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Organisms, Diversity & Evolution 5 (2005) 203–236
ORGANISMS DIVERSITY & EVOLUTION
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Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): Evidence from behaviour, morphology and DNA

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Received 12 May 2004; accepted 15 December 2004

Abstract

The African whip spider, *Damon variegatus*, exhibits a broad, discontinuous distribution from the Congo, through western Tanzania and Zimbabwe, to South Africa and Namibia. Variation in size, number of antenniform leg segments, and colouration, taken together with a discontinuous distribution, suggest that allopatric populations of *D. variegatus* may be reproductively isolated, and more than one species may be involved. Furthermore, many morphological characters of *D. variegatus* appear to be plesiomorphic if compared to closely related species, suggesting that *D. variegatus* might be paraphyletic, regardless of whether it is a single panmictic species or a group of partly or entirely reproductively isolated populations. This contribution attempts to determine whether *D. variegatus* is monophyletic and comprises more than one species, by investigating three sources of evidence: behaviour, morphology and DNA. Mating behaviour is observed and mate-recognition trials conducted between males and females from several populations of *D. variegatus* and related species of *Damon*. The morphology of spermatophores obtained during these matings is studied and a matrix of somatic and genitalic characters produced. These morphological data are analysed separately and in combination with DNA sequences from loci of three genes in the nuclear genome (18S rDNA, 28S rDNA and Histone H3) and three genes in the mitochondrial genome (12S rDNA, 16S rDNA and Cytochrome Oxidase I). Neither the comparative behavioural evidence gathered nor the spermatophore morphology conclusively suggest that *D. variegatus* comprises more than one species. However, the molecular data, analysed separately and in combination with the morphological data, reveal that *D. variegatus* is monophyletic and that the population of *D. variegatus* to the west of the Kalahari sand system (Namibia and southern Angola) is specifically distinct from those to the east. This new species is described as *Damon sylviae*, the diagnosis of *D. variegatus* s. str. is revised, and a key to the species of the *D. variegatus* group is provided.

Keywords: Amblypygi; *Damon variegatus*; Behaviour; Morphology; DNA; Systematics

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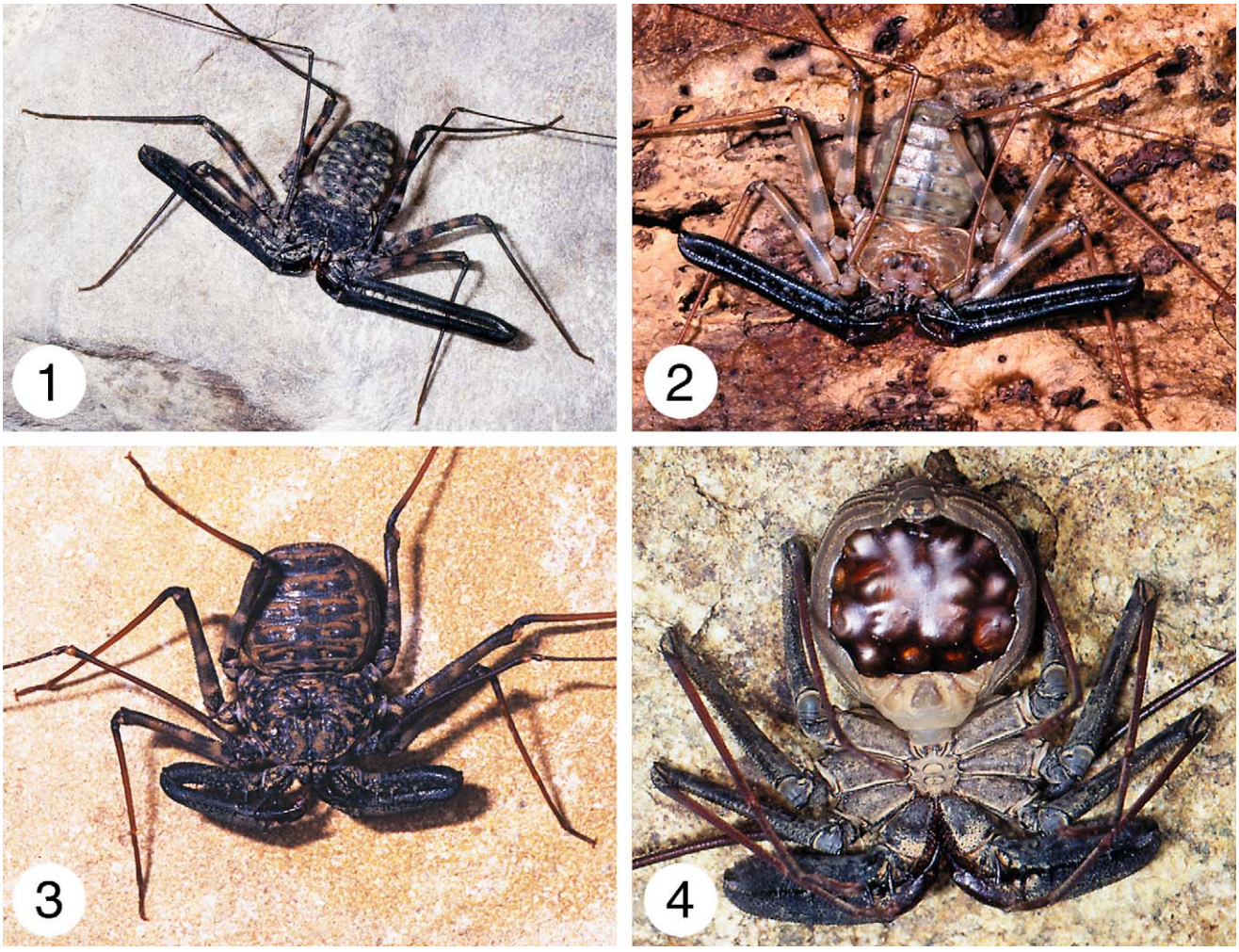
doi:10.1016/j.ode.2004.12.004

Introduction

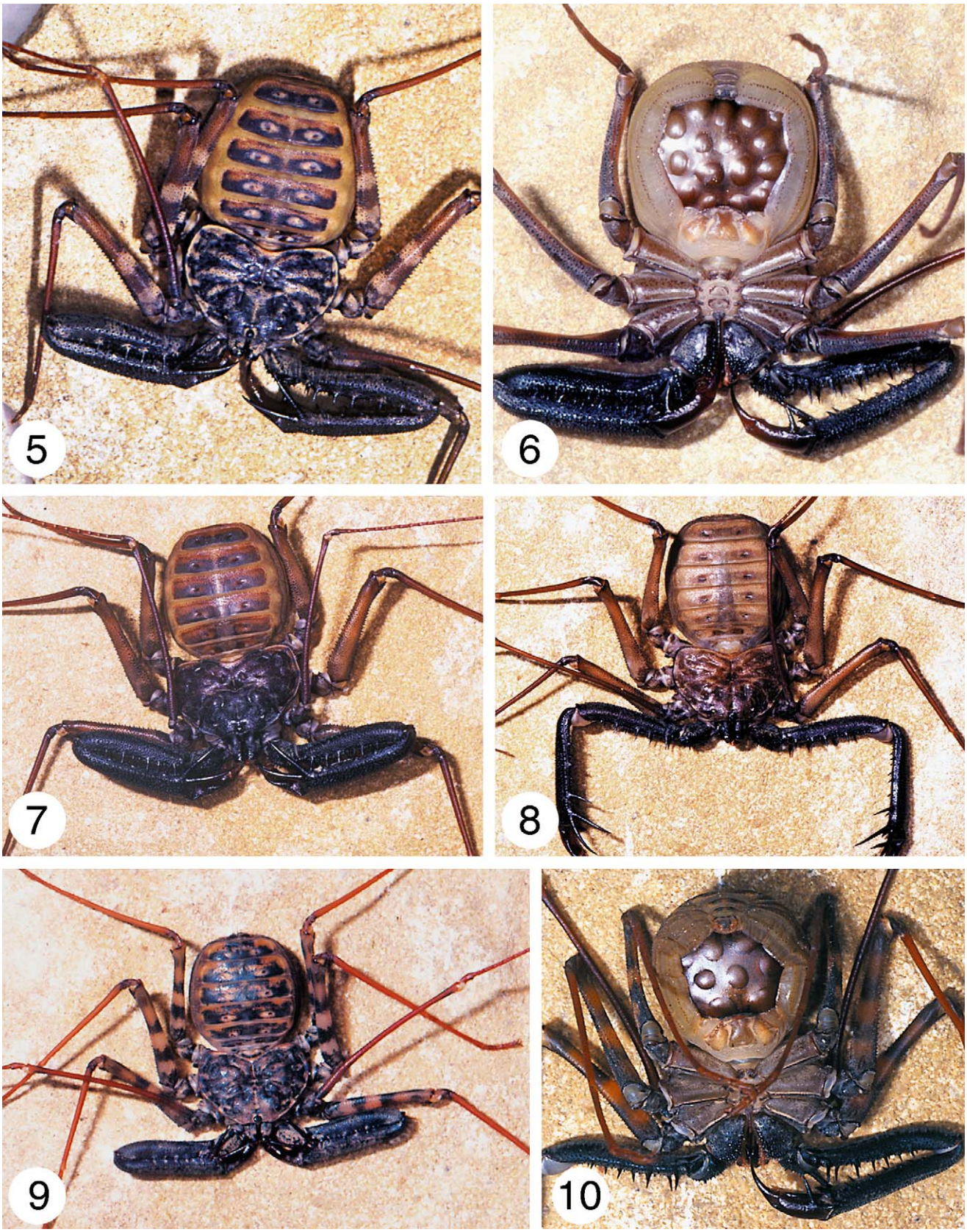
Whip spiders (Amblypygi), also known as tailless whip scorpions, are a conspicuous group of bizarre, dorsoventrally flattened arachnids with raptorial pedipalps and a pair of extremely elongate, antenniform first legs (Figs. 1–10) used as tactile and olfactory organs as well as for communication (Weygoldt 2000a). In the phylogeny of Chelicerata, the Amblypygi are placed either as the sister group of spiders, Araneae (e.g. Platnick and Gertsch 1976; Weygoldt and Paulus 1979; Wheeler and Hayashi 1998), or in the Pedipalpi (e.g. Shultz 1990; Giribet et al. 2002), as sister to a monophyletic group comprising the Thelyphonida and Schizomida, variously assigned to separate orders (Uropygi and Schizomida, respectively), or to a single order (Uropygi).

The catalogue of Harvey (2003) lists five families, 17 genera and 136 species of Amblypygi. A few more species have been described since, so the actual number is between 140 and 150. Most of these inhabit humid tropical and subtropical regions (especially rainforests). However, a few species occur in the temperate zones (e.g. in southern Europe and South Africa), even inhabiting semi-arid to arid regions (e.g. in Morocco, Namibia and the Arabian Peninsula). Most of the latter evidently survived the onset of aridification by retreating into deep caves, as in Arabia, or by adapting to the xeric conditions on the surface, as in Namibia (Weygoldt 2000b).

The genus *Damon* C.L. Koch, 1850 is endemic to subsaharan Africa or the Afrotropical region (Table 1); reports from the New World are erroneous (Weygoldt 1999a). Weygoldt (1999a, 2000a, b) distinguished ten



Figs. 1–4. Species in the *Damon variegatus* group of southern African whip spiders. (1) *Damon diadema* (Simon), male from Shimoni Cave, Kenya. (2) *Damon gracilis* Weygoldt, female from Omabsu, Kaokoveld, Namibia. (3) *Damon annulatipes* (Wood), brooding female from Charter's Creek, KwaZulu-Natal, South Africa. (4) *Damon annulatipes* (Wood), anaesthetised brooding female, showing brood sac, from Charter's Creek, KwaZulu-Natal, South Africa.



Figs. 5–10. Whip spiders formerly attributed to *Damon variegatus* s.l. (l–5) *Damon variegatus* (Perty), female from Hoedspruit, Mpumalanga, South Africa. (6) *Damon variegatus* (Perty), anaesthetised brooding female, showing brood sac, from Medike, Soutpansberg, South Africa. (7) *Damon variegatus* (Perty), female from Tanzania. (8) *Damon variegatus* (Perty), female from Medike, Soutpansberg, South Africa. (9) *Damon sylviae* n. sp., female from Obab Cave, Namibia. (10) *Damon sylviae* n. sp., anaesthetised brooding female, showing brood sac, from Obab Cave, Namibia.

Table 1. The currently accepted species of *Damon* C.L. Koch, 1850 (Amblypygi, Phrynichidae), with countries of distribution compiled from Harvey (2003); dubious records preceded by "?"

Species	Distribution
D. annulatipes (Wood, 1869)	South Africa, Swaziland
D. brachialis Weygoldt, 1999	Malawi, Mozambique, Zambia, Zimbabwe
D. diadema (Simon, 1876)	Ethiopia, Kenya, Somalia, Tanzania, ?Yemen
D. gracilis Weygoldt, 1998	Angola, Namibia
D. johnstonii (Pocock, 1894)	Cameroon, Congo, Democratic Republic of Congo, Equatorial Guinea (incl. Bioko Island), Gabon, Nigeria
D. longispinatus Weygoldt, 1999	Tanzania
D. medius (Herbst, 1797)	Benin, Cameroon, Ghana, Guinea, Ivory Coast, Liberia, Mali, Nigeria, São Tomé & Príncipe, Senegal, Sierra Leone, Togo
D. tibialis (Simon, 1876)	Angola, Democratic Republic of Congo, São Tomé & Príncipe
D. uncinatus Weygoldt, 1999	Cameroon
D. variegatus (Perty, 1834)	Botswana, Democratic Republic of Congo, ?Eritrea, Mozambique, Namibia, South Africa, ?Sudan, Tanzania, Zambia, Zimbabwe

species of *Damon* (Table 1), which is the most diverse genus of whip spiders on the African continent and includes the largest amblypygid species in the region. *Damon johnstonii*, *Damon medius* and *Damon tibialis* (all formerly placed in the genus *Titanodamon* Pocock, 1894), reach body lengths of 30–40 mm, and their antenniform legs may span 440 mm. Most species of *Damon* are epigean, spending the day in the cracks and crevices of rock outcrops, beneath stones, exfoliations, the peeling bark of trees, or in the holes of tree trunks, and only venturing out at night in search of prey.

Damon is clearly monophyletic on the basis of two autapomorphies: leaf-like setae on the tarsal segments of the antenniform legs (Lawrence 1949; Weygoldt 1996a), and pleural folds that surround the egg sac of the brooding female laterally, and in some species even ventrally, to form a brood pouch (Weygoldt 1996a, 1999a; Figs. 4, 6 and 10). The genus can be divided into two groups on biogeographical grounds (Weygoldt 1999a, 2000a, b). The West African group comprises four large and impressive species – *D. johnstonii*, *D. medius*, *D. tibialis* and *Damon uncinatus* – ranging from Senegal along the West African coastline to the western part of the Congo, where they inhabit rainforests, caves and mesic savanna. These species are characterised by their large size (30–40 mm) and the presence of ventral sac covers, but probably represent a paraphyletic assemblage. *D. medius* may be sister to the remaining species of *Damon*, collectively referred to as the East African group (Weygoldt 1999a, 2000a, b).

The East African or *Damon variegatus* group appears to be monophyletic (Weygoldt 1999a, 2000a, b). All species of this group are distinguished from the West African group by the absence of ventral sac covers, by their characteristic spermatophores, and by their generally smaller size (25–30 mm). The largest species is *D. diadema* (reaching nearly 30 mm; Fig. 1). Species of this group range from the eastern part of the Congo and Sudan, through Kenya and Tanzania, to South Africa and Namibia, where they occur in a variety of habitats including rainforests, caves, savannas and even the semi-desert of northern Namibia and southern Angola.

Most species of the *D. variegatus* group are geographically localised. *Damon longispinatus* is known only from the type locality in the Tanga region of Tanzania. *Damon gracilis* (Figs. 2 and 11) is restricted to northwestern Namibia and southwestern Angola. *Damon annulatipes* (Figs. 3, 4 and 11) inhabits forests along the escarpment and eastern coast of South Africa, Swaziland and probably southern Mozambique. *Damon diadema* (Fig. 1) is recorded from eastern Tanzania and Kenya, extending northwards into Ethiopia and Somalia, with a doubtful record from the Arabian Peninsula. *Damon brachialis* occurs in Malawi, Mozambique, Zambia and Zimbabwe.

Compared to the other species, *D. variegatus* (Figs. 5–11) exhibits a broad distribution from the Congo, through western Tanzania and Zimbabwe, to South Africa and Namibia. One specimen has been reported from the Sudan and another from Eritrea. There are large, empty spaces across the broad distributional range of *D. variegatus*, which may reflect true allopatry due to the patchiness of their habitat. However, this discontinuity in distribution must also be partially artifactual, reflecting localised collecting patterns.

D. variegatus displays considerable morphological variation across its wide distribution range. Specimens from southern populations are smaller than those from the Congo, and have fewer antenniform leg segments (28–30 tibial segments in South Africa, 29–30 in Zimbabwe, 30–31 in the Congo). Specimens from various populations also differ in the shade, intensity

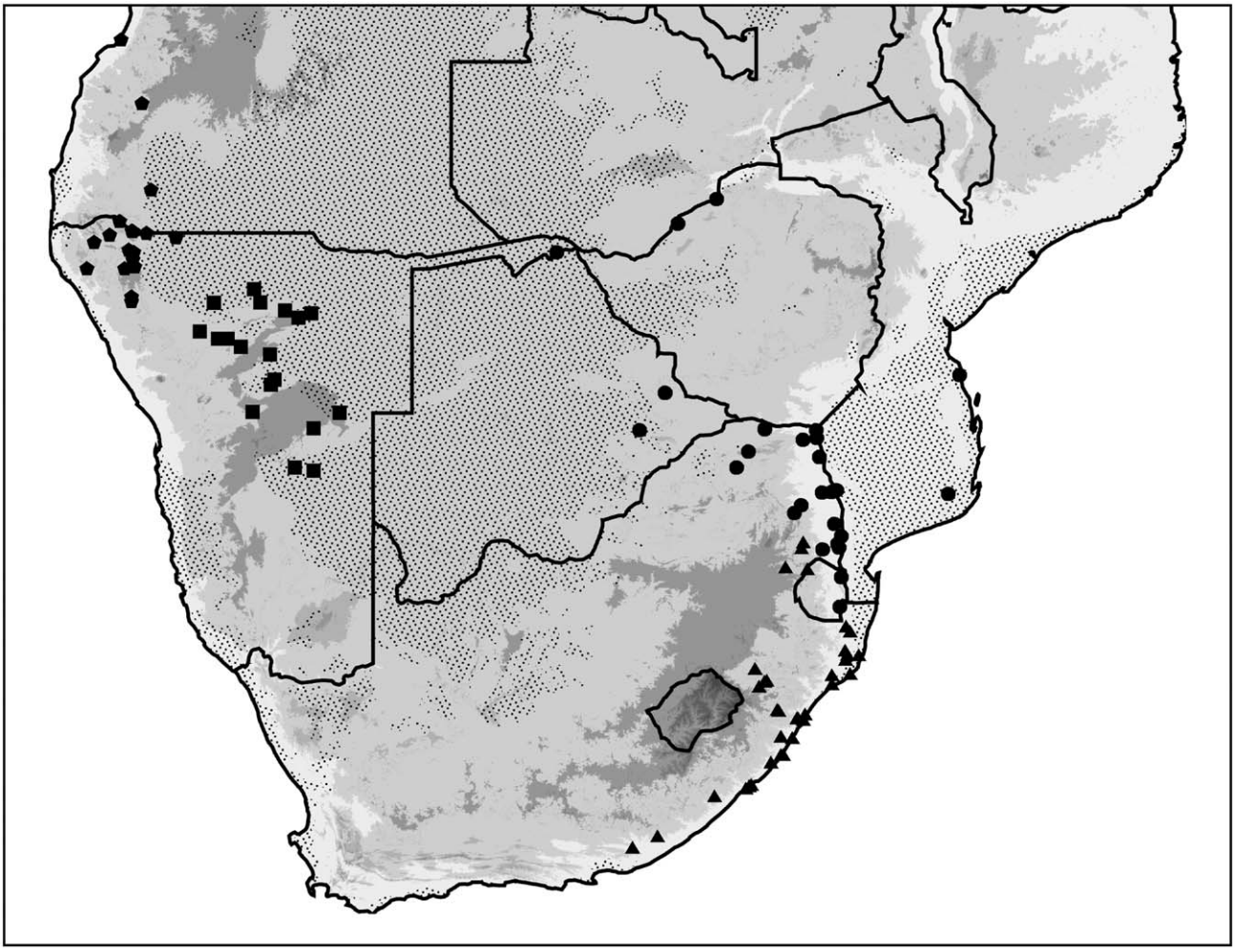


Fig. 11. Geographical distributions of four whip spider species in the *Damon variegatus* group from southern Africa, based on material examined for this study, and that of Weygoldt (1999a): *Damon annulatipes* (Wood), ▲; *Damon gracilis* Weygoldt, ⬟; *Damon sylviae* n. sp., ■; *Damon variegatus* (Perty), ●. Contour interval 500 m; major sand systems stippled.

and patterning of their colouration, e.g. Namibian specimens are more vividly coloured than specimens from localities east of the Kalahari sand system. All of this suggests that populations of *D. variegatus* may be separated and that some might be reproductively isolated, in which case, *D. variegatus* would comprise more than one biological species (sensu Dobzhansky 1937; Mayr 1963). On morphological grounds, it also seems likely that several phylogenetic species (sensu Cracraft 1983, 1989; Nixon and Wheeler 1990) are involved, but the difficulty in partitioning the morphological variation discretely has thus far prevented their delimitation. Furthermore, many morphological characters of *D. variegatus* appear to be plesiomorphic if compared to other species of the *D. variegatus* group (Weygoldt 1999a, 2000a, b). Weygoldt (1999a, p. 40) therefore proposed the following scenario: ''A central group budded off lateral populations which evolved certain apomorphies: *D. longispinatus*, *D. diadema* and *D. brachialis* along the eastern coast, *Damon annulatipes* along the southern coast, *D. gracilis* along the south-western coast, and perhaps an undescribed species in the far north, Sudan. The central group is *D. variegatus*.'' If this scenario were correct, then *D. variegatus* would be paraphyletic, regardless of whether it is a single panmictic species or a group of partly or entirely reproductively isolated populations.

The present contribution attempts to address these questions, i.e. whether the taxon *D. variegatus* is monophyletic and comprises more than one species, by investigating three sources of evidence: behaviour, morphology and DNA. Mating behaviour was observed and mate-recognition trials conducted between males and females from several populations of *D. variegatus* and related species of *Damon*. The morphology of spermatophores obtained during these matings was studied and a matrix of somatic and genitalic characters produced. These morphological data were analysed

separately and in combination with DNA sequences from loci of three genes in the nuclear genome (18S rDNA, 28S rDNA and Histone H3) and three genes in the mitochondrial (mt) genome (12S rDNA, 16S rDNA and Cytochrome Oxidase I). Based on the data collected and analysed here, we deduce not only that *D. variegatus* is monophyletic, but that the population of *D. variegatus* to the west of the Kalahari sand system (Namibia and southern Angola) is specifically different from those to the east. We conclude this contribution by describing this new species as *Damon sylviae* (Figs. 9 and 10), revising the diagnosis of *D. variegatus*, and providing a key to the species of the *D. variegatus* group.

Material and methods

Taxonomic sampling and material examined

Eight exemplars of *D. variegatus*, originating from two localities in Namibia (hereafter referred to as *D. sylviae* n. sp.), four in South Africa, one in Swaziland and one in Tanzania, were included as ingroup taxa in the analysis (Appendix A).

Characters were polarised by means of outgroup comparison (Watrous and Wheeler 1981; Farris 1982; Nixon and Carpenter 1993). In order to test the monophyly of *D. variegatus*, three other species in the *D. variegatus* group, viz. *D. annulatipes*, *D. diadema* and *D. gracilis* (represented by specimens from three, two and one localities, respectively), were included. A single specimen of *D. medius*, from the West African group of *Damon*, was included as a potential outgroup to all exemplars of the *D. variegatus* group. Finally, *Musicodamon atlanteus* Fage, 1939, *Phrynichodamon scullyi* (Purcell, 1902), *Euphrynichus bacillifer* (Gerstaecker, 1873) and *Phrynichus scaber* (Gervais, 1844), also placed in family Phrynichidae Karsch, 1879, were included as outgroups to the exemplars of *Damon*. *Musicodamon* and *Phrynichodamon* are presently included with *Damon* in subfamily Damoninae Simon, 1936, whereas *Euphrynichus* and *Phrynichus* are placed in subfamily Phrynichinae Simon, 1892 (Weygoldt 1999a, 2000b; Harvey 2003). The inclusion of these outgroup genera is justified on the grounds of prior cladistic analyses, based on morphological data (Weygoldt 1996a, b, 1999a, c, 2000a, b). The analysis was rooted on *Xerophrynus machadooi* (Fage, 1951), placed incertae sedis in Phrynichidae by Harvey (2003), but believed to be sister to a monophyletic group comprising the remaining phrynichid genera (Weygoldt 1996b, 1999a, c, 2000a, b).

Material examined, including type specimens, is deposited in the following collections: AMNH = American Museum of Natural History, New York, USA; BMNH = The Natural History Museum, London, U.K.; FMNH = Field Museum of Natural History, Chicago, USA; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MHNG = Muséum d'Histoire Naturelle, Genève, Switzerland; MRAC = Musée Royal de l'Afrique Centrale, Tervuren, Belgium; NCAP = National Collection of Arachnida, Plant Protection Research Institute, Pretoria, South Africa; NHMW = Naturhistorisches Museum Wien, Austria; NMNW = National Museum of Namibia, Windhoek; NMSA = Natal Museum, Pietermaritzburg, South Africa; SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany; ZMHB = Zoologisches Museum, Humboldt-Universität, Berlin, Germany; ZMUC = Zoologisk Museum, University of Copenhagen, Denmark. Personally collected specimens were found by turning stones, lifting tree bark, inspecting rock crevices and entering caves during the day, or by searching with the aid of a torch-light at night.

A distribution map of southern African *Damon* species was produced using ArcView GIS Version 3.2 (Environmental Systems Research Institute, Redlands, CA), by superimposing point locality records, obtained from the material examined, on spatial datasets depicting the topography (500 m contour interval), sand systems, and political boundaries of southern Africa (following Prendini 2003, 2004).

Morphological and behavioural data

Nineteen morphological characters were scored across the 21 terminal taxa for the cladistic analysis (Table 2). Twelve were coded into binary states and seven into multistates. Transformation series could not be inferred for multistate characters, which were therefore treated as unordered, i.e. nonadditive (Fitch 1971). Morphological terminology follows Weygoldt (1996a, b, 1999a). Character data were edited, cladograms prepared, and character optimisations conducted using WinClada, Ver. 1.00.08 (Nixon 2002). Ambiguous optimisations were resolved using accelerated transformation (ACCTRAN) or Farris optimisation, which favours reversals over parallelisms to explain homoplasy (Farris 1970; Swofford and Maddison 1987, 1992; Maddison and Maddison 1992) and therefore maximises homology (Griswold et al. 1998). Four uninformative characters (1, 8, 9, and 11) were excluded from all analyses; hence, tree statistics are calculated from phylogenetically informative characters only (Bryant 1995).

Characters 18 and 19 (concerning the disposition of spermatophores and egg sacs) required that specimens be brought back to the laboratory alive, reared and mated before they could be observed and scored. These investigations allowed additional meristic data to be obtained from the spermatophores (although it was not

Table 2. Morphological character matrix for *Damon variegatus* and other phrynichid taxa

Char	Xmac	Ebac	Psca	Pscu	Matl	Dmed	Ddi1	Ddi2	Dan1	Dan2	Dan3	Dgr1	Dgr2	Dsy1	Dsy2	Dva1	Dva2	Dva3	Dva4	Dva5	Dva6	Steps	CI	RI	Fit	SW
1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	100	100	10	10
2	0	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	100	100	10	10
3	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	100	100	10	10
4	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	100	100	10	10
5	0	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	66	50	8.5/7.5/10	3
6	0	2	1	0	1	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	3/5	66/40	66/0	8.5/5	4
7	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	100	10	10
8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	100	10	10
9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	100	100	10	10
10	–	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	100	10/7.5	10
11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	100	10	10
12	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	100	10	10
13	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	50	50	8.5/10	2
14	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	100	100	10	10
15	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2/3	50/33	66/33	8.5/6	3
16	3	2	2	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	100	100	10	10
17	0	0	0	0	0	0	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	2/3	100/66	100/83	10/7.5	10
18	?	1	1	0	1	2	3	3	3	3	3	4	4	3	3	3	3	3	3	3	3	4/5	100/80	100/66	10/7.5	10
19	0	0	0	?	0	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2/3	100/66	100/87	10/7.5	10

Character states are scored 0–4, ? (unknown), or – (inapplicable); character descriptions are provided below († = uninformative). Length (steps), CI, RI, fit ($k = 3$), and final weights with successive weighting (SW) are reported for the tree obtained from the separate morphological analyses and, if differing, for the trees obtained by simultaneous analysis of morphological and molecular data (with equal weighting, and with weighting regime minimising character incongruence among data partitions). Refer to the Appendix for taxon codes and material examined.

1. Chelicerae, uppermost or distal, bicuspidate tooth: lower cusp larger (0); upper cusp larger (1).†
2. Cheliceral stridulating organ: absent (0); present, type I (1); present, type II, row of setae that may be a stridulating organ (2).
3. Antenniform legs, tibia: not thickened (0); thickened (1).
4. Antenniform legs, tarsal segments with leaf-like setae: absent (0); present (1).
5. Fourth leg tibia (basitibia IV): divided into three articles, i.e. 3-segmented (0); divided in two articles, i.e. 2-segmented (1); undivided, i.e. 1-segmented (2).
6. Pedipalps, shape: short and stout (0); slightly elongated (1); greatly elongated and slender (2).
7. Pedipalp trochanter, number of large spines on ventral surface: one (0); two (1).
8. Pedipalp femoral spines: well developed, spiniform (0); reduced to bacilliform apophyses (1).†
9. Pedipalp tibia, arrangement of spines: three large dorsal spines (1–3) form a catching basket, with smaller spines between the large ones (0); three large dorsal spines (1–3) are shifted to the distal end and form the phrynichid 'hand' (1).†
10. Pedipalp tibia, development of phrynichid 'hand': weakly developed, with straight spines (0); well developed, with curved spines (1); inapplicable (–).
11. Pedipalp tibial spine I: normal (0); bifid (1).†
12. Pedipalp tibial spine II: does not participate in formation of 'hand' (0); has shifted distally and participates in formation of 'hand' (1).
13. Pedipalp basitarsus with backwardly directed spine: absent (0); present (1).
14. Pedipalp distitarsus with two small denticles above cleaning organ: absent (0); present (1).
15. Ventral sac covers: absent (0); present (1).
16. Female genitalia, gonopodial appendage vestiges: soft finger-like (0); hook-like (1); reduced or missing (2); flat, with a sharp edge (3).†
17. Gonopods with unpaired sclerotized bar or plate anteriad: absent (0); present, of *D. variegatus* type (1); present, of *D. gracilis* type (2).
18. Spermatophores: simple, with free sperm packages (0); sperm packages on distal ends of movable bars (1); with reduced bars (2); of *D. variegatus* type (3); with reduced stalk (4); unknown (?).
19. Egg sac development: brood pouch absent (0); brood pouch present, weakly developed, eggs visible from the sides (1); brood pouch present, well developed, egg sac surrounded by large lateral and posterior pleural folds (2); unknown (?).

possible to code these data into discrete characters for cladistic analysis), and provided supplementary evidence on mating behaviour.

Captive husbandry and observation of amblypygids follows the methods of Weygoldt (1997/98, 1999b, 2002, 2003) and Weygoldt and Hoffmann (1995). All specimens were housed individually in small containers with a piece of paper towel lining the bottom, an inclined piece of cork bark to provide a retreat, and a small water dish.

Mating behaviour and mate recognition trials were observed in larger containers, the back walls of which were furnished with a substrate on which the animals could move and walk (stone slabs, cork or painted styrofoam). The bottom of the containers contained a humid mixture of sand and peat with some leaf litter. A piece of cork bark leaning against the back wall served as a retreat.

All observations were conducted at night under red light and videotaped. A male and a female from different populations were placed into the same container for the mate recognition trials. Fresh spermatophores were obtained by interrupting mating immediately after the spermatophore was deposited. After mating behaviour had been observed and videotaped several times, further trials were conducted without observation. The presence of an empty spermatophore served as an indication that mating had been successful.

Acquisition and preservation of samples for DNA isolation

DNA was isolated from pedipalp or leg muscle tissues dissected from specimens that were fixed in 95–100% ethanol (Prendini et al. 2002). Live specimens, collected in the field or obtained from colleagues, were usually brought back to the laboratory for tissue fixation at –20 °C, as this has been found to significantly increase the yield of high molecular weight DNA (Prendini et al. 2002). However, when collecting trips took more than 14 days, tissues were fixed in the field at ambient temperature. Tissue samples were mostly taken from juveniles and subadults and are stored (in the vapour phase of liquid nitrogen at –150 °C) in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the AMNH (Table 3; Appendix A). Adult *D. variegatus* and *D. annulatipes*, collected from the same populations, have been retained as voucher specimens in the collection of the AMNH. A few live specimens of *D. annulatipes* and *D. variegatus* are maintained in culture by PW.

Choice of gene loci

It is generally accepted that more than one gene locus should be used for phylogenetic reconstruction and that

Table 3. Tissue samples used for DNA isolation from *Damon variegatus* and outgroup taxa

Species	Country	AMCC	18S rDNA	28S rDNA	12S rDNA	16S rDNA	CO I	HIS H3
Xerophrynus machadoi	Namibia	124710	AY829900	AY829921	AY829860	AY829879	—	AY829961
Euphrynichus bacillifer	Kenya	124711	AY829902	AY829923	AY829862	AY829881	AY829943	AY829963
Phrynichus scaber	Seychelles	124712	AY829901	AY829922	AY829861	AY829880	AY829942	AY829962
Phrynichodamon scullyi	South Africa	124713	AY829904	AY829925	AY829864	AY829883	AY829944	AY829965
Musicodamon atlanteus	Morocco	124714	AY829903	AY829924	AY829863	AY829882	—	AY829964
Damon medius	Senegal	124715	AY829905	AY829926	AY829865	AY829884	AY829945	AY829966
Damon diadema 1	Kenya	124716	AY829906	AY829927	AY829866	AY829885	AY829946	AY829967
Damon diadema 2	Tanzania	124717	AY829907	AY829928	AY829867	AY829886	AY829947	AY829968
Damon annulatipes 1	South Africa	124718	AY829908	AY829929	AY829868	AY829887	AY829948	AY829969
Damon annulatipes 2	South Africa	124719	AY829909	AY829930	AY829869	AY829888	AY829949	AY829970
Damon annulatipes 3	Swaziland	124720	AY829910	AY829931	AY829870	AY829889	AY829950	AY829971
Damon gracilis 1	Namibia	124721	AY829919	AY829940	AY829877	AY829898	AY829959	AY829980
Damon gracilis 2	Namibia	124722	AY829920	AY829941	AY829878	AY829899	AY829960	AY829981
Damon sylviae 1	Namibia	124723	AY829911	AY829932	AY829871	AY829890	AY829951	AY829972
Damon sylviae 2	Namibia	124724	AY829912	AY829933	AY829872	AY829891	AY829952	AY829973
Damon variegates 1	South Africa	124725	AY829913	AY829934	—	AY829892	AY829953	AY829974
Damon variegates 2	South Africa	124726	AY829914	AY829935	AY829873	AY829893	AY829954	AY829975
Damon variegates 3	South Africa	124727	AY829915	AY829936	AY829874	AY829894	AY829955	AY829976
Damon variegates 4	South Africa	124728	AY829916	AY829937	AY829875	AY829895	AY829956	AY829977
Damon variegates 5	Swaziland	124729	AY829917	AY829938	AY829876	AY829896	AY829957	AY829978
Damon variegatus 6	Tanzania	124730	AY829918	AY829939	—	AY829897	AY829958	AY829979

All samples, for which accession numbers are listed, are deposited in the Ambrose Monell Collection for Molecular and Microbial Research (AMCC) at the American Museum of Natural History, New York. GenBank accession codes are provided for the respective sequences.

at least one locus should be from the recombinant nuclear genome. Six loci were selected for the present investigation, not only on the basis of the availability of primers that could consistently amplify sufficiently large, phylogenetically informative fragments, but also because they have been reported to evolve at different rates and thus would be expected to provide phylogenetic resolution at different, overlapping taxonomic levels (e.g., Simon et al. 1994; Hayashi 1996; Wahlberg and Zimmermann 2000; Giribet et al. 2001b; Prendini et al. 2003).

Three gene loci from the nuclear genome were included primarily to resolve relationships among the outgroup taxa. The complete sequence of the small-subunit ribosomal RNA gene (18S rDNA), a variable fragment (D3 region) of the large-subunit ribosomal RNA gene (28S rDNA) and a variable fragment of the Histone H3 protein-coding gene were amplified. These fragments have been used in various studies of arthropod phylogeny at higher and lower levels, e.g. see Giribet et al. (2001b), Prendini et al. (2003), and references therein.

In order to provide resolution among the ingroup taxa, three gene loci were selected from the more labile mt genome. Comparatively labile fragments of the mt homologs of the nuclear small-subunit ribosomal RNA gene (12S rDNA) and the nuclear large-subunit ribosomal RNA gene (16S rDNA), both of which also contain conserved regions, were chosen, together with a more conserved fragment of the Cytochrome c Oxidase subunit I (CO I) protein-coding gene. These fragments have been used in studies of inter- and intraspecific variation within insects, scorpions, and spiders, as well as for studies of arthropod higher phylogeny, e.g. see Giribet et al. (2001b), Prendini et al. (2003), and references therein.

DNA isolation, amplification and sequencing

Laboratory work was conducted at the Molecular Systematics Laboratory of the AMNH. Genomic DNA was isolated from ethanol-preserved tissues using homogenisation buffers. Most tissue samples were homogenised in a buffer solution comprising 1 vol (400 µl) of 4 M guanidinium isothyocyanate (5 g/ml guanidinium thyocyanate, 1 M Tris.Cl, pH 7.5) and 0.14 M β-mercaptoethanol, by agitation for 1–2 h at ambient temperature, following a modified protocol for RNA extraction (Chirgwin et al. 1979) used by Edgecombe et al. (1999), Giribet et al. (1999a, b) and Giribet and Ribera (2000). After homogenisation, DNA was cleaned in a standard 25:24:1 phenol/chloroform/isoamyl alcohol series (Palumbi et al. 1991), precipitated in 100% ethanol and 3 M NaOAc (pH 5.2), dehydrated in a speed-vac at 60 °C, and resuspended in water. Tissue samples that proved difficult to amplify during the polymerase chain reaction (PCR) were re-extracted using the Qiagen® Dneasy Tissue Kit: Dneasy Protocol for Animal Tissues. Consult Nishiguchi et al. (2002) for further details of DNA isolation protocols used in this study.

Double-stranded template, suitable for sequencing, was prepared by PCR amplification with the primers listed in Table 4. The 18S rDNA fragment was amplified in three overlapping sections, using the following primer pairs: 18S1F/18S5R, 18S3F/18Sbi, 18SA2.0/18S9R. Primer pairs 28Sa/28Sbout, H3AF/H3AR, 12Sai/12Sbi, 16Sar/16Sbr and HCOoutout/LCO were respectively used to amplify fragments of 28S rDNA, H3, 12S rDNA, 16S rDNA and CO I. Amplification was conducted in a 50 µl volume reaction, with 1.25 units of AmpliTaq® DNA Polymerase (Perkin Elmer), 200 µM of dNTPs and 1 µM of each primer, or using

Table 4. Primers used in amplification and sequencing of Amblypygi

Primer name	Sequence (5′–3′)	Other names (references)
18S1F	TACCTGGTTGATCCTGCCAGTAG	
18S5R	CTTGGCAAATGCTTTCGC	
18S3F	GTTCGATTCCGGAGAGGGA	
18Sbi	GAGTCTCGTTCGTTATCGGA	
18SA2.0	ATGGTTGCAAAGCTGAAAC	
18S9R	GATCCTTCCGCAGGTTCACCTAC	
28Sa	GACCCGTCTTGAAACACGGA	D3A (Nunn et al. 1996)
28Sbout	CCCACAGCGCCAGTTCTGCTTACC	
H3AF	ATGGCTCGTACCAAGCAGACVGC	
H3AR	ATATCCTTRGGCATRATRGTGAC	
12Sai	AAACTAGGATTAGATACCCTATTAT	SR-N-14588 (Kocher et al. 1989; Simon et al. 1994)
12Sbi	AAGAGCGACGGGCGATGTGT	SR-J-14233 (Kocher et al. 1989; Simon et al. 1994)
16Sar	CGCCTGTTTATCAAAAACAT	LR-N-13398 (Simon et al. 1994)
16Sbr	CTCCGGTTTGAACTCAGATCA	LR-J-12887 (Simon et al. 1994)
HCOoutout	GTAAATATATGRTGDGCTC	
LCO	GGTCAACAAATCATAAAGATATTGG	LCO-1490-J-1514 (Folmer et al. 1994)

Ready-To-Go PCR beads (Amersham Pharmacia Biotech), to which were added 1 µl per reaction of each 10 µM primer, 23 µl of water, and 2 µl of DNA. The PCR program consisted of an initial denaturing step at 94 °C for 5 min, 40 amplification cycles (94 °C for 15 s, 49 °C for 5 s, 72 °C for 15 s), and a final step at 72 °C for 7 min in a GeneAmp® PCR System 9700 (Perkin Elmer) thermocycler or in Tetrad 4-head thermocyclers. Specific conditions were optimised for taxa and primer pairs (e.g., a lower annealing temperature was used to amplify the CO I fragment).

PCR products were verified on 1% agarose/TBE electrophoretic gel. Products were then purified with the Qiagen Qiaquick 96 PCR Purification Kit by eluting into 60 µl buffer EB (using a Biomek Robot with a 96-well format), dehydrated in a speed-vac at 60 °C, and resuspended in 10 µl water (again using the Biomek Robot).

Double-stranded sequencing of the PCR products was conducted by the dideoxy termination method (Sanger et al. 1977) using an automated Applied Biosystems Inc. (ABI) Prism™ 3700 DNA sequencer. Cycle-sequencing with AmpliTaq® DNA Polymerase, FS (Perkin-Elmer) using dye-labelled terminators (ABI Prism™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kit) was performed in a GeneAmp® PCR System 9700 (Perkin Elmer) thermocycler and in Tetrad 4-head thermocyclers. Cycle-sequencing was conducted in a 10 µl volume reaction, comprising 2 µl of Big Dye, 2 µl of Big Dye Extender, 1 µl of 3.2 µM primer, 3 µl of water, and 2 µl of DNA, 96 reactions at a time using the Biomek Robot. The cycle-sequencing program consisted of 25 amplification cycles (96 °C for 15 s, 50 °C for 15 s, 60 °C for 4 min).

Dye-labelled cycle-sequence products were cleaned by isopropanol/ethanol-precipitation (40 µl 70% isopropanol added; centrifuged for 30 min at 3500 rpm; microtiter plate inverted and centrifuged for 1 min at 500 rpm; 40 µl 70% ethanol added; centrifuged for 30 min at 3500 rpm), air-dried for 30 min, resuspended in 10 µl formamide and loaded directly (in microtitre plates) onto the 3700, four plates at a time.

DNA sequence editing

The accuracy of sequences was verified, in all cases, by independently amplifying and sequencing the complementary strands of all fragments. If complementary strands disagreed (except by minor mismatches), the sample was reamplified and sequenced to resolve discrepancies. Chromatograms obtained from the automated sequencers were edited, primer sequences removed, and consensus sequences created from the complementary strands using Sequencher™ Ver. 4.0.5 (Gene Codes Corporation, Ann Arbor, MI).

A total of 122 sequences were generated for this study (Table 3). The CO I fragments could not be amplified from the samples of *Xerophrynus* and *Musicodamon*, whereas the 12S rDNA fragments could not be amplified from the samples of *D. variegatus* 1 and *D. variegatus* 6.

The protein-coding H3 and CO I fragments were exactly 328 and 815 bp, respectively, in all terminal taxa, whereas the ribosomal 18S rDNA, 28S rDNA, 12S

Table 5. Frequency distribution of length variation (number of base-pairs) in homologous sequences of the 18S rDNA, 28S rDNA, 12S rDNA and 16S rDNA genes of *Damon*, compared with other genera of Phrynichidae

		Xerophrynus	*Phrynichus*	*Euphrynichus*	*Phrynichodamon*	*Musicodamon*	*Damon*	Total
	n	1	1	1	1	1	16 (12S: 13)	21 (12S: 18)
18S rDNA	Range	1760	1761	1761	1764	1763	1763	1760–1764
	Mean						1763	1763
	Mode						1763	1763
28S rDNA	Range	521	522	522	522	523	522–523[a]	521–523
	Mean						522	522
	Mode						522	522
12S rDNA	Range	339	337	341	345	343	340–345[b]	337–345
	Mean						343	342
16S rDNA	Range	507	516	527	509	513	516–522[c]	507–527
	Mean						519	518
	Mode						518	518

Numbers in parentheses refer to the frequencies with which sequence lengths were observed. Actual frequencies as follows:
[a]522 (15), 523 (1).
[b]340 (3), 341 (1), 342 (3), 343 (2), 344 (2), 345 (2).
[c]516 (4), 518 (6), 519 (1), 520 (3), 522 (1), 525 (1).

rDNA and 16S rDNA fragments varied from 1760–1764 bp (mean: 1763; mode: 1763), 521–523 bp (mean: 522; mode: 522), 337–345 bp (mean: 342), and from 507–527 bp (mean: 518; mode: 518), respectively (Table 5). The six fragments collectively comprise 4268–4302 bp per terminal taxon.

Phylogenetic analysis

The present investigation applies the ''simultaneous analysis'' sensu Nixon and Carpenter (1996a) or ''total evidence'' sensu Kluge (1989) approach to analysing molecular and morphological data, the advantages and disadvantages of which have been thoroughly reviewed and shall not be elaborated here. The arguments of Nixon and Carpenter (1996a) concerning explanatory power, character independence, and the emergence of secondary signals are considered sufficient justification for this approach. Separate analyses of the morphological and molecular data were conducted only in order to assess character incongruence by means of the incongruence length difference (ILD; Mickevich and Farris 1981; Farris et al. 1994, 1995) discussed further below.

The inclusion of morphological data, in turn, provides justification for the use of parsimony in the present investigation, and simultaneous analysis is a logical extension of the parsimony criterion (Nixon and Carpenter 1996a). The use of multiple analytical techniques predicated on fundamentally different philosophies (''syncretism'' sensu Schuh 2000; ''pluralism'' sensu Giribet et al. 2001a; ''methodological concordance'' sensu Grant and Kluge 2003) has been criticised elsewhere (Giribet et al. 2001a; Grant and Kluge 2003; Prendini et al. 2003).

Separate analysis of the morphological data under equal weighting was conducted with Hennig86 Ver. 1.5 (Farris 1988), using the implicit enumeration (**ie*;**) command. The effects of successive approximations weighting (Farris 1969) and implied weighting (Goloboff 1993) were also investigated. Successive weighting was implemented using the command sequences **xs w; ie*;** in Hennig86 and **run swt.run; mswap+;** in Pee-Wee Ver. 2.6 (Goloboff 1997). Pee-Wee was used for analyses with implied weighting, according to the following command sequence: **hold10000; hold/10; mult*100; jump50; max*;**. There is currently no philosophical justification for the choice of any particular k value; hence the analyses with implied weighting employed six values for k, spanning the input range permitted by Pee-Wee (specified with command **conc N;**).

The method of ''optimisation alignment'' or ''direct optimisation'' (Wheeler 1996), which allows DNA sequence alignment and phylogenetic analysis to be undertaken simultaneously and dynamically, was used for analysis of the molecular data separately and in combination with the morphological data. Although computationally intensive, direct optimisation has become increasingly popular, whereas the traditional approach to analysing DNA sequence data by first aligning and then subjecting the prealigned sequences to a normal parsimony analysis has come under increasing criticism (summarised in Prendini et al. 2003).

There are two advantages to using direct optimisation instead of fixed alignment. Firstly, aligning prior to phylogenetic analysis clearly violates the logic of parsimony because whether or not an indel is postulated depends on the phylogeny in question. As has been argued by Wheeler (1996), a phylogeny should be evaluated according to how many substitutions and how many indels it requires postulating; so that analyses should simultaneously consider the indels and substitutions required by alternative phylogenies, instead of taking them as given. Not only is direct optimisation philosophically superior in this regard, but the method has been empirically demonstrated to yield more congruent results than fixed alignment when using character congruence among partitions as a criterion (Wheeler and Hayashi 1998; Wahlberg and Zimmermann 2000; Wheeler 2000, 2001a, b; Giribet 2001; Wheeler et al. 2001). Fixed alignment may not yield objective, precise results due to various computational difficulties, which are most severe when sequences are of greatly different lengths (see Phillips et al. 2000 and references therein).

As in other studies using direct optimisation, a ''sensitivity analysis'' (sensu Wheeler 1995) was undertaken to assess the sensitivity of phylogenetic results to variation in the analytical parameters. Although some authors disagree (e.g. Kluge 1997a, b; Frost et al. 2001; Grant and Kluge 2003), we concur with Giribet (2003) that data exploration is important for discerning between robust relationships, which appear under a wide range of parameters, and unstable relationships, which appear only under particular parameters.

The parameters of primary interest were the indel or gap cost ratio (the relative cost of the insertion or deletion of a base versus a base substitution), the transversion-transition or change ratio (the relative cost of a transversion versus a transition), and the relative weight of morphology. Thus, if an indel ratio of 2:1 was specified, two base substitutions would equal a single indel, whereas if a tv–ts ratio of 4:1 was specified, four transitions would equal a single transversion. When the tv–ts ratio was set at a value other than unity, the indel cost was set according to the cost of transversions. The relative indel cost was varied from equal to base substitutions to twice and four times as costly (the 2:1 weighting approximates the gap:change ratio used during alignment). The tv–ts cost was similarly specified and, in addition, a transversion-only scheme (transition

Table 6. Molecular stepmatrices used in sensitivity analyses with POY (Gladstein and Wheeler 1996–2000)

Tv:ts		∞	1	2	4
Gap:change	1	110: 0 1 0 1 1 1 0 1 0 1 0 1 0 1 1 1 0 1 0 1 1 1 1 1 0	111: 0 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 1 0 1 1 1 1 1 0	121: 0 2 1 2 2 2 0 2 1 2 1 2 0 2 2 2 1 2 0 2 2 2 2 2 0	141: 0 4 1 4 4 4 0 4 1 4 1 4 0 4 4 4 1 4 0 4 4 4 4 4 0
	2	210: 0 1 0 1 2 1 0 1 0 2 0 1 0 1 2 1 0 1 0 2 2 2 2 2 0	211: 0 1 1 1 2 1 0 1 1 2 1 1 0 1 2 1 1 1 0 2 2 2 2 2 0	221: 0 2 1 2 4 2 0 2 1 4 1 2 0 2 4 2 1 2 0 4 4 4 4 4 0	241: 0 4 1 4 8 4 0 4 1 8 1 4 0 4 8 4 1 4 0 8 8 8 8 8 0
	4	410: 0 1 0 1 4 1 0 1 0 4 0 1 0 1 4 1 0 1 0 4 4 4 4 4 0	411: 0 1 1 1 4 1 0 1 1 4 1 1 0 1 4 1 1 1 0 4 4 4 4 4 0	421: 0 2 1 2 8 2 0 2 1 8 1 2 0 2 8 2 1 2 0 8 8 8 8 8 0	441: 0 4 1 4 16 4 0 4 1 16 1 4 0 4 16 4 1 4 0 16 16 16 16 16 0

cost of zero) was employed. In total, 12 combinations of indel and tv–ts costs were employed (with indel ratios of 1, 2, 4 and tv–ts ratios of 1, 2, 4, ∞). Parameters are named 110, 111, 121, 141, 210, 211, 221, 241, 410, 411, 421, 441 (Table 6). According to this notation, parameter set 221 (gap:tv:ts) means that the indel (gap) cost is set at twice the highest tv–ts (change) cost, in this case the tv, which is twice the ts cost; hence the ratio 221 implies costs for gap, tv and ts of 4, 2 and 1, respectively.

While the indel and tv–ts ratios were varied, the morphological data were assigned weights relative to the molecular data. In one group of analyses, morphological characters were weighted equal to the highest of the molecular costs (indels), whereas in a separate group of analyses, morphological data were weighted equal to the base change cost. This resulted in 20 simultaneous analyses, in addition to the 12 separate analyses of the molecular data in which indel and tv–ts ratios were varied.

All analyses in which indel ratio, tv–ts ratio, and relative weight of morphology were varied, were performed using batch files spawning the program POY Ver. 2.0 (Gladstein and Wheeler 1996–2000) in a cluster of 564 500–1000 MHz processors connected in parallel using PVM software (see Janies and Wheeler 2001). Stepmatrices were invoked by the command –**molecularmatrix**, with an argument for the relevant stepmatrix, e.g. –**molecularmatrix 221**, and morphological weights assigned with the command –**weight N**. The following commands were used for the search (Gladstein and Wheeler 1996–2000; Wheeler et al. in press):

–**parallel**: executes in parallel using PVM.

–**jobspernode 2**: sets two processes running per node.

–**controllers 10**: assigns ten clusters to the parallel search.

–**buildsperreplicate 25**: performs 25 addition sequences in the build phase of a single replicate.

–**random 10**: performs 10 random addition sequence builds (through swapping) on slave nodes; since the option –**norandomiseoutgroup** is specified, the outgroup is unaffected.

–**multibuild**: performs random addition sequence builds (no swapping), of which the best are submitted to branch swapping.

–**multirandom**: spawns individual random addition replicates to slave nodes.

–**treefuse**: performs tree fusing (Goloboff 1999).

–**fuselimit 100**: holds a maximum of 100 tree fusing pairs in memory.

–**fusemingroup 3**: allows a minimum of three taxa to be exchanged in a subtree during tree fusing.

–**dpm**: performs load balancing by using dynamic process migration (dpm), which moves processes from overutilised to underutilised nodes and causes additional slave processes to be spawned, thereby significantly improving performance.

–**dpmacceptratio 1.5**: sets the threshold parameter for dpm to 1.5; the performance ratio is a combined measure of processor load and processor speed.

–**ratchettbr 20**: performs 10 iterations of the parsimony ratchet (Nixon 1999), using TBR branch-swapping.

–**ratchettrees 2**: holds two starting trees in memory at each iteration.

–**trailinggap 1**: sets the cost of leading and trailing gaps in a sequence to unity.

–**norandomiseoutgroup**: prevents randomisation of the outgroup in –**random** and –**multibuild**.

–**noleading**: leading and trailing gaps are ignored in calculating tree cost.

–**fitchtrees**: ensures the randomness of the subset of trees stored in memory by adding additional trees to full buffers through random replacement of stored trees.

–**maxtrees 20**: holds a maximum of 20 trees in memory during processing.

–**seed –1**: sets seed value for pseudorandom number generation, using system time, in seconds (–**1**).

–**slop 5**: checks all suboptimal trees within 0.5% of the current minimum value during a search; this option slows down the search but is less affected by the heuristics of tree calculation shortcuts (Edgecombe et al. 1999; Giribet and Ribera 2000).

–**checkslop 10**: checks all suboptimal trees within 1% of the minimum value during a final TBR refinement.

The complete command sequence for a simultaneous analysis under equal weighting (using stepmatrix 111 and morphology weighted 1), where the files 18S, 28S, H3, 12S, 16S, COI and morph represent the various partitions and T111.tre the output file, is as follows: **poy –parallel –jobspernode 2 –controllers 10 –buildsperreplicate 25 –random 10 –multibuild –multirandom –treefuse –fuselimit 100 –fusemingroup 3 –dpm –dpmacceptratio 1.5 –ratchettbr 20 –ratchettrees 2 trailinggap 1 –norandomiseoutgroup –noleading –fitchtrees –maxtrees 20 –seed –1 –slop 5 –checkslop 10 –molecularmatrix 111 18S 28S H3 12S 16S COI –weight 1 morph –printtree –plotfile T111.tre**.

As in other studies (e.g., Prendini et al. 2003), results of the sensitivity analyses are summarised by means of 50% majority rule (Margush and McMorris 1981), or 50% compromise (sensu Nixon and Carpenter 1996b), and strict consensus trees. The problems with using majority rule consensus trees as a means of resolving ambiguous strict consensus trees have been well elaborated by Nixon and Carpenter (1996b) and Sharkey and Leathers (2001), among others. The use of such trees in the present context is justified on the grounds that they serve a different purpose. Here, majority rule consensus trees are presented, alongside strict consensus trees, to provide a graphical representation of the results of the sensitivity analyses. Nodes that appear in the majority rule trees but are collapsed in the strict consensus trees were obtained under the majority of parameter combinations; hence more confidence may be placed in the supposition that they are robustly supported by the data than in the alternatives that were retrieved only under specific parameter combinations.

Congruence between morphological and molecular data partitions was used as an optimality criterion to select the optimal (most corroborated) tree – that which minimises character conflict among the data – from among the various alternatives. This is an extension of parsimony for, just as the aim of parsimony analysis is to locate the tree that minimises the number of steps, the aim of sensitivity analysis is to determine the parameter set that minimises incongruence among the data (Wheeler 1995; Edgecombe et al. 1999). Incongruence among data partitions was measured by the ILD (Mickevich and Farris 1981; Farris et al. 1994), calculated by dividing the difference between the overall tree length and the sum of its data partitions:

$$\mathrm{ILD} = (\mathrm{Length}_{\mathrm{Combined}} - \sum \mathrm{Length}_{\mathrm{Partitioned}})/\mathrm{Length}_{\mathrm{Combined}}.$$

In view of recent criticisms of the ILD test (e.g. Cunningham 1997a, b; Dolphin et al. 2000; Yoder et al. 2001; Barker and Lutzoni 2002, Darlu and Lecointre 2002; Dowton and Austin 2002), it is important to distinguish between using the ILD in the incongruence test and its use as an optimality criterion. When the ILD is employed as a simple heuristic measure of incongruence, as in this study, objections to its use for determining incongruence between data partitions do not apply.

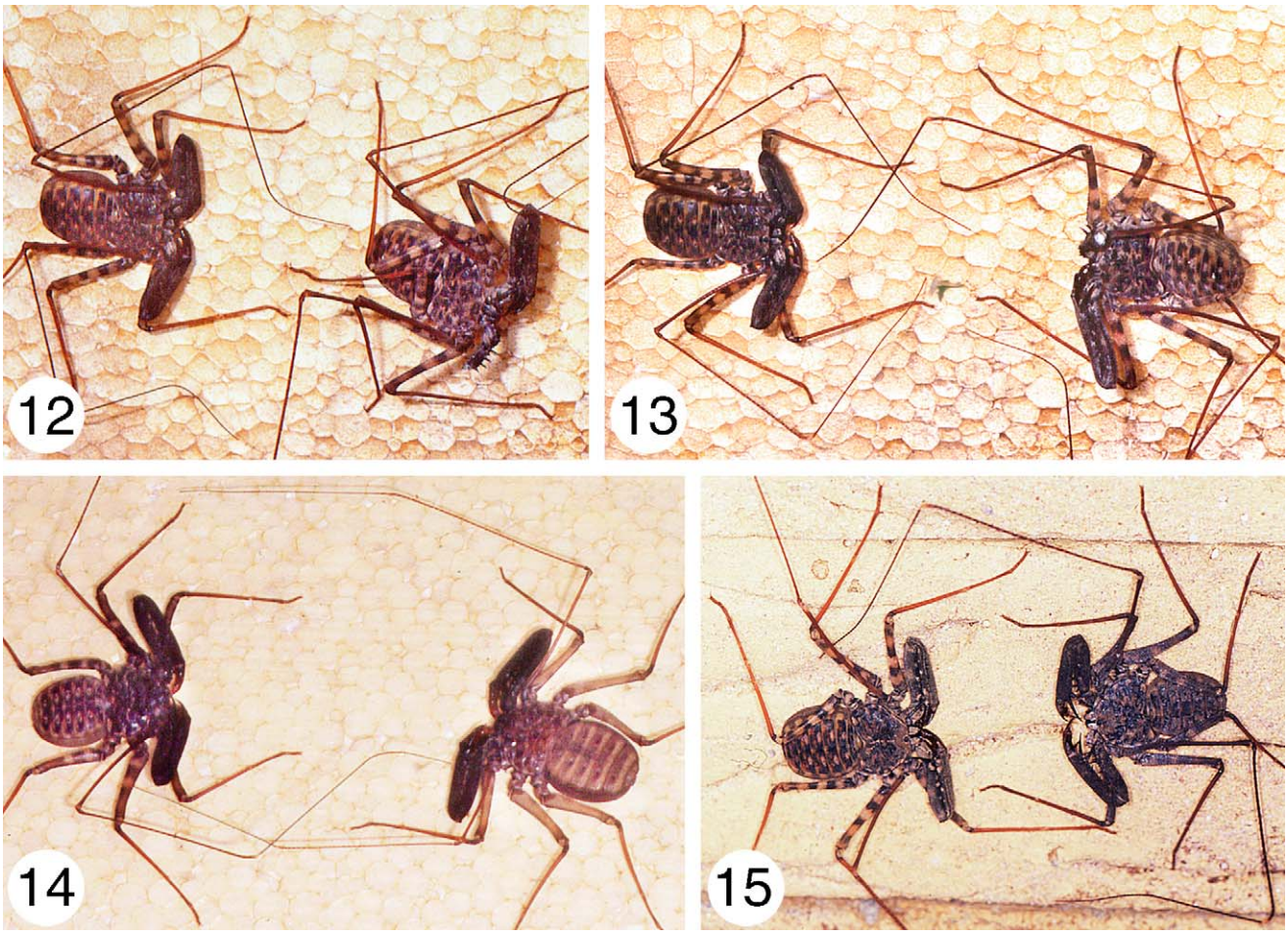
The relative degree of support of branches in the optimal tree was assessed with branch support or decay indices (Bremer 1988, 1994; Donoghue et al. 1992), calculated in POY by invoking the –**bremer** command.

Results

Courtship and mating behaviour

This section describes the mating behaviour observed among putatively conspecific specimens of *D. sylviae* n. sp. from different populations, and *D. variegatus* from the same populations.

D. sylviae 1 (♂) × *D. sylviae* 2 (♀): The courting male taps the female with irregular movements of his antenniform legs. At intervals of 0.25–2 min he pulls his antenniform legs back and then throws them forward towards the female, shaking them heavily above and in front of her 2–15 times. The male then continues the slower, irregular movements, during which the front legs (second pair) are alternatingly lifted off the ground and placed back at intervals of 2–10 s. These movements are irregular; sometimes the left or right foreleg is lifted twice before the opposite leg is lifted. The receptive female crouches close to the male and taps him slowly. During later phases of the courtship dance, the antenniform legs of the male are not only thrown forward towards the female, but vibrated in front of her so quickly that they become almost invisible in the video recordings. Occasionally the male steps forward and grasps at or in front of the



Figs. 12–15. Courtship and mating among species of *Damon* C.L. Koch. 12–13. Courtship in *Damon sylviae* n. sp. 12. Male depositing a spermatophore. 13. Male luring female to spermatophore close to his left forefoot. 14. *Damon variegatus* (Perty) from Hoedspruit courting female from Medike; these matings were usually successful. 15. *Damon annulatipes* (Wood) male courting female *D. sylviae* n. sp.; mating and sperm transfer never ensued.

female with his pedipalp (the forward approach). Finally, the male turns to deposit the spermatophore.

During spermatophore formation, the male stretches first one then the other antenniform leg over the female and touches her, then throws both antenniform legs forward 3–4 times, then again touches the female (Fig. 12). Spermatophore formation takes about 2 min. Thereafter, the male turns towards the female again and begins to lure her to the spermatophore by alternatingly touching her in a firm rhythm with his left or right antenniform leg (Fig. 13). The female approaches, picks up the sperm and the pair separate, the male at first continuing the rhythmic movements of his antenniform legs. The whole mating dance lasts for 3–4 h.

D. variegatus 3 (♂ × ♀); *D. variegatus* 4 (♂ × ♀); *D. variegatus* 6 (♂ × ♀): The courting male approaches the female and, after irregularly tapping the female for some minutes, performs a distinctive display: the male's body jerks forward slightly, and both antenniform legs are symmetrically thrown against the female, quickly vibrated back and forth and then pulled back. These jerks are performed about every 0.5–1 s. At intervals of 1–2 min he interrupts this series and touches and taps the female with irregular movements of the antenniform legs. The receptive female crouches down in front of the male and also touches him with an irregular pattern of antenniform leg movements. Throughout courtship, the male frequently lifts one or the other foreleg (leg II) off the ground and places it back down. Occasionally, the male unfolds his pedipalps and rushes forward, attempting to grasp at the female (the forward approach). The female usually withdraws and the male grasps the air, not touching the female. As the female often withdraws to the side, these forward approaches often lead to the pair circulating around each other. During later phases of courtship, a regular pattern of forward jerks, forward approaches with grasping, and irregular tapping becomes evident, and the antenniform legs, when thrown forward, are so rapidly moved back and forth that they become invisible in the video recordings. After a final

forward approach, the male turns to deposit the spermatophore.

During spermatophore formation, the male regulary and rapidly throws both antenniform legs forward several times and, every 3–5 s, stretches one antenniform leg backward and touches the female (Fig. 14). The male also regularly taps and touches the female with irregular antenniform leg movements. After about 2 min, the male turns to the female again. He then lures the female to the spermatophore with a firm pattern of antenniform leg movements, alternatingly touching her in a firm rhythm with his left or right antenniform leg. The female approaches, picks up the sperm, and the pair separate, the male at first continuing his rhythmic antenniform leg movements. The whole mating dance lasts for 3–8 h.

This general description holds for pairings of members of all populations studied. There are minor differences. For example, one male may perform more forward jerks before he pauses to tap the female with irregular movements of the antenniform legs. The forward jerks are more pronounced in some males than in others. However, differences among males from the different populations are not greater than those among males from the same populations.

Mate-recognition experiments

This section presents the results of mate-recognition experiments among putatively heterospecific specimens (*D. sylviae* n. sp. and *D. variegatus*), and putatively conspecific specimens of *D. variegatus* from different populations. Males and females of *D. variegatus* from Hoedspruit (*D. variegatus* 3) and Medike (*D. variegatus* 4) in South Africa, a female *D. sylviae* n. sp. from Christirina, Namibia (*D. sylviae* 2), and the sole male from Obab Cave, Namibia (*D. sylviae* 1), were available for these experiments. The Tanzanian specimens (*D. variegatus* 6) could not be included in these observations because they refused to mate, even with members from the same brood, probably a captivity artifact. For comparison, females of *D. annulatipes* 2 were also included.

These trials were not female-choice experiments. The females had no choice because only one male was present. They were conducted to see whether mate recognition works among different populations. As only a few specimens were available, there are only a few trials, and the results cannot be evaluated statistically.

D. variegatus 3 (♂) × *D. sylviae* 2 (♀); *D. variegatus* 4 (♂) × *D. sylviae* 2 (♀): Besides mating with the only male from Namibia, the females from Christirina mated readily with males from Hoedspruit several times and twice (three trials) with males from Medike. Mating and spermatophore transfer were successful, although the spermatophores of males from Hoedspruit, and particularly those from Medike, were much thicker, with larger sperm packages that protruded from the female gonopore for some hours after mating. Two of the females that had mated with a Hoedspruit male laid eggs, but these failed to develop. The eggs laid after mating with the Namibian male also failed to develop.

D. variegatus 4 (♂) × *D. variegatus* 3 (♀): Only one of five trials between males from Medike and females from Hoedspruit was successful, and yielded an empty spermatophore.

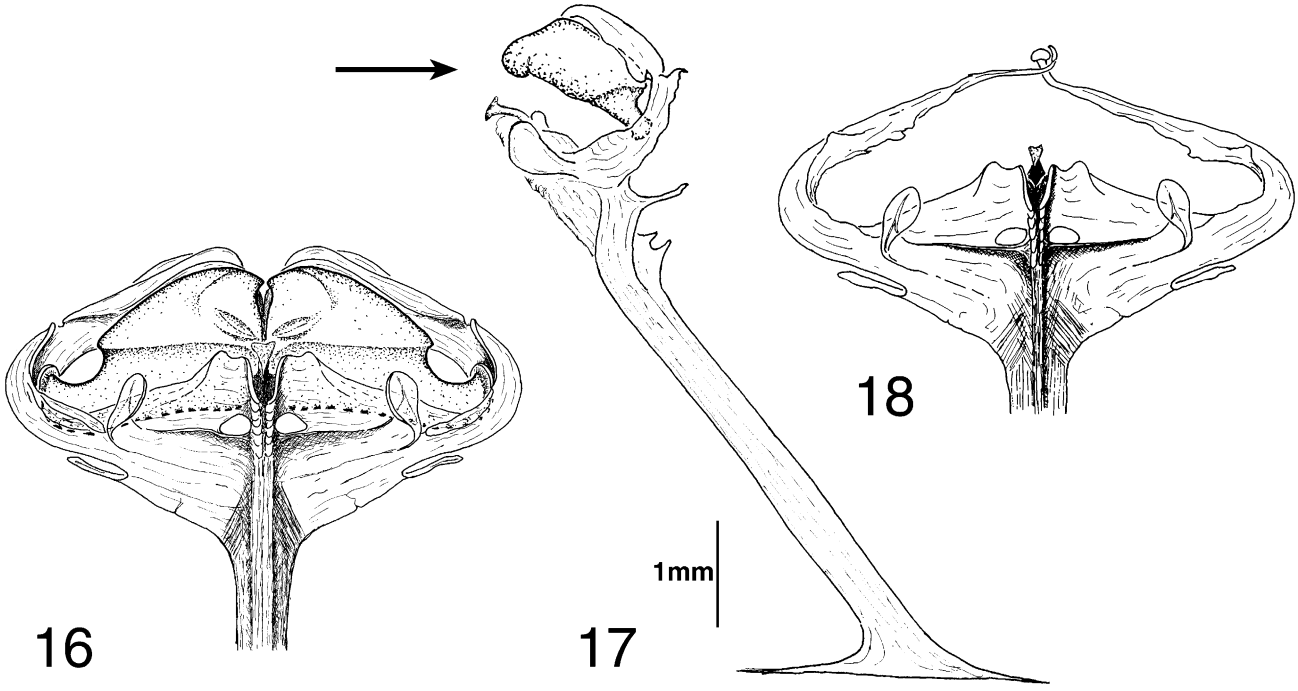
D. variegatus 3 (♂) × *D. variegatus* 4 (♀): Two trials between males from Hoedspruit and females from Medike were successful. One male deposited three spermatophores during 24 h.

None of the males used in these trials mated with *D. annulatipes* females (Fig. 15). Courtship between the specimens of *D. annulatipes* and *D. variegatus* never led to spermatophore formation, because the animals ceased courtship dancing after a short while. This was not because the females were unreceptive. They mated with conspecific males the next day. Mate recognition obviously worked between members of *D. variegatus* from the different populations in Namibia and South Africa, as well as between members of the Namibian and South African populations, but not between these populations and *D. annulatipes*.

Comparative spermatophore morphology

Figs. 16–18 illustrate a spermatophore of *D. sylviae* n. sp. (from Obab Cave, Namibia). It consists of an inclined stalk, 5.0–5.5 mm long and about 0.5 mm thick, carrying the spermatophore head on its upper end, and attached to the substratum by a foot. This spermatophore head consists of two curved arms that embrace two large, medially fused sperm packages. The sperm packages are attached to the frame laterally by means of lateral anchors, and distally by two spoon-like appendages that become visible in the emptied spermatophore. The sperm packages are composed of a thick secretion, into which the spermatozoa are embedded ventrally. The spermatophore head bears a conductor medially and two leaf-like structures of unknown function laterally.

Spermatophores of *D. variegatus* males from the other populations are nearly identical, but there are some differences. Those of males from Hoedspruit have a shorter and thicker stalk, 3.7–4.0 mm long and 0.7–0.9 mm thick, whereas those of males from Medike are more robust and even shorter and stouter, 3.2–3.5 mm long and 1.1–1.5 mm thick. In some spermatophores, the stalk displays a thickening in the upper half (Table 7). In contrast, the spermatophores of *D. annulatipes* and the Namibian *D. sylviae* 1 are very slender, with a thin stalk.



Figs. 16–18. The spermatophore of *Damon sylviae* n. sp. 16. Anterior view of spermatophore head. 17. Entire spermatophore in lateral view; arrow indicates site where female receives sperm packages. 18. Anterior view of head of an emptied spermatophore.

Table 7. Meristic data (mm) for spermatophores of several *Damon* species

Population	Collection locality	Stalk height	Stalk breadth	Head breadth
D. annulatipes 1	Charter's Creek, South Africa	5.0–5.5	0.7	3.0–3.3
D. sylviae 1	Obab Cave, Namibia	6.5	0.6	3.5
D. variegatus 3	Hoedspruit, South Africa	6.0	0.9	4.3
D. variegatus 4	Medike, South Africa	5.0–5.5	1.2–1.6	3.5–4.0
D. variegatus 6	Tanzania	5.0	0.8	4.9

The spermatophores from *D. annulatipes* are similar, but smaller. Those of *D. diadema* are also similar but considerably larger. Spermatophores of *D. gracilis* differ markedly; their stalk is reduced (Weygoldt 1997/98).

Phylogenetic analysis of the morphological data

Separate analysis of the 15 informative morphological characters with equal weighting retrieved a single most parsimonious tree (MPT) of 29 steps, fit 26, consistency index (CI) 84, and retention index (RI) 89. This MPT was also located by the analyses with successive weighting and implied weighting under $k = 3-6$. The rescaled fit percentile of the MPT varied among the implied weighting analyses as follows: 84 ($k = 3$), 85 ($k = 4$), 86 ($k = 5$ and 6).

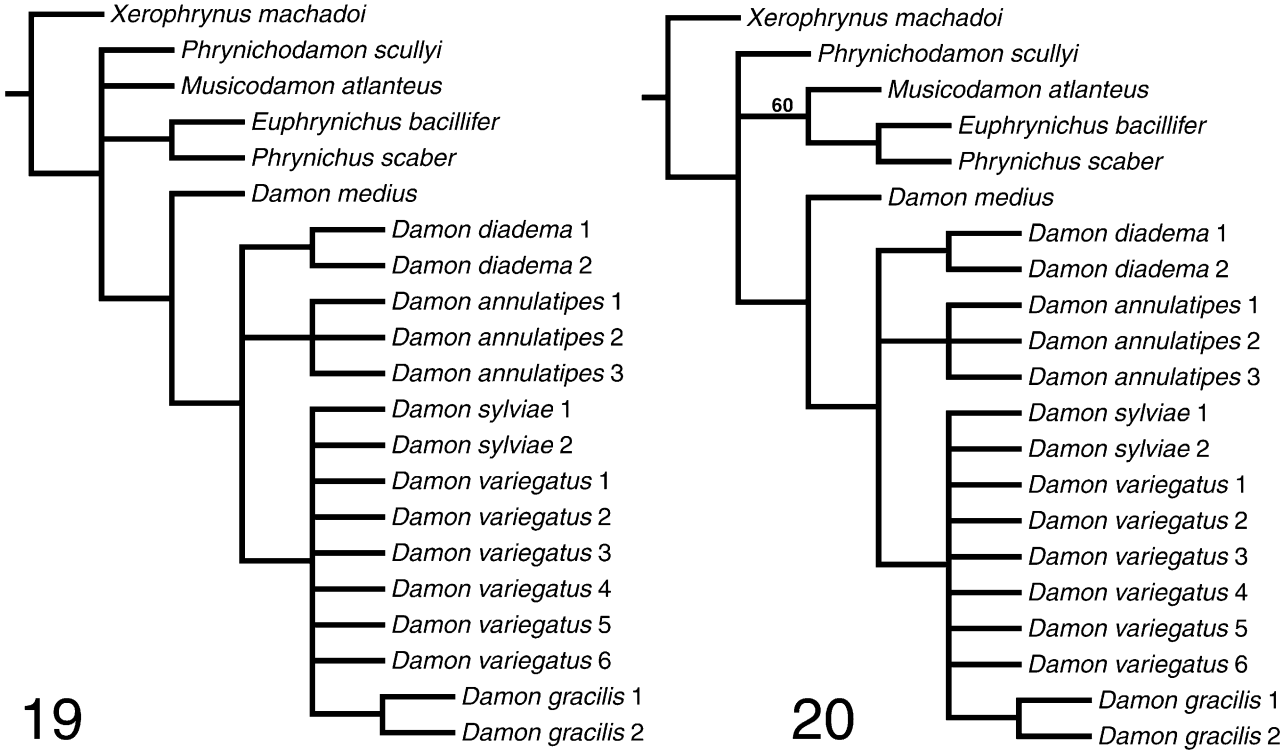
The MPT portrays a monophyletic *Damon*, in a monophyletic group with *Phrynichodamon*, *Musicodamon*, *Phrynichus*, and *Euphrynichus*. *Musicodamon* forms a monophyletic group with the exemplars of *Euphrynichus* and *Phrynichus*, which in turn form a more inclusive monophyletic group, in accordance with the topology of Weygoldt (1996a, Fig. 52; 1996b, Fig. 31; 1999a, Fig. 78; 1999c, Table 1; 2000a, Fig. 303). The relative positions of *Damon*, *Phrynichodamon* and the group comprising *Musicodamon*, *Euphrynichus*, and *Phrynichus* are unresolved. Within *Damon*, the sole exemplar of the West African group, *D. medius*, is placed sister to the East African or *D. variegatus* group, retrieved as monophyletic, in accordance with Weygoldt

(1999a, Fig. 76). Three monophyletic groups, corresponding to *D. annulatipes*, *D. diadema* and (*D. gracilis* + *D. variegatus*), are retrieved within the East African group, but their relationships are unresolved. The (*D. gracilis* + *D. variegatus*) group was also retrieved by Weygoldt (1999a, Fig. 77). A monophyletic *D. gracilis* is obtained within the (*D. gracilis* + *D. variegatus*) group, but the monophyly of *D. variegatus* is not supported, and no phylogenetic structure is retrieved among its populations (including the Namibian exemplars described below as *D. sylviae* n. sp.). The CI, RI, fit and final successive weights for the morphological characters on the MPT are provided in Table 2.

Analyses with implied weighting under $k = 1$ and 2 located two MPTs of 30 steps, fit 27, CI 81, and RI 87, which differed from the MPT obtained by the other analyses only in the positions of *Musicodamon* and *Phrynichodamon*. In one MPT, *Musicodamon* was placed as the sister taxon of *Damon*, and *Phrynichodamon* as the sister taxon of (*Musicodamon* + *Damon*), to the exclusion of (*Euphrynichus* + *Phrynichus*), in accordance with the "alternative hypothesis" of Weygoldt (1999a, Fig. 79; 2000b,: Fig. 1). In the other MPT, the positions of *Musicodamon* and *Phrynichodamon* were reversed. The rescaled fit percentile of these MPTs was 81 in the analysis under $k = 1$, and 82 in the analysis under $k = 2$. The strict and majority rule consensus trees of the separate morphological analyses are provided in Figs. 19 and 20.

Phylogenetic analysis of the molecular data

Separate analyses of the molecular data by direct optimisation, with 12 combinations of indel and tv–ts costs, retrieved a single MPT in all cases except with gap:tv:ts ratios of 211, 410 and 421, when two MPTs were retrieved, and with a ratio of 121, when four MPTs were retrieved. Tree lengths are provided in Table 8. Comparison of the results of the separate molecular analyses, summarised by strict and majority rule (50%) consensus trees (Figs. 21, 22), revealed considerable topological concordance and stability, despite the range of weighting regimes applied to the data. All except six nodes, which collapsed in the strict consensus tree (Fig. 21), were obtained by the 12 analyses and may thus be regarded as robustly supported by the molecular data. None of these nodes was incompatible with the MPTs retrieved by separate analyses of the morphological

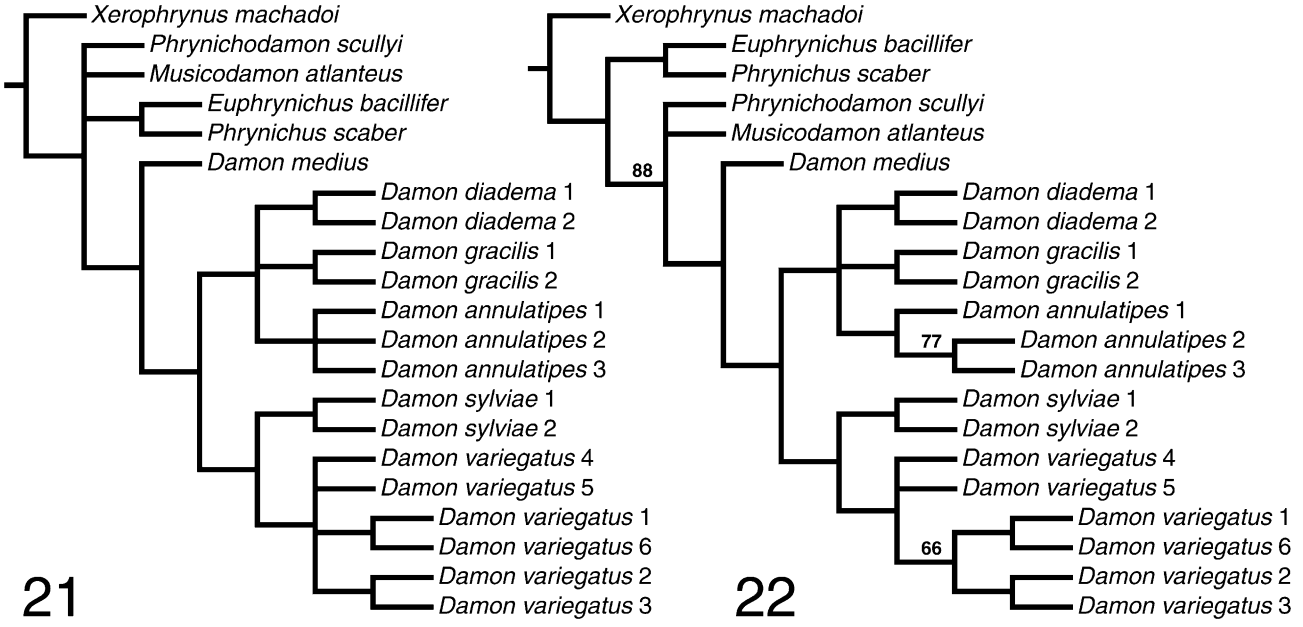


Figs. 19–20. Consensus of the MPTs obtained by eight separate analyses of the morphological character matrix (Table 2) under weighting regimes that maximised fit and minimised length. 19. Strict consensus. 20. Majority rule (>50%) consensus. Frequencies with which nodes were retrieved in >50% of analyses are indicated above branches for frequencies of >50% but <100%; nodes retrieved in <50% of analyses are collapsed; remaining uncollapsed nodes were retrieved in all analyses. This topology was retrieved by analyses with equal weighting, successive weighting and implied weighting under $k = 3-6$.

Table 8. Character incongruence (ILD) among the MPTs obtained by separate analysis of the morphological and molecular data (gaps included) under direct optimization, where: W_{Mor} and W_{Mol} denote the weighting schemes for morphological and molecular data, respectively; L_{Mor}, L_{Mol} and L_{Comb} denote the length of the MPT(s) for the morphological, molecular and combined data sets, respectively; Σ denotes the summed lengths of the MPT(s) for the separate data sets

W_{Mor}	W_{Mol}	L_{Mor}	L_{Mol}	L_{Comb}	Σ	ILD
1	110	29	1209	1244	1238	0.0048232
1	111	29	2954	2990	2983	0.0023411
2	121	58	4230	4300	4288	0.0027907
4	141	116	6653	6793	6769	0.0035330
1	210	29	1376	1411	1405	0.0042523
1	211	29	3156	3191	3185	0.0018803
2	221	58	4573	4644	4631	0.0027993
4	241	116	7326	7466	7442	0.0032146
1	410	29	1594	1630	1623	0.0042945
1	**411**	**29**	**3391**	**3426**	**3420**	**0.0017513**
2	421	58	5046	5116	5104	0.0023456
4	441	116	8248	8388	8364	0.0028612
2	210	58	1376	1446	1434	0.0082988
2	211	58	3156	3226	3214	0.0037198
4	221	116	4573	4714	4689	0.0053034
8	241	232	7326	7606	7558	0.0063108
4	410	116	1594	1736	1710	0.0149770
4	411	116	3391	3531	3507	0.0067969
8	421	232	5046	5326	5278	0.0090124
16	441	464	8248	8808	8712	0.0108992

The weighting scheme that minimized character incongruence between the data sets is indicated in boldface.



Figs. 21–22. Consensus of the MPTs obtained by 12 separate analyses of the molecular data in which indel (gap) cost and tv–ts ratio were varied (Tables 6, 8). 21. Strict consensus. 22. Majority rule (>50%) consensus. Frequencies with which nodes were retrieved in >50% of the analyses are indicated above branches for frequencies of >50% but <100%; nodes retrieved in <50% of analyses are collapsed; remaining uncollapsed nodes were retrieved in all analyses.

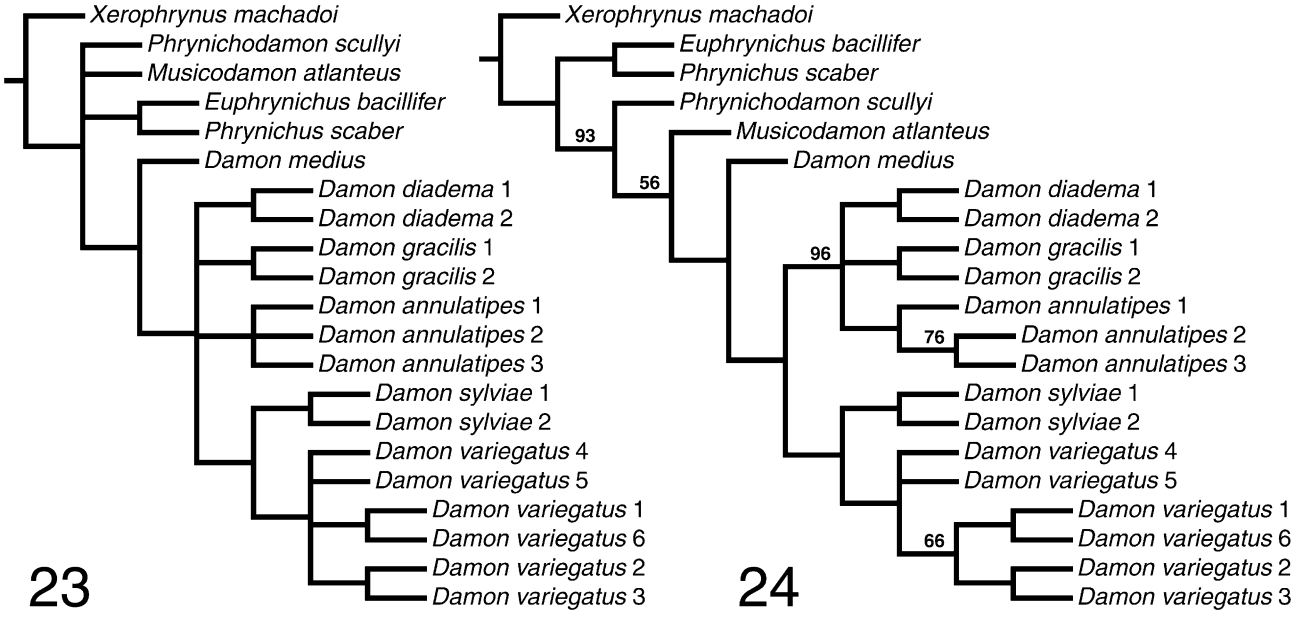
data, with the exception of the node that placed *D. gracilis* in a monophyletic group with *D. annulatipes* and *D. diadema*, rather than with *D. sylviae* n. sp. and *D. variegatus*, portrayed in Fig. 19. The monophyly of (*Euphrynichus* + *Phrynichus*), *Damon*, the *D. variegatus* group, *D. annulatipes*, *D. diadema*, and *D. gracilis*, were again unanimously supported. Additionally, the monophyly of the Namibian exemplars of *D. variegatus* (described below as *D. sylviae* n. sp.) was supported, as was the monophyly of *D. variegatus* s. str. (the remaining exemplars from localities east of the Kalahari sand system in South Africa, Swaziland and Tanzania). A further two monophyletic groups were retrieved within *D. variegatus* s. str., corresponding to relatively southern (*D. variegatus* 2 + 3) and northern (*D. variegatus* 1 + 6) populations.

Three nodes that appeared in the majority rule consensus tree (Fig. 22), but collapsed in the strict consensus tree (Fig. 21), were obtained in >50% of the separate analyses of the molecular data. The first of these, retrieved in 88% of the topologies, placed *Phrynichodamon* and *Musicodamon* in a monophyletic group with *Damon*, to the exclusion of (*Euphrynichus* + *Phrynichus*), as portrayed by Weygoldt (1999a, 2000b). This result was contrary to the topology obtained in the majority of separate analyses of the morphological data, in which *Musicodamon* was placed in a monophyletic group with (*Euphrynichus* + *Phrynichus*), to the exclusion of *Phrynichodamon* and *Damon* (Fig. 20), following Weygoldt (1996a, b, 1999a, c, 2000a). The other nodes, retrieved in 77% and 66% of the topologies, respectively, concerned internal groupings within *D. annulatipes* and *D. variegatus* s. str., which were not retrieved in the separate morphological analyses. The relative positions of *Phrynichodamon*, *D. annulatipes*, *D. diadema* and *D. gracilis*, and of *D. variegatus* 4, could not be resolved in more than 50% of the separate molecular analyses.

Phylogenetic analysis of the combined data

Simultaneous analyses of the morphological and molecular data by direct optimisation, with 12 combinations of indel and tv–ts costs, retrieved a single MPT in all cases except with gap:tv:ts ratios of 211, 410 and 421 (morphology weight = 2) when two MPTs were retrieved; with a ratio of 421 (morphology weight = 8) when three MPTs were retrieved; and with a ratio of 121 when four MPTs were retrieved. Tree lengths are provided in Table 8. Results of the simultaneous analyses, summarised by strict and majority rule (50%) consensus trees (Figs. 23, 24), compared favourably with those obtained by the separate molecular analyses but revealed greater topological concordance and stability than the latter.

All except seven nodes, which collapsed in the strict consensus tree (Fig. 23), were obtained by the 12 analyses and may thus be regarded as robustly



Figs. 23–24. Consensus of the MPTs obtained by 20 simultaneous analyses of the morphological data (Table 3) and optimised molecular data in which morphological weight, indel (gap) cost and tv–ts ratio were varied (Tables 6, 8). 23. Strict consensus. 24. Majority rule (>50%) consensus. Frequencies with which nodes were retrieved in >50% of analyses are indicated below branches for frequencies of >50% but <100%; nodes retrieved in <50% of analyses are collapsed; remaining uncollapsed nodes were retrieved in all analyses.

supported by all the data. None of these nodes was incompatible with the MPTs retrieved by separate analyses of the morphological or molecular data. The node that placed *D. gracilis* in a monophyletic group with *D. annulatipes* and *D. diadema* (Fig. 21), rather than with *D. sylviae* n. sp. and *D. variegatus* (Fig. 19), was only retrieved in 96% of the analyses (Fig. 24) and thus collapsed in the strict consensus (Fig. 23). The monophyly of (*Euphrynichus* + *Phrynichus*), *Damon*, the *D. variegatus* group, *D. annulatipes*, *D. diadema*, and *D. gracilis*, were again unanimously supported, as were the monophyly of the Namibian exemplars of *D. variegatus* (described below as *D. sylviae* n. sp.), of *D. variegatus* s. str., and of (*D. variegatus* 1 + 6) and (*D. variegatus* 2 + 3).

The majority rule consensus of the topologies obtained by the simultaneous analyses (Fig. 24) was more resolved than that obtained by the separate molecular analyses (Fig. 22), suggesting that the simultaneous analyses were more stable, i.e. less sensitive to parameter variation, than the separate molecular analyses. Aside from the node grouping *D. annulatipes*, *D. diadema* and *D. gracilis* mentioned above, another five nodes that appeared in the majority rule consensus (Fig. 24), but collapsed in the strict consensus (Fig. 23), were obtained in >50% of the simultaneous analyses. The most significant of these, retrieved in 56% and 93% of the topologies, respectively, again placed *Musicodamon* in a monophyletic group with *Damon*, and *Phrynichodamon* in a monophyletic group with (*Musicodamon* + *Damon*), to the exclusion of (*Euphrynichus* + *Phrynichus*), following Weygoldt (1999a, 2000b). As in the separate molecular analyses, the positions of *Musicodamon* and *Phrynichodamon* portrayed in this topology contrast with those in the topology obtained by the separate morphological analyses, in which *Musicodamon* was placed in a monophyletic group with (*Euphrynichus* + *Phrynichus*), to the exclusion of *Phrynichodamon* and *Damon* (Fig. 20), following Weygoldt (1996a, b, 1999a, c, 2000a). The other nodes, retrieved in 76% and 66% of the topologies, respectively, again concerned internal groupings within *D. annulatipes* and *D. variegatus* s. str., which were retrieved in the separate molecular analyses but not in the separate morphological analyses. The relative positions of *D. annulatipes*, *D. diadema* and *D. gracilis*, *D. variegatus* 4 and *D. variegatus* 5 could not be resolved in more than 50% of the simultaneous analyses.

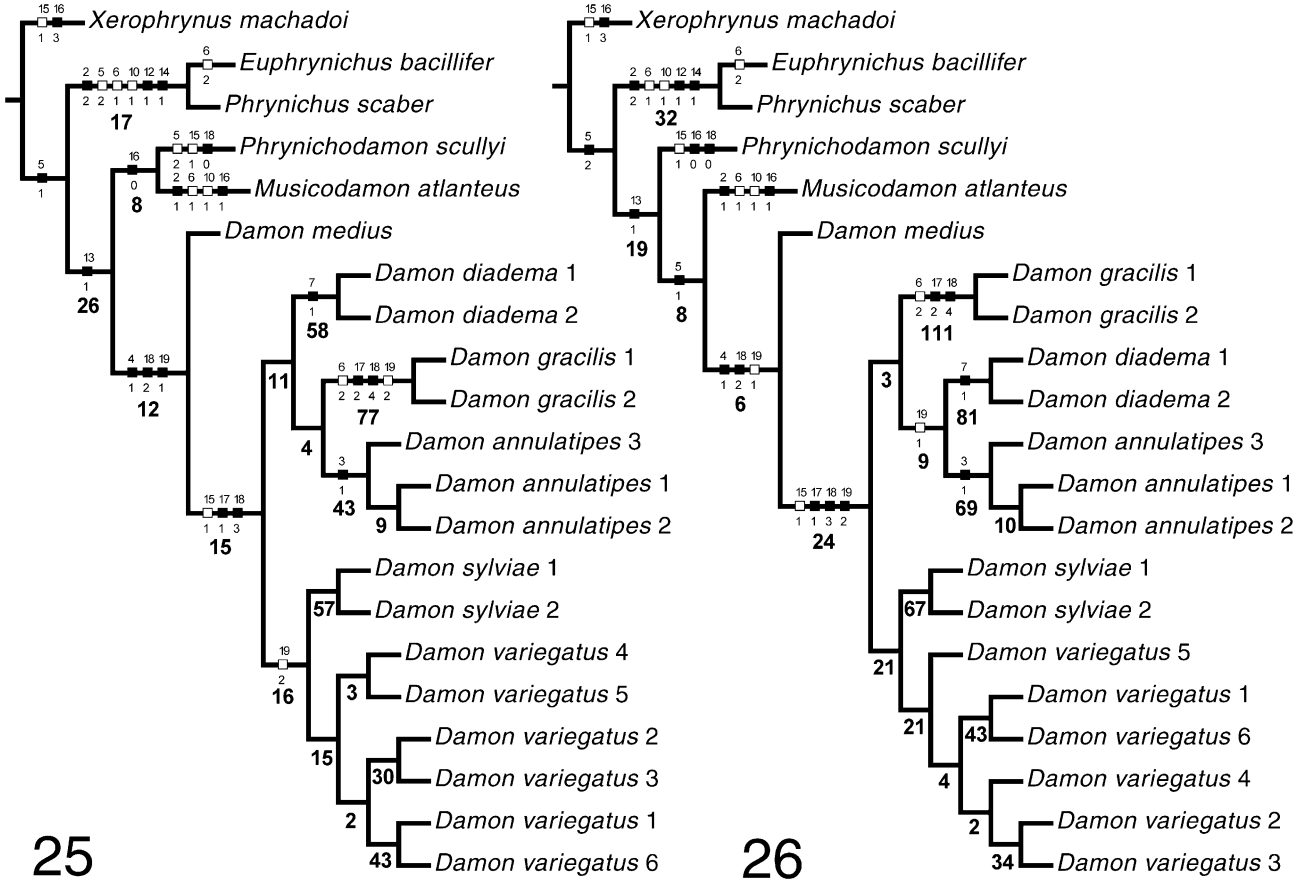
Fig. 25 illustrates the MPT obtained by simultaneous analysis of the morphological and molecular data with equal weighting. This tree supports the monophyly of Phrynichinae (*Euphrynichus* + *Phrynichus*) and Damoninae (*Phrynichodamon* + *Musicodamon* + *Damon*), following Weygoldt (1999a, 2000b) and Harvey (2003), as well as the monophyly of *Damon*, of the East African or *D. variegatus* group, and of its component species, as recognised in the revision by Weygoldt (1999a): *D. annulatipes*, *D. diadema*, *D. gracilis* and *D. variegatus* s. l. Placement of *Phrynichodamon* in a monophyletic group with *Musicodamon* contradicts the relationships among these taxa proposed by Weygoldt (1996a, b, 1999a, c, 2000a, b), as does placement of *D. gracilis* in a monophyletic group with *D. annulatipes*. The morphological synapomorphies of these taxa are optimised on the tree in Fig. 25.

The optimal tree obtained by simultaneous analysis of the morphological and molecular data with the weighting regime that minimised character incongruence among the data partitions (ILD = 0.0017513) is provided in Fig. 26. This MPT was obtained by analysis with a gap:tv:ts ratio of 411 (Table 6) – implying costs for indel (gap), tv and ts of 4, 1 and 1, respectively – and morphological data weighted equal to the tv–ts cost, i.e. 1 (Table 8). This optimal parameter set compares favourably with that found in other studies of arthropod phylogeny, where optimal parameter sets have been experimentally found to be for gap:tv:ts = 211, 221, 411 (Wheeler 1995, 1997, 1998; Wheeler and Hayashi 1998; Edgecombe et al. 1999; Wheeler et al. 2001; Prendini et al. 2003).

The optimal tree again supports a monophyletic Phrynichinae and a monophyletic Damoninae, following Weygoldt (1999a, 2000b) and Harvey (2003). It further supports the internal relationships among the damonine genera proposed by Weygoldt (1999a, 2000b): (*Phrynichodamon* (*Musicodamon* + *Damon*)). The optimal tree also supports the monophyly of *Damon*, of the East African or *D. variegatus* group, and of its component species as recognised in the revision by Weygoldt (1999a): *D. annulatipes*, *D. diadema*, *D. gracilis* and *D. variegatus* s. l. However, placement of *D. gracilis* in a monophyletic group with *D. annulatipes* and *D. diadema* contradicts the relationships among these taxa proposed by Weygoldt (1999a, 2000b). The morphological synapomorphies of these taxa are optimised on the tree in Fig. 26, whereas the length, fit (fi), CI and RI of the morphological characters on this tree are provided in Table 2.

There are no discrete morphological characters to support the remaining groups in the equal weights tree or the optimal tree. However, the molecular data in both cases support monophyletic western (Namibian) and eastern groups of *D. variegatus* s. l., providing novel justification for describing the western (Namibian) population of *D. variegatus* as *D. sylviae* n. sp., while restricting the name *D. variegatus* to the eastern populations.

Both trees portray further structure within *D. variegatus* s. str. obtained by the molecular data alone. In the optimal tree (Fig. 26), the Swazi exemplar (*D. variegatus* 5) is placed basal to the remaining exemplars



Figs. 25–26. Most parsimonious trees with morphological synapomorphies optimised on branches using ACCTRAN; solid bars indicate uniquely derived apomorphic states, whereas empty bars indicate parallel derivations of apomorphic states; number above each bar gives the character number, number below gives the character state; branch support values of nodes provided below branches. 25. The MPT obtained by simultaneous analysis of the morphological data (Table 2) and molecular data with equal weighting. 26. The optimal tree obtained by simultaneous analysis of the morphological data and molecular data under the weighting regime that minimised character incongruence among the data partitions; this MPT was obtained by analysis with costs for indel (gap), tv and ts of 4, 1 and 1, respectively, and morphological data weighted equal to the tv–ts cost, i.e. 1 (Tables 6, 8).

from populations further to the north, which in turn separate into two monophyletic groups. One of these monophyletic groups contains the three exemplars from geographically intermediate populations at Hoedspruit, Blyderivierspoort and Medike (*D. variegatus* 2, 3 and 4), although the Medike population groups with the Swazi population in the equal weights tree (Fig. 25). The other monophyletic group, obtained in the equal weights tree and the optimal tree, contains the exemplars from northern populations, Messina (*D. variegatus* 1) and Tanzania (*D. variegatus* 6).

Discussion

This study set out to address whether *D. variegatus* s. l. is a valid, panmictic species or a group of two or more similar but allopatric and reproductively isolated species. The currently recognised species of the *D. variegatus* group are easily distinguished morphologically. *D. diadema* bears two ventral spines on the pedipalp trochanter, a character shared with *D. brachilis*. The remaining species (*D. annulatipes*, *D. gracilis*, *D. longispinatus* and *D. variegatus* s. l.) display only one ventral spine on the pedipalp trochanter. *D. gracilis* differs from all other species in its slender habitus, elongate and strongly sexually dimorphic pedipalps, and thick spermatophore without a stalk. *D. annulatipes* and *D. variegatus* s. l. are similar morphologically. However, *D. variegatus* s. l. contains several populations that differ in colour pattern and other minor details.

Neither the comparative behavioural evidence (mating behaviour and mating experiments) gathered during this study, nor spermatophore morphology conclusively

suggested that *D. variegatus* s. l. comprises more than one species. The reproductive behaviour and spermatophores of all populations studied were very similar. Indeed, only the thickened spermatophores of specimens from the Soutpansberg (Medike, *D. variegatus* 4) were in any way distinctive. We conclude that mating behaviour and spermatophore morphology in this group of *Damon* species is of minor importance in mate recognition.

Nevertheless, our genetic evidence indicates that *D. variegatus* s. l. is not a panmictic population. Nuclear and mt DNA sequence data obtained during this study suggested that *D. variegatus* s. l. comprises at least two species: *D. variegatus* s. str., comprising several populations with different colour patterns (some of which may yet prove to be cryptic species as more data are gathered) from countries in the eastern half of southern Africa, as far north as Tanzania; and *D. sylviae* n. sp from Namibia and southern Angola. The occurrence of *D. variegatus* s. str. and *D. sylviae* n. sp. as sister species on eastern and western sides of the Kalahari sand system, a formidable barrier to the dispersal of lithophilous taxa, mirrors a biogeographic pattern already known among scorpions of the genera *Hadogenes* Kraepelin, 1894, *Opistophthalmus* C.L. Koch, 1837 and *Parabuthus* Pocock, 1890 (L. Prendini, unpublished data).

Morphologically, *D. sylviae* n. sp. differs from *D. variegatus* s. str. in several respects. The habitus of *D. sylviae* n. sp. differs because the colour pattern is more vivid and the outline of the opisthosoma more circular than in *D. variegatus* s. str. The carapace of *D. sylviae* n. sp. is also more heavily granulated than that of *D. variegatus* s. str., exhibiting large, prominent granules along the anterior margin, as well as anterior and posterior granules on the median ocular tubercle (Fig. 30). The trichobothrial series *sbc* contains three, occasionally only two trichobothria, whereas in all populations of *D. variegatus* s. str. this row contains five or occasionally four trichobothria. The antenniform legs of *D. sylviae* n. sp. are composed of only 28 tibial and 65 tarsal articles, versus 29–30 tibial and 66–67 tarsal articles in *D. variegatus* s. str.

In most of these characters, *D. sylviae* n. sp. is more similar to *D. annulatipes* than to *D. variegatus*. For example, *D. annulatipes* is also heavily granulated, with prominent granules on the median ocular tubercle and along the anterior carapace margin (Fig. 28), also possesses only three trichobothria in series *sbc*, and possesses an even lower number of antenniform leg segments than *D. sylviae* n. sp., comprising 25–27 tibial and 58–60 tarsal articles. However, there is one interesting difference between *D. sylviae* n. sp. and *D. annulatipes*. Brooding females of *D. sylviae* n. sp., like those of *D. variegatus* and *D. gracilis*, develop a brood pouch from pleural folds that protect large parts of the egg sac even ventrally (Figs. 6 and 10; Table 2, character 19), probably an adaptation to the relatively more arid regions inhabited by these species, compared with *D. annulatipes*. The majority of simultaneous analyses (Fig. 24), including the optimal topology (Fig. 26), placed *D. annulatipes* in a monophyletic group with *D. diadema* and *D. gracilis*, to the exclusion of *D. sylviae* n. sp., which was instead placed as the sister species of *D. variegatus* s. str. As *D. medius*, all species of the *D. variegatus* group, and even one species of *Phrynichus* (Weygoldt 2003) display pleural folds protecting the eggs laterally, we assume that an enlargement of these folds is easy to develop. Similarly, the low number of trichobothria in row *sbc* is most likely the result of convergent reduction. A greater number of trichobothria, as in *D. diadema* and *D. gracilis*, is the plesiomorphic condition. The low numbers of antenniform leg articles in *D. annulatipes* and *D. sylviae* n. sp. must also be regarded as the result of convergent reductions. In conclusion, the morphological comparison supports the molecular results that *D. variegatus* s. l. contains two species, *D. variegatus* s. str. and *D. sylviae* n. sp., described below.

The results of this study also shed some light on relationships among the genera of Phrynichidae. In particular, they falsify the hypothesis of relationships proposed by Weygoldt (1996a, b, 1999a, c), and instead support the "alternative hypothesis" of Weygoldt (1999a, 2000b) also accepted by Harvey (2003), according to which the Phrynichidae contains two subfamilies, Damoninae and Phrynichinae (besides the most likely basal *Xerophrynus*). The spermatophores of *Phrynichus*, *Euphrynichus*, and *Musicodamon* are complex and composed of similar parts. However, those of *Phrynichodamon* are simple and seemingly primitive, as are the female genitalia of this species. Weygoldt (1999b, 2002) suggested that a spermatophore like that of *D. medius* could have evolved from one like that of *Musicodamon*, a hypothetical evolutionary pathway supported by the relative placements of these taxa in the optimal topology (Fig. 26). However, results of the present analysis also imply that the spermatophore of *Phrynichodamon* is not primitive but evolved by the reduction of parts from much more complex spermatophores like those of *Musicodamon* and the Phrynichinae. Simplification of spermatophores does of course occur, as shown by *D. medius* and especially the *D. variegatus* group, the spermatophores of which are simplified in another direction. Nevertheless, this hypothesis is contingent on the relative positions of *Phrynichodamon* and *Musicodamon*, which were the most unstable in the present analyses, and the matter warrants further investigation.

Systematic account

Key to the species of the *Damon variegatus* group

1. Ventral sac covers large and well-developed; pedipalp tibial spine 3 less than half length of spine 2 in large specimens only ..... western group of *Damon* species
– Ventral sac covers reduced to small vestiges or absent; pedipalp tibial spine 3 less than half length of spine 2 in most species ..... *Damon variegatus* group (2)
2. Pedipalp trochanter with two proximal spines ventrally..... 3
– Pedipalp trochanter with one large spine ventrally 4
3. Female genitalia with sclerotisation in front of soft, cushion-like gonopods forming a flat, crescent-shaped sclerotised plate; recorded from Kenya, Tanzania ..... *D. diadema* (Simon)
– Female genitalia with sclerotisation in front of soft, cushion-like gonopods forming a vertical, curved bar at anterior margin of gonopods; recorded from Malawi, Mozambique, Zambia ..... *D. brachialis* Weygoldt
4. Pedipalp tibial spine 3 as long as or longer than spine 2, even in large specimens; pedipalps elongate and slender in males; recorded from Tanzania ..... *D. longispinatus* Weygoldt
– Pedipalp tibial spine 3 much shorter than spine 2 in large specimens 5
5. Female genitalia with sclerotisation in front of soft, cushion-like gonopods forming a partially flat plate with posterior and lateral margins bent upwards and forming part of the anterior wall of the gonopods; pedipalps strong and stout in males 6
– Female genitalia with sclerotisation in front of soft, cushion-like gonopods forming a vertical, narrow, curved bar; pedipalps extremely elongate in males; recorded from Angola, Namibia ..... *D. gracilis* Weygoldt
6. Trichobothrial series *sbc* with 3 (occasionally 2) trichobothria; median ocular tubercle granulated 7
– Trichobothrial series *sbc* with 5 (occasionally 4) trichobothria; median ocular tubercle smooth. Antenniform legs with 28–31 tibial and 67–68 tarsal articles (depending on locality); colour in life variable, with a strong pattern and annulated legs in most but almost without pattern and leg annulations in others; recorded from Congo, Mozambique, SouthAfrica, Tanzania, Zimbabwe ..... *D. variegatus* (Perty)
7. Antenniform legs with 25 (occasionally 25 or 27) tibial and 58–60 tarsal articles; antenniform leg tibia thickened in males; colour in life greyish-black with a strong pattern of lighter cream-coloured and annulated legs; recorded from South Africa ..... *D. annulatipes* (Wood)
– Antenniform legs with 28 tibial and 65 tarsal articles; antenniform leg tibia not thickened in males; colour in life brownish with a bright pattern of reddish and cream-coloured areas, and annulated legs; recorded from Angola, Namibia ..... *D. sylviae* n.sp.

Damon sylviae n. sp.

Damon variegatus (Perty, 1834); misidentifications, nec *Phrynus variegatus* Perty, 1834. – Lampe (1918, p. 206); Lawrence (1949, p. 2, Fig. 1 part); Fage (1951, p. 13 part); Fage (1954, p. 181 part, Fig. 2 part); Lawrence (1955, p. 260 part); Weygoldt (1999a, pp. 35–37 part, Figs. 64, 80 part); Weygoldt (2000a, Fig. 67, 155 part), 293 part); Weygoldt (2000b, pp. 342–343 part, Fig. 11 part, Table 1 part).

Etymology

The species is named in honour of Sylvia Weygoldt who collected the type specimens in Obab Cave.

Type material

Holotype: NAMIBIA: Otjozondjupa Region: Grootfontein District: Obab Cave, Farm Obab 856 [19°10′S 17°07′E], 27.iv.1999, S. Weygoldt, in cave, 1 ♂ (SMNS). Paratypes: same data as holotype, 2 ♀ (SMNS).

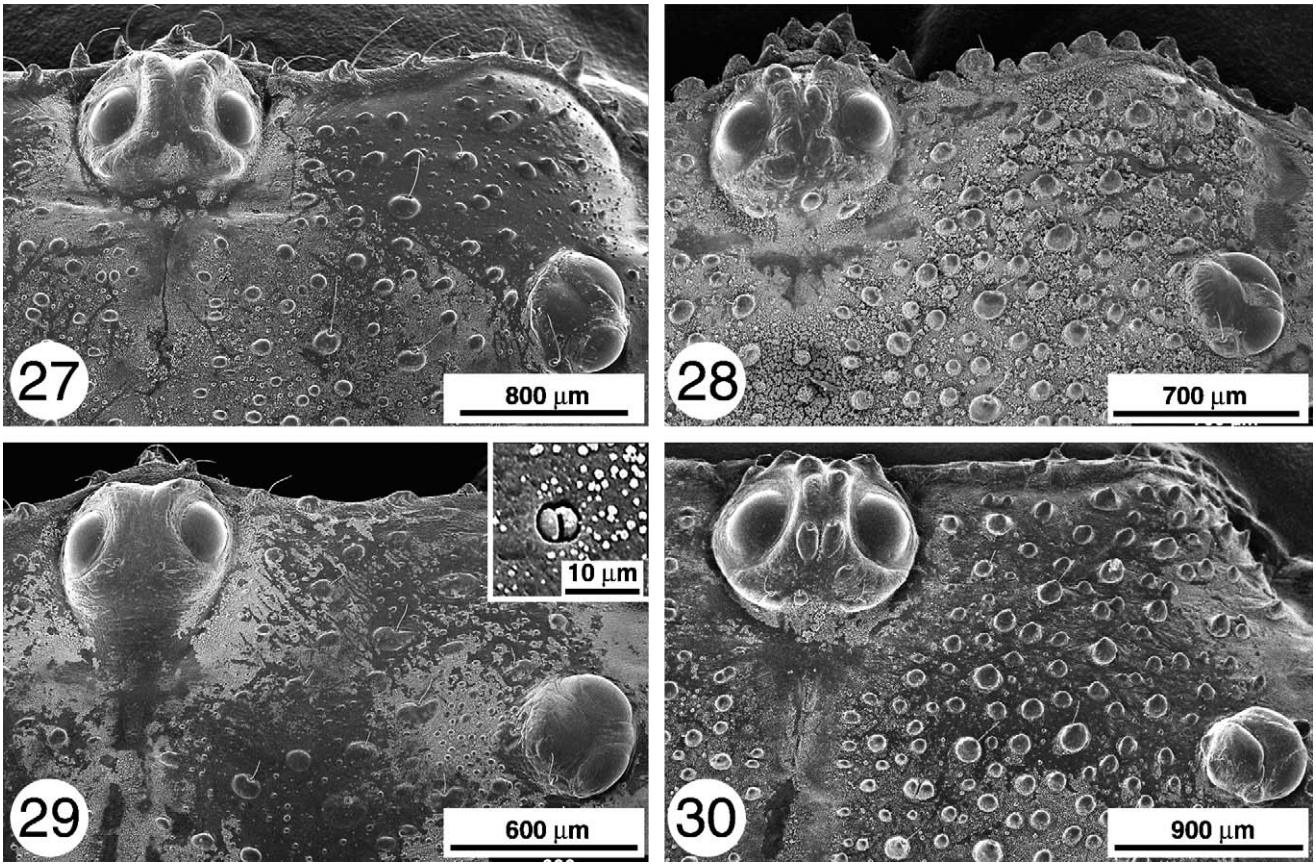
Additional material examined

NAMIBIA: 5 ♀ [ovigerous] (ZMHB). Khomas Region: Windhoek District: Farm Christirina 259 [23°24′S 18°00′E], J. Henschel, 1 ♀ (AMCC 124724). Kunene Region: Outjo District: Farm Belina 132 [20°06′S 16°02′E], 14.ii.1964, A.S. Oberholzer, 2 ♀ (NMNW 21062); Farm National 129 [20°06′S 16°17′E], viii.1987, Mr. Doll, in borehole, 1 ♀ (NMNW 21077); Road between Otjikango [Otjikondo] and Outjo [19°55′S 15°34′E], iii.1978, Roodt, 1 ♂ (NMNW 21075). Etosha National Park: Okaukuejo Rest Camp [19°11′S 15°56′E], 1.xi.1989, M. Lindeque, 1 ♂ (NMNW 21088); Raymund se Gat, Bloubokkiesdraai [18°50′S 16°57′E], 13.iv.1989, E. Marais & J. Irish, in cave, 1 ♂ 1 ♀ (NMNW 21086). Omaheke Region: Gobabis District: Farm Dipcardi 389, Sandveld Research Station [22°00′S 19°09′E], iii.1984, A. Steyn, in house, 1 ♂ (NMNW 21090); Witvlei [22°24′S 18°29′E], 1984, G. Kubisch, 1 ♀ (NMNW 21089); Zanie [Farm Zania 451, 23°29′S 18°29′E], Botswana border, 27.v.1974, R. Greeff, 1 ♂

(NMNW 21073). Otjozondjupa Region: Grootfontein District: Farm Gaikos 729 [19°27′S 18°25′E], iii.1987, v. Gressmann, 1 ♀ (NMNW 21087); Grootfontein [19°34′S 18°06′E], 3.ii.1990, P. von Wrede, found in outhouse, 1 ♂ (NMNW 21079); Obab Cave, Farm Obab 856 [19°10′S 17°07′E], 13–24.viii.1994, E. Marais, in cave, 1 ♂ (NMNW 21091), 27.iv.1999, S. Weygoldt, in cave, 2 ♀ 1 ad. (AMCC 124723). Otjiwarongo District: Farm Erindi Osombaka 223 [21°17′S 17°23′E], 26.xi.1988, A. Kotze, in bathroom, 1 ♂ (NMNW 21078); Farm Hoasas 16 [20°19′S 16°37′E], 20.iv.1964, A. Oelofse, 1 ♀ (NMNW 21063); Farm Okambukonde West, 183 km from Grootfontein [20°31′S 17°22′E], 3.iv.1989, C.H.G. Schlenwein, 1 ♀ (NMNW 21033); Farm Okapanda Yokahandja [Farm Okapanda 248, 21°09′S 17°29′E], 19.iii.1933, W. Hoesch S.G., 1 ♀ (ZMHB).

Diagnosis

A species of the *D. variegatus* group, morphologically similar to *D. variegatus*, from which it differs by the following combination of character states: smaller size; trichobothrial series *sbc* with 2–3 trichobothria (*D. variegatus*: 4–5); stronger colour pattern (some *D. variegatus* populations also have a distinct pattern, but it is less vivid); coarser granulation of the carapace, which exhibits large, prominent tubercles (the latter smaller and flatter in *D. variegatus*); presence of large tubercles on the median ocular tubercle (the latter in *D. variegatus* is smooth with very few, small elevations, each bearing a seta); elevated, almost pyramidal lateral ocular triads (the latter flat and rounded in *D. annulatipes*, *D. gracilis* and *D. variegatus*; Figs. 25–30,). The new species shares all except the last character state with *D. annulatipes* from which it may be distinguished by its vivid colouration (*D. annulatipes* also has a strong pattern with leg annulations, but it is greyish-black in colour with a light, cream-coloured pattern). *Damon annulatipes* is further distinguished by means of an autapomorphy, the thickened antenniform leg tibia of the male. *Damon gracilis* is further distinguished from the new species by means of its extremely elongate pedipalps in the adult male.



Figs. 27–30. Scanning electron micrographs of anterior region of carapace between median ocular tubercle and right lateral ocular triad in several species of *Damon* C.L. Koch. 27. *Damon gracilis* Weygoldt. 28. *Damon annulatipes* (Wood). 29. *Damon variegatus* (Perty) from Medike, Soutpansberg, South Africa; inset: glandular pore on carapace of a specimen from Tanzania. 30. *Damon sylviae* n. sp.

Description

Colour in life: a very distinct pattern with some individual variation; carapace brownish with cream-coloured lateral markings, blackish above brain region with cream to reddish and black markings radiating from the central depression; pedipalps dark reddish-brown, almost black; tergites with dark, nearly blackish base colour and cream to reddish markings around the muscle depression and along the postero-lateral margins; leg femora dark brown with two distinct bright annulations and a less distinct annulation distally, leg tibiae reddish-brown.

Colour in ethanol: the distinct colour pattern remains unchanged in ethanol; in many specimens the light-coloured parts become even lighter, rendering the pattern more distinct.

Carapace: 1.8 times wider than long; coarsely granular with many large, pointed tubercles and smaller granules in between, most of the pointed tubercles bearing a seta; anterior and antero-lateral margin with similar pointed tubercles; carapace heavily sculptured, median and lateral depressions, and those radiating from the medial depression, deep and obvious; frontal process triangular, the tip visible from above; ocelli well developed, lateral triads high, almost pyramidal, median ocular tubercle also high, without median groove, instead with some large tubercles.

Chelicera: with a few large and several small granules anterodorsally; with typical phrynichid dentition, only one external tooth opposite the space between internal teeth 2 and 3, though closer to 2 than to 3; fang with three large and one small teeth, internal surface posteriorly with a loose group of small setae, with a distinct groove behind the compound slit sense organs at the base of the fang, and with some folds behind the external compound slit sense organ.

Pedipalp: coarsely granular; trochanter with one ventral and one anterior spine and numerous large tubercles; femur with five primary spines dorsally, spine F3 smaller than F2 and F4 and closer to F4 than to F2, with five spines ventrally; tibia with four spines dorsally (spine 5 min), spine 3 shorter than one-fourth of spine 1 or 2, with five spines ventrally, spine III, IV, and V minute; pedipalps grow allometrically and exhibit little sexual dimorphism, tibia of male 1.9 times carapace length, of female 1.6 times carapace length.

Antenniform legs: 28 tibial and 65 tarsal articles.

Walking legs: carapace:femur 2 ratio 0.5–0.6; carapace:tibia 4 ratio 0.3–0.4; basitibia 1 2.6 times longer than basitibia 2; basitibia 2 6–7.0 times longer than wide.

Trichobothria: series *sbc* with 3 (occasionally 2) trichobothria; *bf* and *bc* almost level, *nbf* farther down, uppermost trichobothrium of series *sbc* higher than *bf* and *bc*.

Sternum: tritosternum long and narrow, tetra- and pentasternum flat, thickened around the lateral and posterior margins; setae present on the thickened margins only.

Ventral sacs: without ventral sac covers.

Genitalia: female genital operculum, posterior margin concavely curved, with a dense fringe of yellow-golden setae medially; gonopods flat, with a narrow, curved sclerotisation anteriorly; male genital operculum, posterior margin slightly concavely curved, with numerous small and a few larger, medially curved marginal setae; spermatophore organ unknown (the only ♂ available escaped and died of desiccation, leaving a shrunken and distorted spermatophore organ).

Measurements (mm), holotype ♂: total length 19; carapace length 7.2, width 12.6, distance between lateral ocelli 4.4; pedipalp tibia length 14.0, width 2.1, spine 1 4.85, spine 2 4.3, spine 3 0.9; first leg femur 23.3; second leg femur 13.5, basitibia 13.5, distitibia 7.8, basitarsus 1.3, other tarsal articles 2.3; third leg femur 13.4, basitibia 14.8, distitibia 8.5, basitarsus 1.3, other tarsal articles 2.4; fourth leg femur 11.9, basitibia 1 9.9, basitibia 2 3.85, ratio 2.6, width 0.55, ratio 7, distitibia 8, basitarsus 1.5, other tarsal articles 2.45; carapace:femur 2 ratio 0.53; carapace:tibia IV ratio 0.33.

Measurements (mm), ♀ exuviae: total length 20; carapace length 7.2, width 13.2, distance between lateral ocelli 4.5; pedipalp tibia length 11.7, width 1.6, spine 1 5.0, spine 2 4.7 spine 3 0.7; first leg femur 22, tibia 38.5, tarsus 39; second leg femur 12.6, basitibia 13.4, distitibia 7.9, basitarsus 1.4, other tarsal articles 2.5; third leg femur 12.5, basitibia 13.6, distitibia 8.3, basitarsus 1.6, other tarsal articles 2.8; fourth leg femur 11.9, basitibia 1 9.4, basitibia 2 3.5, ratio 2.6, width 0.5, ratio 6.7, distitibia 7; basitarsus 1.5, other tarsal articles 2.8; carapace:femur ratio 2 0.6; carapace:tibia IV ratio 0.36.

Distribution

D. sylviae n. sp. is recorded from central-northern Namibia, west of the Kalahari sand system and east of the western escarpment, and probably also occurs in southern Angola (Fig. 11).

Ecology

D. sylviae n. sp. inhabits a region of arid to semi-arid savanna and spends most of its time underground, in caves or deep rock crevices and fissures, only appearing in the open after heavy rain. Therefore, although the species is widely distributed in Namibia, it is seldom seen. Most specimens contained in the collection of the National Museum of Namibia were captured during house-building or road construction.

Damon variegatus (Perty, 1834)

Phrynus variegatus Perty, 1834, p. 200, pl. XXXIX, Fig. 10. – de Lamarck (1838, p. 118); Koch (1840,

pp. 10–11, Fig. 599); Gervais (1844, pp. 5–6); Butler (1873, p. 118, pl. VI, Fig. 4 misidentification?); Butler (1879, p. 315).

Damon variegatus (Perty, 1834). – Koch (1850, p. 81); Kraepelin (1895, pp. 18–19 part, Fig. 9); Kraepelin (1899, pp. 239–240 part); Kraepelin (1901, p. 264); Börner (1904, p. 5, Figs. 5, 88–89, 91); Kraepelin (1913, p. 188 part); de Mello-Leitão (1931, pp. 38–39, Fig. 16); Werner (1934, p. 472 part, Figs. 21b, 50, 108); Fage (1939, p. 108 part, Fig. 6 part); Lawrence (1949, pp. 1, 2, 4–10 part, Figs. 1 part, 2c–d, 3a–b, 4a–c, 5a–d, 6a–b); Fage (1951, pp. 12–13 part); Roewer (1952, p. 26); Fage (1954, pp. 180–181 part, Fig. 2 part); Lawrence (1954, pp. 168–169); Lawrence (1955, p. 260 part); Lawrence (1958, Fig. 1e); Alexander (1962a, pp. 380–382, Fig. 2); Alexander (1962b, pp. 25–36 part, Figs. 2a–c, 3d, 5); Lawrence (1964, p. 39); Lawrence (1967, p. 86); Cloudsley-Thompson (1968, pp. 156, 159); Kaestner (1968, p. 123); Besch (1969, p. 730); Lawrence (1969, pp. 82, 86 part); Schaller (1971, p. 425); Delle Cave and Simonetta (1975, pp. 157–160 misidentification?); Cloudsley-Thompson (1978, p. 188); Newlands (1978, pp. 691–693 part, Fig. 1 part); Schaller (1979, pl. 10.II, Fig. 5); Weygoldt (1996a, Fig. 8); Weygoldt (1999a, pp. 35–37 part, Figs. 62–63, 76–77, 80 part); Weygoldt (1999b, pp. 61, 63); Weygoldt (2000a, Figs. 155 part, 263–264, 293 part); Weygoldt (2000b, pp. 342–343 part, 345, 346 part, Figs. 1, 11 part, 12–13); Harvey (2003, pp. 13–14 part).

Nanodamon cinctipes Pocock, 1894, pp. 293–294. – Synonymised by Kraepelin (1899, p. 239).

Type material

Originally, but mistakenly Amazon River (''Amazon flumen''). Neotype (designated by Weygoldt 1999a): DEM. REP. CONGO: Katanga Prov.: Albertville [Kalémié, 05°57′S 29°12′E], xii.1918, R. Mayne, 1 ♂ (MRAC 004.539).

Additional material examined

BOTSWANA: Central District: Swaneng Hill [Swanend, 22°26′S 26°50′E], Serowe, 20.viii.1978, 1 ♀ (ZMUC); Tonota [21°29′S 27°29′E], Shashe River School, 1970–1971, D. Carmichael, under leaf litter, 1 ♂ (MCZ). DEM. REP. CONGO: Katanga Prov.: Albertville [Kalémié, 05°57′S 29°12′E], J.J. Verhoustraete, 1 ♀ (MRAC 134.180), 1959, J.J. Verhoustraete, 1 ♀ [ovigerous] (MRAC 115.069); Albertville [Kalémié], Lubunduye [05°59′S 29°11′E], 1936, Hässli, 1 ♂ (MRAC 23.691); Bassin de la Lukuga [05°40′S 26°55′E], 14.vii.1934, De Saeger, 1 ♀ [ovigerous] (MRAC 23.695); Funda Biabo [09°50′S 25°33′E], L. Charliers, 1 ♀ (MRAC 4.535); Kabalo [06°03′S 26°55′E], H. Schouteden, 1 ♂ (MRAC 23.694); Kiamba [07°20′S 28°01′E], Muarungu [07°42′S 30°00′E], iii.1927, Q. Bayet, (MRAC 004.517–4.531); Kiambi [07°19′S 28°01′E], 10–15.v.1931, G.F. de Witte, 1 ♂ (MRAC 23.698); Kina [07°21′S 25°34′E], 1933, R.P. Stocky, 1 exempl. (MRAC 23.696); Lukonzolwa [Lukonzalwa, 08°47′S 28°38′E], 20.xi.1911, Dr. Stappers, 1 ♀ (MRAC 4.532); Mwanza [08°56′S 26°12′E], v.1927, Mission catholique, 1 ♂ (MRAC 4.534); Mwema [08°13′S 27°28′E], vii.1927, A. Bayet, 10 exempl. (MRAC 023.700–710); Riv. Lukuga [05°40′S 26°55′E], 1918, Dr. Gerard, 1 ♀ [ovigerous] (MRAC 4.536); Sankisia [09°24′S 25°48′E], 1911, Dr. Rodhain, 1 ♂ (MRAC 23.693). Parc National Upemba: Kaswabilenga, riv. Lufira [08°51′S 26°43′E], x.1947, G.F. de Witte, 680 m, 29 exempl. (MRAC 114.079); Kaziba, affl. g. Senze et sous-affl. dr. Lufira [09°10′S 26°45′E], 17.ii.1948, G. F. de Witte, 1140 m, 35 exempl. (MRAC 114.084); Lusinga (Colline) [08°56′S 27°12′E], 12.xii.1947, G. F. de Witte, 1800 m, 13 exempl. (MRAC 114.085); Munoi, bifurcation riv. Lupiala, affl. dr. Lufira [08°45′S 26°44′E], 31.v–1.vi.1948, G. F. de Witte, 890 m, 1 ♂ 2 ♀ [1 ovigerous] (MRAC 114.087). North Kivu Prov.: Ituri Forest [01°51′N 29°58′E], Mr. Barnes, 1 ♀ (BMNH 1922.12.23.1). MOZAMBIQUE: 1 ♀ (MHNG); Portuguese East Africa, A. Berger, 1 ♀, dissected (AMNH). Inhambane Prov.: Manbone [Mambone, 21°01′S 35°01′E], viii.1971, E.N. Kjellesvig-Waering, 2 ♂ (FMNH); Panda [24°04′S 34°44′E], 17.iv.1971, E.N. Kjellesvig-Waering, 1 ♀ (FMNH). NAMIBIA: Caprivi Region: Katima Mulilo District: Ngoma bridge [17°53′S 24°43′E], 20.viii.1974, C.H.G. Schlenwein, 1 ♂ (NMNW 21076). SOUTH AFRICA: Transvaal, 1890, 1 ♂ (ZMUC). Limpopo Prov.: Messina District: Messina Nature Reserve: Hunter's camp (Farm Prinzenhage 47) [22°24′S 30°02′E], L. Prendini & K.M.A. Prendini, xii.1991, 1 ♂ (SMNS), 6.i.2000, L. Prendini, E. Scott & J. Scott, 1 ad. (AMCC 124725). Phalaborwa District: Hoedspruit [24°21′S 30°58′E], 4.vii.1999, A. Leroy, 3 ♂ 4 ♀ several juv. (SMNS), 3 ♂ 2 ♀ (Universität Freiburg), 1 ad. (AMCC 124727); Ingwelala Game Reserve [24°02′S 31°30′E], v.1990, R. & C. Dehning, 1 ♂ (AMNH). Pietersburg District: Farm Amsterdam, Dendron [23°23′S 29°19′E], J. Viljoen, on ground, 1 ♂ 5 ♀ (NCAP 77/193), xii.1969, J. Viljoen, on ground, 1 ♂ 1 ♀ [ovigerous] 1 juv. (NCAP 94/530), ix.1970, J. Viljoen, on ground, 2 ♀ (NCAP 77/183), 2.ii.1971, J. Viljoen, on ground, 1 ♂ (NCAP 78/109). Soutpansberg District: Medike, Sand River valley [22°59′S 29°37′E], Soutpansberg, 10–11.v.1999, P. Weygoldt, 1 ad., 19 juv. (AMCC 124728), 11.v.1999, P. & S. Weygoldt, 4 ♂ 6 ♀ several juv. (SMNS). Kruger National Park: Punda Milia Camp [22°41′S 31°01′E], 8.v.1968, J.A. & S. Slater, R.T. Schuh, 1 ♂, dissected (AMNH). Mpumalanga Prov.: Pilgrim's Rest District: Blyde River Canyon Nature Reserve: Blyderivierspoort Dam, Peninsula trail [24°33′S 30°48′E], 13.vii.2000, L. Prendini, M. MacFarlane & K.M.A. Prendini, 1 ad. (AMCC 124726). SWAZILAND: Mlawula Nature Reserve: Croc Pool

[26°17′20″S 31°57′46″E], 3.iv.2001, L. Prendini, G. Giribet & R. Boycott, mixed bushveld at base of western slopes of Lebombo Mountains, under stones and in crevices, 1 ♀ 1 subad. ♂ 2 juv. (AMNH), 1 juv. (AMCC 124729); Sara Camp [26°11′44″S 31°59′24″E], 2.iv.2001, L. Prendini, G. Giribet & R. Boycott, 188 m, mixed bushveld on rocky hill, under tree bark and in rock crevices, 1 ♀ 1 subad. ♀ 2 juv. (AMNH). TANZANIA: ex pet trade, acqu. 12.xii.1998, P. Weygoldt, 1 ♀ (AMCC 124730), 1 ♀ several juv. (SMNS). Rukwa Region: Kirando [07°25′S 30°36′E], 23.x.1926, Dr. C. Christy, 1 ♂ (BMNH 1928.4.24.11). ZAMBIA: Luapula Prov.: Lake Mweru Wantipa [08°42′S 29°46′E], iii.1945, P.D.L. Guilbride, 1 ♀ (BMNH 1946.12.31.271). ZIMBABWE: 30.xi.1989, J. Rechter, probably from wood, 1 ♂ (NMNW 21084), 29.vi.1991, T. Mosterd, between bark of tree, 2 ♂ (NCAP 91/1002), beneath bark of tree, 1 ♂ (NCAP 91/663). Mashonaland West Prov.: Nuffield Kariba Research Station, Sinamwenda [17°09′S 27°49′E], Lake Kariba, 11.ix.1969, J.P. Loveridge, in laboratory, 1 ♂ (NMSA); Sinamwenda [17°09′S 27°49′E], Kariba, 15.iv.1969, P.R. Alp, in laboratory, 1 ♂ 1 ♀ (NMSA); U.C.R.N., Sinamwenda [17°09′S 27°49′E], 27.v.1970, 1 ♀ (NMSA).

Dubious records: SOUTH AFRICA: Gauteng Prov.: Pretoria District: Pretoria [25°45′S 28°10′E], xi.1971, Mrs. A. Kruger, 1 ♀, dissected (AMNH). Sudan: Fluß Sedith, Palme, 1 ♂ (NHMW 1439).

Diagnosis

A medium to large (up to 30 mm) *Damon* species, distinguished from *D. gracilis* by its strong and stout pedipalps; from the similar *D. annulatipes* and *D. sylviae* n. sp. by its larger size, greater number of antenniform leg segments, and greater number of trichobothria in series *sbc*; and from *D. diadema* by the presence of only one large ventral spine on the pedipalp trochanter. It shares the presence of a well-developed brood pouch with *D. gracilis* and *D. sylviae* n. sp.

Description

Colour in life (Hoedspruit): Pedipalps almost black; tarsus, especially in small specimens, reddish; carapace blackish with light brown patches along lateral and posterior margins, and light brown, curved streaks radiating from the central depression; tergites blackish with light brown, occasionally reddish spots surrounding the muscle depressions, and light brown caudal markings; walking leg femora distinctly annulated, dark greyish-brown, each with two light brown annulae; tibiae uniformly brown.

Colour in ethanol (Hoedspruit): The distinct colour pattern is retained in ethanol, although the individual hues may fade somewhat.

Colour in life (*Medike*): Although juveniles and young specimens display a pattern similar to the specimens from Hoedspruit, the pattern is increasingly blurred in adults and, especially, in large specimens; pedipalps blackish; carapace dull brownish; tergites cream-coloured to brownish, the anterior portion slightly darker; leg femora also cream-coloured to brownish, annulations nearly completely blurred.

Colour in ethanol (*Medike*): Dull reddish-brown; the original pattern of the carapace and tergites is revived in some ethanol specimens.

Colour in life (*Tanzania*): Pedipalps blackish; carapace blackish with faint reddish-brown markings at the posterior and lateral margins; tergites dark-brown anteriorly, fading to reddish-brown posteriorly and close to the muscle depressions; walking leg femora brown, each with two slightly lighter annulations; tibiae reddish-brown; pattern more distinct in juveniles.

Colour in ethanol (*Tanzania*): Pattern similar to that in life, but much more lightly coloured, faded.

Carapace: 1.6–1.7 times wider than long; coarsely granular, with large, flat, rounded and smooth, densely packed granules, many bearing a seta at their anterior margin; anterior granules form almost transverse rows close to the midline; frontal process triangular, pointed, the tip visible from above; lateral ocelli large, well developed, median ocular tubercle large, rounded, with shallow longitudinal groove, smooth with very few, small elevations.

Chelicera: With large granules anteriorly; with typical phrynichid dentition, only one sharp external tooth opposite the space between internal teeth 2 and 3; fang with three to four large and one or two small teeth, medial or internal surface with an irregular group of small setae.

Pedipalps: trochanter with one ventral, one anterior and two small dorsal spines, and numerous spinelets or large tubercles, many bearing a seta; femur also densely covered by large tubercles, with up to six spines dorsally, spine F3 about midway between F2 and F4, but in some specimens slightly closer to F4, as long as spine F4, with up to six spines ventrally, decreasing in length from FII to FVI, tibia also with numerous large tubercles, with four to five spines dorsally, with four to five spines ventrally, spine 3 in large adults more than half the length of spine 2 or 1, but in large specimens, in which it is less than one-fourth of spine 2, tarsus also with strong tubercles basally; cleaning brush of tarsus with 20 ventral setae; pedipalps grow allometrically with a slight sexual dimorphism, tibia in large males nearly twice carapace length.

Antenniform legs: 29–31 tibial and 67–68 tarsal articles.

Walking legs: Carapace:femur 2 ratio 0.56–0.61; carapace:tibia 4 ratio 0.4–0.46; basitibia 1 2.9–3.6 times longer than basitibia 2; basitibia 2 5.5–8.0 times longer than wide.

Trichobothria: Series *sbc* with 4 or 5 trichobothria.

Sternum: tritosternum long and narrow, tetra- and pentasternum broad, each with 2–4 setae; lateral and latero-caudal margins thickened and darker, also setose; metasternum paired.

Ventral sacs: Eversible; without ventral sac covers.

Genitalia: Female genital operculum, posterior margin concavely curved, with a few large setae exteriorly, but with more setae on the interior, dorsal margin; gonopods flat and wide, with a crescent-shaped sclerotisation anteriorly; male genital operculum posterior margin with only a slight indentation, with an irregular group of small tubercles, each carrying a thin seta, ventrally; spermatophore organ almost without dorsal sclerotisation, lobes protruding from the gonopore wide, with a thin sclerotisation separating dorsal and ventral lobes.

Measurements (mm), ♂ (Hoedspruit): Total length 23.2, carapace length 8.6, width 14.6, distance between lateral ocelli 5.6; pedipalp tibia length 15.4, width 2.2, spine 1 4.8 spine 2 4.4, spine 3 0.95; first leg femur 23, tibia 40; second leg femur 13.9, basitibia 13.1, distitibia 6.9, basitarsus 1.3, other tarsal articles 2.1; third leg femur 14.3, basitibia 13.9, distitibia 7, basitarsus 1.5, other tarsal articles 2.5; fourth leg femur 12.6, basitibia 1 10.2, basitibia 2 3.3, ratio 3.0, width 0.6, ratio 5.5, distitibia 6.5, basitarsus 1.4, other tarsal articles 2.5; carapace:femur 2 ratio 0.6; carapace:tibia IV ratio 0.4.

Measurements (mm), ♂ (Medike): Total length 23.2; carapace length 8.3, width 13.2, distance between lateral ocelli 5.0; pedipalp tibia length 16.5, width 2.3, spine 1 15.4, spine 2 5.2, spine 3 2.0; first leg femur 26.5, tibia 43, tarsus 45; second leg femur 14.6, basitibia 14.5, distitibia 6.45, basitarsus 1.2, other tarsal articles 2.05; third leg femur 14.9, basitibia 15, distitibia 6.6, basitarsus 1.3, other tarsal articles 2.4; fourth leg femur 12.9, basitibia 1 10.3, basitibia 2 3.5, ratio 2.9, width 0.6, ratio 5.8, distitibia 6.8, basitarsus 1.3, other tarsal articles 2.3; carapace:femur 2 ratio 0.6; carapace:tibia IV ratio 0.4.

Measurements (mm), largest ♀ (probably from Venda): Total length 29; carapace length 9.4, width 15.2, distance between lateral ocelli 5.2; pedipalp tibia length 16.4, width 2.5, spine 1 6.4, spine 2 6.0, spine 3 1.3; first leg femur 24.5, tibia 42, tarsus 43; second leg femur 15.4, basitibia 13, 8, distitibia 7,4, basitarsus 1.2, other tarsal articles 2.3; third leg femur 15.3, basitibia 14.8, distitibia 7.5, basitarsus 1.3, other tarsal articles 2.4; fourth leg femur 13.5, basitibia 1 11.2, basitibia 2 3.1, ratio 3.6, width 0.45, ratio 8.0, distitibia 6.1, basitarsus 1.2, other tarsal articles 2.2; carapace:femur 2 ratio 0.6; carapace:tibia IV ratio 0.46.

Measurements (mm), ♀ (Tanzania): Total length 33.4; carapace length 7.85, width 13.2, distance between lateral ocelli 4.8; pedipalp tibia length 13.3, width 2.2, spine 1 4.8, spine 2 4.3, spine 3 1.3; first leg femur 19.8, tibia 33, tarsus 35.3; second leg femur 12.9, basitibia 11.5, distitibia 6.2, basitarsus 1, other tarsal articles 1.9; third leg femur 12.3, basitibia 12, distitibia 6.5. basitarsus 1.2, other tarsal articles 2.2; fourth leg femur 11.5, basitibia 1 9.0, basitibia 2 3.2, ratio 2.8, width 0.6, ratio 5.3, distitibia 6.2, basitarsus 1.2, other tarsal articles 2.2; carapace:femur 2 ratio 0.6; carapace:tibia IV ratio 0.4.

Distribution

Damon variegatus is widespread in southern Africa, east of the Kalahari sand system, from southern Swaziland to the Democratic Republic of Congo and western Tanzania (Fig. 11). It has been recorded from Botswana, the Democratic Republic of Congo, Malawi, Mozambique, Namibia, South Africa, Swaziland, Tanzania, Zambia, and Zimbabwe. Isolated records from Eritrea (Delle Cave and Simonetta 1975) and Sudan (Kraepelin 1895) are either erroneous or referable to another species.

Ecology

Damon variegatus inhabits a region of semi-arid to mesic savanna. During the day, it shelters in rock crevices, fissures and spaces behind the peeling bark of trees, but at night it is commonly found on the surface.

Appendix A

Terminal taxa, codes, specimens and tissue samples used for behavioural observations and cladistic analyses on the *D. variegatus* group (Amblypygi). Tissue samples are deposited in the AMCC at the American Museum of Natural History, New York (AMNH).

1. *Xerophrynus machadoi* (Xmac): Namibia: Erongo Reg.: Omaruru Distr.: Amis valley [21°11′S 14°28′E], Brandberg, 24.iv.1999, P. Weygoldt, 1 ad. (AMCC 124710). Several specimens were collected during three visits to the Brandberg. They lived for several years and grew well in captivity but never mated or reproduced.
2. *Euphrynichus bacillifer* (Ebac): Kenya: Coast Prov.: Kilifi [03°38′S 39°51′E], ca. 60 km N of Mombasa, 11.i.1995, S. Huber, 1 ad. (AMCC 124711), offspring raised in captivity. The species was reared through several generations. The specimen used was bred in captivity.
3. *Phrynichus scaber* (Psca): Seychelles: Aride Isld. [04°12′S 55°40′E], 1–3.ix.1997, P. Weygoldt, 1 ad. (AMCC 124712). Six specimens were collected and observed in captivity. Mating was observed several times (Weygoldt 1999b).
4. *Phrynichodamon scullyi* (Pscu): South Africa: Northern Cape Prov.: Calvinia Distr.: Farm Klippe Rivier 630, 1.5 km from Nieuwoudtville on R27 to Vanrhynsdorp [31°22.226′S 19°05.521′E], 18.ii.2003,

L. Prendini & E. Scott, sandstone outcrops, arid fynbos next to seep, under rock on rock, 1 ad. (AMCC 124713). Behavioural studies were not conducted on this specimen, but on others collected in the Cederberg (Western Cape Prov.).

5. *Musicodamon atlanteus* (Matl): Morocco: Tata Prov.: Tata [29°45′N 07°59′W], 11–12.vii.1999, S. Huber, 1 ad. (AMCC 124714). Several specimens were collected during this and two further visits. Successful mating in captivity occurred twice, reproduction once (Weygoldt 2002). The specimens used were from the first visit.
6. *Damon medius* (Dmed): Senegal: Ziguinchor Reg.: near Ziguinchor [12°34′N 16°16′W], vii.1997, S. Huber, under tree bark in hotel garden, 13 juv. (AMCC 124715). Two males and three females were collected in Senegal and Gambia. They readily mated and reproduced in captivity. Many spermatophores were recovered. The specimens used were bred in captivity.
7. *Damon diadema* 1 (Ddi1): Kenya: Coast Prov.: Shimoni Cave [Shimoni, 04°39′S 39°23′E], viii.1992, P. Weygoldt, 1 ad. [AMCC 124716]. Several specimens were collected in the Shimoni Cave, S of Mombasa. The species was reared through several generations. Two fresh and six emptied spermatophores were preserved.
8. *Damon diadema* 2 (Ddi2): Tanzania: acquired from T. Gearheart, 5.ix.2001, 1 ad. (AMCC 124717). Behavioural studies were not conducted on this specimen.
9. *Damon annulatipes* 1 (Dan1): South Africa: KwaZulu-Natal Prov.: Pietermaritzburg Distr.: Natal Botanical Gardens, Pietermaritzburg [29°36′09″S 30°20′47″E], 5–8.iv.2001, L. Prendini & G. Giribet, 1228 m, Afromontane forest, in rock crevices at top of hill, 2 ♂, 2 ♀, 1 subad. ♂ (AMNH), 1 ad. (AMCC 124718). Behavioural studies were not conducted on these specimens.
10. *Damon annulatipes* 2 (Dan2): South Africa: KwaZulu-Natal Prov.: Hlabisa Distr.: Charter's Creek, Lake St. Lucia [28°12′S 32°26′E], i.1997, L. Prendini & K.M.A. Prendini, 15 juv. (AMCC 124719). Several adult specimens were collected from the vicinity of Charter's Creek on the western shore of Lake St. Lucia, and sent to Freiburg. These readily mated and reproduced in captivity.
11. *Damon annulatipes* 3 (Dan3): Swaziland: Malolotja Nature Reserve (northern section): Mgwayiza Forest and nearby grassland [25°59′49″S 31°07′08″E], 1.iv.2001, L. Prendini, G. Giribet & R. Boycott, 1138 m, under stones on hillside, 1 ♂, 1 ♀ (AMNH), 4 juv. (AMCC 124720). Behavioural studies were not conducted on these specimens.
12. *Damon gracilis* 1 (Dgr1): Namibia: Kunene Reg.: Opuwo Distr.: Omabsu, ca. 38 km N of Opuwo [17°49′S 13°45′E], 20.iv.1996, P. Weygoldt, 1 ad. (AMCC 124721). Five specimens were collected. They readily mated and reproduced in captivity and were easily cultured. A few breeding specimens are still in the possession of several hobby and professional arachnologists in Germany. The specimens used here were bred in captivity.
13. *Damon gracilis* 2 (Dgr2): Data and comments as above, 1 ad. (AMCC 124722).
14. *Damon sylviae* 1 (Dsy1): Namibia: Otjozondjupa Reg.: Grootfontein Distr.: Obab Cave, Farm Obab 856 [19°10′S 17°07′E], 27.iv.1999, S. Weygoldt, in cave, 1 ad. (AMCC 124723). Four females and one male were collected in a small cave on the Farm Obab 856 near the border of Etosha National Park. The male was found with only one pedipalp, but readily mated with the females in spite of this. It was accidentally killed after two matings. One fresh and one emptied spermatophore were studied.
15. *Damon sylviae* 2 (Dsy2): Namibia: Khomas Reg.: Windhoek Distr.: Farm Christirina 259 [23°24′S 18°00′E], J. Henschel, 1 ♀ (AMCC 124724). The sole female collected at Christirina mated with the male from Obab Cave.
16. *Damon variegatus* 1 (Dva1): South Africa: Limpopo Prov.: Messina Distr.: Messina Nature Reserve: Hunter's camp (Farm Prinzenhage 47) [22°24′S 30°02′E], xii.1991, L. Prendini & K.M.A. Prendini, 1 ♂ (SMNS), 6.i.2000, L. Prendini, E. Scott & J. Scott, 1 ad. (AMCC 124725). Behavioural studies were not conducted on these specimens.
17. *Damon variegatus* 2 (Dva2): South Africa: Mpumalanga Prov.: Pilgrim's Rest Distr.: Blyde River Canyon Nature Reserve: Blyderivierspoort Dam, Peninsula trail [24°33′S 30°48′E], 13.vii.2000, L. Prendini, M. MacFarlane & K.M.A. Prendini, 1 ad. (AMCC 124726). Behavioural studies were not conducted on this specimen.
18. *Damon variegatus* 3 (Dva3): South Africa: Mpumalanga Prov.: Phalaborwa Distr.: Hoedspruit [24°21′S 30°58′E], 4.vii.1999, A. Leroy, 3 ♂, 4 ♀, several juv. (SMNS), 3 ♂, 2 ♀ (Univ. Freiburg), 1 ad. (AMCC 124727). Several specimens, mostly immatures, were collected close to the border of Kruger National Park, near Hoedspruit. All specimens survived to adulthood and several are still alive. They mated whenever given the opportunity, and most of the females laid eggs subsequently. Three fresh and seven emptied spermatopohores were studied.
19. *Damon variegatus* 4 (Dva4): South Africa: Limpopo Prov.: Soutpansberg Distr.: Medike, Sand River valley [22°59′S 29°37′E], Soutpansberg, 10–11.v. 1999, P. Weygoldt, 1 ad., 19 juv. (AMCC 124728), 11.v.1999, P. & S. Weygoldt, 4 ♂, 6 ♀, several juv. (SMNS). About ten specimens, most of them immatures and small adults, were collected under

stones near Medike in the Sand River Valley, Soutpansberg. All specimens were reared to adulthood and a few are still alive. They mated whenever given the opportunity, and subsequently most females laid eggs. Four fresh and five emptied spermatophores were available.

20. *Damon variegatus* 5 (Dva5): Swaziland: Mlawula Nature Reserve: Croc Pool [26°17′20″S 31°57′46″E], 3.iv.2001, L. Prendini, G. Giribet & R. Boycott, mixed bushveld at base of western slopes of Lebombo Mts., under stones and in crevices, 1 ♀, 1 subad. ♂, 2 juv. (AMNH), 1 juv. (AMCC 124729). Behavioural studies were not conducted on these specimens.
21. *Damon variegatus* 6 (Dva6): Tanzania: acquired from pet store, 12.xii.1998, 1 ♀ (AMCC 124730). An ovigerous female was obtained from a German pet shop. The exact origin is unknown but believed to be in Tanzania. The offspring of the female were reared to adulthood but only one male survived. This male mated once with his mother and one emptied spermatophore was recovered.

Acknowledgements

PW thanks Colin Craig and Dieter Morsbach (Ministry of Environment and Tourism, Government of Namibia) for permission to collect and export Amblypygi from Namibia during 1999 (permit application process kindly facilitated by Eryn Griffin, formerly of the National Museum of Namibia, Windhoek); John Nevill (Ministry of Foreign Affairs, Planning and Environment, Government of the Seychelles) and Terence Coopoosamy (Seychelles Bureau of Standards) for permission to collect and export Amblypygi from the Seychelles during 1997 (permit to visit the island Aride kindly facilitated by Adrian Skerret). LP thanks Morris Mtsambiwa (Swaziland National Trust Commission) for permission to collect and export Amblypygi from Swaziland during 2001 (permit application process kindly facilitated by Richard Boycott). LP also thanks the following South African provincial nature conservation departments for permission to collect Amblypygi in the reserves under their jurisdiction during the period 1997–2003: KwaZulu-Natal Nature Conservation Service (formerly Natal Parks Board); Mpumalanga Parks Board; Northern Province Environmental Affairs. For congenial company on the field trips during which Amblypygi were collected, PW thanks Mike and Eryn Griffin, Norman Larsen, John and Astri Leroy, and Pat Matyot; LP thanks Richard Boycott, Gonzalo Giribet, Marco MacFarlane, Ken Prendini, Elizabeth Scott, and Jane Scott. Additional thanks are extended to Louisa and Eric van der Merwe for hospitality while visiting Farm Obab 856, to Retha and Ian Gaigher for hospitality while visiting Medike, Soutpansberg, and to Richard Boycott for hospitality while visiting the Malolotja and Mlawula Nature Reserves. Further specimens and tissue samples for DNA isolation were generously provided by Todd Gearheart, Astri Leroy, Johannes Henschel and Siegfried Huber. We gratefully acknowledge the assistance of the following people in loaning specimens from their institutions or allowing access to the collections during various visits: Norman Platnick, Lou Sorkin (AMNH); Paul Hillyard and Janet Beccaloni (BMNH); Petra Sierwald, Phil Parrillo (FMNH); Herb Levi (MCZ); Bernd Hauser (MHNG); Rudy Jocqué (MRAC); Ansie Dippenaar-Schoeman (NCAP); Jürgen Gruber (NHMW); Eryn Griffin (NMNW); Michelle Hamer (NMSA); Margie Cochrane (SAMC); Wolfgang Schawaller (SMNS); Jason Dunlop (ZMHB); Henrik Enghoff and Nikolaj Scharff (ZMUC). We thank Anne Keller and Diana Pietri for generating the DNA sequence data, Steve Thurston for preparing the figures and cover illustration, Jason Dunlop and an anonymous reviewer for comments on the manuscript. Some of the fieldwork and sequencing for this project was supported by National Science Foundation grant EAR-0228699 to W.C. Wheeler, J. Coddington, G. Hormiga, L. Prendini, P. Sierwald, M. Arnedo, J. Bond, P. Goloboff, C. Grismado, C.G. Griswold, C. Hayashi, M. Hedin, W. Maddison, J. Miller, M.J. Ramírez, N. Scharff, and C. Vink.

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