenberg-University Mainz, and the Senckenberg Research Institute Frankfurt. Film sequences of *Heteropoda maxima* were made in Laos by H. Heltorff.

Terminology for claw teeth follows Barrows [1925] (Figs 1–3): 'primary tooth' is used for the terminal tooth, 'secondary teeth' for all others. A tooth was included as such in the analysis, when its length was larger than the width of its base. Shorter teeth are here called 'primordial teeth'. Secondary teeth are numbered from distal to proximal. Measurements included in the analysis are shown in Fig. 3. The relation of length and width of the primary and the longest secondary tooth respectively were used as a comparison index between the taxa, i.e., to judge the elongation rate of the teeth. The minimum length of the claw was taken, as in some cases the claw base was broken off during preparation or the base was hidden in the palpal tip in tiny and poorly prepared individuals. The length of each prosoma was taken as a general reference for the size of the individual. All measurements were taken using a millimetric grid attached to the ocular piece of the compound microscope. Values on scale bars in illustrations are in millimetres.



Figs 1–3. Female palpal claws of Sparassidae: 1 — *Palystella* sp. (PJ 1869, paired sclerotized base omitted); 2 — *Heteropoda maxima* (PJ 1845, tendons omitted); 3 — *Sinopoda forcipata* (PJ 356, schematic diagram). ET = extensor tendon, FT = flexor tendon, H(bas) = height of claw base, H(max) = maximum height, L1 = length of primary tooth, L2 = length of longest secondary tooth, L(max) = maximum length, L(min) = minimum length, MT = medial tendon, PR = primordial teeth, PSB = paired sclerotized plate (= tendon plate), PT = primary tooth, SC = supplying channel, SSC = secondary supplying channel, ST = secondary teeth, W1 = width of primary tooth, W2 = width of longest secondary tooth, α1 = angle of primary tooth, α2 = angle of longest secondary tooth. Scale: 0.1 mm.

Рис. 1–3. Коготь пальпы самки у Sparassidae: 1 — *Palystella* sp. (PJ 1869, парные склеротизированные основания не показаны); 2 — *Heteropoda maxima* (PJ 1845, сухожилия не показаны); 3 — *Sinopoda forcipata* (PJ 356, схематическая диаграмма). ET = сухожилие разгибатель, FT = сухожилие сгибатель, H(bas) = высота основания когтя, H(max) = максимальная высота, L1 = длина первичного зуба, MT = среднее сухожилие, PR = изначальные зубцы, PSB = парная склероизированная пластинка (= сухожильная пластинка), PT = первичный зуб, SC = проводящий канал, SSC = вторичный проводящий канал, ST = вторичные зубцы, W1 = ширина первичного зуба, W2 = ширина самого длинного вторичного зуба, α1 = угол первичного зуба, α2 = угол самого длинного вторичного зуба. Масштаб: 0,1 мм.

In the introduction and discussion the three terms ‘taxonomy’, ‘systematics’ and ‘phylogenetics’, which are often used interchangeably to a degree, or are used without distinct differentiation are distinguished. In this paper I use these in the following sense: taxonomy distinguishes and describes species (‘alpha-taxonomy’), systematic research groups the species by means of shared apomorphies to taxa (‘beta-taxonomy’) and phylogenetic research traces the lineages back in the past and tries to reconstruct an entire course of evolution [Simpson, 1961; Janich *et al.*, 2001].

Abbreviations: PJ = subsequent number for Sparassidae examined by P. Jäger. For further explanations see legend of Figs 1–3.

Collections: CDPC = Dr. Christa Deeleman-Reinhold’s personal collection, Ossendrecht, The Netherlands; MHNG = Museum d’Histoire Naturelle Geneve (P. Schwendinger); MNHN = Muséum National d’Histoire Naturelle Paris (C. Rollard); NHM = Natural History Museum London (J. Beccaloni); NHMB = Naturhistorisches Museum Basel (A. Hänggi); NHMW = Naturhistorisches Museum Wien (J. Gruber); NRMS = Naturhistoriska Riksmuseet Stockholm (T. Kronestedt); QMS = Queensland Museum South Brisbane (R. Raven); SMF = Forschungsinstitut und Naturmuseum Senckenberg Frankfurt (P. Jäger); SMN = State Museum of Namibia Windhoek (T. Bird); ZFMK = Zoologisches Forschungsinstitut und Museum Alexander König (B. Huber); ZMH = Zoologisches Museum Hamburg (M. Dastych); ZMUC = Zoological Museum of the University Copenhagen (N. Scharff).

Results

General morphology of the sparassid palpal claw

In all Sparassidae, one primary, three to ten secondary teeth and up to three additional primordial teeth are present. The claw is connected by at least two tendons (Figs 1, 2): the dorsal extensor tendon and the ventral flexor tendon; the latter is first connected to the paired sclerotized structures of the base of the claw (tendon plate) and then to the muscles [Barrows, 1925; this study]. An additional distinct tendon-like element is present in all cases on the proximal dorsal part of the claw. It could not be identified unequivocally as a tendon, but its structure within the claw and the extending parts as seen in a 1 000× magnification suggests that it is a tendon (Fig. 1). However, in contrast to the others, the function of this single tendon remains unclear.

In most cases a main channel is visible within the claw, which runs from the proximal end to the tip of the primary tooth. In several cases the branching off of smaller channels into the secondary teeth is visible (Figs 1, 2). Partly visible channels are illustrated in Fig. 54.

The surface structure of the secondary teeth and of the ventral part of the primary tooth can generally be identified (Fig. 1). Differences are present only in the distinctness of the texture.

The following characters are size-dependent (Fig. 3): L(max), L(min), H(max), H(bas), L1, L2, W1, W2. The ratios L1/W1 and L2/W2 showed a slight (not significant) trend to be negatively correlated to the body size. Number of teeth, angles of teeth and the position of the longest secondary teeth are not size-dependent.

Outgroup analysis

ARANEAE (non-sparassids). In almost 75 percent of the spider taxa examined a pectinate claw is present. The primary tooth is the dominant element in every case (Figs 4–13). These findings hold true for the basal spider taxa, such as the Liphistiidae, Atypidae, Ctenizidae, Theraphosidae and Hypochilidae. In *Liphistius* spp. one to three secondary teeth are present in juveniles, whereas the adult possesses three to four teeth [Schwendinger, 1990; this study]. Dunlop [2002] illustrated an apparently smooth palpal claw of *Liphistius desultor* (Schiödte, 1849). As the claw is shown in a slightly oblique dorsolateral view, the presence of minute secondary teeth, as occur in juvenile stages cannot be excluded. In adult females of *Theraphosa blondi* (Latreille, 1804), secondary teeth were absent, whereas in a juvenile a small secondary tooth was present. In the following 34 spider families secondary teeth were present: Agelenidae, Amaurobiidae, Anyphaenidae, Araneidae, Argyronetidae[1], Atypidae, Ctenidae, Ctenizidae, Dictynidae, Eresidae, Filistatidae, Gnaphosidae, Hahniidae (in part, *Cryphoeca silvicola*), Hersiliidae, Hexathelidae, Hypochilidae, Liocranidae (in part, *Agroeca proxima*), Liphistiidae, Lycosidae, Mimetidae, Nesticidae, Oecobiidae, Oxyopidae, Philodromidae, Pisauridae, Psechridae, Selenopidae, Tetragnathidae, Theridiidae, Thomisidae, Uloboridae, Zodariidae, Zoridae and Zoropsidae. Secondary teeth of all taxa examined were shorter than the primary tooth and not elongated (ratio L2/W2 = 1.5–4.3). In Clubionidae, Dysderidae, Hahniidae (in part, *Antistea elegans*), Linyphiidae (in part, Fig. 6), Liocranidae (in part, *Phrurolithus festivus*), Nemesiidae, Segestriidae and Trochanteriidae a smooth claw is present. In Linyphiidae in part. (*Tenuiphantes mengei*, *Erigone atra*), Oonopidae, Palpimanidae, Pholcidae, Scytodidae, Sicariidae and Theridiosomatidae the palpal claw is absent. In this respect, Coddington [1990] gives an overview for Araneoidea and Deinopoidea, Hormiga [2000] for the Erigoninae and a few Araneoidea. In the Salticidae, a claw is present only in the primitive subfamilies Lyssomaninae and Spartaeinae. In *Lyssomanes viridis* (Walckenaer, 1837) and *Chinoscopus maculipes* Crane, 1943 a small smooth claw is present, whereas in *Portia fimbriata* (Doleschall, 1859) the claw is pectinate [Logunov, pers. comm.].

SPARASSIDAE (non-heteropodines). In all the studied representatives from subfamilies other than Heteropodinae, a pectinate claw with a dominant primary tooth is present (Figs 14–21). In all groups the secondary teeth are consistently shorter than the primary tooth and not elongated (ratio L2/W2 = 1.5–5.0). The angles of the teeth varies between 95° and 165° (secondary teeth: 95°–141°, primary tooth: 103°–165°). Higher values (122°–165°) refer to members of *Arandisa*, *Palystella* (Fig. 21) and *Leucorchestris*.

Heteropodinae

Within the Heteropodinae a quite inconsistent set of different character states is found (Figs 22–29). In the majority of Heteropodinae the primary tooth is shorter than most of the

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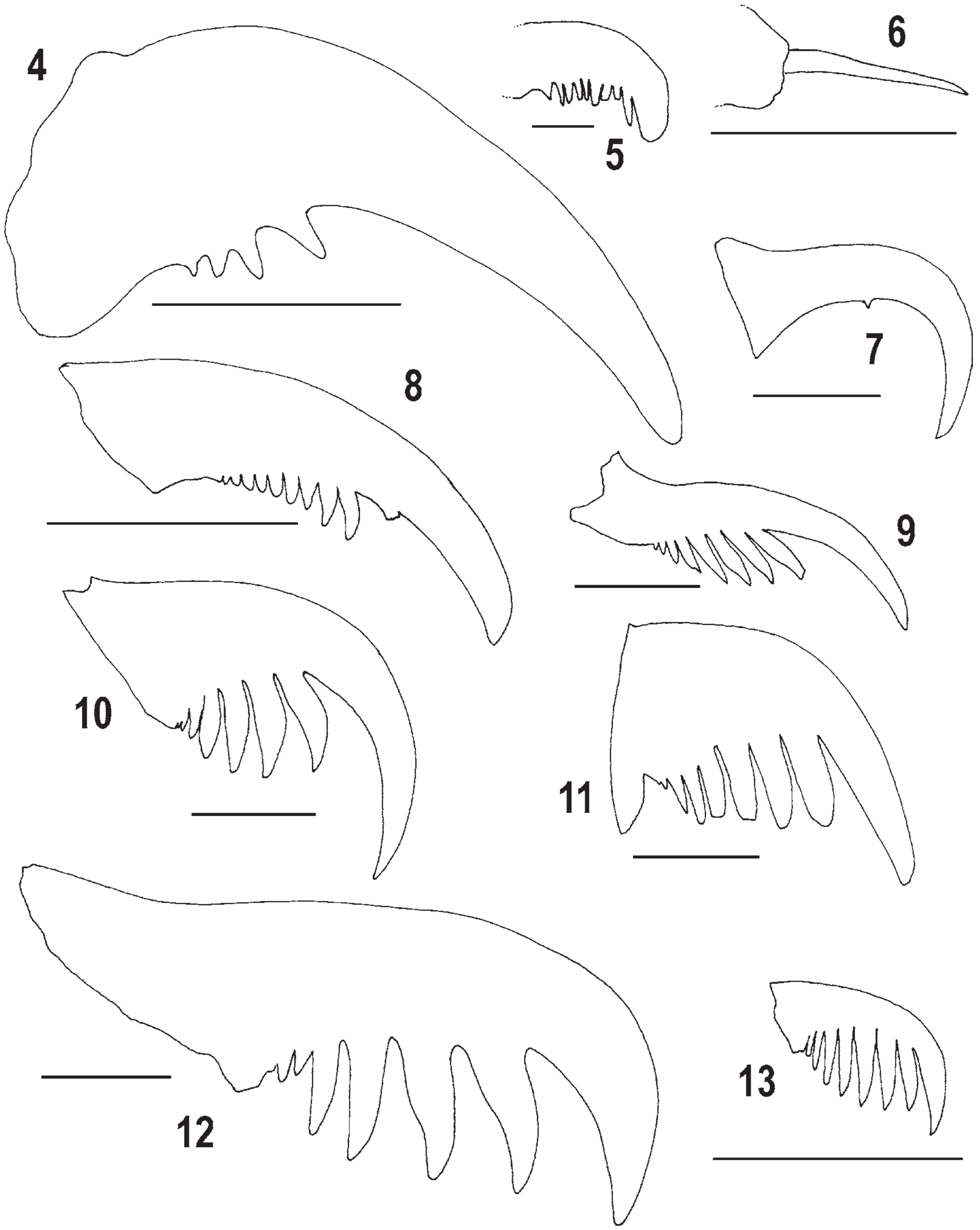
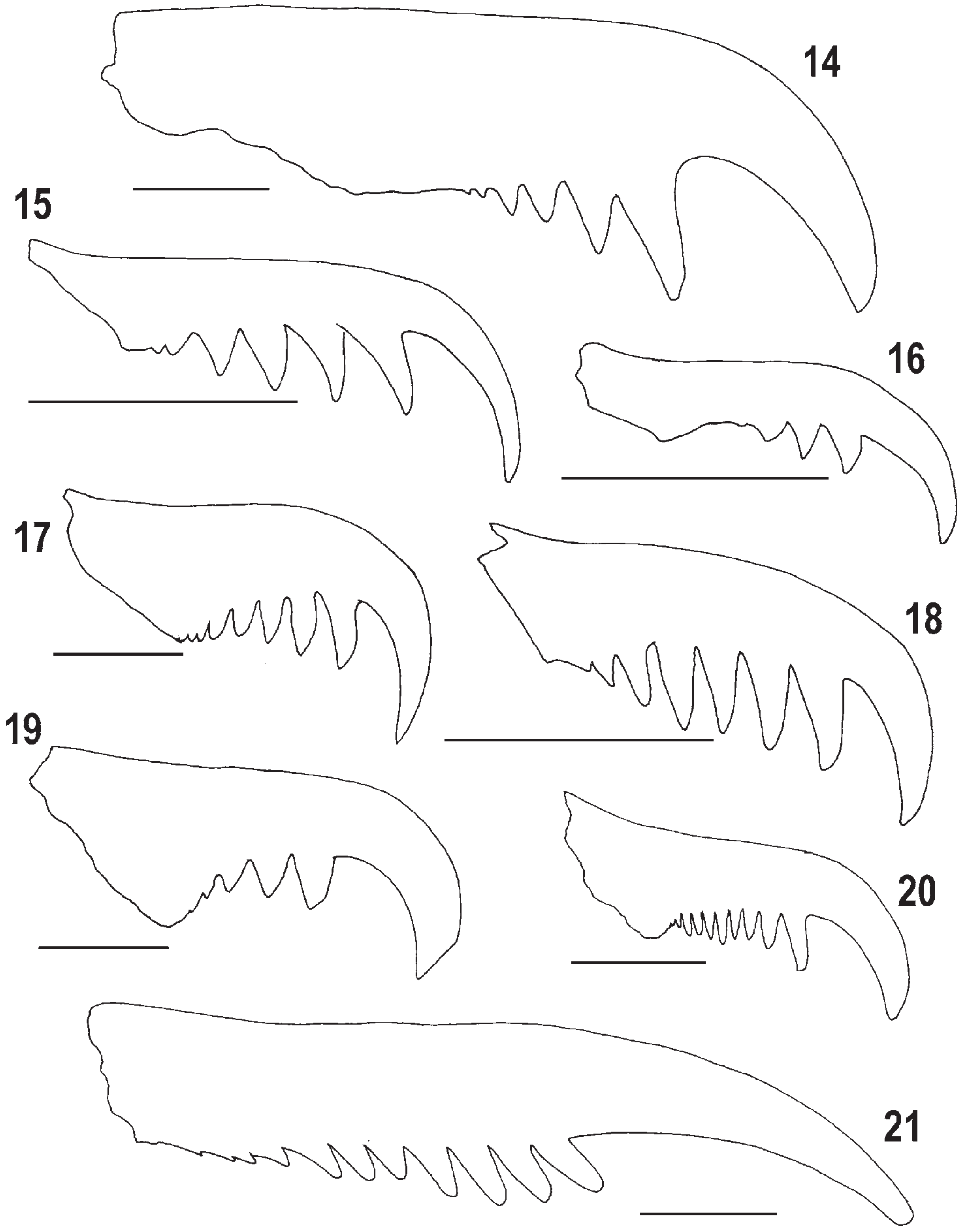
[1] In contrast to Platnick [2003] I retain the valid family name Argyronetidae Thorell, 1870 for *Argyroneta* and former Cybaeidae according to the International Code of Zoological Nomenclature [ICZN 1999: Article 23.3], i.e., Argyronetidae is not a *nomen oblitum*.



Figs 4–13. Female palpal claws of Araneae (exceptions indicated): 4 — *Liphistius malayanus*; 5 — *Uroctea* sp.; 6 — Linyphiidae sp.; 7 — *Theraphosa blondi*, juvenile; 8 — *Hypochilus gertschi*, 9 — Pisauridae sp., subadult male; 10 — Pisauridae sp.; 11 — Araneidae sp.; 12 — *Cupiennius salei*; 13 — Thomisidae sp. Scale: 4–6, 8–13 (0.1 mm), 7 (0.5 mm).

Рис. 4–13. Коготки пальпы самок у Araneae (исключения указаны): 4 — *Liphistius malayanus*; 5 — *Uroctea* sp.; 6 — Linyphiidae sp.; 7 — *Theraphosa blondi*, juvenile; 8 — *Hypochilus gertschi*, 9 — Pisauridae sp., subadult male; 10 — Pisauridae sp.; 11 — Araneidae sp.; 12 — *Cupiennius salei*; 13 — Thomisidae sp. Масштаб: 4–6, 8–13 (0,1 мм), 7 (0,5 мм).



Figs 14–21. Female palpal claws of Sparassidae (other than Heteropodinae): 14 — *Damastes* sp. (PJ 1874); 15 — *Anaptomecus* sp. (PJ 1878); 16 — *Keilira sparsomaculata* (PJ 954); 17 — *Gnathopalystes* sp. (PJ 113); 18 — *Olios lutescens* (PJ 1881); 19 — *Anchonastus plumosus* (PJ 1879); 20 — *Eusparassus* sp. (PJ 1861); 21 — *Leucorchestris arenicola* (PJ 1860). Scale: 0.1 mm.

Рис. 14–21. Коготки пальпы самок у Sparassidae (другие чем Heteropodinae): 14 — *Damastes* sp. (PJ 1874); 15 — *Anaptomecus* sp. (PJ 1878); 16 — *Keilira sparsomaculata* (PJ 954); 17 — *Gnathopalystes* sp. (PJ 113); 18 — *Olios lutescens* (PJ 1881); 19 — *Anchonastus plumosus* (PJ 1879); 20 — *Eusparassus* sp. (PJ 1861); 21 — *Leucorchestris arenicola* (PJ 1860). Масштаб: 0,1 мм.

secondary teeth, which are elongated (ratio L2/W2 = 3.4–9.9), this is in contrast to other Sparassidae subfamilies. To answer the question as to whether the Heteropodinae have the secondary teeth elongated compared to other Sparassidae, or the primary tooth reduced, or both, L(min) and H(bas) were taken as the reference sizes: the ratio L2/L(min) = 0.26–1.07 in Heteropodinae (0.11–0.33 in other Sparassidae), L1/L(min) = 0.27–0.71 in Heteropodinae (0.30–0.58 in other Sparassidae). Ratio L2/H(bas) = 0.94–3.35 in Heteropodinae (0.34–1.18 in other Sparassidae), L1/H(bas) = 0.59–2.40 in Heteropodinae (0.90–3.30 in other Sparassidae). Despite some overlapping, it is clear from these comparisons that the secondary teeth are elongated in the Heteropodinae compared to other Sparassidae. A reduction of the primary tooth in the Heteropodinae is only weakly supported using H(bas) as the reference.

The angles of the claw teeth in the Heteropodinae (excluding *Sinopoda*) are 90° to 122° (secondary teeth: 90°–104°, primary tooth: 90–122°). The range is slightly shifted towards lower angles in contrast to other Sparassidae, lower than 100° were present in 75 percent of specimens examined.

Sinopoda

Palpal claws of the 17 *Sinopoda* species examined varied distinctly in shape and the ratios investigated, in contrast to the preliminary observations (Figs 23, 30–43). Besides having really shorter secondary teeth (ratio L2/W2 = 3.8–4.9), the majority of *Sinopoda* species have intermediate to very long secondary teeth (ratio L2/W2 up to 9.4). In some cases it was not even clear whether the original length of each tooth was present. It is assumed that in some cases (see Fig. 36) the teeth could be worn down due to walking on rocky substrates, e.g., in cave ecosystems. In addition, the angles of the claw teeth are more variable (78°–143°). No correlation could be found between the different states of the characters listed and the habitat in which the spider lives (cave, under tree bark, rock crevices, leaf litter). In conclusion, *Sinopoda* species have numerous different claw tooth character states; shorter secondary teeth are present in only a few species.

Claw teeth in ontogeny

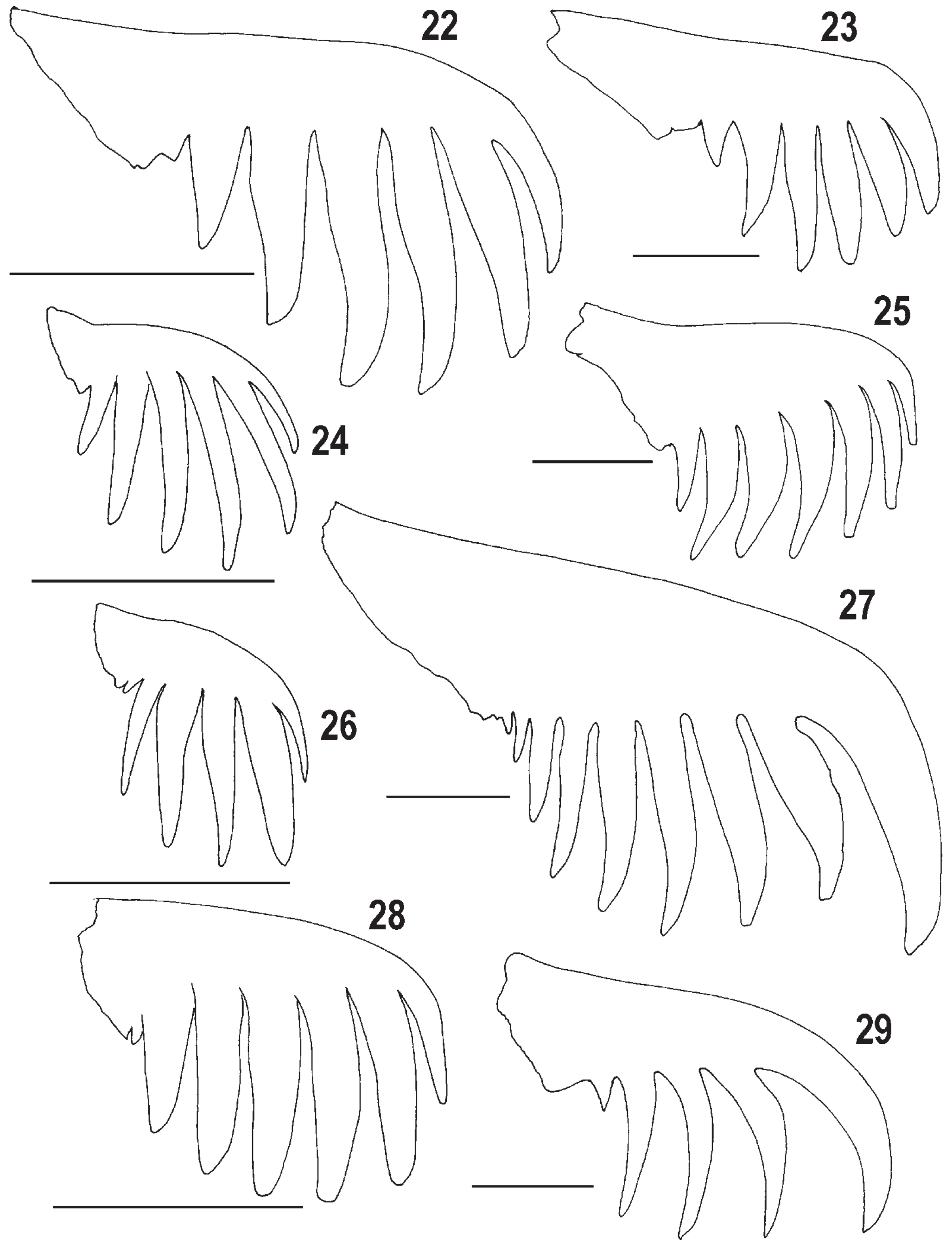
Due to the lack of large, suitable series, ontogenetic investigations could only be done for four species: *Heteropoda maxima* from Laos, two *Sinopoda* species, one from China and one from Indonesia (Sulawesi), and *Spariolenus* sp. from Oman; the last is treated in the following paragraph. First instars of the first three species have long secondary teeth (Figs 38–46) (ratio L2/W2 = 6.7–8.6), which are retained in *H. maxima* (7.5; adult 9.9). In the two *Sinopoda* species, the ratio decreased during individual growth (4.8–5.3; adult 4.5–5.5).

The number of teeth increases during the ontogenetic development of a spider. This was observed for *Liphistius* spp., *Heteropoda maxima* (Figs 44–46), *Sinopoda* spp. (Figs 38–43) and *Spariolenus* sp. (Figs 47–49). In *Theraphosa blondi*, the juvenile examined had one tooth, which was absent (reduced?) in the adult female. From the position of the primordial teeth and the consistent shape and arrangement of the distal teeth it is hypothesized that new teeth originate on the proximal part (base) of the claw.

Intermediate forms and geographical distribution

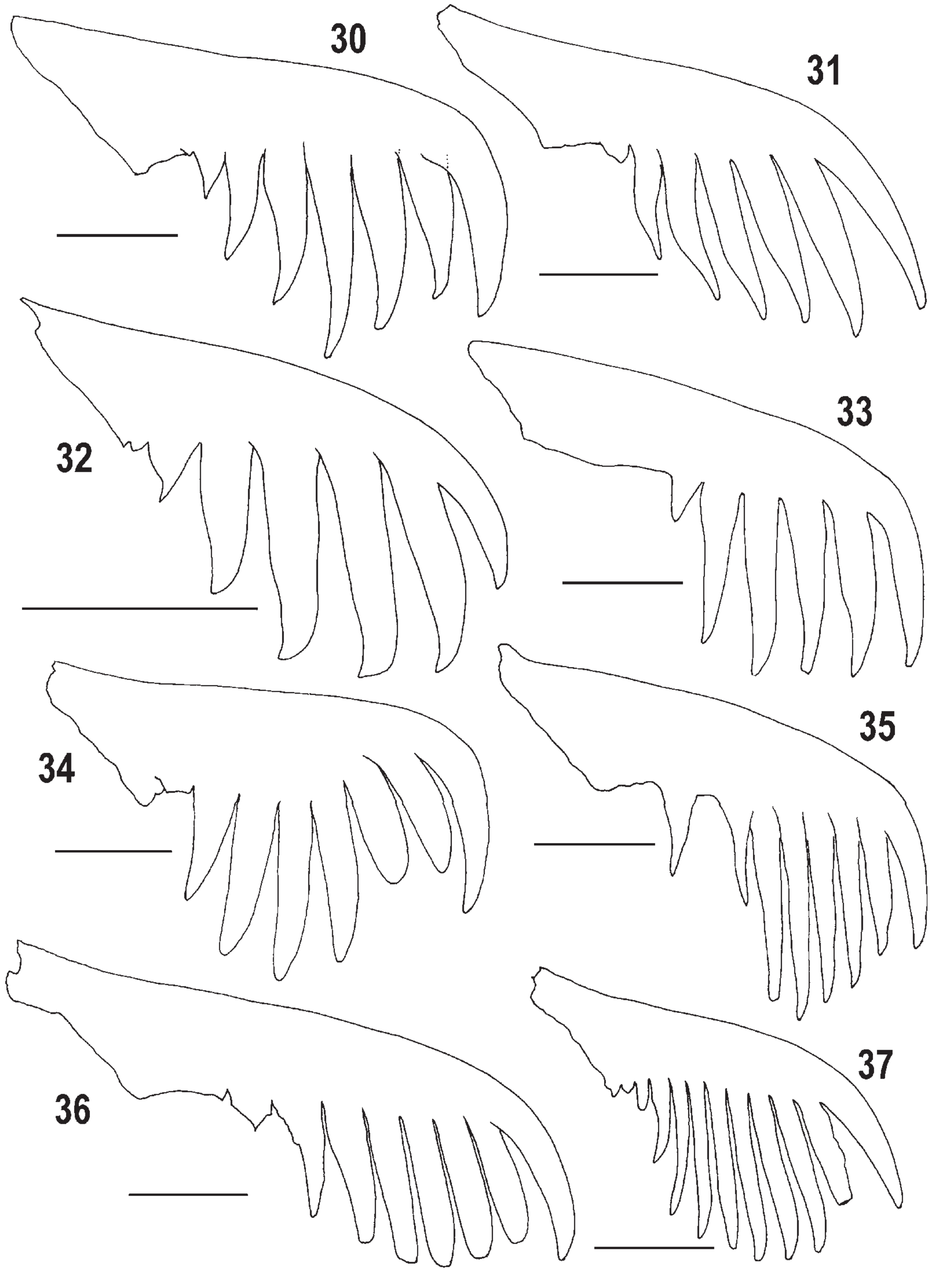
Representatives of Heteropodinae are found in Asia, Australia and one genus (*Barylestis*) is known from Africa [Jäger, 2001, 2002]. The majority of Heteropodinae species found in Asia and Australia belong to the genera *Heteropoda* and *Pseudopoda* and have claws with elongated secondary teeth (Fig. 57). In only a few Heteropodinae (genera *Barylestis, Pandercetes* and *Spariolenus*), are the secondary teeth not distinctly elongated, in one *Spariolenus* species from Oman they are even shorter than the primary tooth (Figs 47–49, 57). The ontogenetic pattern reveals that even the younger stages of the latter species have no elongation of the secondary teeth. In *Pandercetes*, a genus with bark-dwelling representatives, all teeth except for a very small one are of similar size (Fig. 29), whereas in *Barylestis* spp. the primary tooth and the third secondary tooth are similar in size, but all others are smaller (Fig. 27).

Three Sparassidae show a potential relationship with the Asian Heteropodinae through



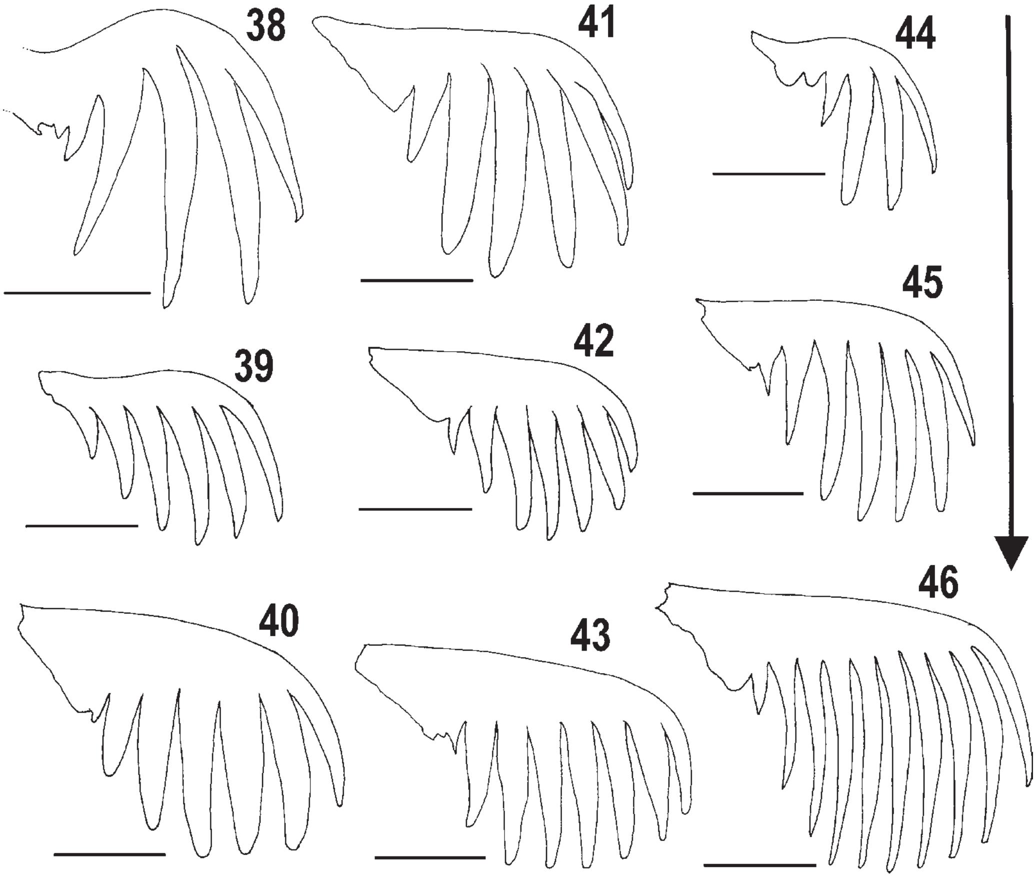
Figs 22–29. Female palpal claws of Heteropodinae: 22 — *Pseudopoda bibulba* (PJ 1716); 23 — *Sinopoda* sp. (PJ 917); 24 — Heteropodinae sp. (PJ 1228); 25 — *Heteropoda* sp. (PJ 1864); 26 — Heteropodinae sp. (PJ 1205); 27 — *Barylestis occidentalis* (PJ 1608); 28 — Heteropodinae sp. (PJ 1205); 29 — *Pandercetes* sp. (PJ 1867). Scale: 22–24, 26–29 (0.1 mm), 25 (0.2 mm).

Рис. 22–29. Коготки пальпы самок у Heteropodinae: 22 — *Pseudopoda bibulba* (PJ 1716); 23 — *Sinopoda* sp. (PJ 917); 24 — Heteropodinae sp. (PJ 1228); 25 — *Heteropoda* sp. (PJ 1864); 26 — Heteropodinae sp. (PJ 1205); 27 — *Barylestis occidentalis* (PJ 1608); 28 — Heteropodinae sp. (PJ 1205); 29 — *Pandercetes* sp. (PJ 1867). Масштаб: 22–24, 26–29 (0,1 мм), 25 (0,2 мм).



Figs 30–37. Female palpal claws of *Sinopoda* spp.: 30, 32–37 — *Sinopoda* sp. (30 — PJ 323, 32 — PJ 895, 33 –PJ 1816, 34 –PJ 919, 35 — PJ 1815, 36 — PJ 1804, 37 — PJ 916); 31 — *Sinopoda microphthalma* (PJ 696). Scale: 0.1 mm.

Рис. 30–37. Коготки пальпы самок у *Sinopoda* spp.: 30, 32–37 — *Sinopoda* sp. (30 — PJ 323, 32 — PJ 895, 33 — PJ 1816, 34 — PJ 919, 35 — PJ 1815, 36 — PJ 1804, 37 — PJ 916); 31 — *Sinopoda microphthalma* (PJ 696). Масштаб: 0,1 мм.



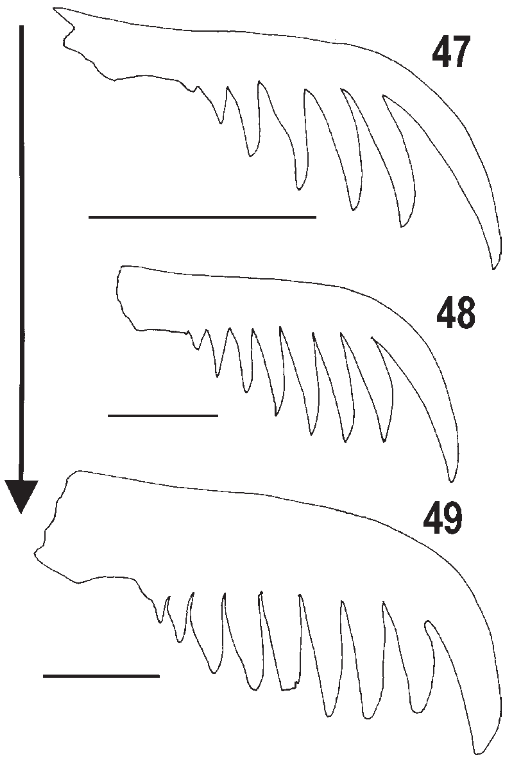
Figs 38–46. Ontogenetic stages of palpal claws of Heteropodinae (arrow indicates the course of development): 38–43 — *Sinopoda* sp. (38 — PJ 1832, juv.; 39 — PJ 1825, juv.; 40 — PJ 1822, ♀; 41 — PJ 1833, juv.; 42 — PJ 1819, juv; 43 — PJ 909, ♀); 44–46 — *Heteropoda maxima* (44 — PJ 1843, juv.; 45 — PJ 1848, juv.; 46 — PJ 1844, subadult ♀). 41 — mirrored from original. Scale: 38 (0.025 mm), 39, 41, 44 (0.05 mm), 40, 42–43, 45 (0.1 mm), 46 (0.2 mm).

Рис. 38–46. Стадии онтогенеза коготков пальпы у Heteropodinae (стрелка указывает направление развития): 38–43 — *Sinopoda* sp. (38 — PJ 1832, juv.; 39 — PJ 1825, juv.; 40 — PJ 1822, ♀; 41 — PJ 1833, juv.; 42 — PJ 1819, juv; 43 — PJ 909, ♀); 44–46 — *Heteropoda maxima* (44 — PJ 1843, juv.; 45 — PJ 1848, juv.; 46 — PJ 1844, неполовозрелая ♀). 41 — зеркально изображение. Масштаб: 38 (0,025 мм), 39, 41, 44 (0,05 мм), 40, 42–43, 45 (0,1 мм), 46 (0,2 мм).

their congruity in somatic and genitalic characters [P. Jäger, pers. data]. In one undescribed Sparassidae from Tanzania, the secondary teeth are slightly elongated, whereas the primary tooth is distinctly shorter (Fig. 52). This conformation resembles the typical Heteropodinae lineage, which is represented by the majority of known species. Another undescribed Sparassidae from Madagascar shows a dominant primary tooth and an only slightly elongated first secondary tooth, which is distinctly different from those in non-heteropodine Sparassidae (Fig. 51). The palpal claw of *Berlandia* spp. from Tanzania shows a similar shape (Fig. 50), as do at least the younger stages of *Spariolenus* sp. from Oman: a dominant primary tooth and similar angles of all teeth (102°–126° in *Spariolenus*, 123°–133° in *Berlandia*).

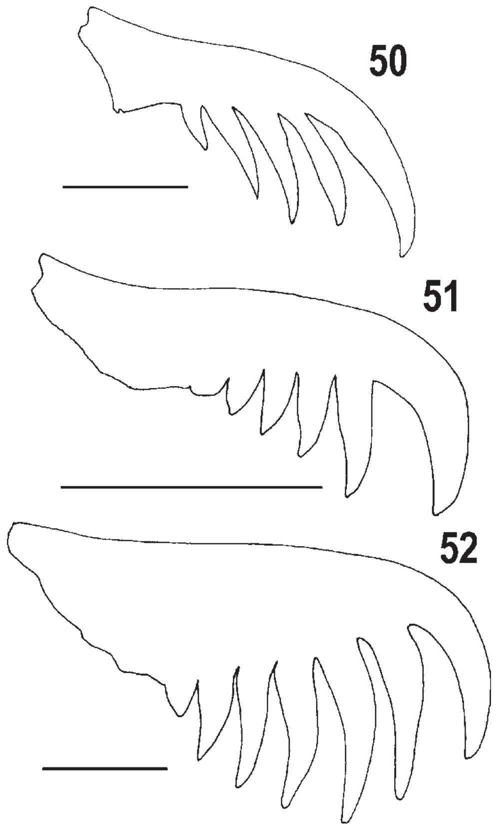
Additional findings on morphology and behaviour

In a juvenile of *Sinopoda microphthalma* (PJ 1835), a partly doubled claw tooth was found (Figs 53, 54). Hartman [1904] illustrated only entire doubled claws or entire claw rows as malformations.



Figs 47–49. Ontogenetic stages of palpal claws of *Spariolenus* sp. (arrow indicates the course of development): 47 — PJ 1865, juv.; 48 — PJ 1866, juv.; 49 — PJ 1470, ♀. Scale: 0.1 mm.

Рис. 47–49. Стадии онтогенеза коготков пальпы у *Spariolenus* sp. (стрелка указывает направление развития): 47 — PJ 1865, juv.; 48 — PJ 1866, juv.; 49 — PJ 1470, ♀. Масштаб: 0,1 мм.



Figs 50–52. Female palpal claws of Sparassidae: 50 — *Berlandia* sp. (PJ 1870); 51–52 — Sparassidae sp. (51 — PJ 1360, 52 — PJ 1291). Scale: 0.1 mm.

Рис. 50–52. Коготки пальпы самок у Sparassidae: 50 — *Berlandia* sp. (PJ 1870); 51–52 — Sparassidae sp. (51 — PJ 1360, 52 — PJ 1291). Масштаб: 0,1 мм.

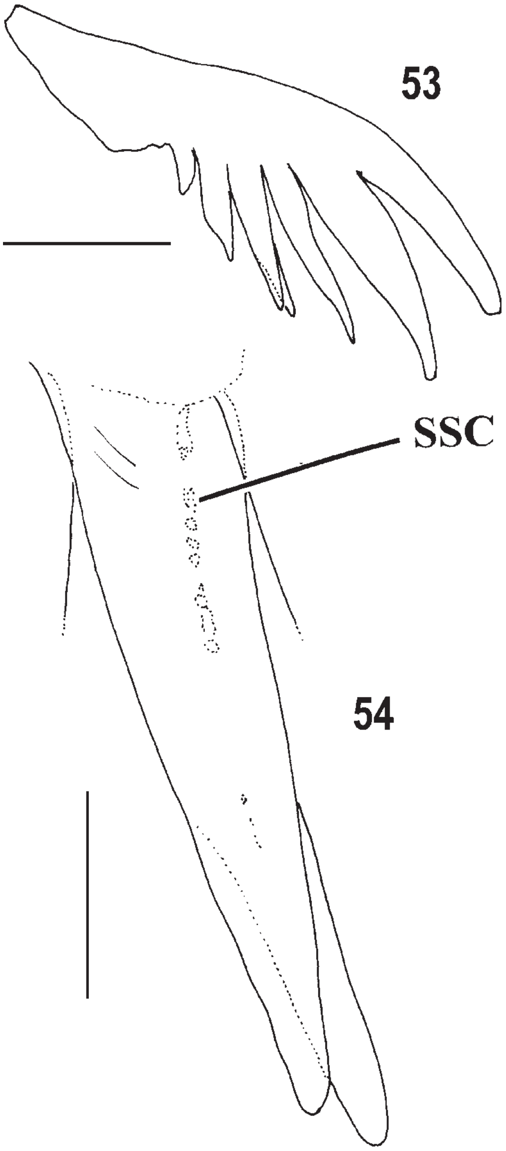
The special brood care behaviour (carrying the egg-sac) was observed exclusively in species of Heteropodinae (*Heteropoda maxima, H. venatoria*). Levy [1989] observed the behaviour in*Heteropoda variegata* (Simon, 1874). The tips of the palpal claws are in direct contact with the egg-sac. More detailed observations on living specimens were not possible due to the great speed of the individuals and because of their large size, which inhibits observations, e.g., in a petri-dish under the stereomicroscope. Tests with claws of preserved specimens reveal that the claw teeth of *Heteropoda maxima* can penetrate the outer layers of the cocoon silk (Fig. 56). Moreover, they could hold the weight of the egg-sac, i.e., claw teeth did not break off, although the wet (alcohol-preserved) egg-sac was far heavier than a dry one.

Discussion

In recent phylogenetic (cladistic) analyses, many taxonomic characters are often examined to analyse relationships within animal groups [e.g., Giribet *et al.*, 2002]. The characters are usually considered to be equally weighted in these analyses. Graybeal [1998] demonstrated that in order to produce a better phylogenetic analysis it is preferable to include more taxa than more characters. In the present study, the focus is set only on the palpal claw to better evaluate it in a more appropriate way.

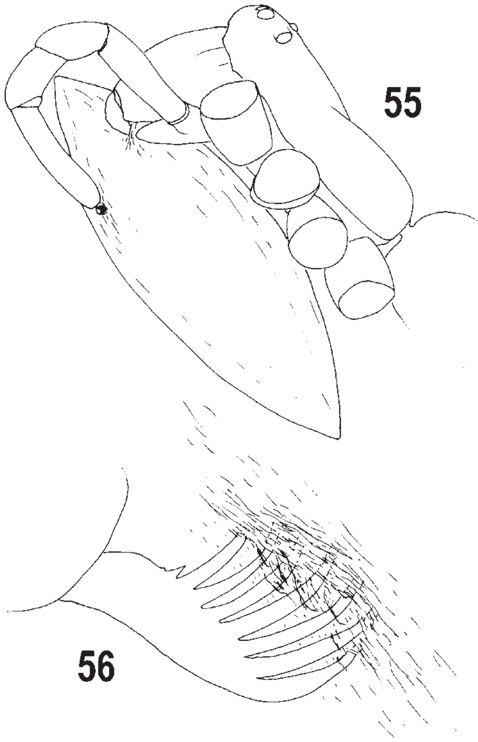
Sub-characters of the palpal claw

Several sub-characters were apparently size-dependent and were therefore excluded as single characters from the analysis. However, some



Figs 53–54. *Sinopoda microphthalma*, juv. (PJ 1835): 53 — palpal claw; 54 — doubled claw tooth, magnified. SSC — secondary supplying channel. Scale: 53 (0.1 mm), 54 (0.025 mm).

Рис. 53–54. *Sinopoda microphthalma*, juv. (PJ 1835): 53 — коготок пальпы; 54 — двойной коготок пальпы, увеличено. SSC — вторичный проводящий канал. Масштаб: 53 (0,1 мм), 54 (0,025 мм).



Figs 55–56. Schematic diagram showing the position of a female spider of Heteropodinae, carrying its egg-sac. 55 — overall view (opisthosoma and all appendages omitted, excluding the left palp); 56 — detail of palpal tip showing how the elongated claw teeth interlock in the outer layer of the egg-sac silk.

Рис. 55–56. Схематическая диаграмма, показывающая позицию самки Heteropodinae, несущую яйцевой кокон. 55 — общий вид (опистосома и все конечности, кроме левой пальпы, не показаны); 56 — lеталь кончика пальпы, показывающая как длинные зубцы когтя цепляют внешний слой шелка яйцевого кокона.

of them were included in ratios and their comparisons. The channels observed in the palpal claws are interpreted here as supply channels for the growing claw, which become redundant when filled and sclerotized like the surrounding chitin. Partially visible channels are considered partly filled. As the channels do not show distinct and consistent differences throughout the taxa examined, they are also excluded as an analytical character. The cuticular texture of the palpal claw teeth (Fig. 1) varies between different taxa without a recognizable pattern and seems to have no diagnostic value. It is interpreted here as 'fabricational noise' (as defined by Seilacher [1973]), i.e., a consequence of growth. Therefore this character was not considered further in this study.

'Palpal claw' in Araneae

For determining the polarity of the character states, 'smooth claw' vs. 'pectinate claw', a

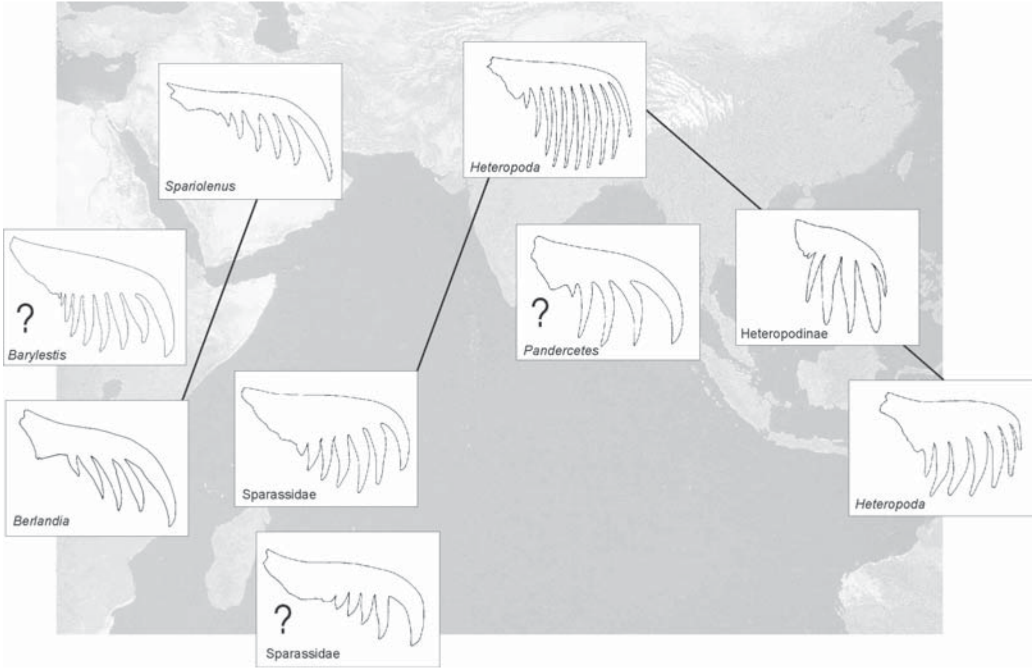


Fig. 57. Different character states of the palpal claws of female Sparassidae, and their geographical distribution with hypothetical interrelationships. For further explanations see text.

Рис. 57. Различные состояния признака когтя пальпы самки у Sparassidae, их географическое распространение и гипотетические взаимоотношения. Остальные объяснения в тексте.

closer look at Chelicerata other than Araneae could be helpful. Dunlop [2002] showed that a triple appendage ('apotele') without any teeth seems to be the plesiomorphic state within the Chelicerata. In the Araneae palp, the three different parts of the apotele are reduced to one single element, only in adult males is the apotele entirely reduced. A pectinate claw is likely to be a synapomorphy for the Araneae, whereas smooth claws or the absence of a claw (e.g., in Linyphiidae or Salticidae) are considered reductions [Hormiga, 2000; present data]. In the Opiliones, the opposite polarity has been proposed: a smooth claw is considered plesiomorphic and a pectinate claw is thought to be a derived state [Giribet *et al.*, 2002], whereas the absence or presence is polarized in the same way as in the Araneae: the presence of the claw as plesiomorphic and its reduction or absence as apomorphic [Shultz, 1998; Giribet *et al.*, 2002]. No matter, how often and under which circumstances a pectinate claw has been evolved and further retained or reduced within the Chelicerata, all these data support a pectinate claw as being a synapomorphy for the Araneae.

'Palpal claw' in Heteropodinae

From the distribution of character states within the Sparassidae it seems likely that the elongated teeth in the Heteropodinae represent a synapomorphy for this subfamily. However, the distribution of character states alone can act only as a weak source of information for the polarization of character states. In contrast, the analysis and understanding of the functional significance of certain characters, and recognition of a possible increase in their efficiency in the course of evolution are far more important [Peters & Gutmann, 1971; Kraus, 1998; Grasshoff, 2001]. Do the elongated teeth in Heteropodinae represent a more efficient structure to carry an egg-sac than shorter teeth do? Before addressing this question, it has to be clarified as to whether there is a functional correlation between this morphological character and the behaviour. Two observations support a functional link: both characters occur exclusively in the Heteropodinae and the tips of the palpal claws are in direct contact with the egg-sac. Moreover, tests with preserved specimens and egg-sacs have shown that the elongated palpal claw teeth can be practically used as a securing structure, because the teeth can penetrate the outer layer of the cocoon-silk and can endure the weight of an egg-sac. When a spider is sitting on a vertical surface, e.g., a tree trunk or a cave wall, the palpal claw will act most efficiently, in those positions in which the palps do not protect the egg-sac from a 'fall down', i.e., when the spider is facing upwards. In this position the bent claw teeth are directed upwards and when embedded in the cocoon silk, stop the egg sac from falling due to gravity (Figs 55, 56).

An increased need for an additional securing mechanism, whilst carrying the egg-sac in Heteropodinae may also be explained by the running speed of these spiders and their life style: free-living in contrast to web-building, egg-sac carrying spiders, such as Scytodidae or Pholcidae [Montgomery, 1903; Dabelow, 1958; Bürgis, 1990].

In general, it has to be stated that the palpal claws or other structures of the palpal tips would most likely only be useful for carrying the egg-sac during an emergency-type situation, e.g., where the chelicerae are not working properly or have to be removed from the egg-sac during an escape. The general necessity for such an emergency situation is apparently present at least for *Heteropoda maxima*, as few females lost their egg-sac during their escape from capture in Laotian caves. Nevertheless, if we presuppose a functional link between elongated claw teeth and egg-sac carrying, those spiders who can carry their brood, may have advantages: they can defend their offspring against parasites, predators or unsuitable climatic conditions, and are even able to take the young spiders to a place with good prey abundance or climatic conditions, just before they hatch. This trait is probably one of the secrets behind the success of the Heteropodinae, particular genera of which represent the dominant groups of Sparassidae in south-east Asia.

It may be added that *Pandercetes* species, which have no palpal claws with elongated secondary teeth, fix their cocoon to the bark of trees [Mascord, 1970] and guard it by sitting over it.

Which evolved first: longer claw teeth or egg-sac carrying?

Representatives of subfamilies of Sparassidae other than Heteropodinae are known to fix their cocoon in rolled leaves (*Rhitymna ingens*) [Jäger, 2003], in silken nests (*Micrommata virescens; Nonianus pictus; Palystes castaneus, P. superciliosus*) [Nielsen, 1932; Levy, 1989; Croeser, 1996], behind bark (*Delena cancerides*) [Mascord, 1970] or in burrows in the soil (*Cebrennus villosus*) [Jäger, 2000]. It seems most likely that the special behaviour of egg-sac carrying in Heteropodinae has to be considered apomorphic, as was suggested for the elongated teeth of the palpal claw. With reference to one of the initial questions, i.e., which evolved first: the long-toothed claw or the egg-sac carrying behaviour, I hypothesize in terms of the engineering morphology of the 'Frankfurter Evolutionstheorie' [Gudo *et al*., 2002; Campbell & Reece, 2003: 564] that if the teeth had evolved first (an idea supported by the appearance of long teeth in all ontogenetic stages), then the behaviour could be seen as a response to this morphological structure, to obtain all possible advantages arising from the available morphology in a specific environment. When the cocoon has previously been carried with shorter teeth, followed by the subsequent evolution of longer teeth, a correlation is more unlikely, but cannot be excluded. In the latter case a non-correlation should seriously be taken into account. In any case, the direction of the evolution seems to be clear: from shorter teeth in Araneae and Sparassidae other than Heteropodinae, to elongated teeth in Heteropodinae.

Analytical value of the character 'palpal claw'

Apart from all the above considerations of the function of the palpal claw and its long teeth in the Heteropodinae, there is strong evidence that this character has a high value for analyzing systematic relationships between sparassid spiders. For example, the exclusion of the Australian genus *Keilira* from the Heteropodinae by Jäger [2001, 2002; cf. Hirst, 1989] is also supported by the absence of elongated palpal claw teeth, (in conjunction with the fact that *Keilira* spp. lack other characters typical of Heteropodinae). The same seems to be true for the related genus *Irileka*, which was also placed in the Heteropodinae by Hirst [1998]. The general taxonomic value of the claw teeth in spiders was rejected by Hartmann [1904]. As he only referred to the number of teeth and its variability, he apparently did not recognize that the claw may possess differences in its shape, which can sometimes be used to distinguish taxa at species level. He was right though, that the number of teeth should only be included in a taxon's diagnosis if the number remained consistent in individuals of a population.

The examples of the 'palpal claw' character states found in *Barylestis*, *Pandercetes*, *Spariolenus* and the undescribed Sparassidae, in conjunction with the zoogeographical considerations, illustrate that this character may be of some use when reconstructing phylogenies (Fig. 57). However, it may be recognized that the Heteropodinae as diagnosed by Jäger [2001, 2002] are probably polyphyletic. If *Berlandia* and the undescribed taxa from Africa were included in Heteropodinae *sensu lato*, it would contain at least two different lineages: one represented by *Berlandia* and *Spariolenus*, and the second consisting of the undescribed taxa from Africa with the typical representatives of the Heteropodinae (Fig. 57).

Conclusions

The following conclusions are drawn: (1) A pectinate claw is synapomorphic for all Araneae; (2) long teeth and egg-sac carrying behaviour in Heteropodinae are apomorphic for Sparassidae; (3) shorter teeth in some *Sinopoda* species are secondarily reduced; (4) the special brood care behaviour is probably linked with the long palpal claw teeth, which probably evolved first; (5) The character 'palpal claw' is useful for systematic analyses in the Sparassidae and should also be considered in studies of other spider groups.

Further studies should concentrate on investigating the brood care behaviour of representatives of other Heteropodinae genera and related taxa. A geographical focus on east Africa and Madagascar may help discern the origins of the Heteropodinae and their special traits.

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Appendix

Alphabetical lists of the taxa examined (taxon name, sex, collection, PJ number: [translated] text of label) sorted by taxon group and name, sex, PJ number and locality respectively.

Sparassidae (Heteropodinae)

Barylestis occidentalis (Simon, 1887): 1 ♀ (ZMUC, PJ 1608), Uganda, Tank Hill, Kampala, 29.06.1970, H. Gorget [Gonget?].

Heteropoda cf. *maxima* Jäger, 2001: 1 juvenile (SMF, PJ 1846), Laos, Khammouan Prov., Ban Tathot, Karst cave Tham Deua, entrance *c*. 200 m a.s.l., 21.02.2003, P. Jäger; 1 juvenile (SMF, PJ 1848), same locality, entrance area and Karst cave Tham Kamouk, entrance *c*. 200 m a.s.l., 20.02.2003, P. Jäger.

Heteropoda maxima Jäger, 2001: 1♀ (SMF, PJ 1838), Laos, Khammouan Prov., Thakek, Ban Tham, 161 m a.s.l., cave, P. Jäger, egg sac, leg. 27.02.2003, dead: 10.03.2003; 1 juvenile (SMF, PJ 1839), same province, Thakek, Kouanphavang, cave, P. Jäger, egg sac, leg. 28.02.2003, hatched: 1.04.2003, dead: 5.05.2003, 2. nymphal stage; 1 juvenile (SMF, PJ 1840), same locality, P. Jäger, egg sac, leg. 28.02.2003, hatched: 10.04.2003, dead: 20.05.2003, 3. nymphal stage; 1 juvenile (SMF, PJ 1841) same locality, P. Jäger, egg sac, leg. 28.02.2003, hatched: 1.04.2003, dead: ?, 4. nymphal stage; 2 juveniles (SMF, PJ 1844–1845), same prov., Thakek, Kouanphavang, *c*. 180 m a.s.l., cave, 28.02.2003, P. Jäger; 1 juvenile (SMF, PJ 1842), same locality, P. Jäger, egg sac, leg. 28.02.2003, hatched: 1.04.2003, dead: 25.06.2003, 5. nymphal stage; 1 juvenile (SMF, PJ 1843), same locality, P. Jäger, egg sac, leg. 28.02.2003, hatched: 1.04.03, dead: 1.04.03, 1. nymphal stage.

Heteropoda sp.: 1 ♀ (SMF, PJ 1864), W Malaysia, Ulu Gombak FSC, on bamboo, spider with prey, 16.08. 1994, D. Kovac.

Heteropodinae sp.: 1 ♀ (NHM, PJ 1228), Malaysia, Sarawak, Mulu Exped., Camp I, MDF, leaf litter or? waterfall, 24.05.1978, F. Wanless; 1 ♀ (NHM, PJ 1205), same area, Melnian Gorge [?], Shrub layer, 20.06.1978, F. Wanless.

Heteropodinae sp.: 1 ♀ (ZMH, PJ 926), Neu Pommern, S.W. Küste, Liebliche Inseln, Fam. Sparassidae, Genus *Heteropoda*, N° 339, Hambg. Südsee-Exp., 01.1909, Dr. G. Duncker.

Pandercetes sp.: 1 ♀ (SMF, PJ 1867), Sri Lanka, Duballa, Upul inragith, WHTS[5?].0003, Photo, S. Benjamin ded. 2003, 28.04.1999.

Pseudopoda bibulba (Xu et Yin, 2000): 1 subadult ♂, 1 ♀ (SMF, PJ 1868, 1716), China, Yunnan Prov., Kunming, Xi Shan, forest, leaf litter, 02.04.1999, P. Jäger.

Sinopoda forcipata (Karsch, 1881): 1 ♀ (NHMB-551 det. as *Heteropoda aulica*, PJ 356), Japan, Yokohama, G. v. R. Merian.

Sinopoda hamata (Fox, 1937): 1 ♀ (SMF, PJ 1799), China, Sichuan, Prov., Emei Shan, 03.1999, dead 20.07. 1999, P. Jäger; 3 juvenile ♀ (SMF, PJ 1801), same locality, walls of monastery, at night, 29.03.1999, P. Jäger.

Sinopoda microphthalma (Fage, 1929): 1 ♀ (MNHN-1758, the holotype of *Panaretidius microphthalmus*, PJ 696), Selangor, Batu Caves, Buston 1913, Pendlebury; 2 juveniles (MNHN-1758, PJ 1834–1835), Selangor, Batu Caves, Buston, 1913, Pendlebury.

Sinopoda sp.: 1 ♀ (MHNG, PJ 1804), Thailand, Mae Hong Son Prov., Tham Lond, in the cave Pai, 19.11.2000, P. Dankittipakul; 1 ♀ (MHNG, PJ 1815), same prov., Pha Tai Cave, in the cave, *c*. 700 m a.s.l., 25.07.2002, P. Dankittipakul.

Sinopoda sp.: 1 ♀ (NHM, PJ 1816), India, Assam, Coll. Miss Steele, „Heteropodidae, det. PJK“, 1935-36 prob.

Sinopoda sp.: 1 ♀ (NHM-99.1.20.8., PJ 1818), China, N.W. Sechuan, J.[?]W. Slyan, (Seuy,..?).

Sinopoda sp.: 1 ♀ (QMS-28039, PJ 192), Thailand, Doi Ithanon, 1 600 m a.s.l., 17.12.86.

Sinopoda sp.: 1 ♀ (NHMB-1963-a [1460], PJ 323), China, Tsingtao, 7.09.1932, Mus. Hoangho-Paiho.

Sinopoda sp.: 1 ♀ (CDPC, PJ 895), Malaysia, Sarawak, Matang Reserve, about 26.03.1985, 1 000 ft a.s.l., + 28.05.1985 under bark, C.L. & P.R. Deeleman; 1 ♀ (CDPC, PJ 899), same locality, Mt. Serapi, 1 000 ft a.s.l., 25.03.1985 + 04.1985, C.L. & P.R. Deeleman; 1♀ (CDPC, PJ 905), same locality, 1 000 ft a.s.l., tree bark.

Sinopoda sp.: 1 ♀ (CDPC, PJ 907), Malaysia, N.P. Kinabalu, HQ, 1 550 m a.s.l., grass etc. along the trail, 21.07.80.

Sinopoda sp.: 6 ♀♀ (SMF, PJ 908-910, 912, 914, 917), China, Shaanxi, Taibaishan, 1 250–1 600 m a.s.l., sifting, at night, on rocks, 8.06.–3.07.1997.

Sinopoda sp.: 1 ♀ (CDPC, PJ 919), China, Guangxi, Nashan, Gin Lun near show cave, visual, habitat: dry fossil passage, 8.01.1988, P. Fogg.

Sinopoda sp.: 1 subadult ♂, 1 ♀ (CDPC, PJ 1822), Indonesia, N-Sulawesi, Dumoga, prim. Forest, dry litter, 27–30.07.1982.

Sinopoda sp.: 1♀ (CDPC, PJ 916), W-Thailand, Cave Phra Dath, Erawan W. Park, 13.03.1986, leg. C.L.& P.R. Deeleman.

Sinopoda sp.: 1 subadult ♂, 2 juvenile ♀ (SMF, PJ 1819, 1833), China, Shaanxi Prov., Taibaishan, S flanks, above Houshenzi, secondary broad-leaved forest, 1300–1 700 m a.s.l., 17–20.06.1997, J. Martens & P. Jäger; 1 subadult ♂ (SMF, PJ 1814), same locality, above Houshenze, 1 250–1 550 m a.s.l., 21.06.1997, P. Jäger.

Sinopoda sp.: 1 juvenile (CDPC, PJ 1832), N. Sulawesi, Dumoga, prim. Forest, dry litter, 27–30.07.1982.

Spariolenus sp.: 1 ♀ (SMF, PJ 1470), N-Oman, W of Nizwa, Al Hamra area, al Hota Cave, 09.2000, S. Huber.

Spariolenus sp., 1 juvenile (NHMW, PJ 1865), Oman, Jebal Akhdar, E of al Hambra, Wadi Fallah, Al Ghubrat, area around spring Ghubrat, 16–18.11.2001, H. Sattmann; 1 juvenile (NHMW, PJ 1866), same area, Hoti-cave, entrance, Wadi Huta, abseil spot, 16.11.2002, H. Sattmann.

Sparassidae (non-heteropodines)

Anaptomecus sp.: 1 ♀ (NRMS, PJ 1878), Guyana, Colleg. Bovallius.

Anchonastus plumosus (Pocock, 1899): 1 ♀ (ZMUC, PJ 1879), Tanzania, coast region, Kisarawe District, Kazimzumbwi Forest reserve, 39°03′E, 6°57′S, 01–02.1991, Frontier Tanzania leg.

Arandisa sp.: 1 ♀ (SMN-44721, PJ 1849), Messum Crater, 21°26.430′S, 14°33.215′E, on rocky hillside at night, 8.04.2000, E. Griffin; 1 ♀ (SMN-44693, PJ 1851), same locality, on ground at night on gravel plain, 5.04. 2000, E.& M. Griffin.

Berlandia sp.: 1 ♀ (ZMUC, PJ 1870), Tanzania: Tanga; Amboni Caves, 5°4–6′S, 39°0–3′E, 80 m, C. Griswold, N. Scharff & D. Ubick.

Damastes sp.: 1 ♀ (NRMS, PJ 1874), Madagascar.

Eusparassus sp.: 1 ♀ (SMF, PJ 1861), Tschad, Guelta bei Zonar, 08.1997, H. Nickel.

Gnathopalystes sp.: 1 ♀ (SMF-RII 13660/222, PJ 113), Indonesia, Sumatra, Fort de Kock.

Keilira sparsomaculata Hirst, 1989: 1 ♀ (SMF, PJ 954), South Australia, 1 km N. Bucks Camp Well, Mt. Reserve Conservation Park, 35°56′S, 140°18′E, 18.3.1992, D. Hirst det., Coll. D. Hirst, South Australian Museum, ded. to SMF.

Leucorchestris arenicola Lawrence, 1962: 1 ♀ (SMN-44171, PJ 1860), Euphorbia Hills, 23.34ºS, 15.38ºE, JH 422, 19.07.1988, J.R. Henschel.

Olios argelasius (Walckenaer, 1805): 1 subadult ♂ (SMF-19323/1, PJ 1880), Spain, (Sp. 97), Franz leg., Wiehle det., Slg. Wiehle.

Olios lutescens (Thorell, 1894): 1 ♀ (SMF, PJ 1881), India, Goa, Canacona, Cabo de Rama Fort, 19.01.2003, S. Huber.

Palystella (?) sp.: 1 ♀ (SMF, PJ 1869), SW Afrika, surroundings of Okahandja, 1957, Gaerdes.

Sparassidae sp.: 1 ♀ (ZMUC, PJ 1291), Tanzania, Tanga Reg., Muheza Distr., Manga Forest reserve, 38°47′E, 5°0′S, August 1997, Frontier Tanzania leg.

Sparassidae sp.: 1 ♀ (NRMS, PJ 1877), Brazil, Nova Teutonia, Fritz Plaumann, 27°11′B, 52°23′L, Museum Thorell.

Sparassidae sp.: 1 ♀ (NHMG, PJ 1360), Madagascar, Achat Le Mault, 1916/ 23.

Araneae (non-sparassids)

Agroeca proxima (O. Pickard-Cambridge, 1871): 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, Kaserne, Düne, 18.09.–02.10.1994, P. Jäger.

Amaurobius ferox (Walckenaer, 1830): 1 ♀ (SMF), France, Luc sur Mer, park, 24.09.1992, P. Jäger.

Antistea elegans (Blackwall, 1841): 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, Tongrube, 06–20.02. 1994, P. Jäger.

Anyphaena accentuata (Walckenaer, 1802): 1 ♀ (SMF), Germany, Rösrath, Im Frankenfeld 15, 1.07.1994, P. Jäger.

Araneidae sp.: 1 ♀ (SMF), Laos, Khammouan Prov., Ban Tathot, village and surroundings, shrubs, 20.02.2003, P. Jäger.

Argenna subnigra (O. Pickard-Cambridge, 1861): 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, barrack, sand dune, 6–20.03.1994, P. Jäger.

Atypus piceus (Sulzer, 1776): 1 ♀ (SMF), Germany, Mainz, Draiser Senke, loess slope, 30.06.1996, P. Jäger.

Cheiracanthium virescens (Sundevall, 1833): 1 ♀ (SMF), Germany, Mechernich, Kalenberg, Malaise trap, 31.03.–08.04.1990, B. Franzen.

Clubiona pallidula (Clerck, 1757): 1 ♀ (SMF), Rees/ Nieder-Rhein, Bienen-Hueth I, 18–21.06.1992, P. Jäger.

Clubiona stagnatilis Kulczyński, 1897: 1 ♀ (SMF), Germany, Vilkerath, Schlingenbach, meadow, herb-layer, 19.05.1995, P. Jäger.

Conothele sp.: 1 juvenile (SMF) Laos, Khammouan Prov., Ban Tathot, cave Tham Kamouk, entrance area, *c.* 200 m a.s.l., 20.02.2003, P. Jäger.

Cryphoeca silvicola (C.L. Koch, 1834): 1 ♀ (SMF), Italy, Sand in Taufers, Reinbach waterfalls, moss on forest floor, 23.07.1991, P. Jäger.

Cupiennius salei (Keyserling, 1877): 1 ♀ (SMF, PJ 449), bred by Stefan Ebert, über B. Hayen, dead: 12.06. 1996, P. Jäger.

Cybaeus tetricus (C.L. Koch, 1839): 1 ♀ (SMF), Austria, Riezlern, Auenhütte, *c.* 1 400 m a.s.l., under log, wet ground, 17.08.1996, P. Jäger.

Erigone atra Blackwall, 1833: 1 ♀ (SMF), Germany, Rösrath, Im Frankenfeld, under stone, 4.08.1994, P. Jäger.

Ero furcata (Villers, 1789): 1 ♀ (SMF), Germany, Rösrath, Wahner Heide, Geisterbusch, inner part of spruce forest, 14.09.1994, P. Jäger.

Evarcha arcuata (Clerck, 1757): 1 ♀ (SMF), Austria, Stopfenreuth, Donau-Auen, 2.06.1993, P. Jäger.

Filistatidae sp.: 1 ♀ (SMF), China, Yunnan Prov., Dali, town, 2 000 m a.s.l., on walls, 05.04.1999, P. Jäger.

Harpactea hombergi (Scopoli, 1763): 1 ♀ (SMF), Germany, Cologne, Melatenfriedhof, under bark of *Platana acerifolia*, 24.01.1995, P. Jäger.

Harpactea rubicunda (C.L. Koch, 1838): 1 ♀ (SMF), Germany, Borgentreich-Borgholz, building, inside, dead in web of *Zygiella x-notata*, 13.06.1992, P. Jäger.

Hersiliidae sp.: 1 ♀ (SMF), Laos, Khammouan prov., Ban Tathot, entrance area of limestone cave, 20.02.2003, H. Steiner.

Histopona torpida (C.L. Koch, 1837): 1 ♀ (SMF), Germany, Hintersee Nature Reserve, Standgraben, empty bed of stream, 11.05.1994, P. Jäger.

Holocnemus pluchei (Scopoli, 1763): 1 ♀ (SMF), Germany, Mainz, Draisberghof, inside, 1.02.1998, P. Jäger.

Linyphiidae (Linyphiinae) sp.: 1 ♀ (SMF, Jä-39), China, Yunnan Prov., Kunming, Xi-Shan, leaf litter, 19.04.1999, P. Jäger.

Liphistius lannaianus Schwendinger, 1990: 1 juvenile (SMF; third instar spiderlings), Thailand, Huay Nam Dang, P. Schwendinger.

Liphistius malayanus Abraham, 1923: 1 ♀ (SMF), Malaysia, Pahang, Genting Highlands, 1 200 m a.s.l., 27.02.2002, A. Kovac.

Liphistius yamasakii Ono, 1988: 1 juvenile (SMF), Thailand, Doi Inthanon, 8.02.1986, P. Schwendinger.

Loxosceles rufescens (Dufour, 1820): 1 ♀ (SMF), Spain, Andalusia, 12.10.2002, S. Heist, B. Hayen ded.

Macrothele sp.: 1 juvenile ♀ (SMF), Laos, Khammouan Prov., Thakek, rockface in front of cave Them En, *c.* 180 m a.s.l., 28.02.2003, P. Jäger.

Nemesiidae sp.: 1 ♀ (SMF), Spain, Andalusia, no date, S. Heist, B. Hayen ded.

Nesticidae sp.: 1 ♀ (SMF), China, Yunnan Prov., Kunming, Xi Shan, 2 000 m a.s.l., forest and macchie, under stones, 2.04.1999, P. Jäger.

Oonopidae sp.: 1 ♀ (SMF), Laos, Khammouan Prov., Thakek, Ban Phôunggam Mai, *c.* 180 m a.s.l., leaf litter and shrubs in front of cave Tham Payat, 1.03.2003, P. Jäger.

Oxyopes ramosus (Martini et Goeze, 1778): 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, barrack, sand dune, 10.07.1994, P. Jäger.

Pachygnatha clercki Sundevall, 1823: 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, munitions depot, heath, 7–15.03.1991, T. Stumpf.

Palpimanus sp.: 1 ♀ (SMF), Spain, Andalusia, Alma Ria, 23.05.2001, S. Heist, B. Hayen ded.

Pardosa pullata (Clerck, 1757): 1 ♀ (SMF), Germany, Inzell, bog, 13.05.1994, P. Jäger.

Philodromus cespitum (Walckenaer, 1802): 1 ♀ (SMF), Germany, Gönnersdorf, garden, 02.06.1992, P. Jäger.

Pholcus phalangioides (Fuesslin, 1775): 1 ♀ (SMF), France, Luc sur Mer, Biological Research Station, inside, 29.09.1992, P. Jäger.

Phrurolithus festivus (C.L. Koch, 1835): 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, clay mine, 1–15.05. 1994, P. Jäger.

Pisaura mirabilis (Clerck, 1757): 1 ♀ (SMF), Germany, Cologne, Zülpicher Straße, Inst. Chemistry, shrubs, 30.05.1995, P. Jäger.

Pisauridae sp.: 1 ♀ (SMF, Jä-16), China, Sichuan, Emei, Emei Shan, village, river, under stones, 750 m a.s.l., 25.03.1999, P. Jäger; adult: 5.04.1999.

Pisauridae sp.: 1 subadult ♂ (SMF, Jä-1), China, Sichuan, Emei, Emei Shan, village, river, under stones, 750 m a.s.l., 25.03.1999, P. Jäger; adult: 5.4.1999.

Plator sp.: 1 subadult ♀ (SMF), China, Yunnan prov., Dali, Cangshan, 2200–2400 m a.s.l., stream, gravels, 6.04.1999, P. Jäger.

Psechridae sp.: 1 ♀ (SMF), Laos, Khammouan prov., Ban Tathot, cave Tham Kamouk, *c.* 200 m a.s.l., entrance area, between rocks, 19.02.2003, P. Jäger.

Pseudeuophrys lanigera (Simon, 1871): 1 ♀ (SMF), Germany, Mainz, Botanical garden of the university, warm house, 20.03.1996, P. Jäger.

Psilochorus simoni (Berland, 1911): 1 ♀ (SMF), Germany, Mainz, Draisberghof, inside, no date, P. Jäger.

Scytodes sp.: 1 juvenile (SMF), Papua New Guinea, S-Pacific, 3°19.491′S, 152°35.370′E-3°19.352′S, 152° 35.462′E, F.S. ‘Sonne’ 133, S Edison Seamount, 26.07.1998.

Scytodes thoracica (Latreille, 1802): 1 ♀ (SMF), Germany, Mainz, Draisberghof, outside walls of a building, –6°C, 11.01.1997, P. Jäger; 1 subadult ♀ (SMF), Germany, Cologne, Bachemer Straße, inside, 2.11.1992, P. Jäger.

Segestria bavarica C.L. Koch, 1843: 1 ♀ (SMF), Italy, Toskany, Sassello, 8.04.1996, P. Jäger.

Segestria florentina (Rossi, 1790): 1 ♀ (SMF), France, Choisy le Roi, on the base of a tree, 11.04.1992, P. Jäger.

Selenops cf. *zuluanus* Lawrence, 1940: 1 ♀ (SMF), South Africa, M. Staib; B. Hayen ded.

Steatoda triangulosa (Walckenaer, 1802): 1 ♀ (SMF), Germany, Mainz, Draisberghof, building, inside, 18.12. 1995, P. Jäger.

Stegodyphus lineatus (Latreille, 1817): 1 ♀ (SMF), Spain(?), St. Antonio, no date, S. Heist; B. Hayen ded.

Tegenaria ferruginea (Panzer, 1804): 1 ♀ (SMF), Germany, Rösrath, Plantage 18, wooden house, 9.09. 1994, P. Jäger.

Tenuiphantes mengei (Kulczyński, 1887): 1 ♀ (SMF), Italy, Toskany, San Filippo, wall, 6.04.1996, P. Jäger.

Tetragnatha extensa (Linnaeus, 1758): 1 ♀ (SMF), Germany, Troisdorf, Wahner Heide, clay mine, 15.05.1994, P. Jäger.

Theraphosa blondi (Latreille, 1804): 1 ♀ (SMF), bred by Hayen, no data.

Theraphosa blondi (Latreille, 1804): 1 juvenile (SMF), bred by Hayen, no data.

Theridiosomatidae sp.: 1 ♀ (SMF), China, Shaanxi Prov., Taibai Shan, S flanks, above Houshenzi, secondary broad-leafed forest, 1300–1700 m a.s.l., 19.06.1997, J. Martens & P. Jäger.

Thomisidae (Tmarini) sp.: 1 ♀ (ZFMK), Uganda, Semliki Forest, 0°48′N, 30°8′E, 5–12.02.1997, T. Wagner.

Uloborus plumipes Lucas, 1846: 1 ♀ (SMF), Germany, Mainz, Augustinergasse, flower-shop, 10.05.1998, P. Jäger.

Uroctea sp.: 1 ♀ (SMF), China, Sichuan Prov., Emei Shan, Wannian Temple, 20–21.03.1999, P. Jäger.

Zelotes subterraneus (C.L. Koch, 1833): 1 ♀ (SMF), Italy, South Tyrol, Neves reservoir, *c.* 1880 m a.s.l., under stones, 19.08.1996, P. Jäger.

Zodarion italicum (Canestrini, 1868): 1 ♀ (SMF), Germany, Rösrath, Im Frankenfeld, railway, 30.04.1993, P. Jäger.

Zora spinimana (Sundevall, 1833): 1 ♀ (SMF), Germany, Rösrath, Wahner Heide, Quereinflugschneise, 26.04–10.05.1991, T. Stumpf.

Zoropsis spinimana (Dufour, 1820): 1 ♀ (SMF), Italy, Toskany, San Filippo, wall, 6.04.1996, P. Jäger.