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Phylogeny and zoogeography of the Australian genus *Storena*

(Araneae, Zodariidae)

By Barbara Baehr & Rudy Jocqué

Baehr, B. & R. Jocqué (1994): Phylogeny and zoogeography of the Australian genus *Storena* (Araneae, Zodariidae). – Spixiana 17/1: 1-12

It has been hypothesized (Jocqué in press) that the Australian Zodariidae have a double origin: a majority of old endemic taxa, and a few genera which have invaded Australia in recent geological times. The revision of *Storena*, supposed to belong to the former group, provides ideal data to test the hypothesis.

The revision of the genus (Jocqué & Baehr 1992) revealed that *Storena* is a clearly delimited genus with a very stable somatic morphology. In contrast there is a clear tendency towards increased complexity in the structure of the male palp. The cladistic analysis was therefore only based on male palpal morphology (of the 27 species mentioned in the revision only 19 males are known).

Both the conventional cladistic analysis in the sense of Hennig (1966) and a numerical cladistic analysis yielded the same important monophyletic groups: the *cyanea*-group (5 species) and the *formosa*-group (7 species). The *raveni*-group consists of the more primitive species but its size differs according the analysis and contains resp. 5 and 3 species. As the group does not have any autapomorphy its status is uncertain. The numerical analysis leaves the 4 most plesiomorphic species in an unresolved assemblage, the other approach remains with 2 ungrouped species.

The most primitive species of the *raveni*-group are found in northern, western and central Australia. The *cyanea*-group with more apomorphic species has its distribution in the eastern part of Australia. The species of the *formosa*-group form a lineage from north-eastern Australia through eastern to southern und western Australia with increasing complexity of the palps. The origin of that group must have been in northern Australia. The fact that the plesiomorphic ungrouped species are scattered through the continent with species in northern Australia as well as in southern Queensland would indicate that the genus is part from the oldest Gondwanaland element and did not reach Australia from the north.

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Introduction

According to Jocqué (in press), the Australian Zodariidae have a double origin. The majority of the genera are supposed to have originated on the continent itself after separation from the other zodariids as a result of the Gondwanaland breakdwon. Two genera with a large distribution in the Old World, *Asceua* and *Mallinella*, are assumed to have reached Australia from the Oriental region during the recent Ice ages, hence their restricted distribution in the extreme northern part of the Australian continent. It is known though that quite a number of present-day Australian taxa, among which spiders and beetles, arrived there from the Oriental region during the Miocene (B. Baehr 1988, M. Baehr 1990). For zodariids this possibility was excluded by Jocqué (in press) as apart from *Asceua* and *Mallinella*, there is no taxonomic overlap between the Oriental and the Australian zodariid fauna at the specific or generic level.

©Z Table 1. Character states used in the analysis of the phylogenetic relationships of species. Different apomorphic states are distinguished by lower-case letters. States of a morphocline are indicated by a number.

No.Character	Plesiomorphic state	Apomorphic state
1. Tibia	1 apophysis	with spines: 1a 2 apophyses: 1b 2 apophyses connected with an u- or v-shaped ridge: 1c one additional apophysis, cylindrical: 1c ¹ one additional apophysis, conical: 1c ² both apophyses connected at base. Dorsal apophysis curves over the ventral apophysis: 1d
2. Flange (paracymbium)	triangular - rhomboid, with ridge	hooked, tip of flange acute: 2a spoon-like: 2b hooked, tip of flange rounded: 2c
3. Basis of flange	without bristles	with many bristles: 3
4. Ventral tegular apophysis	small or absent	free, desk-like: 4a free, knob-like: 4b free, like a thick finger: 4c free, hooked: 4d free, membranous: 4e free, membranous, like a finger: 4e ¹ free, membranous, like a bent gutter: 4e ² free, membranous, basis of gutter strong: 4e ³ free, membranous, gutter with denticles on margin: 4e ⁴ free, membranous, margin of gutter wing-shaped: 4e ⁵ free, membranous, reduced to a knoblike apophysis: 4e ⁶ reduced: 4e ⁷ closed by the embolus: 4f closed by the spirale of embolus: 4f ¹ closed by the basis of embolus: 4f ²
5. Embolus	rather straight, finger-like	turned to an open o: 5a turned to an open o, with ridges: 5a ¹ turned to an open o, with strong denticles and ridges: 5a ² spirally coiled: 5b spirally coiled 1x: 5b ¹ spirally coiled more than 2 1/2 x: 5b ²
6. Basis of embolus	distal or mediodistal	on lateroproximal side of the bulb: 6a central, visible: 6b central, visible, beginning of torsion mediodistal: 6b ¹ central, visible, beginning of torsion medial: 6b ² central, covered by the spirally coiled embolus: 6c central, beginning of torsion mediodistal, partly covered by the spirally coiled embolus: 6c ¹ central, beginning of torsion medial, partly covered by the spirally coiled embolus: 6c ² central, completely covered: 6c ³
7. Spermaduct	large, s-shaped	large, rounded: 7a small, inconspicuous: 7b
8. Tip of embolus	short, acute	elongate, thin, acute: 8a widened: 8b counter-rotating: 8c widened, semilunar: 8d

The recent revision of *Storena*, a large endemic Australian genus, offered an ideal possibility to test the hypothesis of the origin of the Australian zodariids. The genus was defined and redescribed by Jocqué (1991) and consequently revised by Jocqué & Baehr (1992) who raised the number of species included in the genus from 4 to 27. 19 of these are represented by males, which make up the majority of the specimens in collections. The explanation for this is the fact that males are common in pitfall traps whereas females are rather rare. During fieldwork in New South Wales one of us (BB) stated that females and juveniles live in holes in decaying logs, which might explain their rarity in pitfalls. As for many species the females are still unknown, it made little sense to include these in the cladistic analysis which is thus entirely based on males.

Whereas somatic characters are very stable in this genus, the sexual organs, and primarily the male palps, are quite variable. There is an obvious increase in complexity of the male palp and several evolution lines can be recognized.

Material

The species considered in the cladistic analysis include all those for which the males are described in Jocqué & Baehr (1992): *Storena aspinosa* Jocqué & Baehr, *S. cochleare* Jocqué & Baehr, *S. colossea* Rainbow, *S. cyanea* Walckenaer, *S. deserticola* Jocqué, *S. digitulus* Jocqué & Baehr, *S. formosa* Thorell, *S. fungina* Jocqué & Baehr, *S. ignava* Jocqué & Baehr, *S. mathematica* Jocqué & Baehr, *S. martini* Jocqué & Baehr, *S. metallica* Jocqué & Baehr, *S. paucipunctata* Jocqué & Baehr, *S. procedens* Jocqué & Baehr, *S. raveni* Jocqué & Baehr, *S. recta* Jocqué & Baehr, *S. rotunda* Jocqué & Baehr, *S. scita* Jocqué & Baehr, *S. sinuosa* Jocqué & Baehr.

Phylogenetic relationships

Methods

The phylogeny is reconstructed following the well-known Hennigian (sensu Hennig 1966) or cladistic principles. The reconstruction of the history of a fauna is based on the history of the acquisition of adaptations, i.e. the history of characters (Sudhaus & Rehfeld 1992).

Both authors independently made a cladistic analysis. The senior author used the conventional Hennigian method (see Sudhaus & Rehfeld 1992), the junior one made a numerical cladistic analysis with the computer program Hennig'86 of Farris. The initial results were very different. The inclusion of somatic characters (presence of hinged hairs, hair cover of carapace and some other characters of sternum and carapace) proved very inappropriate and these characters are seemingly highly subject to homoplasy. By using the same characters both the cladograms became practically congruent. Some small differences remained due to the fact that in the conventional analysis more than 10 states of the same character (tibial apophyses) were used whereas Hennig'86 can only take up to 10.

Characters

All but a few characters were from the male palp. Tibia with 1-4 tibial apophyses (TA). Cymbium (C) with big basolateral flange (FI) variable in size and shape. Embolus (E) very variable, ranging from a short, broad prong to a long, twice coiled, whip-like appendage or a massive s-shaped structure. Tegulum provided with a ventral tegular apophysis (VTA) which may be membranous (mVTA) and a distal tegular apophysis (DTA).

Although a cladistic analysis of the zodariid genera is available (Jocqué 1991) the polarization of the characters posed some problems. The generic revision was mainly based on the type species of the genera which implies that the taxa in the cladogram may be at any level in the clade of a particular genus. A species with a complex palp may belong to a genus in which the most plesiomorphic species have simple palps or vice versa. Therefore, the comparison of the palps of *Storena* with those of its sister-group or other closely related outgroups is not very relevant. It would seem though that an increase in complexity of the palps is the rule in the zodariids. Most of the genera in which there is no obvious change

©Z in complexity (e.g. *Lachesana*, *Lutica*) tend to have simple palps. Large genera for which the revision has been done (*Diores*, Jocqué 1990) or is in preparation (*Tenedos*) have distributions that can only be understood when it is assumed that the palps gain in complexity with time. In *Storena* itself, some of the evolution lines only make sense if one admits increasing complexity of the male palps. Some particular species have small sclerites or membranes that are obviously purposeless; their presence can be understood in the light of previous stages in the development in which these structures were much larger and had an obvious function (e.g. the ventral tegular apophysis in *S. martini*, see below).

Results

The numerical cladistic analysis initially yielded 24 equally parsimonious trees of length 39 and with a high consistency index of 82. The consistency index increased to 91 after two rounds of successive weighting. Finally the Nelson consensus tree was calculated.

Both the conventional analysis and the Nelson consensus tree of the numerical analysis yielded the same important monophyletic groups: the *cyanea*-group (5 species) and the *formosa*-group (7 species). The *raveni*-group consists of the more primitive species but its size differs according the analysis and contains resp. 5 and 3 species. As the group does not have any autapomorphy its status is uncertain. The numerical analysis leaves the 4 most plesiomorphic species in an unresolved assemblage, the other approach remains with 2 ungrouped species. Since both cladograms are so similar only the one reached with the conventional analysis is shown (Fig. 4).

The species of *Storena*, except for two species (*S. procedens*, *S. digitulus*; Fig. 1), can thus be grouped in three groups, two of which are well defined. The uncertain relationships are marked in the cladogram with a dotted line.

The *raveni*-group contains the most primitive species of the genus *Storena*. So far there is no synapomorphic character to support the monophyly of the *raveni*-group. Their bulbus is equivalent to the "basic conformation (Grundplan)" with well exposed tegulum and only a tiny ventral tegular apophysis (VTA)

Table 2. Character states of species of *Storena* numbered as in Table 1: - plesiomorphic state; numbers: apomorphic states.

species	1	2	3	4	5	6	7	8
<i>procedens</i>	—	—	—	4c	—	—	—	—
<i>digitulus</i>	1a	—	—	4a	—	—	—	—
<i>deserticola</i>	1c	—	—	—	—	—	—	—
<i>ignava</i>	1c	—	—	—	—	—	—	—
<i>mathematica</i>	1c ¹	—	—	4d	—	—	—	—
<i>raveni</i>	1c ¹	—	3	4d	—	—	—	—
<i>paucipunctata</i>	1c ¹	—	—	4b	—	—	7a	—
<i>scita</i>	1c	2c	—	4f ¹	5b ²	6b ¹	7b	8a
<i>metallica</i>	1c	2c	—	4f ¹	5b ²	6b ²	7b	8a
<i>cochleare</i>	1c ²	2b	—	4f ²	5b ¹	6b ¹	7b	8b
<i>cyanea</i>	1c ²	2b	—	4f ²	5b ¹	6b ²	7b	8b
<i>colossea</i>	1c ²	2b	—	4f ²	5b ¹	6b ³	7b	8a
<i>recta</i>	1b	—	—	4e ¹	—	—	—	—
<i>rotunda</i>	1b	2a	—	4e ²	5a	6a	7b	8a
<i>fungina</i>	1d	2a	—	4e ³	5a	6a	7b	8a
<i>aspinosa</i>	1d	2a	—	4e ⁴	5a	6a	7b	8a
<i>martini</i>	1d	2a	—	4e ⁶	5a ²	6a	7b	8a
<i>sinuosa</i>	1d	2a	—	4e ^{7*}	5a ¹	6a	7b	8c
<i>formosa</i>	1d	2a	—	4e ^{7*}	5a ¹	6a	7b	8d

* reduced apomorphic character

1

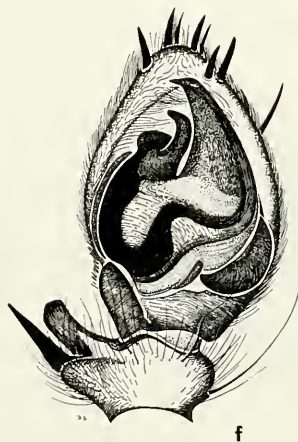
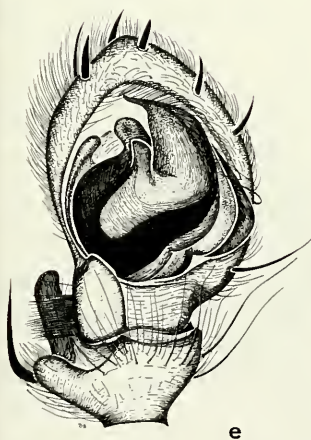
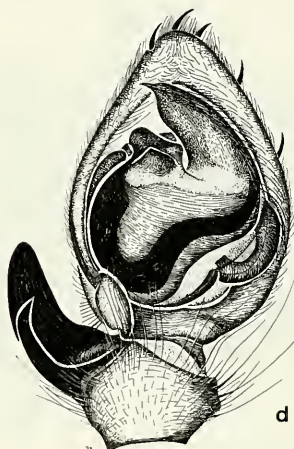
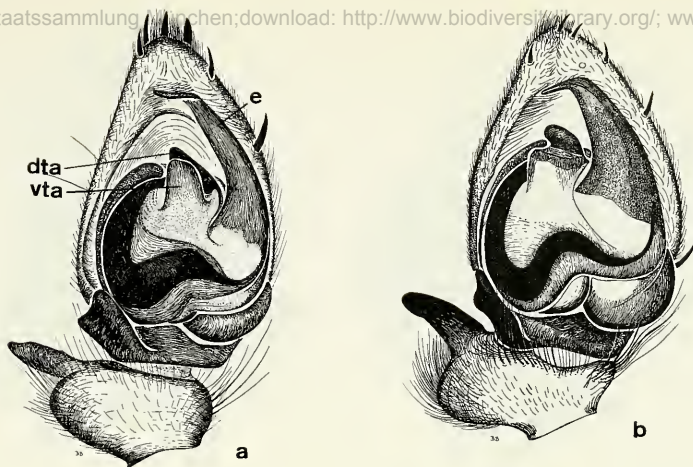


Fig. 1. Male palps of the most plesiomorphic species of *Storena*. a. *S. procedens*. b. *S. digitulus*. c. *S. deserticola*. d. *S. ignava*. e. *S. raveni*. f. *S. mathematica*. g. *S. paucipunctata*. dta: distal tegular apophysis; vta: ventral tegular apophysis.

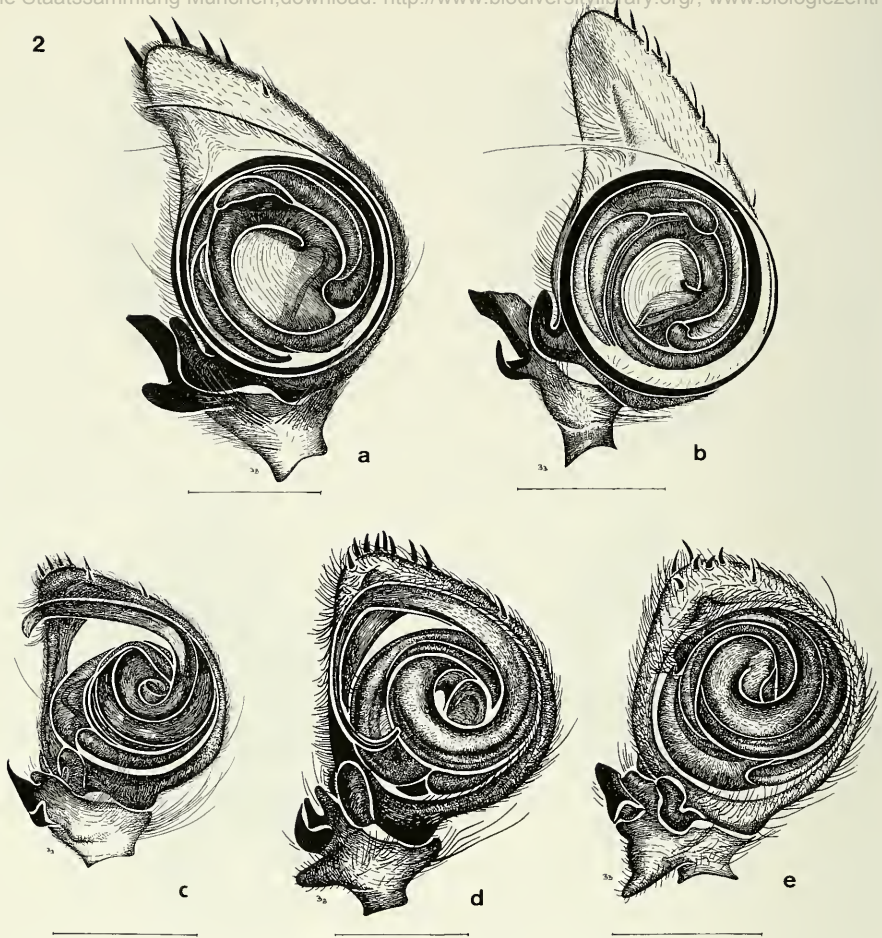


Fig. 2. Male palps of species of *Storena* from the *cyanea*-group. a. *S. metallica*. b. *S. scita*. c. *S. cochleare*. d. *S. colossea*. e. *S. cyanea*.

and with a short, straight, fingerlike embolus (Fig. 1). As usual in primitive groups, the species only possesses a few apomorphic characters (see cladogram). Because of the problems with the outgroup comparison the status of the u-shaped tibial apophysis is doubtful. Either it is the basic conformation and thus a plesiomorphy, either a synapomorphy it shares with the *cyanea*-group.

The *cyanea*-group is characterized by a high number of synapomorphies (Tab. 2: 4f, 5b, 7b) of which the spirally coiled embolus is the most conspicuous one. The individual species and clades are supported by several synapomorphies, confirming the sister-group relationships.

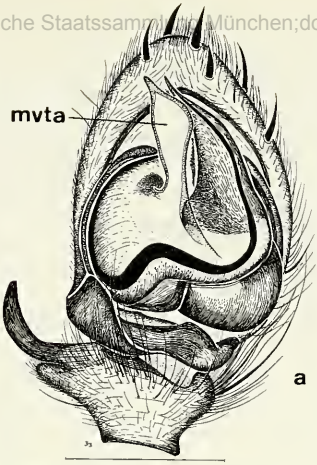
Also for the palps of the species in the *formosa*-group there is a distinct morphocline. This monophyletic group is based on the presence of a membraneous ventral tegular apophysis (mVTA, Fig. 3). This mVTA obviously serves as a conductor for a long and slender embolus. As soon as the embolus becomes massive and strengthened by the presence of ridges and notches, and hence self-supporting, the mVTA is reduced and only present as a tiny left-over (*S. martini*) or disappears completely (*S. formosa*, *S. sinuosa*). This case confirms the polarization which assumes increasing palpal complexity.

An additional synapomorphy of this group is the shape of the complex tibial apophysis, which is quite uniform in all its species except *S. recta* and *S. rotunda*.

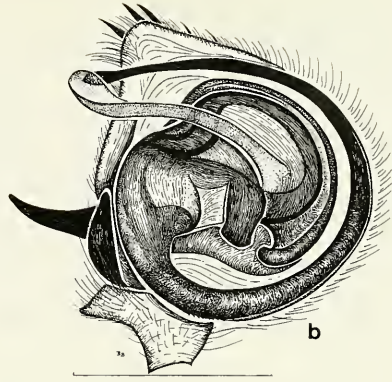
The interrelationships of the remaining single species-groups are uncertain, because we found no synapomorphies with other groups. The status of *S. digitulus* and *S. procedens* is also doubtful. In the

3

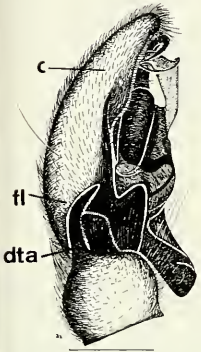
mvta



a

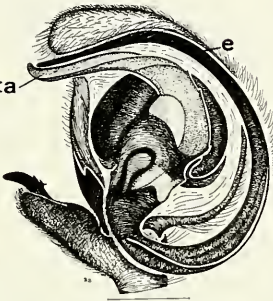


b

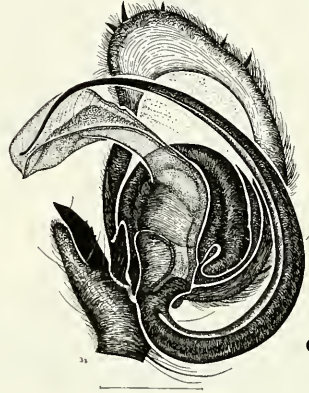


vta

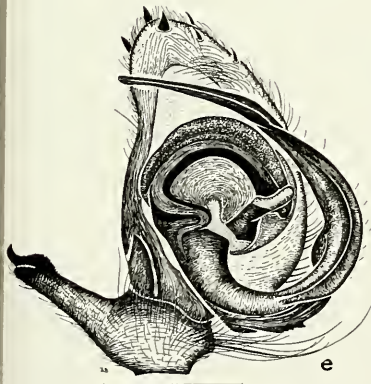
c



e



d



e



f



g

Fig. 3. Male palps of species of *Storena* from the *formosa*-group. a. *S. recta*. b. *S. rotunda*. c. *S. aspinosa*. d. *S. fungina*. e. *S. martini*. f. *S. sinuosa*. g. *S. formosa*. c: cymbium; dta: dorsal tibial apophysis; e: embolus; fl: flange; mvta: double membranous ventral tegular apophysis; vta: ventral tegular apophysis.

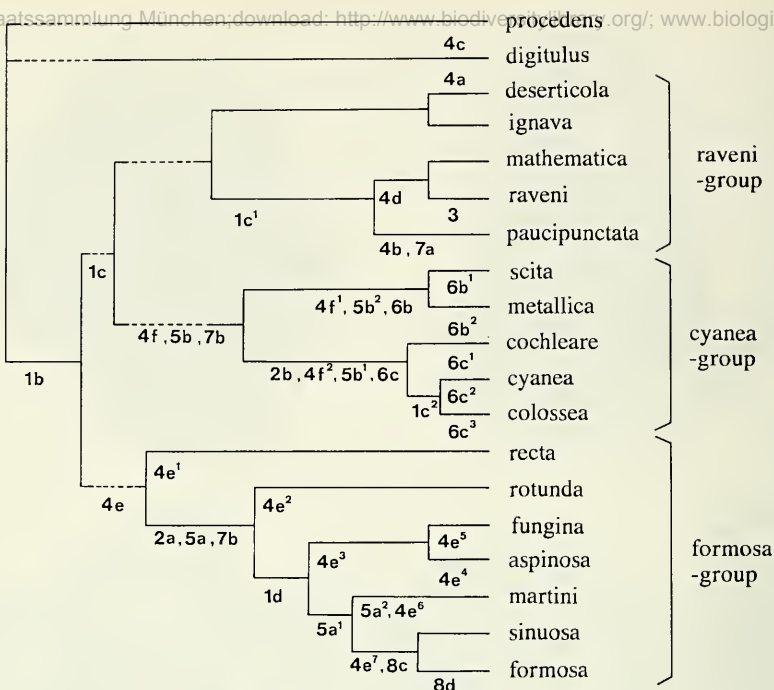


Fig. 4. Cladogram of the males of *Storena*.

structure of the bulbus they hardly differ from the “basic conformation”. Nevertheless, their tibial apophysis could be a synapomorphy, because the plesiomorphic state of the structure of the tibial apophysis is unknown. Since this apophysis is essential for fixing the male palp to the epigyne, it is regarded a character of the utmost importance. The fact that both species possess only one tibial apophysis can thus be

1. a plesiomorphic character, when the sister-group has only one tibial apophysis in its basic conformation;
2. secondary reduced and therefore apomorphic, when the sister-group possesses a tibia with two apophyses forming a “U”.

In the first case *S. digitulus* and *S. procedens* are the most primitive living species (as figured in the cladogram) but if they are apomorphic in their tibial structure, they could be the sister-group of the *formosa*-group.

Only the *cyanea*-group (5 species) and the *formosa*-group (7 species) are monophyletic units. For the remaining, plesiomorphic species it is at present difficult to find clear relationships.

The origin of the genus *Storena*

For most species we only have very reduced number of records. The ideas about their distribution patterns and about the historical biogeography are therefore tentative. In general, we follow the considerations of Hennig (1966) and Brundin (1966) in that plesiomorphy of a taxon and place of origin are correlated.

According to the actual zoogeographical knowledge (Baehr 1990, Cranston & Naumann 1991), the fauna and flora of Australia is mainly composed of three ecologically and taxonomicall distinct elements.

1. A very old autochthonous (endemic) tropical or subtropical Gondwanaland element. The most primitive members of this faunistic element are presently found in the tropical and subtropical regions of northern, and eastern Australia where they mainly live in rainforest or in semiarid and arid deserts



Map 1. Records of the most primitive species of *Storena* in Australia: ○ *S. digitulus*, ● *S. procedens*. Raveni-group: ▼ *S. deserticola*, ▲ *S. ignava*, ◆ *S. mathematica*, □ *S. raveni*, ■ *S. paucipunctata*. Arrows indicate hypothetical expansion of the group.

with *Eucalyptus* and *Acacia*. These taxa are generally very isolated and relics of sister-groups can sometimes be found in the tropical and subtropical parts of Africa and India.

2. A younger Antarctic element of Gondwanaland origin, found in temperate, southern rainforest and mainly characterized by the southern beech *Notofagus*. If a group belongs to this element, the most primitive species are to be found in the temperate regions of south-western and south-eastern Australia. Sister-groups are likely to exist in New Zealand and South America.
3. A young tropical or subtropical Indo-Malayan element with south-eastern Asian affinities. The most primitive species are found in tropical and subtropical monsoon and rainforest habitats of the northern and eastern part of Australia. The group is not as isolated as the former and sister-groups may be found on the Asian islands and in New Guinea.

The most primitive species of the genus *Storena* are recorded from *Storena procedens* (south-eastern Queensland), *Storena digitulus* (Queensland), raveni-group (northern western Australia, Northern Territory, eastern Queensland).

The derived species of the *cyanea*-group with complex apomorphic characters are found in Queensland and New South Wales.

The species of *formosa*-group form a morphocline starting with *S. recta* (north-eastern Queensland) ending with *S. formosa* (western Australia, South Australia, Victoria, New South Wales, Queensland), which is the most apomorphic species.

The most primitive species of the genus *Storena* are thus living mainly in the Northern Territory and in Queensland. According to the theories of Brundin (1966) and Hennig (1966) the origin of the genus *Storena* is most likely to be in the tropical, subtropical and semiarid part of northern and eastern Australia. The genus is thus most likely part of the old Gondwanaland heritage of the Australian continent.



Map 2. Records of species of the *cynea*-group: ▼ *S. cochleare*, ▲ *S. colossea*, ○ *S. cyanea*, ◆ *S. metallica*, □ *S. scita*. Arrows indicate hypothetical expansion of the group.

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

As Baehr (1992) described in detail, 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. During the Pleistocene there were repeated successions of wet pluvials and dry interpluvials.

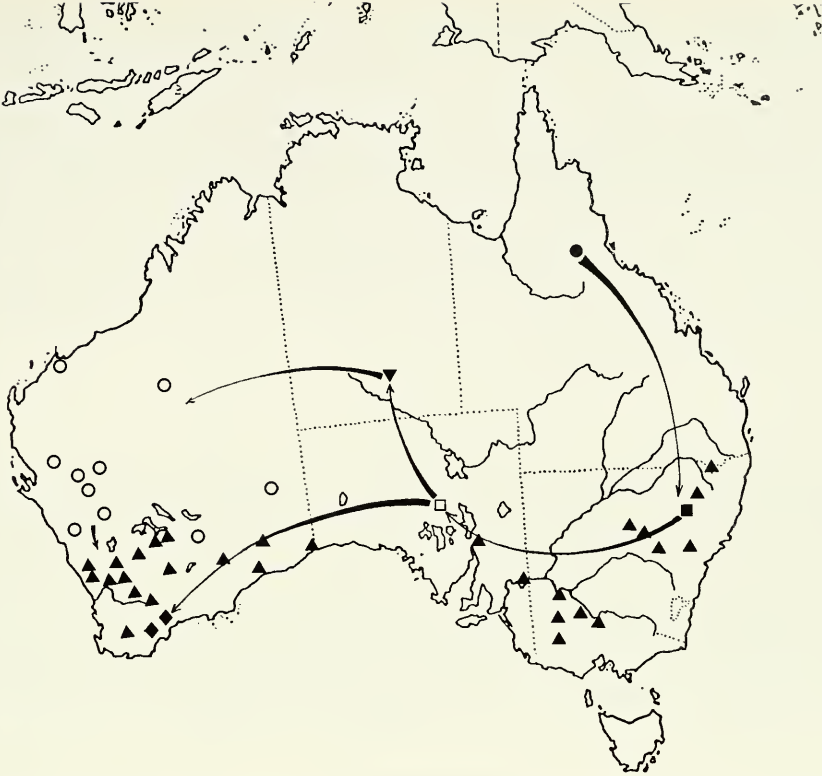
The temperate vegetation belts retreated to the south during the northbound movement of the continent. Hence, northern Australia was colonized by tropical fauna and flora elements. When Australia came in contact with the Asiatic archipelago, the original endemic Australian fauna and flora were mixed with the tropical fauna invading Australia from southern Asia.

The most important factors for the expansion of the tropical, temperate and arid vegetation belts were the climate changes in the Pleistocene.

During the pluvials wet belts favouring rich tree growth spread over areas almost devoid of trees today. The northern tropical rainforests expanded along the coast and in southerly direction and met with the temperate rainforests on the eastern coast. In the south (Nullarbor Plain) and in the west (Great Sandy Desert), woodlands formed a connection between south-eastern and south-western Australia. So during wet pluvials, Australia's arid centre was surrounded by a belt of more or less dense forests and woodlands which enabled many species to expand their distribution area.

In the dry interpluvials the arid zones expanded and isolated large forest or woodland regions now recognized as faunal refugia (e.g. Arnhem Land, Kimberley Division, Hamersley Ranges, south-western Australia). Populations were isolated there and endemic species developed. This process of expansion and reduction of climatic and vegetation belts occurred repeatedly during the Pleistocene.

The evolution of the distribution patterns of the species in the genus *Storena* seemingly followed the same principles as mentioned above.



Map 3. Records of species of the *formosa*-group: □ *S. aspinosa*, ▲ *S. formosa*, ◆ *S. fungina*, ▼ *S. martini*, ● *S. recta*, ■ *S. rotunda*, ○ *S. sinuosa*. Arrows indicate hypothetical expansion of the group.

The geographic origin of *Storena* or of its ancestor is obscure because the genus is endemic in Australia. Nevertheless, the distribution pattern, with the most generalized species in the Northern Territory (*S. ignava*, *S. deserticola*) and in Queensland (*S. digitulus*, *S. procedens*), is evidence of the northern, respectively eastern tropical or subtropical origin of the genus.

The climatic changes in the pluvials supported the expansion of this species in two directions. In the dry interglacials founder populations were isolated and gave way to new species. The relatively plesiomorphic character of these related species supports this argumentation. In the west: *S. paucipunctata*; in the south: *S. mathematica*, *S. ignava*.

Further climatic changes increased the distribution in eastern Australia. In the area between Cape York Peninsula in the north and New South Wales in the south, optimal conditions presumably prevailed and enabled speciation of the founder populations. Here could be the origin of the species *S. digitulus*, *S. procedens* and of the *cyanea*- and *formosa*-group (see Maps 1, 2, 3). So southern Queensland and north-eastern New South Wales are obviously a major centre of evolution, at least in the *cyanea*-group, where considerable radiation took place.

The well defined *cyanea*-group is distributed in the eastern coastal region. Remarkable is the large distribution of the most apomorphic species *S. colosseae* (coastal region of New South Wales) and *S. cyanea* (coastal region of north Queensland, New South Wales, Victoria and South Australia). Obviously they were well adapted to the environmental conditions.

The *formosa*-group exhibits a large degree of evolution and forms a distinct morphocline in which the mVTA is of paramount importance to support the monophyly of this clade. This group apparently originated in north-eastern Queensland, where the most primitive species (*S. recta*) live today. The group expanded initially in southern and subsequently in western direction. Evolutionary steps paralleling the expansion may be recognized in the species *S. rotunda* (New South Wales) and *S. aspinosa* (South Aus-

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 tralia): The ancestors of *S. aspinosa* developed the characteristic double tibial apophysis (Fig. 3), the main synapomorphic character of *S. aspinosa* and the four other species in the sister-group of *S. rotunda*: *S. fungina*, *S. martini*, *S. sinuosa* and *S. formosa*. In the following pluvial the ancestors were able to expand their populations in western direction across the Nullarbor Plain and in northern direction to central Australia, where today *S. fungina* (western Australia) and *S. martini* (central Australia) are found. In the ancestors of *S. martini* the mVTA lost its function and was reduced to a tiny left-over. In the following pluvial founder populations expanded to western Australia and speciated after isolation to the ancestor of *S. sinuosa* and *S. formosa*, developing a strong, sinuous embolus. Whereas *S. sinuosa* is presently only found in western Australia, *S. formosa* - the most apomorphic species within this morphocline - is distributed from south-western Australia, through south Australia, Victoria, New South Wales to Queensland. However, so far there are no records from the Nullarbor Plain. Hence, the most derived species of the *formosa*-group, *S. formosa* has the most extensive distribution and is obviously also the best adapted to the recent environmental conditions.

Conclusion

Since the genus *Storena*, as many of its closest relatives, is an isolated endemic genus of Australia and since the most primitive species were recorded from northern and eastern Australia, it apparently belongs to the old tropical and subtropical autochthonous faunistic element of Gondwanaland. This at least partly corroborates Jocqué's (in press) hypotheses about the origin of the Australian zodariids. However, according to Jocqué (1991) the sister-group of *Storena* is a clade comprising *Selamia* Simon and *Pax* Levy (the latter mentioned in the paper as *Storamia* Jocqué), both genera of the Mediterranean. In the light of the probable origin of *Storena* as described above, this is a rather unlikely relationship. It is also one of the branches which is not supported by a synapomorphy. However, the *Storeninae* without femoral organs form a group of very closely related genera which obviously needs further research.

Acknowledgements

We thank Dr. Martin Baehr for reading our manuscript and discussing the main phylogenetic and zoogeographical problems. A. Reygel helped with the graphics for this paper.

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Zeitschrift/Journal: [Spixiana, Zeitschrift für Zoologie](#)

Jahr/Year: 1994

Band/Volume: [017](#)

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