THE GENERIC RELATIONSHIPS OF THE NEW ENDEMIC AUSTRALIAN ANT SPIDER GENUS NOTASTERON (ARANEAE, ZODARIIDAE)

B.C. Baehr: Queensland Museum, P.O. Box 3300, South Brisbane Queensland 4101, Australia. E-mail: BarbaraB@qm.qld.gov.au

ABSTRACT. A revision of the new endemic Australian genus Notasteron revealed two species, Notasteron carnarvon new species (male), Notasteron lawlessi new species (female, male). The genus is characterized by a strongly reticulated, shield-shaped sternum with steep lateral margins and a posteriorly situated boss. The male palp has a semicircular and undulated distal tegular apophysis and the female epigyne has long, convoluted copulatory ducts. Possible relationships of Notasteron with genera of the Asteron complex, Habronestes, Hetaerica, Malinella and Storosa, are analyzed with NONA and also reconstructed using the Hennigian method. The results indicate that the new genus does not belong to the Asteron complex but is the sister genus of Hetaerica. Notasteron lawlessi is quite common and occurs throughout the eastern part of Australia, whereas N. carnarvon is only found in the Carnarvon region of Western Australia.

Keywords: Taxonomy, new species, cladistics

The arachnid family Zodariidae is one of the most dominant ground-living spider families in Australia (Churchill 1998). Most species can be easily recognized by their bright yellow or orange spots on a dark brown abdomen and their annulated legs. With now 232 described and an estimated 350–400 total species, Australia has one of the richest known zodariid spider faunas worldwide. Rudy Jocqué’s generic revision of the Zodariidae (1991) initiated intensive studies of the Australian zodariid fauna (Jocqué 1991, 1995a, b; Jocqué & Baehr 1992, 2001; Baehr & Jocqué 1994, 1996, 2000). With funding from the Australian Biological Resources Study Participatory Program, 130 additional new species, including this revision, were described within the last three years (Baehr & Jocqué 2001; Baehr 2003a, b, c, 2004a, b; Baehr & Churchill 2003).

The two species of the new genus Notasteron described here, were initially thought to belong to the Asteron complex because they share a similar abdominal pattern and the same general palp structure as the derived genera of the Asteron complex, Basasteron (Rainbow 1920), Cavasteron Baehr & Jocqué 2000, Euasteron Baehr 2003, Holasteron Baehr 2004a, Masasteron Baehr 2004b, Minasteron Baehr & Jocqué 2000 and Spinasteron Baehr & Churchill 2003. These genera are characterized by a thin semicircular embolus and an enormous semicircular distal tegular apophysis (DTA). The peculiar structure of the distal tegular apophysis is unique within the Australian zodariids but it occurs also in Tenedos O.P.-Cambridge 1897 (Jocqué & Baert 2002), a large South American genus.

The use of a scanning electron microscope revealed significant differences in the structure of the sternum, the labium, the endites and the coxae between Notasteron and the Asteron complex. The sternum of the species in the Asteron complex is flat or only slightly convex, shiny, finely reticulated and has a smooth, rebordered margin (Fig. 11). The species of Notasteron have a strong reticulated sternum with a weak boss posteriorly and a steep lateral margin (Fig. 12). Species of the Asteron complex have a triangular labium, but it is more rectangular with a narrow base and a broadly rounded tip in Notasteron. The endites within the Asteron complex are triangular and medially straight whereas the Notasteron has medially concave endites. These characters are shared partly with Hetaerica Rainbow 1916 and Storosa Jocqué 1991 (Figs. 13, 14).

METHODS
Descriptions are based on material stored in 70% ethanol. Epigynes were cleared in lactic
Figures 1–4.—Notasteron lawlessi. 1. body dorsal. 2, 4. carapace; 2. lateral; 4. frontal; 3. sternum and coxae. Scale bar = 1 mm.

acid. Descriptions were generated with the aid of Intkey (Dallwitz et al. 1998) and shortened where possible. Location data and maps were created with Biolink version 1.5 (CSIRO Entomology, Canberra, Australia; http://www.biolink.csiro.au/). Descriptions of spination and color patterns follow that in the revision of Euasteron (Baehr 2003a). Abbreviations of characters: ALE = anterior lateral eyes, AME = anterior median eyes, C = concavity on retrolateral part of cymbium, CL/CW = carapace length / width, CD = copulatory duct, CO = copulatory opening, DTA = distal tegular apophysis (in previous papers called dorsolateral tegular apophysis = conductor), DtiA = dorsolateral tibial apophysis, E = embolus, EB = embolus base, EP = external prong on dorso-retrolateral tibial apophysis, IP = internal prong on dorso-retrolateral tibial apophysis, PE = prolateral extension of DTA, PLE
Figures 5–10.—*Notasteron* spp., right male palps. 5, 7. ventral; 6, 8. lateral; 9, 10. epigyne. 9. ventral; 10. dorsal (cleared). 5, 6. *N. carnarvon*; 7–10. *N. lawlessi*. Scale bar = 0.5 mm (male palps), 0.1 mm (epigyne). Abbreviations: DTA = dorsal tegular apophysis; E = embolus; EP = external prong on dorso-retrolateral tibial apophysis (DtiA); IP = internal prong on dorso-retrolateral tibial apophysis (DtiA); PE = prolateral extension of DTA; PR = prong as ventral part of RDTA; RDTA = retrolateral extension of DTA; RE = retrolateral extension on cymbal flange; VtiA = ventral tibial apophysis.

Abbreviations of institutions from which material was borrowed: Australian Museum, Sydney (AM); American Museum of Natural History, New York (AMNH); Museum Victoria, Melbourne (MV); South Australian Museum, Adelaide (SAM); Queensland Museum, Brisbane (QM); Western Australian Museum, Perth (WAM).

**SYSTEMATICS**

Family Zodariidae Thorell, 1881

*Notasteron* new genus

**Type species.**—*Notasteron lawlessi* new species.

**Etymology.**—The generic name reflects the fact that *Notasteron* is not a genus of the *Asteron* complex, and is considered neuter in gender.

**Diagnosis.**—Species of *Notasteron* resemble those of *Hetaerica* in having a sternum with steep lateral margins and of *Storosa* in having a sternum with a posterior boss in males, but can be distinguished by the undulated prolateral part of DTA in the male palp (Figs. 5–8, 12) and the long convoluted epi-gynal ducts (Figs. 9, 10).

**Description.**—Medium sized spiders (4.80–5.70) with oval, roughly reticulated, laterally rebordered carapace, widest between coxae II and III, narrowed in front to about 0.53 of maximum width. Profile flattened, with the highest point behind fovea (Fig. 2). Color of carapace, sternum and chelicerae orange to sepia brown; endites and labium sepia.
brown, distally white. Abdomen sepia brown; dorsally with two pairs of white patches on top and one above the spinnerets; ventrally dark brown. Legs brown. Eyes (Figs. 1, 2, 4) in three rows (2–4–2). ALE in first row, AME, PLE in second, PME third row. AME smallest. Clypeus curved downwards, height about 2.3 times the diameter of ALE. Chilum single. Chelicerae with longitudinal boss and lateral condyle, few setae in front and a dense row of setae on distal promargin, with one tooth on promargin (Fig. 4). Endites broad, median margin concave with anteromesal scopula, no serrula, labium inverted u-shaped, basally constricted. Sternum shield-shaped with straight anterior margin, roughly reticulated and punctated, posteriorly with weak boss, lateral margin steep (Fig. 12). Legs with few spines on pairs I and II, more numerous on III and IV. Metatarsal preening brush on metatarsi II and III weakly developed. Paired tarsal claws with eight teeth on inner side, unpaired claw toothless, on onychium. Abdomen oval with two sigilla. Anterior lateral spinnerets on common base, posterior median and posterior lateral spinnerets tiny, situated in one transverse row behind anterior spinnerets. Colulus represented by group of setae. Tracheal spiracle, tiny slit-like, covered by tiny sclerotized lip.

**Male palp (Figs. 5–8):** Cymbium with dorsal apical scopula, retrolaterally with straight, rectangular extension (RE). Cymbium base retrolaterally with concavity C (Fig. 8). DTA semicircular, distal part folded containing embolus, with short undulated PE; RDTA with well developed tip and prong. Embolus base hidden behind RDTA, embolus thin, semicircular. Tibia: VtIA bipartite, internal prong long needle-shaped, external part flat, rebordered along lateral margin; DtIA bipatite, IP spatulate as long as EP (Figs. 6, 8).

**Epigyne (Figs. 9, 10):** Epigyne with m-shaped copulatory openings, long convoluted copulatory ducts and small, globular spermathecae.

**Distribution.**—The two known species of *Notasteron* have a disjunct distribution. One species is quite common and occurs throughout the eastern part of Australia whereas the more derived species is only found in the Carnarvon region of Western Australia.

**Notasteron lawlessi** new species
(Figs. 1–4, 7–10, 12, 16)

**Type material.**—Holotype male: AUSTRALIA: *Queensland*: Taroom, “Boggomoss” Station, 25°25’S, 150°01’E, 11 November 1996, P. Lawless, pitfall (QM S37401). Paratypes: AUSTRALIA: *Queensland*: 1 male, Barakula State Forest, Hellhole Creek, open woodland, 26°20’S, 150°42’E, 13–15 October 2004, C. Burwell, pitfall (QM S67697); 1 male, Taroom District, BS24, 25°25’S, 149°58’E, 12 November 1996–January 1997, P. Lawless, pitfall (QM S37214); 2 males, 2 females, Expedition Range National Park, “Amphitheatre” yards, 440 m, 25°13’S, 149°01’E, 27 September 1997–4 March 1998, G. Monteith, D. Cook, pitfall (QM S44250, S44798); 1 female, Langlo Crossing, 3 km NW, 26°07’S, 145°39’E, 4 May 2001, G.B. Monteith, pyrethrum (QM S60615); 26 males, Lake Broadwater, via Dalby, site 2, 5, 9, 27°21’S, 151°06’E, 17 May 1985–25 February 1986, M. Bennie, pitfall (QM S47388–91, S47613–15); 2 males, same data (WAM T63078); 1 male, 1 female, Mount Gayndah, summit, 25°36’S, 151°32’E, 18 December 1998–27 January 1999, G. Monteith, pitfall (QM S55161); 1 male, 1 female, Mount Gayndah, 25°35’S, 151°32’E, 16 November 2000, N. Platnick, hand collecting (AMNH); 2 males, 3 females, Mount Gayndah, 25°36’S, 151°32’E, 21 November 1998, R. Raven, vibration (QM S51313); 3 males, Mount Stuart, 23°05’S, 148°41’E, 12 December 1999, D. Hannah, tree clearing, pitfall (QM S60741, S60743, S60744); 1 male, Mount Debatable, 1.5 km NE., 25°37’S, 151°34’E, 11 October–19 December 1998, G. Monteith, pitfall (QM S47569); 3 males, 1 female, Mount Pleasant, site 32.2, 24°52’S, 146°23’E, 30 October 1999, D. Hannah, tree clearing, pitfall (QM S60742, S60754); 3 males, Thylungra, site 3, 26°05’S, 143°27’E, October 1995, T. Churchill, pitfall (QM S60752); 9 males, Fairview, 24°19’S, 147°01’E, 6 November 1998, D. Hannah, tree clearing, pitfall (QM S60749, S60745); 4 males, Narrien, 22°53’S, 146°49’E, 1998, D. Hannah, tree clearing, pitfall (QM S60747); 4 males, Oakleigh, 26°51’S, 151°27’E, 1998, D. Hannah, tree clearing, pitfall (QM S60746); 1 male, Mulga gradient, pitfall traps 14–20, Site 5, October 1995, T. Churchill, pitfall (QM
Figure 11–14.—Sterna and mouthparts. 11. Masasteron queenslandicum; 12. Notasteron lawlessii; 13. Hetaerica scenica; 14. Storosa obscura.

S60751); 13 males, Meta Park, 1998, tree clearing, pitfall (QM S60748); 1 female, Fleurs, site58/2, February 1999, tree clearing, pitfall (QM S60750); 3 females, Texas, 16 km S., 28°56’S, 151°08’E, 25 January 2002, B. Baehr, N. Platnick, R. Raven, vibration (QM S60616); 1 female, Wyeproof, 23°38’S, 146°51’E, 1998, tree clearing, pitfall (QM S60753); New South Wales: 1 female, Kelvin SF, 8 km N. of Kelvin, 30°45’S, 150°20’E, 23 November–14 December 2001, H. Doherty, M. Elliot, pitfall (AM KS82173); 3 males, 2 females, Dowe SF, 30°47’S, 150°30’E, 23 November–14 December 2001, L. Wilkie, H. Smith, pitfall (AM KS82166, KS82168, KS82170–72); 1 male, 2 km from Tamworth on Tintinhull Rd, 31°04’S, 150°57’E, 15 November–6 December 2001, H. Doherty, M. Elliot, pitfall (AM KS82167); 1 male, between Kootingal and Tamworth, Crown Res. 200m past tip, 31°04’S, 151°02’E, 15 November–6 December 2001, G. Carter, pitfall (AM KS82169); 1 male, Gubatta, 33°36’S, 146°31’E, 6–14 December 1999, D. Driscoll, pitfall (QM S53897); 1 male, Morton Plains Station, 1.5 km NE. of Enngonia, 29°05’S, 146°12’E, 15 October 1991, R. Harris (SAM KS32557); 1 female, Pullop, strip site 3P,
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34°01’S, 146°04’E, 3–8 November 1999, D. Driscoll, pitfall (QM S53736); 1 male, Pulletop, reserve, 33°58’S, 146°05’E, 3–8 November 1999, D. Driscoll, pitfall (QM S53840); 9 males, 3 females, Pulletop, roadside, 34°01’S, 146°04’E, 12 October–8 November 1999, D. Driscoll, pitfall (QM S52523, S52642, S52732, S53778, S52919); 2 males, Pulletop site 10P, 33°55’S, 146°06’E, 12 October–8 November 1999, D. Driscoll, pitfall (QM S53279, S52917); 1 male, Rankins Springs, 33°45’S, 146°19’E, December 1999, D. Driscoll, pitfall (QM S52587); 2 males, Round Hill Nature Reserve site 1R, 33°03’S, 146°13’E, 19–23 December 1999, D. Driscoll, pitfall (QM S53101, S53039, S52131); 4 males, 2 females, Taleeban, roadside site 8T, 33°53’S, 146°28’E, 3–8 November 1999, D. Driscoll, pitfall (QM S53930, S52680); 1 male, 2 females, Taleeban site 4T, 33°57’S, 146°26’E, 23 February–18 October 1999, D. Driscoll, pitfall (QM S53101, S53039, S52131); 4 males, 2 females, Taleeban, roadside, 33°52’S, 146°25’E, 12 October–10 November 1999, D. Driscoll, Pitfall (QM S52650, S53127, S53128, S53531); 3 males, Taleeban, roadside site 8T, 33°53’S, 146°28’E, 1–10 November 1999, D. Driscoll, pitfall (QM S52661, S53753); 1 male, Taleeban site 10T, 33°57’S, 146°24’E, 3–10 November 1999, D. Driscoll, pitfall (QM S53761); Victoria: 2 males, Meringur, 5 km ESE., site 114, 34°24’S, 141°23’E, November 1985, A.L.Yen, drift fence pitfall (MV); South Australia: 3 males, 8 females, Danggali Conservation Park, Sandford Dam, 33°22’S, 140°54’E, 22–23 November 1996, D. Hirst, vibration (SAM NN17391–401); 3 males, 6 females, Danggali Conservation Park, 3 km N. Tomahawk Dam, 33°19’S, 140°43’E, 24–26 November 1996, J.A. Forrest, D. Hirst (SAM NN17402–09, NN17411); 1 male, same locality, 4 September 1996, D. Hirst (SAM NN17410); 1 male, 1 female, 8 km NNE. Mount Woodroffe, 26°15’S, 131°47’E, 13–17 October 1994, Pitjantjara Lands Survey, J.A. Forrest, pitfall (SAM NN 11435, NN11439); 1 male, Gluepot Res., 8.5 km W.-WNW. Gluepot Homestead, 33°44’S, 140°02’E, 26 November–6 December 2000, Gluepot survey, Sitella Camp (SAM NN17390); 2 males, 12.5 km E. Mitchell Nob, 26°08’S, 131°57’E, 20–21 October 1994, J.A. Forrest, pitfall (SAM NN11436–7); Northern Territory: 1 male,1 female, Illamurta Spring, 24°18’S, 132°41’E, 26 March 1993, D. Hirst, pitfall (SAM NN17388–89); 1 female, Danggali Conservation Park, 1.5 km S. 3LO Dam, 33°17’S, 140°55’E March 2001, J.A. Forrest, D. Hirst, vibration (SAM NN17412).

Etymology.—The specific name is a patronym in honor of Phillip Lawless, formerly of the Queensland Museum, the collector of the holotype.

Diagnosis.—This species can be distinguished from the other species of the genus by the blunt tip of the RDTA in the male palp.

Description.—Male (holotype): Total length 4.88. Cephalothorax 2.48 long; 1.80 wide; 0.80 high; cl/cw 1.37; sternum 1.20 long; 1.00 wide; sl/sw 1.20; abdomen 2.40 long; 1.52 wide. Color: body orange brown, to sepia brown, endites and labium distally white, abdomen dorsally with weak scutum and two pairs of white patches on top and with one above the spinnerets. Legs brown. Eyes: AME smallest; eye group width 0.50 of head-width; AME 0.10; ALE 0.12; PME 0.12; PLE 0.12; AME-AME 0.04; AME-ALE 0.04; PME-PME 0.02; PME-PLE 0.10; ALE-PLE 0.04; eyes group AME-PME 0.34; AME-AME 0.24; PME-PME 0.26. Clypeus 0.28 high. Male palp (Figs. 7, 8): RDTA with blunt tip and strong prong, equal in length. DtiA IP spatulate as long as EP, EP peg-shaped.

Female (paratype): Total length 5.48. Cephalothorax 2.60 long; 1.64 wide; 0.96 high; cl/cw 1.58; sternum 1.20 long; 1.08 wide; sl/sw 1.11; abdomen 2.88 long; 1.68 wide. Coloration as male, but no scutum. Legs: male palpal claw strong with eight teeth. Epigyne (Figs. 9, 10): CO m-shaped, half way between epigastric fold and end of epigyne. CD curled horizontally and vertically back to circular S.

Variation.—There is some variation in the body color from dark brown to light orange
brown, but the color pattern of the abdomen is the same.

**Distribution.**—This species occurs in South Australia, southern part of Northern Territory, New South Wales, Victoria and Queensland (Fig. 16).

**Notasteron carnarvon** new species

(Figs. 6, 16)

**Type material.**—Holotype male: AUSTRALIA: Western Australia: Francois Peron National Park, W. of Monkey Mia along road

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**Figure 15, 16.**—15. Phylogeny of some genera related to *Notasteron*, based on character matrix in Table 2. Cladogram of supposed relationships in sense of Hennig (1966), consistent with NONA (fast optimization). 16. Records of the genus *Notasteron* in Australia, rectangle *N. lawlessi*, circle *N. carnarvon*. 

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\[\text{Pentasteron simplex}\]

\[\text{Storosa obscura}\]

\[\text{Notasteron lawlessi}\]

\[\text{Notasteron carnarvon}\]

\[\text{Hetaerica scenica}\]

\[\text{Malinella zebra}\]

\[\text{Habronestes jocquei}\]

\[\text{Basasteron leucoseum}\]

\[\text{Euasteron enterprise}\]

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Table 1.—Characters and character states scored for the cladistic analysis.

| Character number | Character                | Character state                                                                 |
|------------------|--------------------------|---------------------------------------------------------------------------------|
| 0                | AME size                 | 0, smallest; 1, largest                                                         |
| 1                | Labium shape             | 0, triangular; 1, inverted u-shaped                                             |
| 2                | Endites medial margin    | 0, straight; 1, concave                                                          |
| 3                | Sternum surface          | 0, smooth, shiny; 1, strongly reticulated, or/and punctated                      |
| 4                | Sternum profile          | 0, flat, rebordered; 1, elevated, with steep lateral margin (in males)           |
| 5                | Sternum posteriorly      | 0, flat; 1, with posterior boss (in males)                                       |
| 6                | Palp DTA shape           | 0, short; 1, cone-shaped, with enrolled lateral margin; 2, with stalk and enrolled tip; 3, semicircular with distinct RDTA and PE |
| 7                | Base of embolus          | 0, part of tegulum; 1, separated from tegulum as a chitinous plate              |
| 8                | Base of embolus, shape   | 0, unmodified; 1, conical; 2, flattened; 3, hidden behind RDTA                   |
| 9                | Retrolateral cymbial flange (RE) | 0, rectangular; 1, with rounded extension; 2, retrolateral concavity         |
| 10               | TBE direction            | 0, pro-lateral; 1, baso-lateral; 2, retro-lateral                                |
| 11               | DTA, prolateral extension (PE) length | 0, PE absent; 1, inside cymbium; 2, reaching tibia                               |
| 12               | Prolateral extension (PE) shape | 0, PE absent; 1, about ¼ of circle; 2, about ½ of circle lateral margin undulated |
| 13               | VTA                      | 0, present; 1, reduced to a tiny spine; 2, absent                                |

to Denham, 25°47′32″S, 113°41′37″E, 7 November 1998, J.M. Waldock, vehicle vibration (WAM T54483). Paratypes: AUSTRALIA: Western Australia: Kennedy Range National Park, 24°31′25″S, 114°57′55″E, 14 January–7 April 1995, W. Muir, wet pitfall (WAM T54696); 3 males, Nerren Nerren Station, 27°03′S, 114°35′E, 11 January–11 May 1995, P. West et al., wet pitfall (WAM T44494); 1 male, same locality, 11 May–18 August 1995, N. Hall (WAM T54699); 1 male, same data (QM S67696); 1 male, Nerren Nerren Station, 27°03′24″S, 114°35′21″E, 25 August–16 October 1994, J.M. Waldock et al., wet pitfall (WAM T44496).

Etymology.—The specific name is a noun in apposition taken from the region in which this species occurs.

Diagnosis.—This species can be distinguished from N. lawlessi by the sharp tip of RDTA in the male palp.

Description.—Male (holotype): Total length 5.60. Carapace 3.00 long; 2.20 wide; 1.08 high; cl/cw 1.36; sternum 1.36 long; 1.16 wide; sl/sw 1.17; abdomen 2.60 long; 1.80 wide. Color: body sepia brown, endites and labium distally white. Abdomen dorsally with two pairs of white patches on top and one above the spinnerets. Legs brown. Eyes: AME smallest; eye group width 0.44 of headwidth; AME 0.11; ALE 0.14; PME 0.14; PLE 0.14; AME-AME 0.04; AME-ALE 0.04; PME-PME 0.04; PME-PLE 0.12; ALE-PLE 0.04; eyes group AME-PME 0.40; AME-AME 0.26; PME-PME 0.32. Clypeus 0.32 high. Male palp (Figs. 5, 6): RDTA with sharp tip and flattened prong. Embolus base flattened; DtiA IP spatulate as long as EP; EP bent ventrally. Female: Unknown.

Distribution.—Found only in the Carnarvon region of Western Australia (Fig. 16).

PHYLOGENETIC ANALYSIS

As the primary tool for the phylogenetic analysis, I used the methods originally proposed by Hennig (1966) and further explained
by Sudhaus & Rehfeld (1992, p.137). Only homologous characters were considered where I was able to determine plesiomorphic and apomorphic character states. I followed the technique of Watrous & Wheeler (1981), using an outgroup, preferably a sister taxon, to determine the polarity of the character states. Based on these character states, I attempted to deduce the phylogenetic history of the species-groups. The result of this phylogenetic analysis (sensu Hennig 1966) was tested with NONA version 2.0 (Goloboff 1997) using the heuristic search option and following settings: 5,000 random taxon addition replications (mult*N), 5 starting trees per replication, and multiple tree-bisection-reconnection (TBR) branch swapping. The NONA bootstrap consensus tree was calculated with 1,000 replications, 10 search replications, and 5 starting trees per replication. I analyzed the same data set using unordered character states. Based on these character states, I attempted to deduce the phylogenetic history of the species-groups. The result of this phylogenetic analysis (sensu Hennig 1966) was tested with NONA version 2.0 (Goloboff 1997) using the heuristic search option and following settings: 5,000 random taxon addition replications (mult*N), 5 starting trees per replication, and multiple tree-bisection-reconnection (TBR) branch swapping. The NONA bootstrap consensus tree was calculated with 1,000 replications, 10 search replications, and 5 starting trees per replication. I analyzed the same data set using unordered character states and fast optimization. Unsupported nodes were collapsed. The analysis is restricted to selected genera of the Asteron complex and the genera Habronestes, Hetaerica, Notasteron and Storosa. It is used here to define where Notasteron should be placed in the Zodariinae. The genera are represented by one species reflecting the “grundplan” in the sense of Hennig (1966) for the considered character states. Yeates (1995) called this the exemplar method. The species Pentasteron simplex Baehr & Jocqué 2001, Basasteron leucoseum (Rainbow 1920), Habronestes jocquei Baehr 2003, Storosa obscura Jocqué 1991 and Hetaerica scenica (Koch 1872) were chosen for the relatively primitive male palpal morphology of the considered genera. Euasteron enterprise Baehr 2003 was added as a representative of the putatively derived genus of the Asteron complex to see how robust the cladogram behaved. Malinella zebra (Thorell 1881), the only known Australian species from a paleotropical zodariid genus, was selected first as the outgroup taxon, then replaced by Pentasteron simplex Baehr & Jocqué 2001, the most basal representative of the analysis.

**Character assessment.**—The sternum, labium and endites provide few distinguishing characters which appear to be informative at the genus and higher level. The eye pattern and particularly the male palps provide synapomorphic features of high value for phylogenetic examinations on species-group level. Derived characters of single species (autapomorphies, e.g., epigynes) are not discussed here. Characters and their states are listed in Table 1.

**Sternum:** The surface of the sternum is smooth and shiny (character 3/0), the profile is flat, the lateral margin is rebordered (character 4/0) in all species of the Asteron complex and in Habronestes. In contrast, all examined species of Notasteron, Hetaerica, and Storosa have a strongly reticulated and/or punctate sternum (character 3/1) with steep lateral margin in Notasteron and Hetaerica (character 4/1), and with a posterior boss in Notasteron and Storosa (character 5/1).

**Mouthparts:** Within the Zodariinae, the shape of the labium and the endites are distinguishing characters at the genus or higher level. All species of the Asteron complex and Habronestes possess a triangular labium (character 1/0) and endites with a straight medial margin (character 2/0). The labium of Hetaerica and Storosa is inverted u-shaped (character 1/1) and the endites of these genera as well as Notasteron are concave on the medial margin (character 2/1).

**Eyes:** In all Zodariinae, both eye rows are so strongly procurved that they appear to be in three rows (2–4–2): ALE in the first row, AME and PLE in the second row, and the third row consists only of PME (Figs. 1, 2, 4). In all Notasteron, Hetaerica and Storosa species, the AME are smaller than the other eyes. This is also the case for the “grundplan” species Basasteron leucoseum, Pentasteron simplex, Habronestes jocquei and Euasteron enterprise (character 0/0). In Malinella zebra, the AME are largest (character 0/1). The increase in size of the AME seems to be derived

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**Table 2.—Character matrix for species used in cladistic analysis.**

| Taxon                  | 0–4 | 5–9 | 10–13 |
|------------------------|-----|-----|-------|
| Pentasteron simplex    | 0000| 0000| 0000  |
| Basasteron leucoseum   | 0000| 0311| 0112  |
| Euasteron enterprise   | 0000| 0312| 1222  |
| Habronestes jocquei    | 0000| 0212| 1000  |
| Malinella zebra        | 1000| 0012| 1000  |
| Notasteron lawlessi    | 0111| 1313| 2132  |
| Hetaerica scenica      | 0111| 0100| 0001  |
| Storosa obscura        | 0110| 1000| 0000  |

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**Table 1.**

| Taxon                  | 0±4 | 5±9 | 10±13 |
|------------------------|-----|-----|-------|
| Pentasteron simplex    | 0000| 0000| 0000  |
| Basasteron leucoseum   | 0000| 0311| 0112  |
| Euasteron enterprise   | 0000| 0312| 1222  |
| Habronestes jocquei    | 0000| 0212| 1000  |
| Malinella zebra        | 1000| 0012| 1000  |
| Notasteron lawlessi    | 0111| 1313| 2132  |
| Hetaerica scenica      | 0111| 0100| 0001  |
| Storosa obscura        | 0110| 1000| 0000  |
but has presumably happened convergently quite frequently in different genera; e.g., in the genus *Habronestes* in the *Habronestes macedonensis* group (Baehr 2003c) and at least four times in the “derived” genera of the *Asteron* complex (some species of *Euasteron*, about half of the species of *Masasteron* and almost all species of *Spinasteron* and *Holasteron*).

**Male palp:** Most characters used in this phylogenetic study are taken from the male palp. Keeping in mind the primitive type of the male palp represented in *Storosa obscura* and *Pentasteron simplex*, the palps of *Notasteron* appear quite derived. The most spectacular change happens in the undulating of the semicircular DTA (character 12/3) and that the embolus base is hidden under the RDTA (character 8/3). The most plesiomorphic short and membranous DTA and a short straight embolus occur in *Storosa obscura* and *Pentasteron simplex* (character 6/0) whereas a cone-shaped DTA with an enrolled margin is synapomorphic for all *Hetaerica* species (character 6/1). The slender stalk-like DTA with an enrolled distal tip is unique for all *Habronestes* species (character 6/2). The main synapomorphy for the genus *Notasteron* and the derived genera of the *Asteron* complex (*Basasteron*, *Cavasteron*, *Euasteron*, *Holasteron*, *Minasteron*, *Spinasteron*, *Tropasteron* and *Masasteron*) is the large semicircular DTA with marginal fold, well developed retrolateral-(RDTA) and prolateral extension (PE) (character 6/3). As this kind of DTA is unique in the Australian Zodariinae, it could be thought that the above-mentioned derived genera of the *Asteron* complex and *Notasteron* are monophyletic. The base of the embolus is separated from the tegulum in the genera *Notasteron* and *Habronestes*, and in all derived genera of the *Asteron* complex. Whereas in *Habronestes* and in the *Asteron* complex, the embolus base is uncovered it is hidden in *Notasteron* (characters 7/1, 8/3). The position of the transbasal area of the embolus (TBE) provides a derived character state for the genus *Notasteron* (character 10/2). The retrolateral cymbial flange (RE) is rectangular and straight in the basal condition (character 9/0) as for *Notasteron*, *Storosa*, *Hetaerica*, *Pentasteron*, *Basasteron* but has a deep groove (character 8/2) as a synapomorphy for all *Habronestes* species. In the derived genera of the *Asteron* complex the flange consists of a rounded extension (character 8/1).

**Results.**—The cladistic analysis of the data matrix (Table 2) with NONA including 14 characters and seven taxa resulted in three most parsimonious trees (length 26 steps, CI = 80, RI = 68). *Euasteron enterprise* was added to the data matrix representing the more derived genera of the *Asteron* complex. In this case, six most parsimonious trees were found (length 31 steps, CI = 77, RI = 65). In all trees, *Notasteron* was matched with only three of eight taxa. The pair *Notasteron-Basasteron* is based exclusively on the advanced male palp character states as synapomorphies. The sister-group constellation *Notasteron-Storosa* is based on the sternum with posterior boss taken as a synapomorphy (5/1). From the analyses; phylogenetic analysis in the sense of Hennig, the cladistic analysis with 7 taxa and 8 taxa, and the bootstrap (“majority rules”), the congruent tree in all was taken as the preferred tree (Fig. 15). The resulting tree shows that *Notasteron* is the sister genus of *Hetaerica* considering the somatic characters of the sternum, the endites and the labium as synapomorphic character states of the genera *Storosa*, *Hetaerica* and *Notasteron*, and the steep lateral margin as the main synapomorphic character state for *Hetaerica* and *Notasteron*.

**Biogeography.**—The Zodariidae are ground dwelling spiders that are not known to disperse aerially. The genus *Notasteron* includes only two species to date. Both species were found in a disjunct distribution pattern. The basal species, *N. lawlessi*, is quite common in the southern and eastern part of Australia (Fig. 16), like the most plesiomorphic species of the *Asteron* complex (*Pentasteron simplex*, *Basasteron leucosemum* and *Euasteron enterprise*); whereas the derived species, *Notasteron carnarvon*, is only found in the Carnarvon region of Western Australia.

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LITERATURE CITED
Baehr, B. 2003a. Revisions of the new endemic genera Basasteron, Euasteron and Spinasteron of Australia (Araneae, Zodariidae): Three new genera of the Asteron-complex. Memoirs of the Queensland Museum 49:1–27.
Baehr, B. 2003b. Revision of the tropical genus Tropasteron gen. nov. of North Queensland (Araneae, Zodariidae): A new genus of the Asteron-complex. Memoirs of the Queensland Museum 49:29–64.
Baehr, B. 2003c. Revision of the Australian genus Habronestes L. Koch (1872) (Araneae: Zodariidae). The species of NSW. Records of the Australian Museum 55:343–367.
Baehr, B. 2004a. Revision of the new Australian genus Holasteron (Araneae, Zodariidae): taxonomy, phylogeny and biogeography. Memoirs of the Queensland Museum 49:495–519.
Baehr, B. 2004b. The systematics of a new endemic Australian genus of ant spiders Masasteron (Araneae: Zodariidae). Invertebrate Systematics 18: 661–691.
Baehr, B. & T.B. Churchill. 2003. Revision of the endemic Australian genus Spinasteron (Araneae, Zodariidae): taxonomy, phylogeny and biogeography. Invertebrate Systematics 17:641–665.
Baehr, B. & R. Jocqué. 1994. Phylogeny and zoogeography of the Australian genus Storena (Araneae, Zodariidae). Spixiana 17:1–12.
Baehr, B. & R. Jocqué. 1996. A revision of Asteron, starring male palpal morphology (Araneae, Zodariidae). Proceedings of the XIII International Congress of Arachnology, Geneva, 3–8 September 1995. Revue Suisse de Zoologie, hors serie 1:15–28.
Baehr, B. & R. Jocqué. 2000. Revisions of the genera in the Asteron-complex (Araneae, Zodariidae). The new genera Cavasteron and Minasteron. Records of the Western Australian Museum 20:1–30.
Baehr, B. & R. Jocqué. 2001. Revisions of the genera in the Asteron-complex (Araneae, Zodariidae). The new genera Pentasteron, Phenasteron, Leptasteron and Subasteron. Memoirs of the Queensland Museum 46:359–385.
Churchill, T.B. 1998. Spiders as ecological indicators in the Australian tropics: family distribution patterns along rainfall and grazing gradients. Bulletin of the British Arachnological Society 11:325–330.
Dallwitz, M.J., T.A. Paine & E.J. Zurcher. 1998. Interactive keys. Pp. 201–212. In Information Technology, Plant Pathology and Biodiversity. (Eds P. Bridge, P. Jeffries, D. R. Morse, and P. R. Scott.) CAB International, Wallingford.
Goloboff, P.A. 1997. NONA version 2.0. Department of Entomology, American Museum of Natural History, New York.
Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.
Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201:1–160.
Jocqué, R. 1995a. Notes on Australian Zodariidae (Araneae). I. New taxa and key to the genera. Records of the Australian Museum 47:117–140.
Jocqué, R. 1995b. Notes on Australian Zodariidae (Araneae). II. Redescriptions and new records. Records of the Australian Museum 47:141–160.
Jocqué, R. & B. Baehr. 1992. A revision of the Australian spider genus Storena (Araneae, Zodariidae). Invertebrate Taxonomy 6:953–1004.
Jocqué, R. & B. Baehr. 2001. Revisions of the genera in the Asteron-complex (Araneae, Zodariidae): Asteron Jocqué and the new genus Pseudoasteron. Records of the Australian Museum 53: 21–36.
Jocqué, R. & L. Baert. 2002. A revision of the Neotropical spider genera Tenedos O.P.-Cambridge and Ishania Chamberlin (Araneae, Zodariidae). Bulletin de l’Institut Royal des Sciences Naturelles de Belgique, Entomologie 72:67–173.
Sudhaus, W. & K. Rehfeld. 1992. Einführung in die Phylogenetik und Systematik. Gustav Fischer Verlag, Stuttgart, Jena, New York.
Watrous, L.E. & Q.D. Wheeler. 1981. The outgroup comparison method of character analysis. Systematic Zoology 30:1–11.
Yeates, D.K. 1995. Groundplans and exemplars: path to the tree of life. Cladistics 11:343–357.

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