European Arachnology 2003 (D.V. Logunov & Penney D. eds.), pp. 41–52.
© Arthropoda Selecta (Special Issue No.1, 2004). ISSN 0136-006X
(Proceedings of the 21st European Colloquium of Arachnology, St.-Petersburg, 4–9 August 2003)

On the taxonomic relations of lynx spiders from the canopy of a tropical Asian rainforest (Araneae: Oxyopidae)

О таксономических связях пауков-рысей из крон тропических дождевых лесов Азии (Araneae: Oxyopidae)

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ABSTRACT. The present generic assignment of ten Oxyopidae species from tree canopies of the rainforest in Borneo is discussed. Somatic and genitalic characters of these species are analyzed and compared with descriptions and some type specimens of *Tapponia* spp. One species is a true *Tapponia*, eight species belong to the pantropical genus *Hamataliwa*, and one species seems to be a member of an undescribed genus. In contrast to many other spider groups, the copulatory organs of *Tapponia-Hamataliwa* appear to be conservative and uniform, whereas the somatic characters are much more diverse.

РЕЗЮМЕ. Обсуждается родовое положение десяти видов Oxyopidae из крон тропического леса в Борнео. Соматические и генитальные признаки этих видов проанализированы в сравнении с описаниями и некоторыми типовыми экземплярами *Tapponia* spp. Один вид оказался настоящей *Tapponia*, восемь видов относятся к пантропическому роду *Hamataliwa*, и один вид вероятно относится к неописанному роду. В сравнении со многими другими группами пауков, копулятивные органы у *Tapponia-Hamataliwa* по-видимому консервативны и униформны, тогда как соматические признаки более разнообразны.

KEY WORDS: Araneae, Oxyopidae, Borneo, canopy, rainforest.
КЛЮЧЕВЫЕ СЛОВА: Araneae, Oxyopidae, Борнео, кроны, дождевой лес.

Introduction

Seven years ago I had the luck to meet Andreas Floren (Würzburg, Germany), who was doing ecological research on the arthropod fauna of the canopy of rainforests in Sabah (Malaysian Borneo) by means of fogging [see Floren & Linsenmair, 1998, 1999, 2001]. This led to many years of cooperation in which one of the targets was assessing comparative species richness of the spider fauna of several habitats. A rich collection from a variety of forests in that region became available and as many species as possible were identified to genus or species. In 80 samples from an area of less than a square kilometre, primary, relatively untouched forest was compared with adjacent patches of clearing (secondary re-growth after clearing of abandoned 'ladangs' or crop fields) of various ages. In total, I studied approximately 5 900 specimens belonging to 535 morphospecies in 31 families. Most species were recognized as belonging to genera which also occur in forests elsewhere in the region, in the ground-storey or on the forest edge. At the species level, however, they were very often different from sympatric species living near the ground.

A comparative study has been carried out in a lowland floodplain forest in Brunei, Borneo [Russell-Smith & Stork, 1995]. From ten fogged

tree crowns, 945 individuals were collected, which were identified to 190 morphospecies in 23 families. Four unnamed oxyopid species were represented as singletons.

Silva [1996] studied the species composition of spiders from a periodically flooded Amazonian lowland forest. Four weeks collecting was done by canopy fogging, ground-storey fogging and three methods of hand collecting. This resulted in a total of 5 895 adult specimens of 1 140 morphospecies in 39 families.

In this study 11 species of oxyopids were collected. One specimen belonged to the genus *Oxyopes*, the remaining oxyopids, consisting of 80 specimens, could not be readily assigned to genus. Very little has been published on tropical Asian Oxyopidae since 1 900, let alone on those species from the rainforest canopy. In this paper, the difficulties encountered during this research are explained and some preliminary results and conclusions are presented.

After the existing types of the species listed in *Tapponia* are examined, these species will be (re)described in a subsequent paper. Synonyms will be established and the description of any new species from the Bornean canopy will be added.

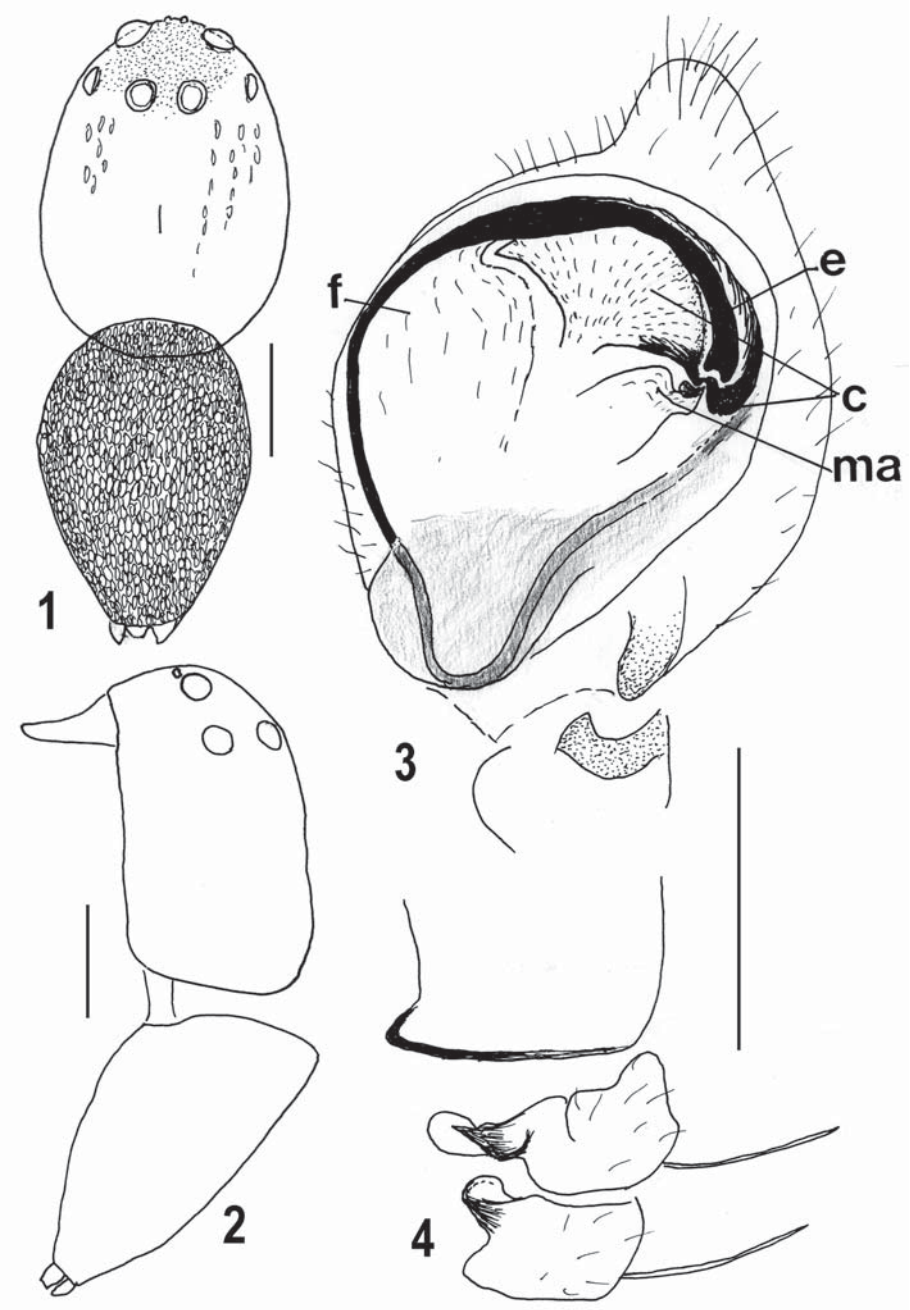
Material and methods

In the primary forest of the Mt. Kinabalu National Park at 700 m elevation at Poring Hot Springs (6°2′75″N, 116°42′2″E), 31 foggings were carried out between 1992 and 1998, on trees belonging to six different species. In three abandoned ladangs, 48 trees belonging to two different species were fogged. Additionally, four different planted crop trees were fogged twice with a one month interval. In total, 5 900 specimens were identified, 81 of which (51 males and 30 females) were oxyopids. Eleven species were distinguished. The lynx spiders of the genus *Oxyopes*, which are common near the ground in open habitats in southern Asia, were represented by one specimen only. The taxonomy of the remaining ten species is discussed below.

In total, 42 species of *Oxyopes* Latreille, 1804, three species of *Peucetia* Thorell, 1869, the monotypic genus *Megullia* Thorell, 1897 and all the 14 species of *Tapponia* Simon, 1885 have been listed for south-east Asia [Platnick, 2002].

The original descriptions of all *Tapponia* species and *Megullia truncata* date from before 1900, were based mainly on single specimens, and were written in Latin without illustrations. None of these species has been reported on since, so it is not surprising that reliable species identifications by means of descriptions alone are virtually impossible. To support identifications, a male and female from Sumatra designated as the types of *Tapponia micans* Simon, 1885 (MNHN, 20886) were studied. The material of *Tapponia superba* (Thorell, 1887) and *T. hieroglyphica* (Thorell, 1887) from Burma identified by Thorell (MNHS, 251/1598b,c, and 250/1595a,b,c, respectively; each series contains specimens collected from their respective type localities, viz., Bhamo), a juvenile specimen of *Megullia truncata* Thorell, 1897 (MNHS, 251/1600; the specimens collected from the type locality, viz., Burma: Palon), and the type specimens of *Tapponia severa* Thorell, 1895 (NHM, BM1971/26) and *Tapponia incompta* Thorell, 1895 (NHM, BM1999/128), all from Burma, were examined. Furthermore, these were compared with all oxyopid specimens, with the exception of *Oxyopes*, in my south-east Asia collection (now in RMNH), from the ground-storey of forests in southern Thailand and the islands Sumatra, Borneo, Sulawesi and Lombok. Finally, a male of the type species *Oxyopes heterophthalmus* (Latreille, 1804) and two species from British Guyana: *Oxyopes salticus* Hentz, 1845 and an unidentified specimen of the pantropical genus *Hamataliwa* were studied for comparison. Unfortunately, most of Thorell's types of species described initially in *Tapponia* or in *Oxyopes* or those subsequently transferred to *Tapponia*, are held in the Museo civico Storia naturale, Genova and were not available for loan. Therefore, at the time of writing no definite identifications could be made.

Abbreviations used in the text and figures: AME = anterior median eyes; ALE = anterior lateral eyes; OQ = ocular quadrangle, formed by ALE and PME; PER = posterior eye row; PME = posterior median eyes; PLE = posterior lateral eyes; c = conductor; d = diameter of eyes; e = embolus; f = membranous flap (attached to base of embolus); ma = median apophysis.



Figs 1–4. The male of *Tapponia* cf. *micans* (from Borneo): 1 — general appearance, dorsal view; 2 — ditto, lateral view; 3 — male palp, ventral view; 4 — palpal tibia, retrolateral view. Scale: 0.5 mm (1–2), 0.25 mm (3–4).

Рис. 1–4. Самец *Tapponia* cf. *micans* (из Борнео): 1 — общий вид, дорзально; 2 — тоже, латерально; 2 — пальпа самца, вентрально; 4 — голень пальпы, ретролатерально. Масштаб: 0,5 мм (1–2), 0,25 мм (3–4).

Type/comparative specimens were examined from the following museums: MNHN = Musée national d'Histoire Naturelle, Paris; MNHS = Swedish Museum of Natural History, Stockholm; NHM = The Natural History Museum, London; RMNH = Rijksmuseum van Natuurlijke Historie (= Nationaal Natuurhistorisch Museum Naturalis), Leiden.

Taxonomy

Ten oxyopid species could be assigned to three groups (groups I–III) based on different shapes of the carapace and abdomen, eye arrangement, features of the integument and male palpal morphology. All species (except number 10, see below) were easily separated from *Oxyopes* by the shape of the carapace (square, rear margin widest, vertical, descending abruptly), the closely set AME and by the lack of black vertical stripes on the clypeus and chelicerae. Epigynes in all species were of similar design, consisting of a posterior horseshoe-shaped rim, from which emanate a pair of elongate spermathecae showing specific shapes after dissection (Fig. 12). There were minor but distinct differences at species level. Similar epigynes are rarely found in other oxyopids.

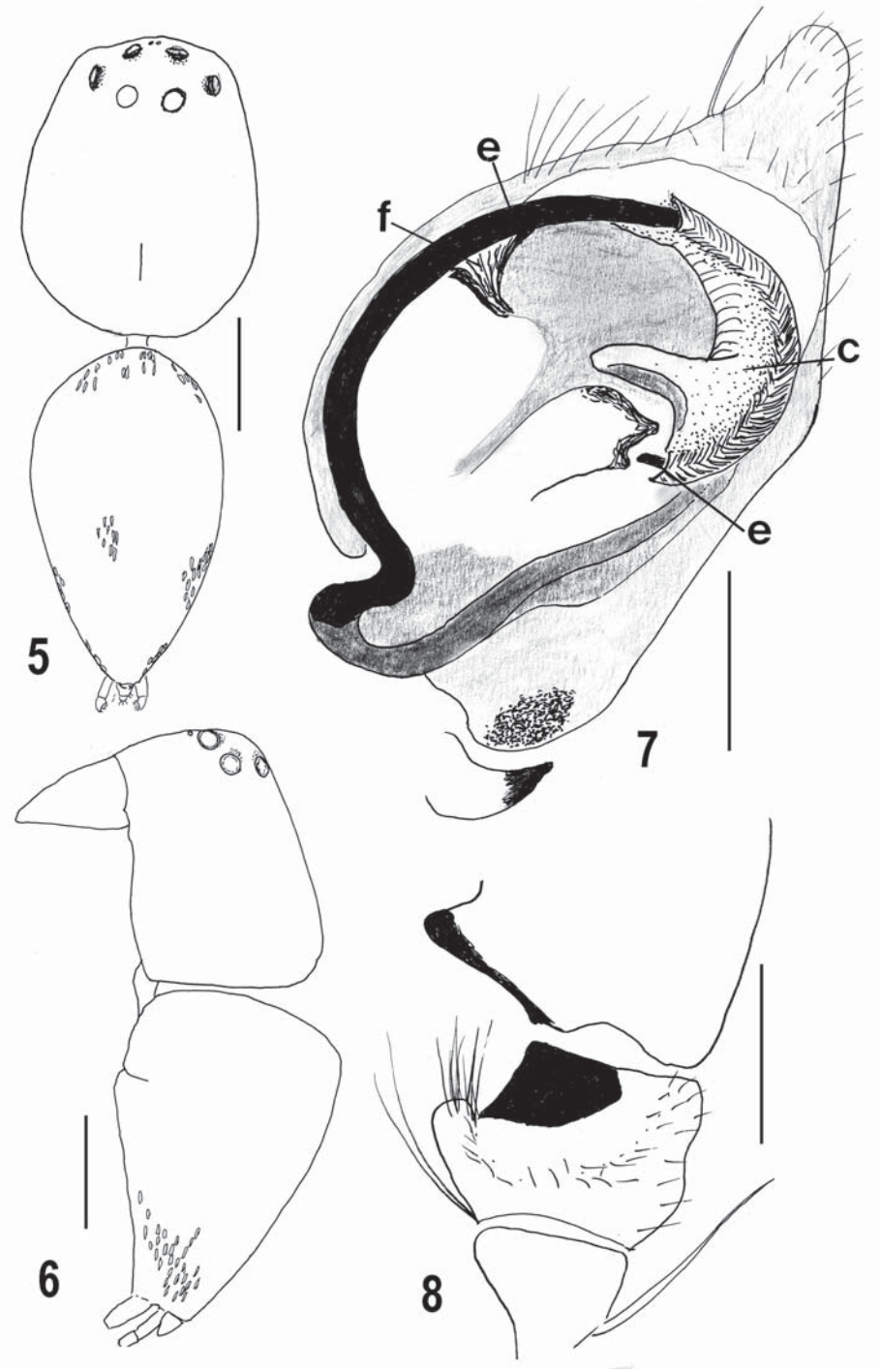
Somatic characters

In species 1 (group I; Figs 1, 2; 3–4 mm long) the carapace is high, rounded in front, with a straight dorsum when viewed laterally. The OQ is longer than wide, widest in front. PME are separated by less than their d. The ocular region is black. The carapace, dorsal aspect of the abdomen and the legs are without a distinct pattern and are densely covered with large adpressed, flattened hairs, giving a gold or silver iridescent appearance.

Species 2–9 (group II; Figs 5, 6, 9) are 4–8 mm long; they share with species 1 the high, square carapace, but the front is almost square (not rounded) and the posterior declivity is almost vertical, sometimes even receding (angle slightly less than 90 degrees). The OQ is as long as wide; the PME are separated by their d or more. The carapace and abdomen of these spiders in alcohol are very often hairless, pigmentless, pale yellowish, or the spiders have patches of non-iridescent reddish, white or blackish, flattened, adpressed hairs on the carapace, abdomen and legs. Fresh specimens are often entirely covered with these hairs (see Fig. 9), but once in alcohol they are easily detached and float to the surface of the fluid. Species 9 has the same features as species 2–8, but the distance between the PME is much greater, 3–4 times their d. This feature is allegedly a diagnostic character of the predominantly American genus *Hamataliwa*.

Species 10 (group III; Figs 10, 11, 15) is a conspicuous, colourful spider of 10–15 mm body length, entirely clothed in thick, colourful, flattened hairs. It is separated from the two other groups by the longer, lower and less steeply sided carapace with a dorsal saddle, the smaller eye group, but the OQ is rectangular and longer than wide. In living specimens, the elongate, often strongly narrowed abdomen is moss-green with a multicoloured pattern of patches of thick hair, often partly iridescent purple or copper; in alcohol, the spider loses the hairs, leaving a hairless tegument which is sometimes heavily pigmented. Pigmented patches on the abdomen may be bright green in life. Spiders of the latter category were also found directly under the canopy of the dark and humid forest.

In what genus should these spiders be placed? After *Oxyopes*, the most common genus known in the region is the endemic *Tapponia* Simon, with 14 species, six of which were originally described in *Oxyopes*. Three species of the panglobal genus *Peucetia* have been described from Burma. *Megullia* Thorell, 1897 is an enigmatic, monotypic genus, known from one female and a subadult male from Burma. The genus *Hamataliwa* is a New World genus with 47 species described from the warmer parts of the Americas and several from Africa and Queensland; one species was recently described from China [Song & Zheng, 1992]. *Peucetia* can be excluded because the low, strongly converging carapace, the relative eye arrangement, the chelicerae and the palpal structure are very different in the specimens studied. All Asian species except for *Hamataliwa* species were described before 1900, in Latin, and rarely with illustrations. It took quite some detective work to find out what distinguishing characters had



Figs 5–8. The male of *Hamataliwa* sp. (from Borneo and Sulawesi): 5 — general appearance, dorsal view; 6 — ditto, lateral view; 7 — male palp, ventral view; 8 — palpal tibia, retrolateral view. Scale: 1 mm (5–6), 0.25 mm (7–8).

Рис. 5–8. Самец *Hamataliwa* sp. (из Борнео и Сулавеси): 5 — общий вид, дорзально; 6 — тоже, латерально; 7 — пальпа самца, вентрально; 8 — голень пальпы, ретролатерально. Масштаб: 1 мм (5–6), 0,25 мм (7–8).

Fig. 9. The female of *Hamataliwa incompta* Thorell, 1895 (Borneo); photo by Mr. Paul Zborowski.
Рис. 9. Самка *Hamataliwa incompta* Thorell, 1895 (Борнео); фотография Mr. Paul Zborowski.

been used to determine generic placement by the earlier authors, and whether these choices would be justified under present-day criteria.

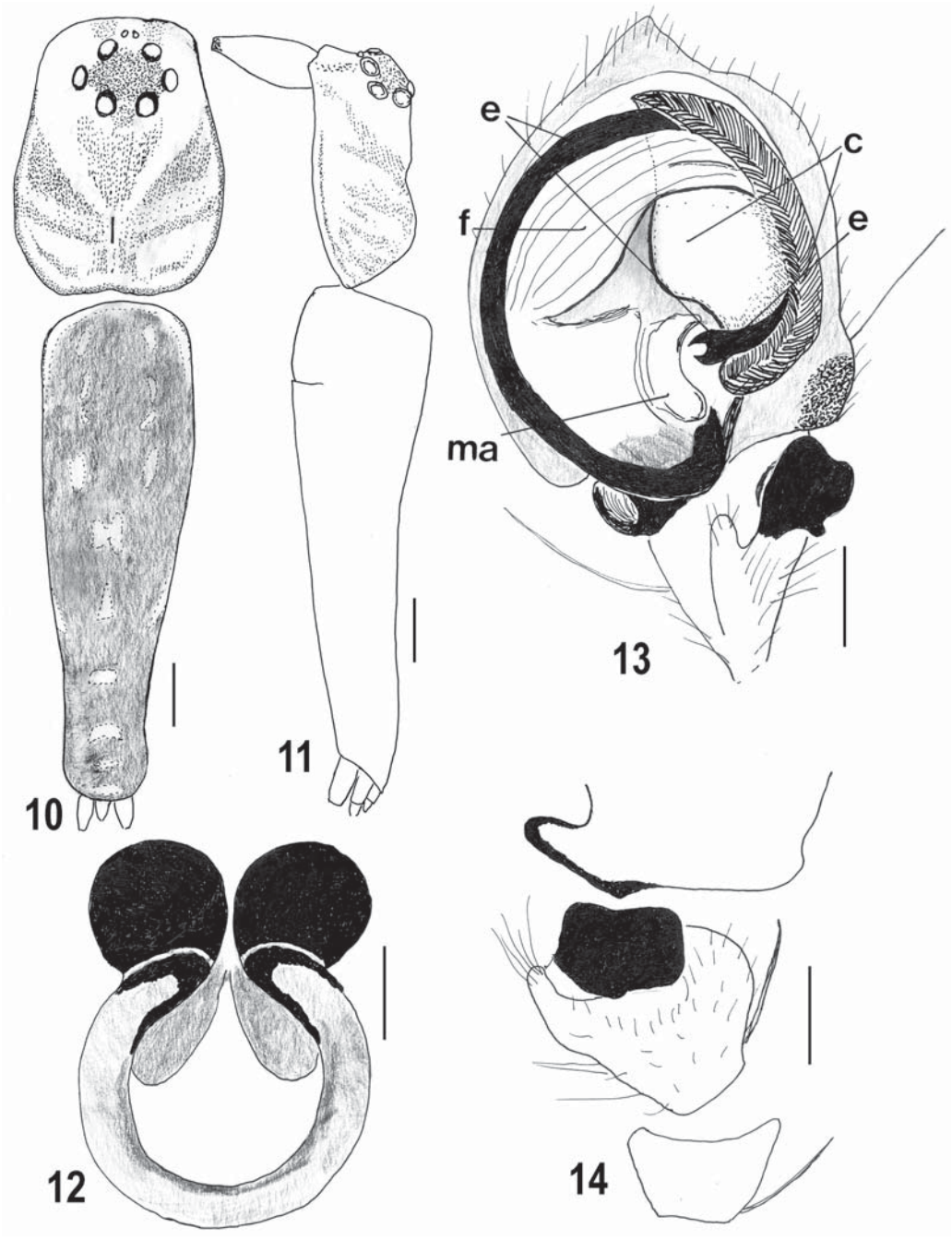
Up until the early twentieth century, the eye arrangement was of paramount importance and often crucial for classification. Virtually the only illustration of eye patterns and the only identification key of any use, which no doubt formed the basis of most placements, was in "Histoire Naturelle des Araignées" [Simon, 1898: p. 377]. Considered crucial was the distance and curvature of the posterior eyes and larger size of the ALE, and the position of the AME: in front of the ALE (*Oxyopes*; [Simon, 1898: figure on p. 373]), rather than between them (*Tapponia*, *Hamataliwa* and in the remaining genera) [Simon, 1898: figure on p. 374]). The eye arrangement of an array of genera presented in the figure on page 374 of Simon [1898], would place species in group I to *Peucetia* or *Tapponia*, species 9 (with the wide PME) to *Hamataliwa*, whereas species 2–8 and 10 would be of doubtful assignment.

The eye position is currently considered unimportant as a key character for classification. Instead, emphasis has been shifted to copulatory organs and, more recently, to other somatic characters often visible only by SEM.

Characters of the copulatory organs

Currently, the copulatory organs of *Tapponia* are almost unknown. One fairly accurate image exists of the epigyne of *T. heterosticta* Pocock, 1897, a large species from Sulawesi; this epigyne is basically similar to that of all the Bornean species considered here. A very sketchy drawing of the palp of *T. austera* Thorell, 1894 was provided by Workman [1896] and is of little use. The South American *Peucetia* were revised by Santos & Brescovit [2003]. New World *Hamataliwa* were revised by Brady [1964, 1970]. Do the structures of the genital organs coincide with somatic features?

Surprisingly, all ten species show a number of characters in palpal structure, which they share with those of the widespread tropical Asian species *Oxyopes birmanicus* Thorell, 1887: viz., the broad and flat tegulum with the embolus arising proximally-prolaterally, the proximal region partly attached to a large membranous flap, the distal part flattened and whip-like, curving all along the outer ledge of the large, flat, fan-shaped conductor; tip of the embolus + conductor adjacent to the small, fleshy median apophysis. Such a structure is not unique; a similar form of the tegulum and its appendages occurs in other spider groups, for instance, the recently described south Australian amaurobioid genus *Therlinya* [Gray & Smith, 2002]; these species are even equipped with a tegular lobe as in the Bornean oxyopids. However, the epigyne is quite different. The configuration described above is not constant in the copulatory organs of all Oxyopidae. In



Figs 10–14. '*Tapponia*' cf. *hieroglyphica* (Thorell, 1887) (from Borneo) (10–14): 10 — female general appearance, dorsal view; 11 — ditto, lateral view; 12 — epigyne; 13 — male palp, ventral view; 14 — palpal tibia, retrolateral view. Scale: 1 mm (10–11), 0.25 mm (12–14).

Рис. 10–14. '*Tapponia*' cf. *hieroglyphica* (Thorell, 1887) (из Борнео) (10–14): 10 — общий вид самки, дорзально; 11 — тоже, латерально; 12 — эпигина; 13 — пальпа самца, вентрально; 14 — голень пальпы, ретролатерально. Масштаб: 1 мм (10–11), 0,25 мм (12–14).

Fig. 15. The female of '*Tapponia*' cf. *hieroglyphica* (Thorell, 1887) with prey (Borneo); photo by Mr. Paul Zborowski.

Рис. 15. Самка '*Tapponia*' cf. *hieroglyphica* (Thorell, 1887) с добычей (Борнео; фотография Mr. Paul Zborowski.

the panglobal genus *Oxyopes*, the palpal structure is variable. In the type species, *O. heterophthalmus* (Fig. 16), the tibial apophysis is deviant, the embolus is very long and thread-like, and the wide, fan-shaped conductor is transparent. In *O. salticus* (Fig. 17), a widespread species in South and Central America, the palpal organ is deviant: the palpal tibia is excavated retrolaterally over its entire length; the sperm duct emerges distally and retrolaterally and follows the outer margin of the tegulum (forming a subcircular coil) and passes into a short, fleshy embolus ending distally in a claw; it converges with the T-shaped conductor and the claw-like median apophysis all superposed in the apex of the bulb. The latter species conforms with the basic pattern in *Tapinillus* [Griswold, 1993: figs 56, 58] and *Peucetia* [Santos & Brescovit, 2003]. The epigynes of both these species are quite different from those in the Bornean material. The male palp of *O. birmanicus* is somewhat similar to that in the canopy species, but lacking the diagnostic characters of the male and female copulatory organs listed below. In some species there is an additional tegular sclerite. *Oxyopes* thus appears to be a polyphyletic genus.

Additionally, the three species groups considered here share several special diagnostic features (see Table): (1) the epigyne with the posterior rim in the shape of a reversed horseshoe; (2) the tibial distal, retrolateral excavation with a shiny black knob, apophysis or tooth in the middle, which corresponds with a sclerotized swelling on the cymbium; (3) the distinct proximal, prolaterally directed tegular lobe; and (4) the heavily sclerotized, almost black conductor, the outer ridge of which partly roofs the embolus. The embolus is black and shiny, broad and flat, distally thinning and extremely flexible and fragile, easily breaking off, often with a terminal widening, completely hidden inside

Table.
Diagnostic characters of *Tapponia* and related genera (abbreviations as explained in Material and methods).

Таблица.
Диагностические признаки *Tapponia* и близких родов (сокращения объяснены в Материалах и методах).

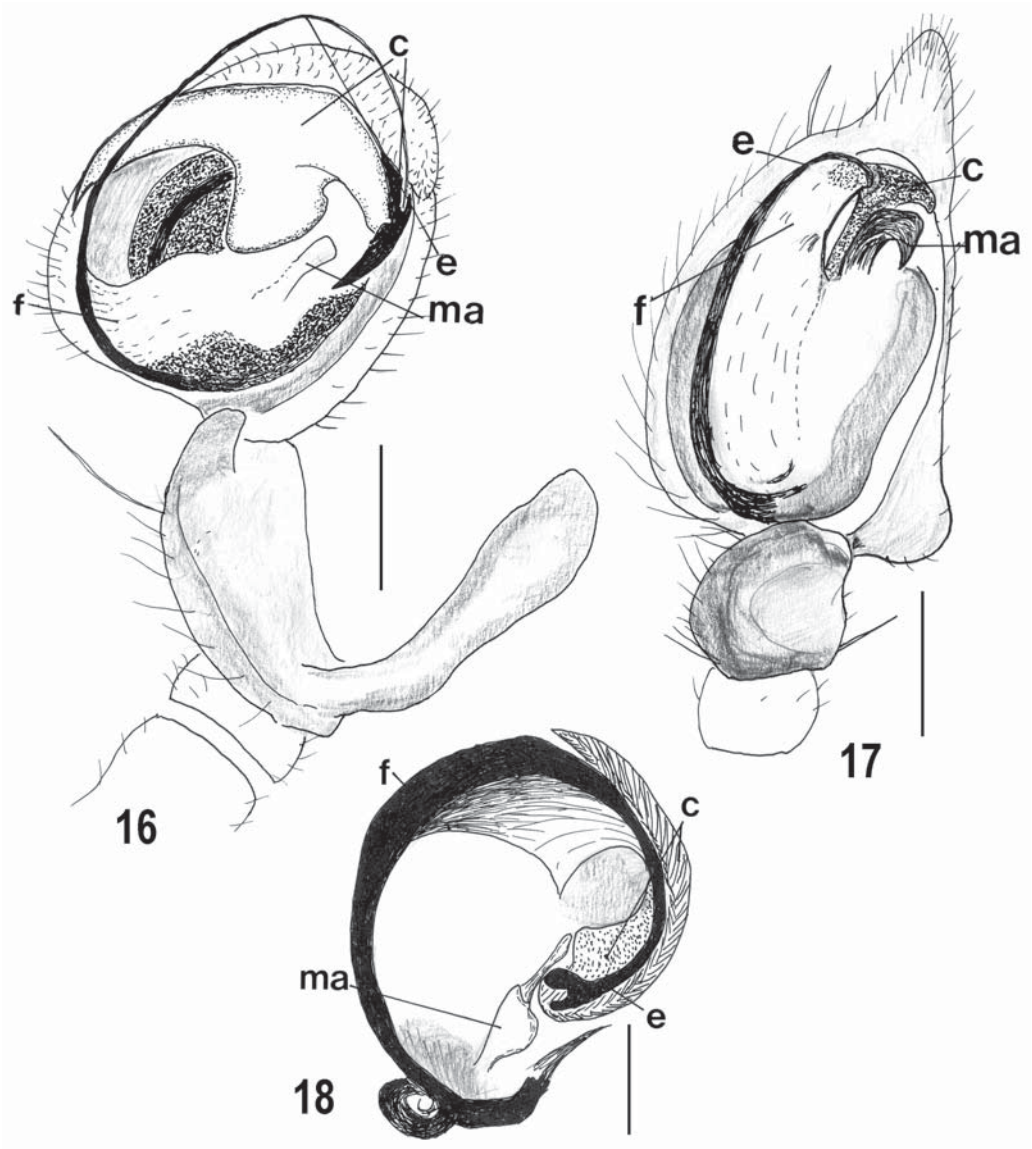
Characters	*Tapponia**	*Hamataliwa***	The *hieroglyphica* group	*Oxyopes****
Carapace	straight; see Fig. 2	straight (dorsally); see Fig. 6	with saddle; see Fig. 11	with saddle
Width of eye field	6/7 of head width	2/3 of head width	1/2 of head width	5/7 of head width
Length of eye field	1/4 of carapace length	1/5 of carapace length	1/5 of carapace length	1/5 of carapace length
AME–AME	1–2 d	< d or = d	< d or = d	> d
ALE–ALE	1–2 d	1–4 d	= d	> d
PME–PME	1/2–1 d	1–4 d	1 d	1 d
Tegument of carapace + abdomen	dense metallic iridescent adpressed spatulate setae	non-iridescent red/black/ white flattened setae	pattern of iridescent flattened setae	pigmented; juveniles with reddish setae
Pigment on abdomen and legs	vague	absent/present	Present	present
Patellar apophysis	present (Fig. 4)	absent (Fig. 8)	absent (Fig. 14)	absent
Tibial apophysis	distal excavation with black knob/tooth (Fig. 3)	distal excavation with black knob/tooth (Fig. 8)	distal excavation with black knob/tooth (Fig. 13)	large V-shaped excavation
Conductor	fan-shaped, distally sclerotized (Fig. 3)	large, sheath-like sclerotized (Fig. 7)	large, sheath-like sclerotized (Fig. 13)	T-shaped membranous
Embolus	flattened, tip slightly widened (Fig. 3)	flattened, tip often widened (Fig. 7)	flattened, tip often widened (Fig. 13)	flattened whip-like
Tegular lobe	small, rounded	hooked	circular	absent
Epigyne	horseshoe rim	horseshoe rim	horseshoe rim (Fig. 12)	V-shaped, flat

* = The characters described are based on *T. micans*.
** = This column refers to the *Tapponia* species to be moved to *Hamataliwa*.
*** = The characters described are based on *Oxyopes birmanicus*.
* = Описанные признаки основаны на изучении *T. micans*.
** = Эта колонка относится к видам *Tapponia*, которые будут переведены в *Hamataliwa*.
*** = Описанные признаки основаны на изучении *Oxyopes birmanicus*.

the sheath-like cavity of the conductor rim. Indeed, the structure of the copulatory organs in these three groups is much more uniform than are the somatic characters.

Examination of the type specimen of the type species of *Tapponia*, *T. micans* Simon, 1885 from Sumatra, showed that it is almost identical to species 1 (group I; Figs 3, 4; *Tapponia* cf. *micans*). In contrast to the species in groups II and III, the palpal patella of this species has a distal apophysis and the tegular lobe is weak.

All species of group II (Figs 7, 8) have a more pronounced, hooked tegular lobe. In the large, colourful species 10 (group III; Figs 12–14, 18), both the structure of the palp and the epigyne are similar to those in group II, except for the tegular lobe which is ring-shaped. After examining material of *T. hieroglyphica* and *T. superba* from Burma (Fig. 18), identified by Thorell (MNHS) and the types of *T. severa* and *T. incompta* (NHM) and carefully reading the descriptions, it became clear that the majority of species listed in *Tapponia* belong with group



Figs 16–18. Male palps of *Oxyopes heterophthalmus* (Latreille, 1804) (from the Pyrenees) (16), *Oxyopes salticus* Hentz, 1845 (from Rupununi, British Guyana) (17) and '*Tapponia*' *superba* (Thorell, 1887) (from Bhamo, Burma) (18). Scale: 0.25 mm.

Рис. 16–18. Пальпы самцов *Oxyopes heterophthalmus* (Latreille, 1804) (из Пиренеев) (16), *Oxyopes salticus* Hentz, 1845 (из Рупунуни, Британская Гвиана) (17) и '*Tapponia*' *superba* (Thorell, 1887) (из Бхамо, Бирма) (18). Масштаб: 0,25 мм.

III, with *T. hieroglyphica* and *T. severa* being the most widespread. *T. incompta* is however a member of group II. In both groups II and III, the colour pattern proved to be an unreliable factor for distinguishing species, as it derives from specialized hairs which quickly become detached in alcohol.

Thus, there are three groups of alleged *Tapponia* species with similar genital organs but with dissimilar habitus and somatic characters. Should the three categories be placed in separate genera, or should they be united in a single genus with variable somatic characters?

Towards a proper assignment

When searching for more exotic *Oxyopes*, I came across some oxyopids collected from the savannah of southern British Guyana. I found a male and a female in this material, which conformed fully, both in somatic and genitalic features, with the species of group II. This species turned out to be one of the numerous New World species of the genus *Hamataliwa* [Brady, 1964]. There is no doubt about the placement of all species of group II; they belong in *Hamataliwa*. In identification keys, *Hamataliwa* keys out as having widely separated PME, but examining Brady's [1964] revision of Central American species, this character appears to be variable among the 45 species treated, and though most species have widely separated PME, there are others that have them much closer together. What then is the status of *Tapponia*? *Tapponia* was established by Simon in 1885, *Hamataliwa* by Keyserling in 1887. The latter genus has been very successful in speciation and is pantropical. Should *Hamataliwa* be synonymized with *Tapponia*? This kind of decision is somewhat arbitrary as no strict rules exist and it sometimes depends on individual judgement.

T. micans, the type species of *Tapponia*, has a few somatic as well as genitalic characters which separate it from *Hamataliwa grisea* Keyserling, 1887, the type species of *Hamataliwa*, as well as from the Asian species. This alone might justify separation at the generic level. I would indeed advocate maintaining them in separate genera. Moreover, placing *Hamataliwa* as a junior synonym of *Tapponia* would have considerable practical nomenclatorial consequences worldwide, and would unnecessarily disturb the current stability in classification.

The species in the third group of '*Tapponia*' *hieroglyphica*, constitute a well definable group of species, incompatible with both *Tapponia* and *Oxyopes*. If Thorell, while transferring the species he had originally described as *Oxyopes* to the genus *Tapponia*, had first studied a specimen of *Tapponia* (established as a genus at that period by his friend and colleague Simon), which he apparently did not, he would have immediately recognized his mistake and left them either in *Oxyopes* or assigned them to a new genus.

The name *Megullia truncata* still figures in Platnick's World Spider Catalogue although Simon placed it in *Hamataliwa* as early as 1898 [Simon, 1898: p. 380]. Thorell personally placed the name "*Hamataliwa truncata*" on the label of the phial containing a subadult male in the collection of the Stockholm Museum. This specimen does not belong in the *hieroglyphica* group, so the name *Megullia* cannot be used for that group of species. Its carapace shape is extraordinary in the height, steepness and width of the front, whilst the rear of the abdomen is unusual in that it is swollen and truncate; the specimen is in poor condition and this trait of the abdomen might be an artefact.

Conclusions

Ten out of the 11 oxyopid species collected from the Bornean rainforest canopy can be recognized as belonging to, or obviously related to, the species currently listed under *Tapponia*. The female copulatory organs are fairly uniform in all these species and so is the male palpal morphology, but there are considerable differences in somatic characters, such that they fall into three distinct species groups. Consistent differences in the tegular lobe of the male palp are found between the three somatic types. Colour patterns are often of little value for separating species, as they are formed by specialized hairs that are readily lost when preserved in alcohol.

Conclusions are as follows:

1. One species is a true *Tapponia*, close to *T. micans*.

2. Eight species belong to the pantropical genus *Hamataliwa*; *Tapponia austera* Thorell, 1894, *T. fronto* (Thorell, 1890), *T. incompta* Thorell, 1895, *T. latifrons* (Thorell, 1890), *T. obtusa* (Thorell, 1892), may also belong in this genus. The final identification is not possible without studying the types of the species described by Thorell.

The position of the monotypic *Megullia truncata* is unclear, it certainly belongs with this group, though a possible transfer into *Hamataliwa* can only be fulfilled after examination of the type specimen.

3. The largest and most colourful species is related to '*Tapponia*' *hieroglyphica* and also cannot be maintained in the genus *Tapponia*. It is closely related to *T. severa* and forms a natural group with several other south-east Asian species that were described in the nineteenth century in the genus *Tapponia*. A new genus should probably be created for them.

ACKNOWLEDGEMENTS. A. Floren is greatly acknowledged for placing all the spiders collected by his fogging experiments in Borneo at my disposal. J. Murphy kindly sent a male of *Oxyopes heterophthalmus* to me for examination; T. Kronestedt generously loaned me all the specimens of *Tapponia superba*, *T. hieroglyphica* and *Megullia truncata* available in the Stockholm museum. C. Rollard loaned me the type of *Tapponia micans* and J. Beccaloni allowed me to see the types of *Tapponia incompta* and *T. severa*. P. Koomen gave me technical assistance.

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