

A revision of *Asteron*, starring male palpal morphology (Araneae, Zodariidae)

Barbara BAEHR¹ & Rudy JOCQUÉ²

¹ Zoologische Staatssammlung, Münchhausenstr. 21, D-81247 München, Germany

² Musée Royal de l'Afrique Centrale, B-3080 Tervuren, Belgium.

A revision of *Asteron*, starring male palpal morphology (Araneae, Zodariidae). - The revision of the genus *Asteron*, described in 1991 on two species, will result in an important diversity increase as more than 100 species are already recognized.

The evolution in the genus is characterized by a spectacular development of the male palp and more precisely by the size increase of the distal tegular apophysis which is directed in the opposite direction of the embolus. A cladistic analysis of the 12 supposedly monophyletic groups (*simplex*, *parasimplex*, *simile*, *reticulatum*, *longiconductor*, *brachyconductor*, *queenslandicum*, *howi*, *crassicalcar*, *mas*, *humphreysi* and *longispina*) is carried out. The most plesiomorphic species of the *simplex*-group has a palpal morphology which is comparably simple as in the most ancestral species of *Storena* (Australia), *Tenedos* (South America) and an as yet undescribed genus from South Africa.

The distribution pattern of the species-groups is presented. Just as for *Storena*, the ancestral groups of *Asteron* are found in the eastern part of Australia whereas the derived groups live in Western Australia.

The details of the distribution corroborate the hypothesis that the Australian Zodariidae have a double origin.

Keywords: Zodariidae - *Asteron* - systematics - phylogeny - zoogeography - historical biogeography

INTRODUCTION

In "We'll meet again", JOCQUÉ (1993) explained the double origin of the Australian Zodariidae. Whereas only *Asceua* and *Malinella* reached Australia from the Oriental region during the recent Ice ages, all other zodariid genera but one are endemic to Australia (JOCQUÉ 1991). *Cyrioctea* belongs to the southern continental fauna and is found in Australia as well as in South Africa and Chile.

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The only Australian genus that has been revised so far is *Storena* (JOCQUÉ & BAEHR 1992, 1995), an excellent example of an isolated endemic Australian genus. According to its phylogenetic relationships and its distribution pattern, it belongs to the old tropical and subtropical fauna of Gondwanaland (BAEHR & JOCQUÉ 1994). The revision of the genus *Asteron* is the next step to review the poorly known, but apparently extremely rich zodariid fauna of Australia. With the analysis of the phylogenetic relationships, we aim to discover the origin of the genus and reconstruct its dispersion on the Australian continent just as we did for *Storena* (BAEHR & JOCQUÉ, 1994).

MATERIAL AND METHODS

Apart from *Asteron mas* Jocqué, 1991 and *Asteron reticulatum* Jocqué, 1991, no other species have been described in that genus. In the course of this study an additional number of about a hundred species was discovered.

As in the genus *Storena*, the females are very rare and so far no strictly female characters were used for the cladistic analysis. Although somatic characters are relatively variable in this genus, it was impossible to recognize any characters we were able to polarize. The male palps on the other hand vary to a large extent and show a spectacular development with increasing complexity. Considering the number of species discovered (around 100) it was decided to limit the analysis to the level of species-groups. All examined males could be included in one of the 12 species-groups so far recognized.

Abbreviations used

BA	base of embolus
DP	distal prong
DTA	distal tegular apophysis
E	embolus
EA	embolar apophysis
LTA	lateral tegular apophysis
P	prong
R	ridge
PD	prolateral prong of DTA
PL	plate
VTA	ventral tegular apophysis

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of the species-groups are reconstructed according to the cladistic principles of HENNIG (1966). We followed the considerations of HENNIG (1966) and BRUNDIN (1966), which establish that plesiomorphy and the place of origin of a taxon are correlated.

Both authors independently made a cladistic analysis. Both methods used to analyse the data yielded a single cladogram with minor differences between them. The extent and the origin of these differences are explained below. The main outgroup

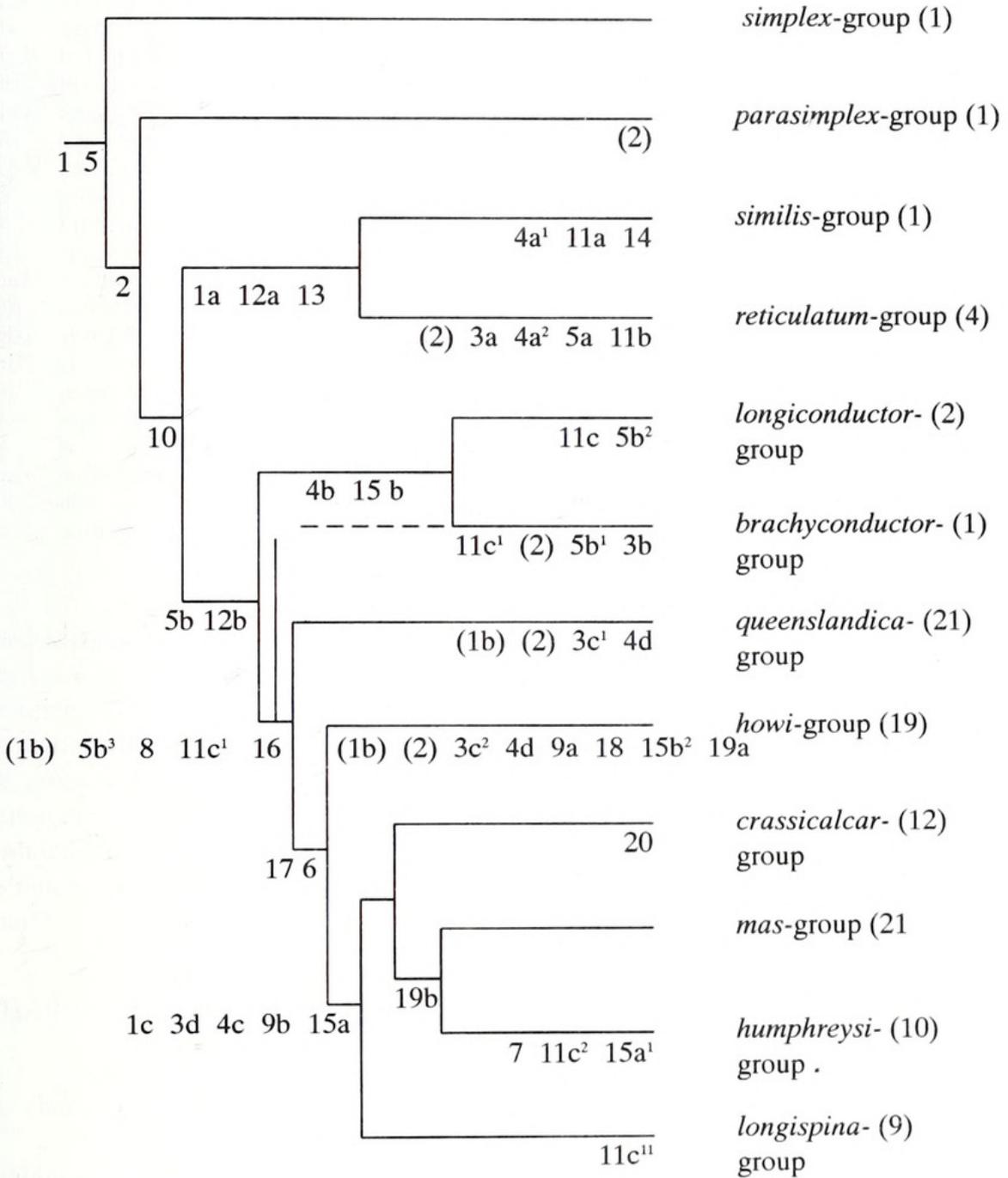


FIG. 1. Cladogram of the species groups of *Asteron*.

TABLE 1

Character states used in the analysis of the phylogenetic relationships of speciesgroups *Asteron*. Different apomorphic states are distinguished by lower case letters. States of a morphocline are indicated by a number.

No.	Character	Plesiomorphic state
1.	Tibia	2 retrolateral apophyses with deep concavity in between
2.	LTA	absent
3.	LTA: structure	conical
4.	VTA: structure	trapezoid
5.	DTA: structure	membranous, spoonlike
6.	DTA: structure	of prolateral appendage short
7.	DTA: shape	of prolateral appendage convex
8.	DTA: tip	of retrolateral appendage blunt
9.	DTA: structure	of retrolateral appendage without prong
10.	Embolus	rigid
11.	Embolus shape	short, not longer than VTA, fingerlike
12.	Base of embolus	embolus merges gradually with tegulum
13.	Embolar apophysis	absent
14.	Embolar apophysis	rounded
15.	Base of embolus,	separate from tegulum, chitinous plate
16.	Prolateral ridge	on tegulum absent
17.	Ridge: length	not reaching the base of bulbus
18.	Ridge: shape	convex
19.	Ridge: structure	without prongs
20.	Cymbium	without strong distal spine

Apomorphic state

- 1a with 3 or 4 apophyses, ventrolateral one pointed
- 1b with 3 or 4 apophyses, ventrolateral one bipointed
- 1c with 3 or 4 apophyses, ventrolateral one distally swollen or hook-shaped
- 2 present
- 3a hookshaped
- 3b small, like a claw
- 3c1 small, spiniform in vertical direction
- 3c2 small, spiniform in horizontal direction
- 3d reduced
- 4a1 large, curved
- 4a2 large, spirally folded
- 4b very large, hook-shaped
- 4c small, reduced to a prong or plate on base of embolus
- 4d reduced
- 5a tunnel-shaped
- 5b large, sickleshaped, with a distal fold
- 5b1 without retro and prolateral appendage
- 5b2 sickleshaped with distal fold and with retro and prolateral appendage, main part on retrolateral side
- 5b3 semicircular, main part on dorsal side, retrolateral appendage as long as prolateral appendage
- 6 prolateral appendage at least as long as half of cymbium and broad
- 7 concave
- 8 sharp tip
- 9a with additional blunt prong near base

- 9b with additional blunt prong at a distance from base
- 10 flexible
- 11a as long as bulbus, cylindrical, semicircular
- 11b as long as bulbus, curled
- 11c as long as bulbus, tapered towards extremity
- 11c1 longer than bulbus, root thin
- 11c2 longer than bulbus, root directed retrolaterad or forwards and bent over $\pm 180^\circ$
- 11c11 longer than bulbus, root widened and flat
- 12a basis bent over $\pm 180^\circ$
- 12b basis separated from tegulum, plate-shaped
- 13 present
- 14 bifurcate
- 15a connected with small prong (VTA), discoidal or semidiscoidal
- 15a1 connected with prolateral plate (VTA), semidiscoidal
- 15b connected with big hook-shaped VTA
- 15b1 elongate, conical, connected with LTA, VTA reduced
- 15b2 elongate, dorsoventrally depressed, connected with LTA, VTA reduced
- 16 present
- 17 reaching basal part of tegulum
- 18 with concavity
- 19a with distal, freestanding prong (DP) on basal part of ridge
- 19b with distal prong (DP) on basal part of ridge, curved under embolar base
- 20 with one strong distal spine

used is *Storena* which is the sister-group of *Asteron* (JOCQUÉ 1991) and has recently been revised (JOCQUÉ & BAEHR 1992, 1995). The results of the character analysis are presented in tables 2 and 3. The senior author used the method of Hennig (see SUDHAUS & REHFELD 1992), whereas the junior author made a numerical cladistic analysis with the program PeeWee (GOLOBOFF 1994). All characters were run unordered. The combination of Whennig and Empezar with default concavity ($K = 3$) resulted in a single tree with length 108.5 and consistency index 0.73. The length of the tree is not very relevant as much depends on the weight of the characters which are attributed by the program itself.

CHARACTERS

Only characters of the male palp were used. The numbers in brackets refer to the character numbers in table 1.

Tibia (1) with 2-4 apophysis. Cymbium (20) without or with distal spine. Embolus (10,11) (E) very variable, ranging from a short, rigid, fingerlike prong to a curled whip-shaped structure with a prolateral embolar apophysis (13, 14) (EA) or to a long semicircular structure. The base of the embolus (12) (BA) can be separated from the tegulum as a plate (15) with various shape, ranging from a short prong (P=VTA?) to a plate (PL). It is not quite sure that this prong is homologous with the VTA. The tegulum is provided with a lateral tegular apophysis (LTA) (2,3), a ventral tegular apophysis (VTA) (4), a membranous distal tegular apophysis (DTA) (5-9) and a prolateral ridge (R) (16-19). The three tegular apophyses and the ridge are variable

in shape or can be lost. In some species-groups the ridge is provided with a distal prong (DP). Only the distal tegular apophysis (DTA) exists in all species and develops into a conductor with a prolateral (PD) and a retrolateral appendage.

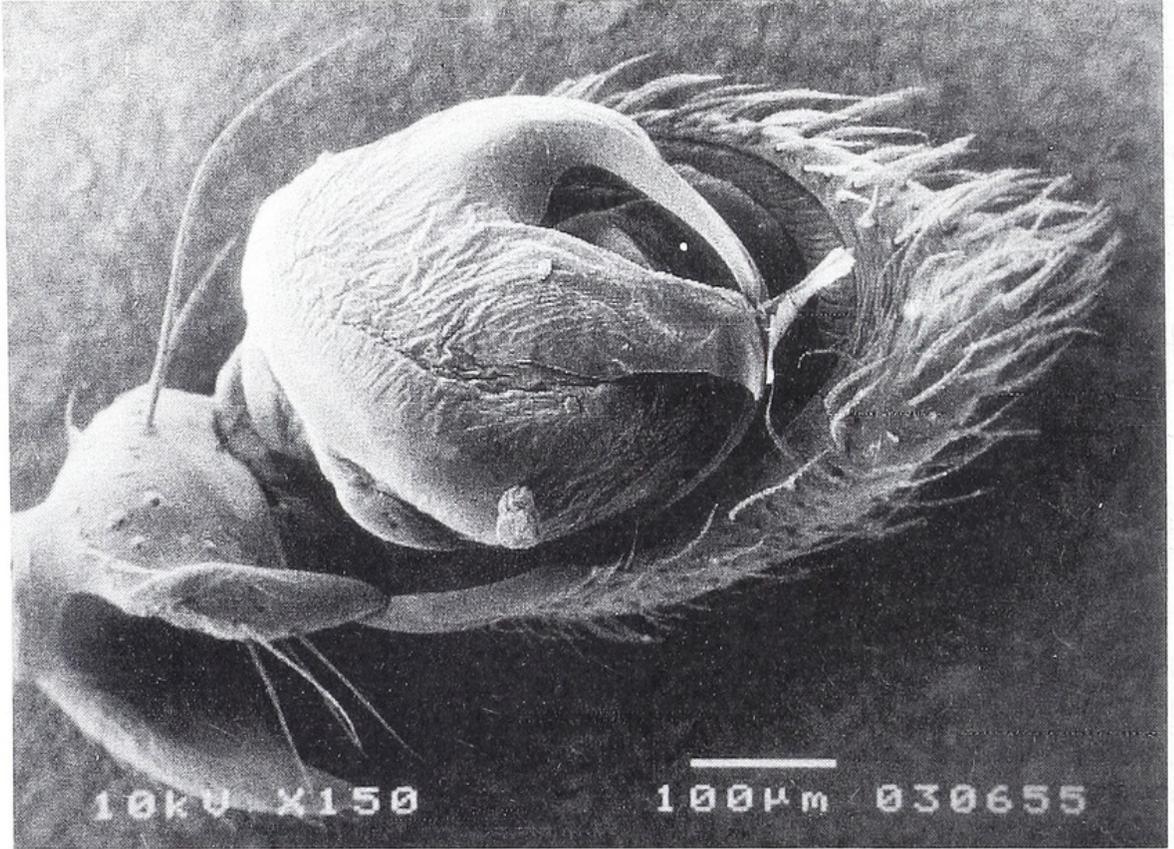


FIG. 2

Asteron simplex-group, 2. Male palp, ventral view.

RESULTS

The species could be divided in 12 supposedly monophyletic species-groups. Although the species have still to be described the groups were given provisional names in order to facilitate the discussion.

The ancestral groups

The species-groups *simplex* (1 species), *parasimplex* (1 species), *simile* (1 species) and *reticulatum* (4 species) are represented by a few species only. With the exception of the *brachyconductor*-group (1 species) and the *longiconductor*-group (2 species), the more derived groups *queenslandicum* (21 species), *howi* (19 species), *crassicalcar* (12 species), *mas* (21 species), *humphreysi* (10 species) and *longispina* (9 species) are rich in species. These more derived groups present a well separated unit, based on the synapomorphies of the DTA (5b) and the structure of the embolar base (12b).

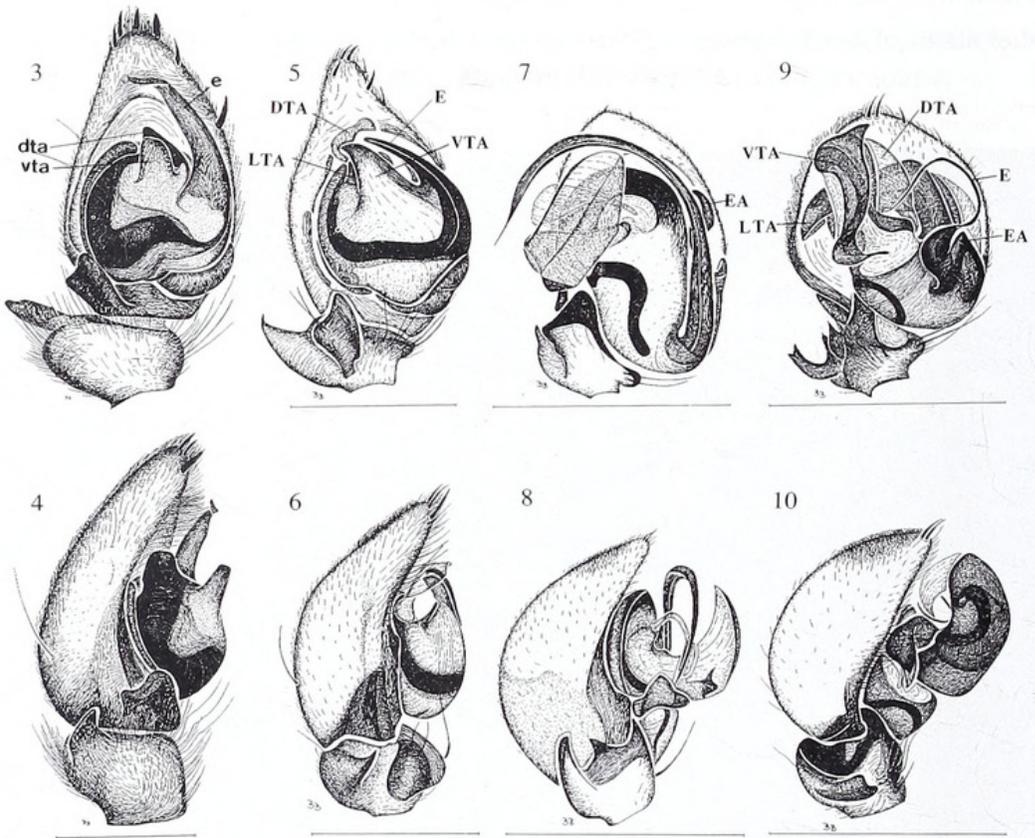
TABLE 2

Character states of species-groups of *Asteron* numbered as in Table 1: - plesiomorphic states; numbers: apomorphic states

	1	2	3	4	5	6	7	8	9	10
<i>simplex</i>	-	-	-	-	-	-	-	-	-	
<i>parasimplex</i>	-	2	-	-	-	-	-	-	-	
<i>simile</i>	1a	-	-	4a1	-	-	-	-	-	10
<i>reticulatum</i>	1a	2	3a	4a2	5a	-	-	-	-	10
<i>brachyconductor</i>	-	2	3b	4b	5b1	-	-	-	-	10
<i>longiconductor</i>	-	-	-	4b	5b2	-	-	-	-	10
<i>queenslandicum</i>	1b	2	4c1	4d	5b3	-	-	8	-	10
<i>howi</i>	1b	2	3c2	4d	5b3	6	-	8	9a	10
<i>crassicalcar</i>	1c	-	3d	4c	5b3	6	-	8	9b	10
<i>mas</i>	1c	-	3d	4c	5b3	6	7	8	9b	10
<i>humphreysi</i>	1c	-	3d	4c	5b3	6	7	8	9b	10
<i>longispina</i>	1c	-	3d	4c	5b3	6	-	8	9b	10
	11	12	13	14	15	16	17	18	19	20
<i>simplex</i>	-	-	-	-	-	-	-	-	-	
<i>parasimplex</i>	-	-	-	-	-	-	-	-	-	
<i>simile</i>	11a	12a	13	14	-	-	-	-	-	
<i>reticulatum</i>	11b	12a	13	-	-	-	-	-	-	
<i>brachyconductor</i>	11c1	12b	-	-	15b	16?	17?	-	-	
<i>longiconductor</i>	11c	12b	-	-	15b	-	-	-	-	
<i>queenslandicum</i>	11c1	12b	-	-	15b1	16	-	-	-	
<i>howi</i>	11c1	12b	-	-	15b2	16	17	18	19a	
<i>crassicalcar</i>	11c1	12b	-	-	15a	16	17	-	-	20
<i>mas</i>	11c1	12b	-	-	15a	16	17	-	19b	-
<i>humphreysi</i>	11c2	12b	-	-	15a1	16	17	-	19b	-
<i>longispina</i>	11c11	12b	-	-	15a	16	17	-	-	-

According to the cladogram of *Asteron* (Fig. 1), based on the matrix of Tab. 2, the most primitive species-group is the *simplex*-group (Fig. 2). It is obviously equivalent with the "basic conformation" with well exposed tegulum, trapezoid ventral apophysis (VTA), membranous spoonlike distal apophysis (DTA) and with rigid, fingerlike embolus. Outgroup comparison with the "basic conformation" of *Storena* (Fig. 3,4) reveals that the synapomorphies of the genus *Asteron* are the deep concavity between the two retrolateral tibial apophyses (1) and the membranous structure of the DTA (5). In the *parasimplex*-group (Fig. 5,6) there is an additional, conical lateral apophysis LTA (2). The shape of this apophysis changed in the remaining groups (3a, 3b, 3c1, 3c2) or was reduced in the more derived groups.

The most conspicuous character of the *simile*-group (Fig. 7, 8) and the *reticulatum*-group (Fig. 9, 10) is the presence of a prolateral embolar apophysis (13) (EA) and the large curved (4a1) or spirally folded (4a2) VTA.

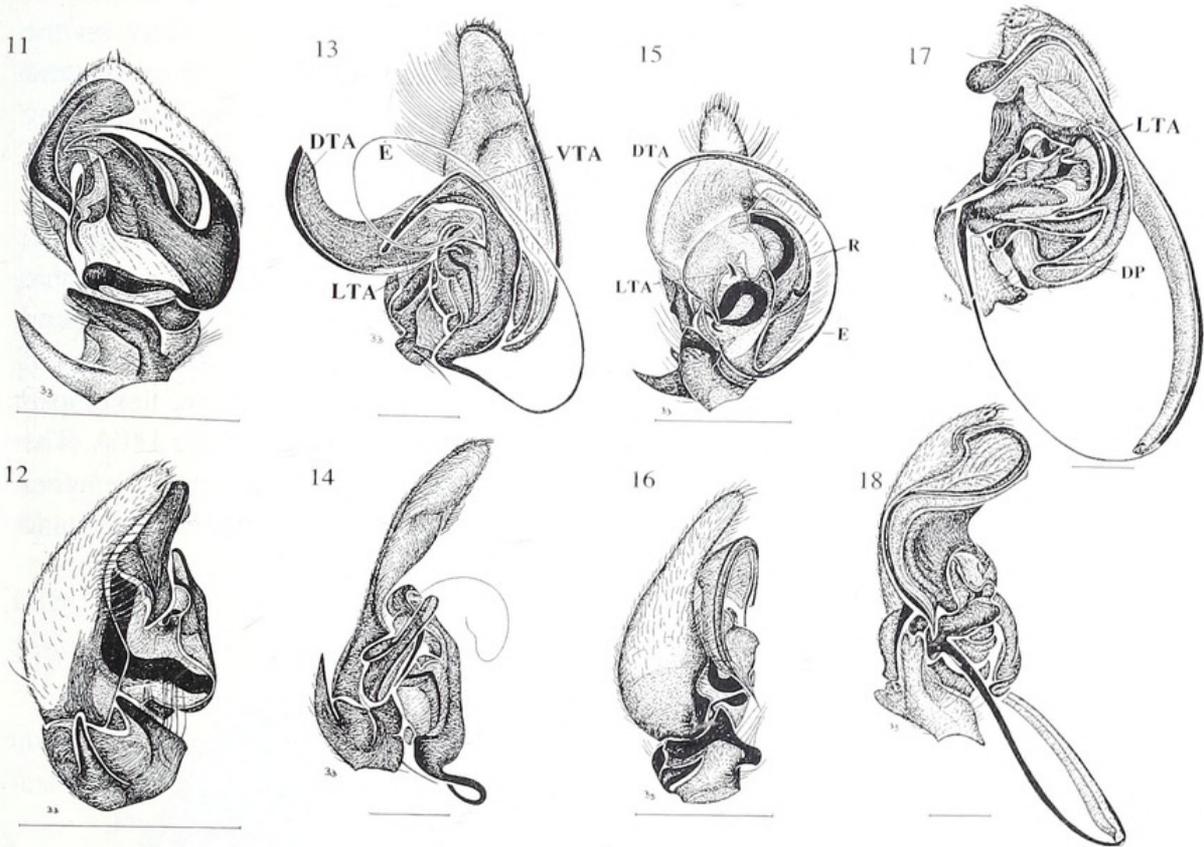


FIGS 3-10

Storena procedens 3. Male palp, ventral view. 4. Male palp lateral view. *parasimplex*-group, 5. Male palp, ventral view. 6. Male palp lateral view. *simile*-group, 7. Male palp, ventral view. 8. Male palp lateral view. *reticulatum*-group, 9. Male palp, ventral view. 10. Male palp lateral view. DTA - Distal tegular apophysis, E - Embolus, EA - Embolar apophysis, LTA - Lateral tegular apophysis, VTA, vta - Ventral tegular apophysis.

As mentioned above, the remaining species-groups are clearly separated from the ancestral ones by the well delimited, chitinous base of the embolus (12b) and the very complex structure of the DTA. The DTA is sickle-shaped or semicircular and with its distal fold (5b), has become a functional conductor.

According to the computer analysis the *longiconductor*-group (Fig. 11,12) and *brachyconductor*-group (Fig. 13, 13) are not sister-groups. The reason for this is that in the *brachyconductor*-group the shape of the embolus (11c1) is very similar to the one of more derived groups. The separate chitinous plate, connected with the big hook-shaped VTA (15b) on the other hand, provides a complex synapomorphy for the *longiconductor*- and *brachyconductor*-group. The big hook-shaped VTA is most probably fixing the palp to the epigyne during copulation. In all other derived groups, the VTA is small or reduced. At the moment we can't decide whether the *brachyconductor*-group is the sister-group of the *longiconductor*-group or whether the latter is the sister-group of all the more derived groups, including the *brachyconductor*-group.



FIGS 11-18

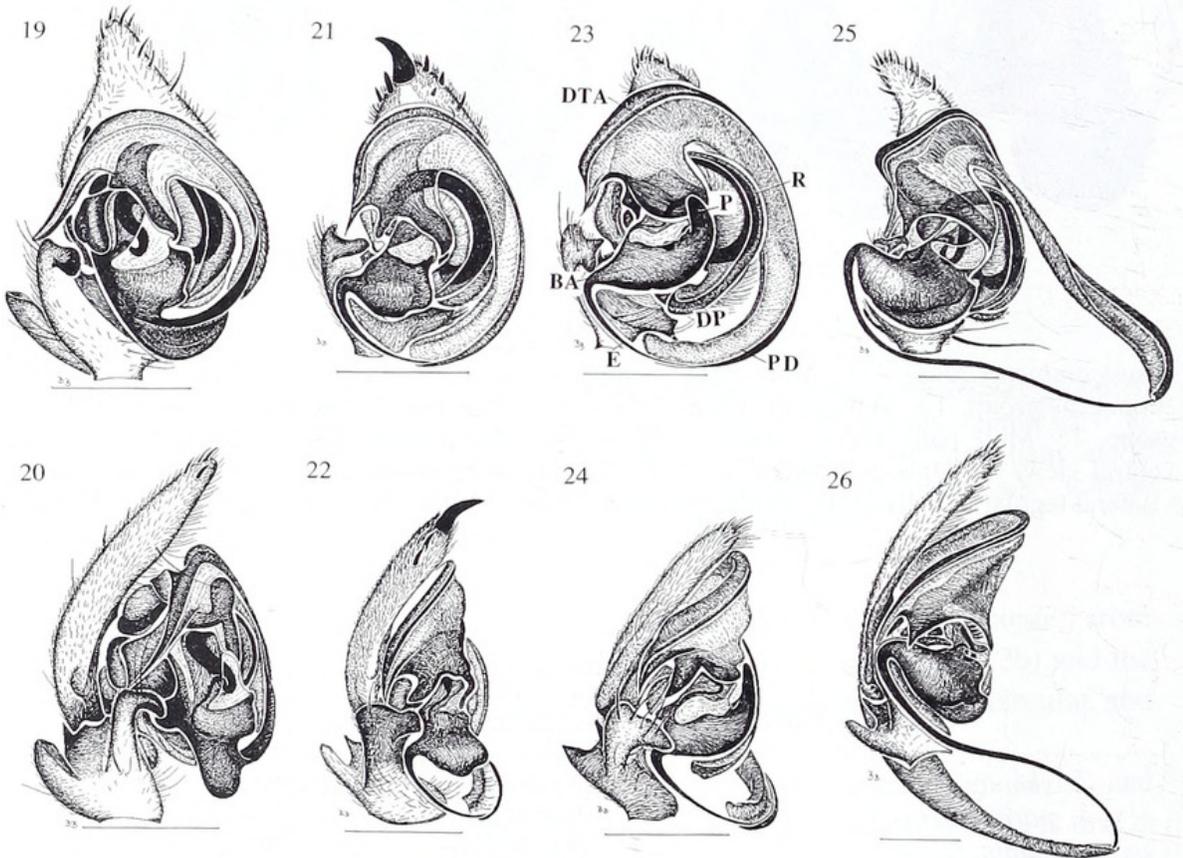
Longiconductor-group, 11. Male palp, ventral view. 12. Male palp lateral view. *brachyconductor*-group, 13. Male palp, ventral view. 14. Male palp lateral view. *queenlandicum*-group, 15. Male palp, ventral view. 16. Male palp lateral view. *howi*-group, 17. Male palp, ventral view. 18. Male palp lateral view. DTA - Distal tegular apophysis, E - Embolus, LTA - Lateral tegular apophysis, R - Prolateral ridge on tegulum, VTA - Ventral tegular apophysis.

TABLE 3

Character matrix based on data in table 2.

<i>simplex</i>	000000000	000000000
<i>parasimplex</i>	010000000	000000000
<i>simile</i>	100100001	111100000
<i>reticulatum</i>	121210001	211000000
<i>brachyconductor</i>	022320001	32003??000
<i>longiconductor</i>	000330001	32003??000
<i>queenlandicum</i>	2235400101	4200410000
<i>howi</i>	2245410111	4200511110
<i>crassicalcar</i>	3054410121	4200111020
<i>humphreysi</i>	3054411121	6200211020
<i>longispina</i>	3054410121	5200111000

The six remaining species-groups show a distinct morphocline here referred to as the *semicirculare*-morphocline. This monophyletic group is based mainly on the semicircular DTA (5b3) with a prolateral appendage and a sharp-tipped retrolateral appendage (8). The concave DTA is obviously functioning as a conductor for the long and slender embolus. The sharp tip is probably inserted together with the slender embolus. A small, spiniform left-over of the LTA seems to be responsible for the fixation of the palp in the *queenlandicum*-group (Fig. 15, 16) and *howi*-group (Fig. 17, 18). The palps of the *queenlandicum*-group must be considered as the plesiomorphic condition of these six groups, with a well developed semicircular DTA, short pro- and retrolateral appendages and a small prolateral ridge on the tegulum. The male palps of the *howi*- and *humphreysi*-group (Fig. 25, 26) are very complicated and have developed an extremely long (twice as long as the bulbus) prolateral appendage of the DTA. The result of both phylogenetic analyses are: the *howi*-group is separated from the other four groups by the elongate, dorsoventrally depressed basis of the embolus (BA) and



FIGS 19-26

Longispina-group, 19. Male palp, ventral view. 20. Male palp lateral view. *crassicalcar*-group, 21. Male palp, ventral view. 22. Male palp lateral view. *mas*-group, 23. Male palp, ventral view. 24. Male palp lateral view. *humphreysi*-group, 25. Male palp, ventral view. 26. Male palp lateral view. BA - Base of embolus, DP - Distal prong on tegulum, DTA - Distal tegular apophysis, E - Embolus, P - Prong on base of embolus, PD - Prolateral prong of DTA, PL - Plate on base of embolus, R - Prolateral ridge on tegulum.

the very long, concave prolateral ridge with a long free prong (DP) on the tegulum. The presence of the small spiniform LTA (3c2) and the elongate base of the embolus relate them with the *queenslandicum*-group.

The last four groups are characterized by a high number of synapomorphies (1c, 3d, 4c, 9b, 15a) of which the most conspicuous are the distally swollen or hook-shaped ventrolateral tibial apophysis (1c) and the discoidal structure of the embolus base (BA, 15a). For the *mas*-group (Fig. 23, 24) we didn't find an autapomorphy. The *crassicalcar*-group (Fig. 21, 22) is characterized by the strong distal spine (20) on the cymbium, also present on the female palp, which is most likely a digging sevice. In the *longispina*-group (Fig. 19-20) the root of the embolus becomes widened and flat (11c11) and the retrolateral appendage of the DTA elongate and grooved. In other characters there is a more or less continuous morphocline from the species in the *mas*-group to those of the *humphreysi*-group. Further research, and possible more new species might reveal whether the *mas*- and *humphreysi*-group must remain separated or not.

DISCUSSION

The origin of the genus *Asteron*

The analysis of the distribution of *Asteron* and its the historical biogeography are tentative because from some regions (Northern Territory, Central Australia) only a few records are available.

The fauna and flora of Australia are mainly composed of three ecologically and taxonomically distinct elements (BAEHR 1990; CRANSTON & NAUMANN 1991), explained in detail by BAEHR & JOCQUÉ (1994).

The ancestral species-groups of the genus *Asteron* are recorded from southeast Queensland (*simplex*-group) and Victoria (*parasimplex*-group). The most plesiomorphic group of the *semicircularis*-morphocline (*queenslandicum*-group) is represented by a high number of species, exclusively found in the rainforests of northeastern Queensland. Therefore *Asteron* most likely originates from the tropical, subtropical or semiarid part of eastern Australia. The simple palpal morphology found in the *simplex*-group is also present in the Australian sister-group *Storena*, in the South American genus *Tenedos* (see JOCQUÉ & BAERT 1996) and in an undescribed taxon from South Africa. This would indicate that *Asteron* belongs to the old Gondwanaland heritage of the Australian continent.

Evolution of the distribution pattern of the genus *Asteron* according to the climatic history of Australia

The climatic conditions of Australia changed during the tertiary because of the rapid drift of the continent to the north, reaching its present position in the Miocene (see BAEHR 1990, 1992, BAEHR & JOCQUÉ 1994). The pleistocene was characterized by repeated successions of wet pluvials and dry interpluvials. In the wet pluvials, a belt of more or less dense forest and woodlands was created around Australia's arid centre. Many species were enable to expand their distribution area in this time.

During the dry interpluvials the arid zones expanded and isolated large woodland regions now recognized as refugia (e.g. Arnhem Land, Kimberly Division,

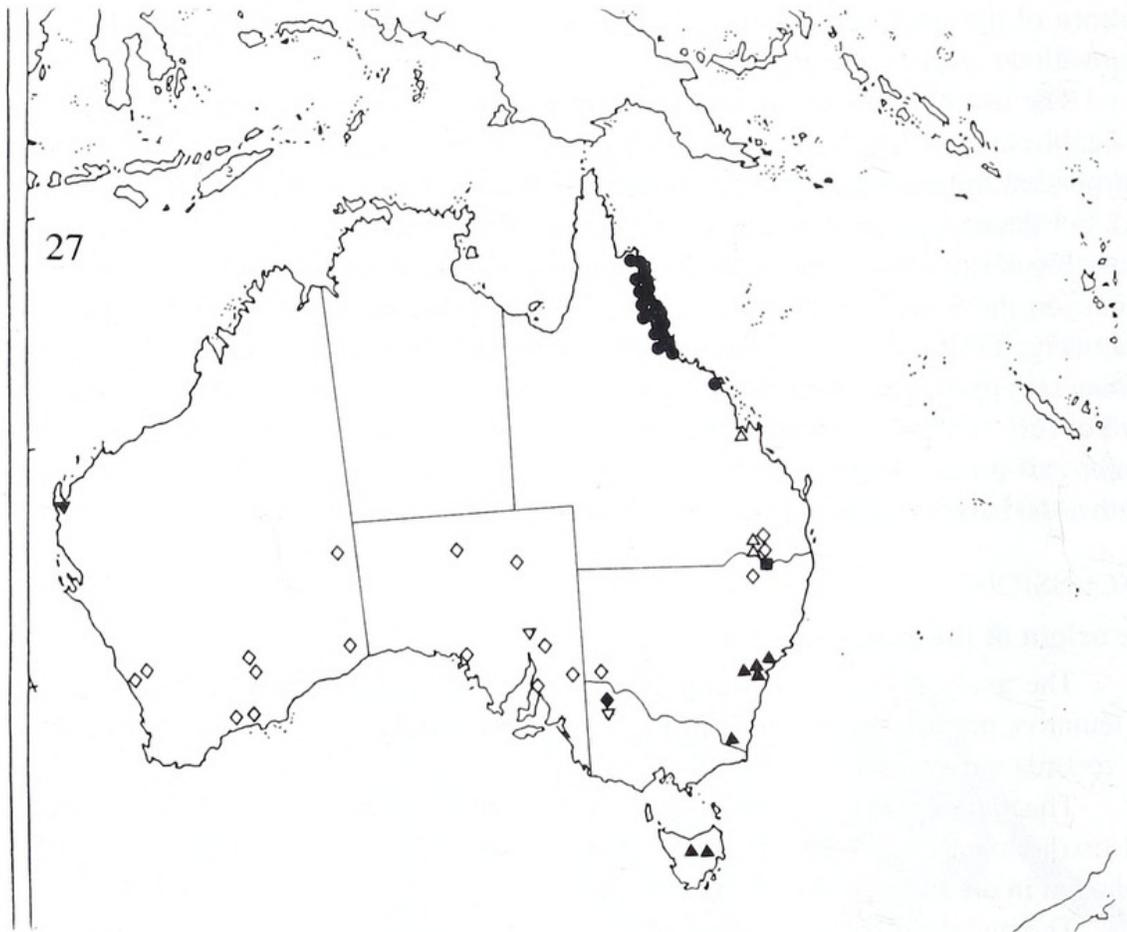


FIG. 27

Distribution pattern of the ancestral species-groups of *Asteron*: ■ *simplex*-group, ◆ *parasimplex*-group, △ *simile*-group, ▲ *reticulatum*-group, ▼ *brachyconductor*-group, ▽ *longiconductor*-group, ● *queenlandicum*-group, ◇ *howi*-group.

Hamersley Ranges, south-western Australia). Populations were isolated and new species developed.

The evolution of the distribution patterns of *Asteron* obviously followed the same scenario. As indicated above, the origin of the genus *Asteron* is supposed to be in the eastern part of Australia (*simplex*, *parasimplex*, *simile*, *reticulatum*) (Fig.27). The ancestors of the *brachyconductor*-group must have been separated very early from the ancestors of the *longiconductor*-group which live today in Victoria and South Australia, because specimens of the *brachyconductor*-group now live in the westernmost part of Western Australia (Fig. 27). After the separation, their palps developed in another, quite different direction.

The well defined *semicirculare*-morphocline colonized the totality of the Australian continent apart from the Northern Territory in different distribution patterns.

An impressive radiation took place in the *queenlandicum*-group (Fig. 27) in small patches of tropical rainforests in Queensland. These forest-dwelling species

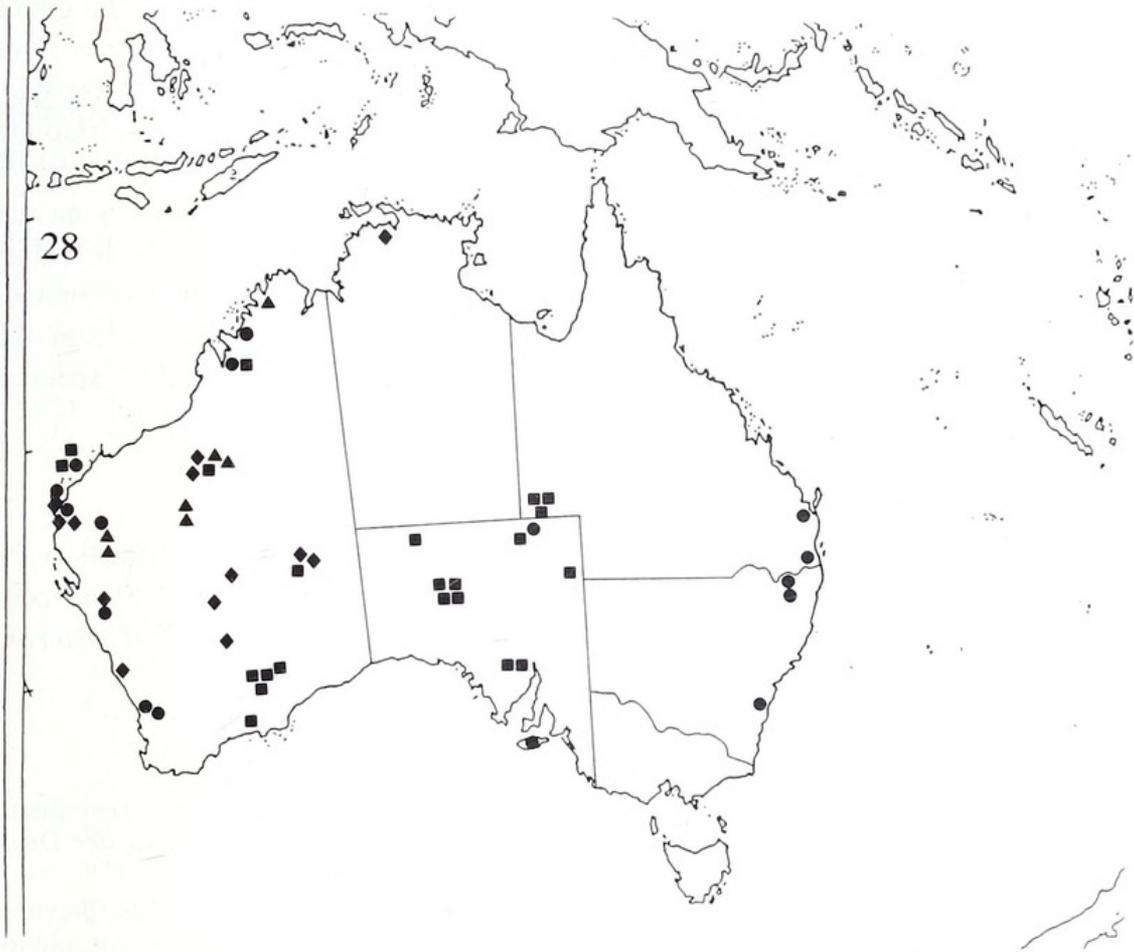


FIG. 28

Distribution pattern of the derived species-groups of *Asteron*: ● *mas*-group, ■ *crassicalcar*-group, ▲ *longispina*-group, ◆ *humphreysi*-group.

have obviously small distribution areas coinciding with the extent of their habitat. These are most likely to be rainforest patches that in certain periods were restricted to high altitude (V. Davies, pers. comm.). On each mountain apparently different species developed. In this group the palps are extremely similar but the pattern of the opisthosoma is specific for each species.

Ancestors of the *howi*-group on the otherhand, colonized the eastern, southern and south-western part of Australia developing many species (Fig. 27).

The same distribution pattern can also be found in the *mas*-group, but the more derived species are only found in Western Australia (Fig. 28). In view of their obviously digging lifestyle, the species of the *crassicalcar*-group have colonized large areas including arid regions (Fig. 28). A few species have a large distribution area unlike the majority of the congeneric taxa. The distribution pattern indicates, that the separation from the *mas*-group took place in South Australia. The most derived species of that group are recorded only from Western Australia just as the entire *humphreysi*- and *longispina*-groups. (Fig. 28).

The above mentioned results indicate that the genus *Asteron* just as the genus *Storena* belongs to the old Gondwanaland fauna. *Storena* as well as *Asteron* have their origin in southeastern Queensland, where the most primitive species of *Storena*, *S. procedens* and the most ancestral species-group of *Asteron*, the *simplex*-group are now found together.

The most derived species-groups and the most diverse and rich fauna are presently located in Western Australia. This rich fauna of Western Australia found its origin in the alternation of wet pluvials (opening of corridors, expansion of founder populations) and dry interpluvials (separation of Western Australia because of the Nullarbor Plain, separation of the founder populations and development of species) during the recent palaeoclimatic history of Australia.

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