

Aops oncodactylus, gen. et sp. nov., the first troglobitic urodacid (Urodacidae:Scorpiones), with a re-assessment of cavernicolous, troglobitic and troglomorphic scorpions

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Abstract. We describe a new genus and species of troglomorphic scorpion from Ledge Cave, Barrow Island, off the north-western coast of Western Australia. This troglobite scorpion was initially difficult to place within the superfamily Scorpionoidea Latreille on account of its unusual morphology. Based on cladistic analysis, we demonstrate that this scorpion is phylogenetically most closely related to the endemic Australian genus *Urodacus* Peters (Urodacidae Pocock). The new taxon, named *Aops oncodactylus*, gen. et sp. nov., is the first troglobitic urodacid and the first troglobitic scorpion recorded from continental Australia. In light of this discovery, we re-assess the known diversity of troglobitic scorpions and the troglomorphic adaptations (troglomorphies) of cavernicolous scorpions. A distinction is recognised between the exclusive occurrence in cavernicolous habitats and the presence of troglomorphies, which are exhibited by some endogean (humicolous) scorpions. The definition of troglobitic scorpions is limited to species that are both restricted to cavernicolous habitats and exhibit pronounced troglomorphies. Only 20 scorpion species meet both criteria and are considered unequivocally troglobitic according to this definition.

Additional keywords: Australia, cladistics, evolution, morphology, phylogeny, taxonomy.

Introduction

Troglobitic scorpions are rarely encountered. The first species was described in the late 1960s (Mitchell 1968) and, in the past 20 years, only seven unequivocally troglobitic species have been added to the previous world total of 13 (Lourenço and Francke 1985), not all of which are unequivocally troglobitic (Table 1). Although fewer troglobitic scorpion species have been discovered in recent years, the number of scorpion families containing troglobitic species has increased, and recent contributions (Volschenk *et al.* 2001; Vignoli and Kovařík 2003; Levy 2007) added three families to the list of those with troglobitic representatives. A fourth family is added in the present contribution.

During a biotic survey of subterranean environments on Barrow Island (Humphreys 2001), off the north-western coast of Western Australia (Fig. 1), a single, juvenile specimen of a new scorpion species, exhibiting remarkable levels of troglomorphism, including complete absence of ocelli and pigmentation, as well as attenuation of the legs and pedipalps (Figs 2, 3), was discovered in Ledge Cave. Although immediately recognisable as a member of the largely Gondwanan superfamily Scorpionoidea Latreille, the troglobite could not, initially, be assigned unequivocally to a family or genus on account of the absence of several crucial character systems (especially ocelli, carapacial sutures, metasomal carinae, shape and setation of the tarsi, and hemispermatophore).

Several characters suggested that the new species was phylogenetically most closely related to two scorpionoid genera, *Urodacus* Peters (Urodacidae Pocock), comprising 20 described species endemic to Australia (Koch 1977; Fet 2000; Volschenk *et al.* 2000), and *Heteroscorpion* Kraepelin (Heteroscorpionidae Kraepelin), comprising five species endemic to Madagascar (Lourenço 1996; Lourenço and Goodman 2002, 2004, 2006; Lourenço *et al.* 2003). For example, the pedipalp chela fingers exhibit more than two primary rows of denticles, accessory trichobothria are present in the *e* and *v* series of the pedipalp patella, and the *V* series of the pedipalp chela, trichobothrium *db* is located dorsally on the fixed finger of the pedipalp chela, and trichobothria *Db*, *Dt*, and *Est* are respectively located externally, proximally, and distally on the chela manus (Prendini 2000). Besides its geographical origin, additional characters (e.g. the presence of accessory trichobothria in the *E* series of the chela manus), suggested a closer relationship to *Urodacus* than to *Heteroscorpion*. The troglobite lacked several putative synapomorphies of both genera, e.g. two pairs of lateral ocelli and a single ventromedian carina on metasomal segments I–IV (Prendini 2000), which might shed light on its phylogenetic relationship with *Urodacus* and *Heteroscorpion* and, in turn, on the respective phylogenetic positions of these genera, a subject of increasing contention (Stockwell 1989;

Table 1. Species of troglobitic and troglomorphic scorpions, tabulated with family ranking, troglomorphy, and relevant references to troglobitic habit or morphology
Higher classification follows Prendini and Wheeler (2005)

	Country	Habitat	Median ocelli	Lateral ocelli	Pigmentation, sclerotisation	Attenuation legs, pedipalps	Proximal pedal spurs	Retrolateral pedal spurs	Telson vesicle	Troglobite	References
Akravidae											
<i>Akrav israhani</i> Levy	Israel	Cave	Absent	Absent	Absent	Present	Present	Present	Unmodified	Yes	1
Buthidae											
<i>Tityus demangei</i> Lourenço	Ecuador	Cave	Unmodified	Unmodified	Reduced	Present	Present	Present	Unmodified	No	2
<i>Troglophopaliurus translucidus</i> Lourenço <i>et al.</i>	Brazil	Cave	Reduced	Reduced	Reduced	Present	Present	Present	Unmodified	Yes	3
<i>Trogloityobuthus gracilis</i> (Fage)	Madagascar	Cave	Present	Present	Reduced	Present	Present	Present	Large	Perhaps	4, 5
Chactidae											
<i>Brotochactas trezzii</i> (Vignoli & Kovarik)	Venezuela	Under stone ^B	Reduced	Present	Reduced	Partial	Absent	Absent	Large	Perhaps	6
Chaerilidae											
<i>Chaerilus cavemicola</i> Pocock	Indonesia	Cave	Present ^C	Present	Well developed	Present	Present	Present	Large	Probably not	7, 8
<i>Chaerilus chapmani</i> Vachon & Lourenço ^A	Malaysia	Cave	Unmodified	Unmodified	Reduced	Present	Present	Present	Unmodified	Yes	9, 10, 11, 8
<i>Chaerilus sabinae</i> Lourenço	Indonesia	Cave	Absent	Absent	Absent	Present	Present	Present	Large	Yes	11, 8
Diplocentridae											
<i>Diplocentrus actian</i> Armas & Palacios-Vargas	México	Cave	Absent	Reduced	Absent	Present	Present	Absent	Unmodified	Yes	12
<i>Diplocentrus anophthalmus</i> Francke ^A	México	Cave	Absent	Reduced	Absent	Present	Present	Absent	Large	Yes	13, 10, 12
<i>Diplocentrus cueva</i> Francke ^A	México	Cave	Reduced	Unmodified	Reduced	Present	Present	Absent	Unmodified	Yes	14, 10
<i>Diplocentrus magnus</i> Beutelspacher & López-Fornet	México	Cave	Unmodified	Unmodified	Well developed	Absent	Present	Absent	Unmodified	No	15
<i>Diplocentrus mitchelli</i> Francke ^A	México	Cave	Unmodified	Unmodified	Absent ^D	Absent	Present	Absent	Unmodified	Probably not	13, 10
<i>Heteronebo clareae</i> Armas	Navassa I. (USA)	Cave ^E	Reduced	Unmodified	Absent	Absent	Present	Absent	Large	Probably not	16
Euscorpidae											
<i>Troglocormus ciegi</i> Francke ^A	México	Cave	Absent	Reduced	Reduced	Present	Present	Present	Large	Yes	17, 10, 18
<i>Troglocormus willisi</i> Francke ^A	México	Cave	Absent	Reduced	Reduced	Present	Present	Present	Large	Yes	17, 10, 18
Liobelidae											
<i>Liobelus polisorum</i> Volschenk <i>et al.</i> ^A	Christmas I. (Australia)	Cave	Reduced or absent	Reduced	Reduced	Present	Present	Absent	Large	Yes	19, 20
Superstitionidae											
<i>Alacran tartarus</i> Mitchell ^A	México	Cave	Absent	Absent	Absent	Present	Present	Absent	Large	Yes	21, 10
<i>Sotanochactas ellioti</i> (Mitchell) ^A	México	Cave	Absent	Absent	Absent	Present	Absent	Absent	Unmodified	Yes	22, 23, 24, 10, 25
<i>Tiphlochactas cavicola</i> Francke ^A	México	Cave	Absent	Absent	Absent	Present	Absent	Absent	Large	Yes	10, 25, 26
<i>Tiphlochactas granulatus</i> Sissom & Cokendolpher ^A	México	Cave	Absent	Absent	Absent	Present	Absent	Absent	Large	Yes	26
<i>Tiphlochactas mitchelli</i> Sissom ^A	México	Leaf litter	Absent	Absent	Absent	Absent	Present	Absent	Large	No	27, 26
<i>Tiphlochactas reddelli</i> Mitchell ^A	México	Cave	Absent	Absent	Absent	Present	Present	Absent	Large	Yes	28, 22, 24, 10, 26
<i>Tiphlochactas rhodasi</i> Mitchell ^A	México	Cave	Absent	Absent	Absent	Present	Absent	Absent	Large	Yes	28, 22, 10, 26
<i>Tiphlochactas sylvestris</i> Mitchell & Peck ^A	México	Leaf litter	Absent	Absent	Absent	Absent	Present	Absent	Large	No	24, 27, 26

(continued next page)

Table 1. (continued)

	Country	Habitat	Median ocelli	Lateral ocelli	Pigmentation, sclerotisation	Attenuation legs, pedipalps	Pro lateral pedal spurs	Retrolateral pedal spurs	Telson vesicle	Troglobite	References
Trogloayosicidae											
<i>Belisarius xambeui</i> Simon ^A	France, Spain	Leaf litter, caves	Absent	Absent	Reduced	Partial	Present	Present	Large	No	29, 30, 31
<i>Trogloayosicus vachoni</i> Lourenço	Ecuador	Cave	Absent	Present	Absent	Absent	Present	Present	Large	Yes	2, 10
Urodacidae											
<i>Aops oncodactylus</i> gen. et sp. n.	Barrow I. (Australia)	Cave	Absent	Absent	Absent	Present	Present	Absent	Unmodified	Yes	32
Vaejovidae											
<i>Pseudouroctonus sprousei</i> Francke & Savary	México	Cave	Reduced	Reduced	Well developed	Partial	Present	Present	Large	Yes	33
<i>Uroctonus grahami</i> Gertsch & Sologlad ^A	USA	Cave	Reduced	Unmodified	Reduced	Present	Present	Present	Unmodified	Yes	34
<i>Vaejovis davidi</i> Sologlad & Fet	México	Cave	Present	Present	Well developed	Partial	Present	Present	Unmodified	Probably not	35
<i>Vaejovis gracilis</i> Gertsch & Sologlad ^A	México	Cave	Reduced	Reduced	Reduced	Present	Present	Present	Unmodified	Yes	34, 10, 36

^ASpecies for which specimens were examined during the present study (refer to Appendix 1 for material examined).^BThe holotype was collected under a stone inside a gorge, 50 m deep; the biotope was characterised as dark and extremely humid.^CPresence assumed based on presence of median ocular tubercle.^DThe holotype is an early instar juvenile specimen, hence the absence of pigmentation could be the juvenile state as observed in most other diplocentrids.^EThe habitat is described as the 'dark zone' of a vertical 'cave' ~1.2 m in diameter and only 5 m deep. The dark zone of all other caves is significantly deeper than 5 m, but given the karstic environment that it was discovered in, there is a chance it may be a troglobite.References: 1, Levy (2007); 2, Lourenço (1981); 3, Lourenço, Baptista and Giupponi (2004); 4, Fage (1946); 5, Lourenço (2000); 6, Vignoli and Kovarik (2003); 7, Pocock (1894); 8, Kovarik (2000); 9, Pocock (1893); 10, Lourenço and Francke (1985); 11, Lourenço (1995); 12, Armas and Palacios-Vargas (2002); 13, Francke (1977); 14, Francke (1978); 15, Beutelspacher and López-Forment (1991); 16, Armas (2001); 17, Francke (1981); 18, Sologlad and Sissom (2001); 19, Humphreys (2001); 20, Volschenk *et al.* (2001); 21, Francke (1982); 22, Mitchell (1971); 23, Reddell and Mitchell (1971); 24, Mitchell and Peck (1977); 25, Francke (1986); 26, Sissom and Cokendolpher (1998); 27, Sissom (1988); 28, Mitchell (1968); 29, Simon (1879); 30, Vachon (1945); 31, Auber (1959); 32, Present contribution; 33, Francke and Savary (2006); 34, Gertsch and Sologlad (1972); 35, Sologlad and Fet (2005); 36, Sissom (1986).

Prendini 2000; Soleglad and Sissom 2001; Soleglad and Fet 2003b; Coddington *et al.* 2004; Soleglad *et al.* 2005; Prendini and Wheeler 2005; Lourenço and Goodman 2006). In the present contribution, we describe the new troglobite, *Aops oncodactylus*, gen. et sp. nov., and present a cladistic analysis that confirms its phylogenetic placement as a basal urodacid (Figs 4–7).

The holotype of *A. oncodactylus* was collected from a cave that is logistically difficult to sample: the chamber in which the specimen was found can only be accessed after diving through a submerged passage (W. F. Humphreys personal communication). It is therefore unlikely that more specimens will be collected in the near future. Despite the fact that Barrow Island possesses biologically rich caves, harbouring numerous endemic taxa, it has been exploited for oil for over thirty years (Humphreys 2001). Additional exploitation for natural gas is under development. The commercial threats facing Barrow Island lend a measure of urgency to the need to describe its biota and, together with the low probability that additional specimens of this (probably endemic) troglotic scorpion will be collected in the near future, and its unique character combination, which differs from all other Australian scorpions, compelled us to describe it on the basis of a single juvenile specimen, something we would not normally consider.

We create a new genus for this species, despite acknowledging the limitations of monotypic genera (Platnick 1976), owing to its basal phylogenetic placement and the fact that it lacks many of the diagnostic character states of *Urodacus*. We are confident in the basal position of this species because our analysis included a range of *Urodacus* exemplars, representing the somatic morphological diversity in that genus, and exem-

plars of all remaining scorpionoid families as outgroup taxa. The acquisition of additional specimens, especially adult males, of *Aops* would provide additional data with which to test its position with respect to other scorpionoid genera, by permitting examination of adult carination and granulation (typically more pronounced in male scorpionoids than in females and juveniles), as well as the hemispermaphore, which includes several synapomorphies for *Urodacus* (Koch 1977). An additional, independent test of its position would be achieved by the analysis of DNA sequences, obviating the inapplicable states introduced into the morphological character matrix by its troglomorphic habitus.

No urodacid species have previously been recorded from caves. Most of the described *Urodacus* species are fossorial and occur in arid to semi-arid habitats west of the Great Dividing Range (in eastern Australia). Some species, however, e.g. *U. manicatus* (Thorell) in south-eastern Australia and *U. planimanus* Pocock in south-western Australia, inhabit mesic forests (L. E. Koch 1977). At least one species, *U. planimanus*, is lithophilous, exhibiting ecomorphological adaptations to this habitat, e.g. dorsoventrally compressed pedipalps and metasoma (Prendini 2001a). Lithophily is probably a precursor to troglomorphy. The four species of *Heteroscorpion* are also lithophilous (Lourenço 1996; Lourenço and Goodman 2002, 2004, 2006; Lourenço *et al.* 2003).

As the first troglotic urodacid and the first troglotic scorpion recorded from continental Australia, *A. oncodactylus* is an important addition to the global troglotic scorpion fauna, which prompted us to summarise the known global diversity of troglotic scorpions, to re-examine the troglomorphic adaptations (troglomorphies) of cavernicolous scorpions, and to recognise a distinction between the exclusive occurrence in cavernicolous habitats and the presence of troglomorphies, which are also exhibited by some endogean scorpions.

Materials and methods

Material examined, photography and terminology

The holotype of the new species is deposited in the Western Australian Museum (WAM). Other material examined to determine its phylogenetic placement and to study troglomorphy is listed in Appendix 1.

Habitus photographs of the holotype were taken under long-wave ultraviolet light using a Microptics ML-1000 digital imaging system (Microptics, Palmyra, VA, USA), illustrations produced using a Leica MZ6 stereo dissection microscope (Leica Microsystems, Wetzlar, Germany), fitted with a drawing tube, and a distribution map plotted with ArcView GIS Version 8.3 (ESRI, Redlands, CA, USA). Figures were subsequently prepared using CorelDraw Version 10. Measurements were taken using the ocular micrometer of a Wild M5 stereomicroscope (Wild, Heerbrugg, Switzerland).

The species description was produced with the assistance of Delta Version 1.04 (CSIRO 2000). Morphological terminology largely follows Vachon (1952), except for trichobothria, following Vachon (1967, 1974), segmentation of appendages, following Couzijn (1976) and Sissom (1990), carinae following Prendini (2000), and sternum following Soleglad and Fet (2003a).

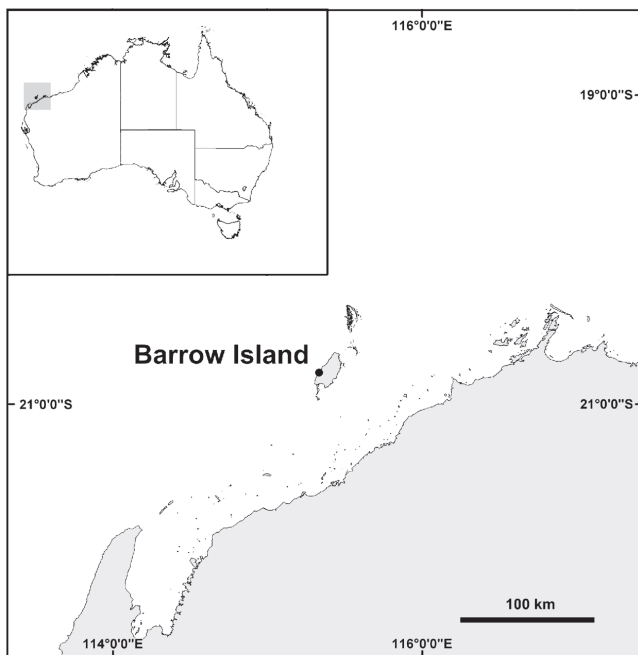


Fig. 1. North-western coastline of Australia, showing locality record for *Aops oncodactylus*, gen. et sp. nov. on Barrow Island. Inset indicating mapped area (shaded) relative to the rest of mainland Australia.

The new species was categorised according to its conservation priority. Prevailing threats to the future survival of the species were considered in recommending its assignment to an IUCN Red List Category (IUCN 2001).

Taxon sampling

The cladistic analysis presented here is based on fifteen terminal taxa (Table 2). The morphological data matrix combines characters and taxa from previous matrices for relationships among the families and genera of Scorpionoidea (Prendini 2000, 2003; Prendini *et al.* 2003), to which the new taxon and six species of *Urodacus* were added to test its phylogenetic placement. The sample of *Urodacus* species included in the analysis represents a wide range of morphological diversity within the genus, including lithophilous (*U. planimanus*) psammophilous (*U. varians* Glauert, *U. yaschenkoi* (Birula)) and pelophilous (*U. manicatus*) ecomorphotypes, thereby providing a strong test of monophyly for *Urodacus*, and for the relationship between its component species and the new taxon (Prendini 2000, 2001b).

In order to confirm that the new taxon described in this paper is a urodacid, a single exemplar species for each of the other scorpionoid families was also included. *Nebo hierichonticus* (Simon) represents Diplocentridae Pocock, *Hemiscorpius lepturus* Peters, Hemiscorpiidae Pocock, *Heteroscorpion opisthacanthoides* (Kraepelin), Heteroscorpionidae Kraepelin, *Opisthacanthus*

validus (Thorell), Liochelidae Simon, *Scorpio maurus mogadorensis* (Birula), Scorpionidae and *Lisposoma josehermana* Lamoral, Bothriuridae Simon. All except *Lisposoma* Lawrence, *Nebo* Simon and *Opisthacanthus* Peters represent the type genera of their respective families. The latter were selected in favour of the type genera because they are more basal (Prendini 2000, 2003), and thus more representative of the ancestral condition for their respective families (Prendini 2001b).

Trees were rooted using the outgroup method (Watrous and Wheeler 1981; Farris 1982; Nixon and Carpenter 1993). *Lisposoma josehermana* was selected as the primary outgroup for the analysis based on prior evidence that Bothriuridae are the sister-group of Scorpionoidea *s. str.* (Stockwell 1989; Prendini 2000, 2003). This taxon was chosen in favour of *Brandbergia* Prendini, the most basal bothriurid (Prendini 2003), because it is known from both sexes (the male of *Brandbergia* is unknown), thus reducing the number of missing entries in the analysis.

Characters

Forty-nine of the 56 characters scored in the fifteen taxa (Table 2, Appendix 2) were included in previous analyses of scorpionoid relationships (Prendini 2000, 2003; Prendini *et al.* 2003). Eight of these (characters 2, 15, 20, 27, 33, 36, 44, 47), pertinent to urodacid relationships but uninformative in the present context, have been retained in the matrix on the grounds



Figs 2, 3. *Aops oncodactylus*, gen. et sp. nov. (holotype), habitus. 2, Dorsal aspect; 3, ventral aspect. Scale bar = 10 mm.

that they contribute to its completeness and future utility, e.g. in diagnostic keys (Yeates 1992), although they were excluded from all analyses. The present analyses are thus based on 48 characters. Nine of these (characters 13, 36, 37, 38, 41, 49, 50, 56) contain missing entries for the new taxon due to the fact that the adults are unknown (hence characters of the male genitalia and secondary sexual dimorphism could not be scored) and the biology is unknown. Character 2 is polymorphic.

Thirty-seven of the informative characters are binary and eleven are multistate (Appendix 2). All multistate characters were treated as unordered, i.e. non-additive (Fitch 1971), defended by invoking the principle of indifference, which asserts that if there is no apparent reason for considering one event to be more probable than its alternatives, then all should be considered equiprobable (Wilkinson 1992).

Twelve of these characters (1, 12, 14, 15, 26, 27, 28, 29, 30, 41, 42, 48) were variously criticised by Soleglad and Fet (2003b), Fet *et al.* (2005) and Soleglad *et al.* (2005). Prendini and Wheeler (2005) responded to these and other criticisms, presented a detailed critique of the work of Soleglad, Fet and coauthors, and concluded that there is no justification for accepting either the criticisms or the results of analyses by these authors. We follow the views of Prendini and Wheeler (2005).

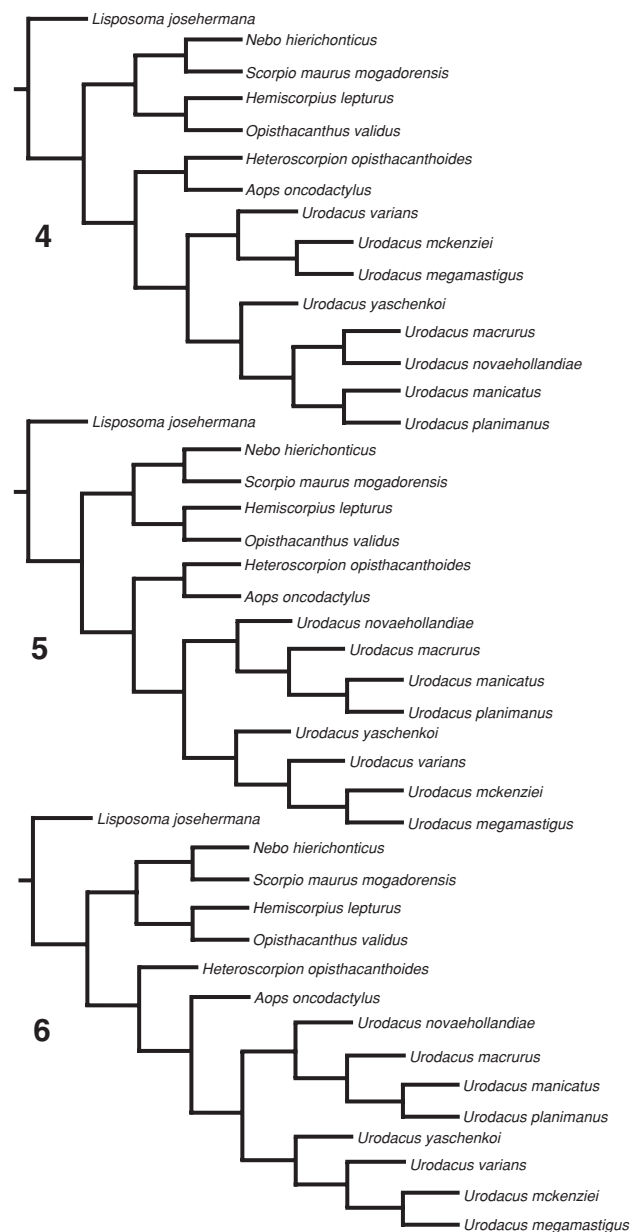
Cladistic analysis

Character data were edited and cladograms prepared using WinClada, version 1.00.08 (Nixon 2002). The eight uninformative characters noted above were excluded from all analyses. Tree statistics are calculated from phylogenetically informative characters only (Bryant 1995).

Characters were not weighted *a priori*. Analyses with equal weighting were conducted using the 'parsimony ratchet' (Nixon 1999) in NONA version 2.0 (Goloboff 1997a), according to the following command sequence: `nix = 50; hold/3; nix[10; nix-10 50 20; preceded by hold10000; hold/100; mult*100; and followed by max*;`. The 'strength' or 'factor' of the ratchet (i.e. the proportion of characters reweighted) was set to 50% (command `nix = 50;`). Fifty initial iterations of the ratchet (command `nix 50;`) were conducted. SPR branch-swapping was applied in the first ten iterations, followed by TBR branch-swapping in the remaining 40 (command `nix-10;`). Three starting trees were held in memory at each iteration (command `hold/3;`) and, every 10 iterations, one of the best trees located at that stage in the search was randomly selected for continued swapping (command `nix[10;`). When the 50 initial iterations were completed, a further 20 iterations were conducted (command `nix 50 20;`).

Implied character weighting (Goloboff 1993, 1995) was conducted to assess the effects of weighting against homoplasious characters, and the resultant topologies compared with those obtained by analysis with equal weighting. In varying the weighting regime applied to the data, we provide a 'sensitivity analysis' (Wheeler 1995), i.e. an assessment of the relative robustness of clades to different analytical parameters, in this case, method and intensity of character weighting (see Prendini 2000, 2004; Prendini *et al.* 2003). If a group is monophyletic only under a very specific combination of parameters, less confidence may be placed in the supposition that the data robustly support its monophyly than may be placed in a group that is monophyletic under a wider range and combination of parameters.

Pee-Wee version 3.0 (Goloboff 1997b) was used for analyses with implied weighting, applying the command sequence: `hold10000; hold/10; mult*100; (hold 10000 trees in memory; hold ten starting trees in memory; perform tree-bisection-reconnection (TBR) branch-swapping on 100 random addition replicates). Additional swapping on up to 1000 trees that are up to 5% longer than the shortest trees (command jump 50;) was performed to help the swapper move between multiple local`



Figs 4–6. Results of cladistic analysis of 48 morphological characters scored for nine species of Urodacidae Pocock, 1893 and six outgroup taxa (Table 2) under weighting regimes that maximised fit and minimised length (Table 3). 4, 5, Two most parsimonious trees (MPTs) retrieved only by the analysis with equal weighting (Table 3). 6, Single MPT retrieved by analyses with equal weighting (one of three MPTs) and implied weighting with $K = 1$ –6 (Table 3).

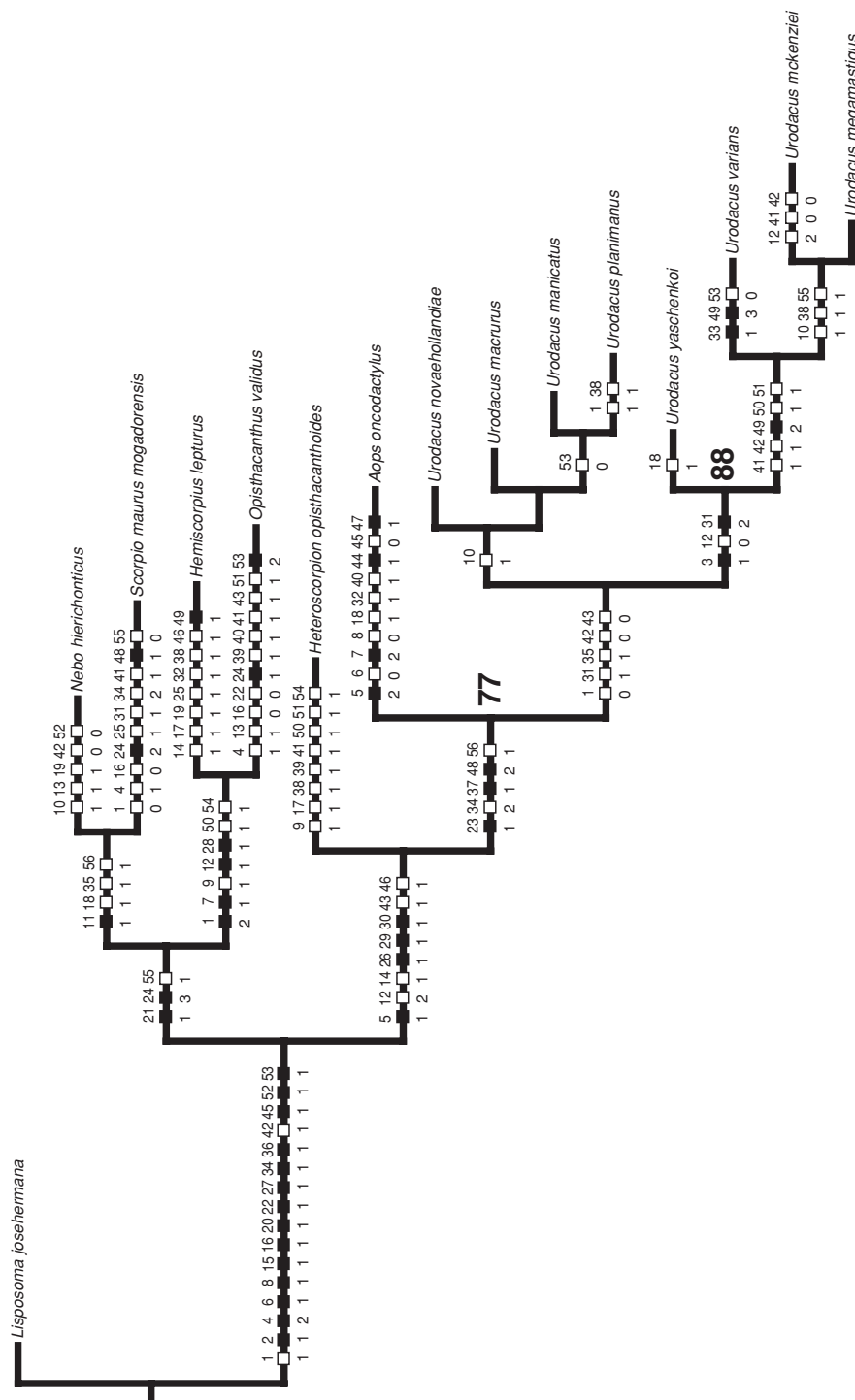


Fig. 7. The optimal tree obtained by cladistic analysis of 48 morphological characters scored for nine species of Urodacidae Pocock, 1893 and six outgroup taxa (Table 2) under weighting regimes that maximised fit and minimised length. This topology was retrieved by analyses with equal weighting (one of three most parsimonious trees (MPTs)) and implied weighting with $K = 1-6$ (Table 3). This topology corresponds to the majority rule (>50%) consensus of MPTs obtained by the seven analyses in which weighting regime was varied. Two nodes retrieved in 77% and 88% of the analyses (collapsed in the strict consensus) are indicated. Synapomorphies optimised with ACCTRAN are indicated with bars. Solid bars indicate uniquely derived apomorphic states, whereas empty bars indicate parallel derivations of apomorphic states. The number above each bar gives the character number. Refer to Appendix 2 for character descriptions.

Table 2. Distribution of 56 characters among nine species of Urodacidae Pocock, 1893 and six outgroup taxa
Character states are scored 0–3, * (polymorphic), ? (unknown), and – (inapplicable)

Taxa	Characters					
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	555555 123456
<i>Lisposoma josehermana</i>	0000000000	0000000000	0000000000	0000000000	00000–0000	000000
<i>Hemiscorpius lepturus</i>	2102011110	0101111011	1103101100	0101010100	0100110011	011110
<i>Opisthacanthus validus</i>	2101011110	0110100001	1001001100	0001010011	1110100001	112110
<i>Nebo hierichonticus</i>	1102010101	1010110111	1103001000	0001110000	0000100000	001011
<i>Scorpio maurus mogadorensis</i>	0101010100	1000100101	1102101000	1002110000	1100100100	011001
<i>Heteroscorpion opisthacanthoides</i>	1102110110	0201111001	010001--11	0001010110	1110110001	111100
<i>Aops oncodactylus</i>	1*02202000	02?1110101	011001--11	01020??01	?1110–1??	01100?
<i>Urodacus macrurus</i>	0102110101	0201110001	011001--11	1002111000	0000110200	011001
<i>Urodacus manicatus</i>	0102110101	0201110001	011001--11	1002111000	0000110200	010001
<i>Urodacus mckenziei</i>	0112110101	0201110001	011001--11	2002111100	0000110221	111011
<i>Urodacus megamastigus</i>	0112110101	0001110001	011001--11	2002111100	1100110221	111011
<i>Urodacus novaehollandiae</i>	0102110101	0201110001	011001--11	1002111000	0000110200	011001
<i>Urodacus planimanus</i>	1102110101	0001110001	011001--11	2012111000	1100110231	110001
<i>Urodacus varians</i>	0112110100	0001110101	011001--11	2002111000	0000110200	011001

optima ('islands' *sensu* Maddison 1991). Finally, trees found with this command were again swapped with TBR, using the command max*; to retain only optimal trees. Analyses with implied weighting investigated the use of six values for the concavity constant, *K*, spanning the input range permitted by Pee-Wee (command: conc N;).

As in previous studies by the second author, results of the sensitivity analyses are summarised by means of 50% majority rule (Margush and McMorris 1981) or 50% compromise (Nixon and Carpenter 1996) consensus trees. Nodes that appear in the majority rule trees but are collapsed in the strict consensus trees were obtained under the majority of weighting regimes, 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 weighting regimes.

Results

Analysis of the 48 informative characters located three most parsimonious trees (MPTs) with equal weighting (Table 3; Figs 4–6). The topology of these MPTs differed only in the relative placements of *A. oncodactylus*, *U. novaehollandiae* and *U. yaschenkoi*. *Aops* grouped sister to *Heteroscorpion* in two of the trees (Figs 4, 5), and sister to *Urodacus* in the third (Fig. 6). *Urodacus novaehollandiae* grouped sister to *U. macrurus* in one tree (Fig. 4), and sister to a group comprising *U. macrurus*, *U. manicatus* and *U. planimanus* in the other two (Figs 5, 6). *Urodacus yaschenkoi* grouped sister to a group comprising *U. novaehollandiae*, *U. macrurus*, *U. manicatus* and *U. planimanus* in one tree (Fig. 4), and sister to a group comprising *U. varians*, *U. mckenziei* and *U. megamastigus* in the other two (Figs 5, 6).

Analyses with implied weighting applying six *K* values located a single MPT with the same topology as one of the three MPTs obtained by the analyses with equal weighting (Table 3; Fig. 6). This topology, obtained by the majority of analyses under weighting regimes that minimised length as well as those that maximised fit (Table 3), is regarded as the optimal hypothesis. Synapomorphies are indicated on this topology in Fig. 7,

which also provides the frequency percentiles for nodes retrieved by >50% but <100% of the analyses (nodes retrieved by <100% obviously collapsed in the strict consensus). The length, fit (*f*_i), consistency indices, and retention indices of informative characters on this topology are listed in Table 4.

All MPTs retrieved in the present analyses were congruent with those obtained in Prendini's (2000, 2003) previous analyses of relationships among the families and genera of Scorpionoidea *s. str.*, a monophyletic group comprising the katoikogenic scorpionoid families (Diplocentridae, Hemiscorpiidae, Heteroscorpionidae, Liochelidae, Scorpionidae and Urodacidae) and excluding Bothriuridae. All analyses confirmed the following relationships among the katoikogenic families on the basis of the placements of their respective exemplars: ((Heteroscorpionidae + Urodacidae) ((Hemiscorpiidae + Liochelidae) (Diplocentridae + Scorpionidae))). All analyses retrieved a monophyletic *Urodacus*, while the majority of analyses, under a range of weighting functions, retrieved a monophyletic Urodacidae, placing *Aops* as the sister-group of *Urodacus*.

The relative positions of Heteroscorpionidae and Urodacidae have been contentious since Prendini (2000) first proposed a sister-group relationship for the families (Soleglad and Sissom 2001; Prendini 2003; Soleglad and Fet 2003b; Coddington *et al.* 2004; Soleglad *et al.* 2005; Prendini and Wheeler 2005; Lourenço and Goodman 2006). According to the alternative hypothesis, first proposed by Stockwell (1989), but also obtained in some analyses by Prendini (2000) and in a reanalysis of Prendini's (2000) data using alternative character interpretations by Soleglad *et al.* (2005), Heteroscorpionidae is sister to (Hemiscorpiidae + Liochelidae), whereas Urodacidae is sister to (Diplocentridae + Scorpionidae). The latter hypothesis was not retrieved in the present analyses and, judging from its character combination and phylogenetic position, the new taxon has increased support for the (Heteroscorpionidae + Urodacidae) sister-group hypothesis first proposed by Prendini (2000). In light of the analytical results, we are confident in creating the second urodacid genus, *Aops*, to accommodate it.

Taxonomy

Genus *Aops*, gen. nov.

Type species: Aops oncodactylus, sp. nov. (by monotypy).

Diagnosis

Aops is most closely related to *Urodacus*. Both genera share the following combination of character states: cheliceral movable finger with distal external and distal internal teeth subequal to unequal, distal external tooth smaller than distal internal tooth, not closely, or at most moderately, opposed; pedipalp patella with anterior process obsolete; trichobothria *ib* and *it* located basally on pedipalp chela fixed finger; *db* located on dorsal surface of fixed finger; *Dt* located basally on dorsal surface of manus; *Db* located basally on external surface of pedipalp chela manus; accessory trichobothria present in *e* and *v* series of patella, and in *E* and *V* series of chela manus; telotarsi without ventromedian row of spinules or spiniform macrosetae; aculeus long, shallowly curved; nongranular surfaces of prosoma, mesosoma, metasoma and legs smooth.

Aops is readily separated from *Urodacus* on the basis of its highly troglomorphic appearance. This species is the only known eyeless member of Urodacidae. Additional autapomorphic character states are as follows: carapacial sutures absent; basitarsi I and II without a retrolateral row of spiniform or setiform macrosetae; laterodistal lobes of telotarsi I–IV truncated; ventrosubmedian macrosetae of telotarsi slender, subspiniform, unlike the stout spiniform macrosetae of *Urodacus*; metasomal carinae obsolete to absent on all segments; pigmentation completely absent.

The holotype of *Aops* is unusual in displaying one subdistal tooth on the movable finger of the left chelicera and two subdistal teeth on the movable finger of the right chelicera. Although the condition of the left chelicera conforms with *Urodacus* and other katoikogenic scorpionoid taxa, additional specimens are required to determine which expression of this character state is fixed in the species. The polymorphic expression of this character within individuals has also been observed in *Belisarius xambeui* Simon, a troglomorphic scorpion from the Pyrenees of France and Spain, and Stockwell (1989: 89) suggested that it might be correlated with troglobitic adaptations. In the superstitioniid subfamily Typhlochactinae Mitchell, endemic to México, four troglomorphic species, *Sotanochactas elliotti* (Mitchell), *Typhlochactas cavicola*

Francke, *T. granulosus* Sissom and Cokendolpher and *T. sylvestris* Mitchell and Peck exhibit a single subdistal tooth, whereas two species, *T. reddelli* Mitchell and *T. rhodesi* Mitchell exhibit two subdistal teeth, again suggesting that this might be correlated with troglomorphism (Sissom and Cokendolpher 1998; Soleglad and Fet 2003b).

Etymology

The name is formed by the Greek prefix *a* [not; without or negative] and *ops* [eye], and describes the absence of eyes in the type species.

Aops oncodactylus, sp. nov.

Material examined

Holotype. Juvenile ♀, Australia, Western Australia, Barrow Island, Ledge Cave (Cave B-1), second chamber, 20°47'53"S 115°19'53"E, 21.viii.1999, coll. W.F. Humphreys & S.M. Eberhard (WAM 99/2109)

Diagnosis

As for genus.

Description

Colour

Chelicerae pale cream. Carapace and tergites yellowish cream. Metasomal segments cream to yellowish cream. Sternites pale yellowish cream; posterior margins white. Pectines creamy white.

Carapace

Anterior margin with well developed median notch and rounded frontal lobes (Fig. 8). Posterolateral margins subparallel. Anteromedian sulcus broad and shallow, anteriorly bifurcated. Paired median lateral and posterolateral sulci obsolete to absent. Posteromedian sulcus distinct, shallow, restricted to posterior depression. Posteromarginal sulcus distinct, shallow. Sutures absent. Median and lateral ocelli absent. Entire surface smooth, without granulation and punctation.

Mesosoma

Tergites smooth, flat, each with paired submedian depressions; I–VI acarinate, but VII with pair of weakly granular submedian carinae. Sternites entirely smooth, acarinate.

Table 3. Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by analysis under equal weighting (EW) and implied weighting (IW) with six values for the concavity constant (*K*), arranged in order of decreasing fit
Alternative topologies indicated in Figs 4–6.

	MPTs	Steps	Fit (<i>F</i> _i)	Rescaled fit	<i>CI</i>	<i>RI</i>	Fig. 4	Fig. 5	Fig. 6
IW: <i>K</i> = 6	1	114	411.2	52	56	60	×		
IW: <i>K</i> = 5	1	114	401.6	51	56	60	×		
IW: <i>K</i> = 4	1	114	388.8	50	56	60	×		
IW: <i>K</i> = 3	1	114	369.9	48	56	60	×		
EW	3	114	369.9	48	56	60	×	×	×
IW: <i>K</i> = 2	1	114	338.2	45	56	60	×		
IW: <i>K</i> = 1	1	114	283.7	40	56	60	×		

Metasoma and telson

Metasomal segments I–V progressively increasing in length, segment V 60% longer than segment I (Figs 2, 3; Table 5). Metasoma slender, width 97% of length for segment I; 80% for II; 60% for III; 53% for IV; and 29% for V. Metasoma short, total length 15% greater than combined length of prosoma and mesosoma. Two carinae on segment I, six carinae on segments II–IV, no carinae on segment V (Figs 23, 24).

Table 4. Length (steps), fit (f_i), consistency indices (CI), and retention indices (RI) of informative characters (Char.) on the optimal tree obtained by analysis under weighting regimes that maximised fit and minimised length (Fig. 7)

Char.	Steps	f_i	CI	RI
1	5	5	40	25
3	1	10	100	100
4	3	7.5	66	0
5	2	10	100	100
6	2	7.5	50	0
7	2	10	100	100
8	2	7.5	50	0
9	2	7.5	50	50
10	3	6	33	66
11	1	10	100	100
12	4	6	50	66
13	2	7.5	50	0
14	2	7.5	50	66
16	3	6	33	0
17	2	7.5	50	0
18	3	6	33	33
19	2	7.5	50	0
21	1	10	100	100
22	2	7.5	50	0
23	1	10	100	100
24	3	10	100	100
25	2	7.5	50	0
26	1	10	100	100
28	1	10	100	100
29	1	10	100	100
30	1	10	100	100
31	3	7.5	66	85
32	2	7.5	50	0
34	3	7.5	66	66
35	2	7.5	50	75
37	1	10	100	100
38	4	5	25	25
39	2	7.5	50	0
40	2	7.5	50	0
41	5	4.2	20	0
42	5	4.2	20	33
43	3	6	33	0
45	2	7.5	50	0
46	2	7.5	50	50
48	2	10	100	100
49	3	10	100	100
50	3	6	33	60
51	3	6	33	50
52	2	7.5	50	0
53	4	6	50	33
54	2	7.5	50	50
55	3	6	33	50
56	2	7.5	50	66

Dorsomedian furrow absent. Dorsal carinae weak, costate, restricted to posterior third of segments I and II; weak, granular, restricted to posterior third of segments III and IV; absent on segment V; not terminating distally in an enlarged, spiniform granule. Dorsolateral carinae weak, costate, restricted to posterior third of segments I and II; weak, costate, continuous for length of segments III and IV; absent on segment V. Lateral carinae restricted to a low mound basally on segment I, absent on segments II–V. Ventrolateral carinae weak to obsolete, costate, continuous for length of segments II–IV; absent on segments I and V. Ventral or ventromedian carinae absent on segments I–V. All intercarinal surfaces smooth. Telson vesicle slightly elongate, oval in shape, with flattened dorsal surface and curved ventral surface (Fig. 25), height 26% of length, not laterally compressed; without anterodorsal lateral lobes, furrows or carinae; surface smooth, sparsely and evenly covered in macrosetae; venom glands presumably folded. Aculeus short and stout, 34% of vesicle length, shallowly curved; subaculear tubercle absent.

Chelicerae

Chelicerai teeth without secondary serrations. Movable finger with distal external and distal internal teeth subequal, distal external tooth smaller than distal internal tooth, and moderately opposed (Fig. 10); movable finger of left chelicera with one subdistal tooth, of right chelicera with two subdistal teeth. Ventral aspect of fingers and manus with dense vestiture of long macrosetae.

Pedipalps

Coxa ventrointernal margin smooth. Femur (Figs 12–14) length 67% greater than width (Table 5); dorsoexternal, dorsointernal, and ventrointernal carinae weak, granular, all other carinae absent or obsolete; intercarinal surfaces smooth, granulation and punctation absent. Patella (Figs 15–18) length 69% greater than width (Table 5); dorsointernal carina weak, smooth, all other carinae absent or obsolete; anterior process weakly developed, dorsointernal and ventrointernal tubercles similar in size; intercarinal surfaces smooth, without granulation and punctation. Chela manus (Figs 19–22) length along ventroexternal carina 42% greater than chela width (Table 5); manus width 15% greater than height; length of movable finger 19% greater than manus length along ventroexternal carina; dorsal secondary carina weak, costate, extending full way across dorsal surface of manus; subdigital carina vestigial, reduced to a low mound basally on manus; digital carina weak, costate; dorsomarginal carina weak, granular; external secondary carina absent; ventroexternal carina weak, costate, parallel to longitudinal axis of chela, with distal edge directed towards a point between external and internal movable finger condyles, but closer to external condyle; ventromedian carina vestigial, reduced to a low mound, basally; ventrointernal carina stronger than ventromedian and internomedian carinae, although indicated only by change in angle of ventral surface of manus; internomedian carina and dorsointernal carinae absent; all intercarinal surfaces smooth, without granulation and punctation. Chela fingers (Fig. 19) with multiple primary rows of denticles in median two thirds and a single row basally and distally; lateral internal and external granules barely noticeable, only slightly larger and more laterally situated than primary rows; finger margins not scalloped and

without sculpturing; fixed finger with a diastema and well developed hook distally; movable finger without lobe and notch basally, but with a small hook distally.

Trichobothria

Pedipalps type C, neobothriotaxic major, with accessory trichobothria in the *v* and *e* series of the patella, and the *V* and *E* series of the chela. Total number of trichobothria per pedipalp, 65: femur, 3 (1 *d*; 1 *i*; 1 *e*), patella, 30 (2 *d*; 1 *i*; 6 *v*; 21 *e*) and chela, 32 (22 on manus, including 14 *E* and 6 *V*). Pedipalp femur (Figs 12, 13) with trichobothrium *i* located basally on dorsointernal surface; *d* and *e* located basally on dorsoexternal surface. Pedipalp patella (Figs 15–18) with trichobothrium *d*₁ located basally on dorsal surface, external to dorsointernal carina; *d*₂ located medially on dorsal surface, between internal tubercle and *i*; *i* located dorsally in distal half of internal surface. Pedipalp chela (Figs 19–22) with trichobothria *ib* and *it* located basally on fixed finger; *db* located on dorsal surface at base of fixed finger; *dsb* located on dorsoexternal surface in basal half of fixed finger; *dst* located on dorsoexternal surface, medially on fixed finger, closer to *dt* than to *dsb*; *dt* located on dorsointernal surface in distal half of fixed finger; *eb* located in basal half of fixed finger, between *dsb* and *db*; *esb* located in basal half of fixed finger, between *dst* and *dsb*, level with *eb*–*est*–*et* axis; *est* located in distal half of fixed finger, between *dst* and *dt*; *et* located in distal half of fixed finger, distal to *dt*; *Dt* located basally on dorsal surface of manus; *Db* located basally on external surface of manus; *Est* located distally on manus; *Et*₁ and *Et*₂ located on external surface of manus. Trichobothrial sulci absent.

Legs

All leg surfaces smooth, without granulation, and almost asetose. Tibiae and basitarsi terete, not dorsoventrally compressed, each with a few scattered spiniform macrosetae on prolateral and retrolateral margins, not arranged into a comb-like row. Telotarsi each with paired ventral rows of subspiniform macrosetae, but without a ventromedian row of spinules or spiniform macrosetae; counts of macrosetae in the pro- and retrolateral rows, 5/6 for telotarsi I and II, 5–6/6–7 for III, and 6/7 for IV, respectively. Telotarsal laterodistal lobes truncated (Fig. 11). Telotarsal unguis short, distinctly curved, and of equal length. Prolateral pedal spurs present. Retrolateral pedal spurs absent.

Coxosternum

Coxapophysis I anterior margin nongranular, expanded and subtriangular, external side fused to anterior of coxa I (Fig. 3). Coxapophysis II ventral margin fused to anterior of coxa II. Sternum type 2, subpentagonal, longer than wide; with pit opening posteriorly (margin absent).

Pectines

First basal median lamella of each pecten with mesal margin subtriangular, pectinal teeth present along entire posterior margin (Fig. 9). Left and right tooth counts, six and five respectively. Pectinal teeth with very large sensory papillae.

Genital operculum

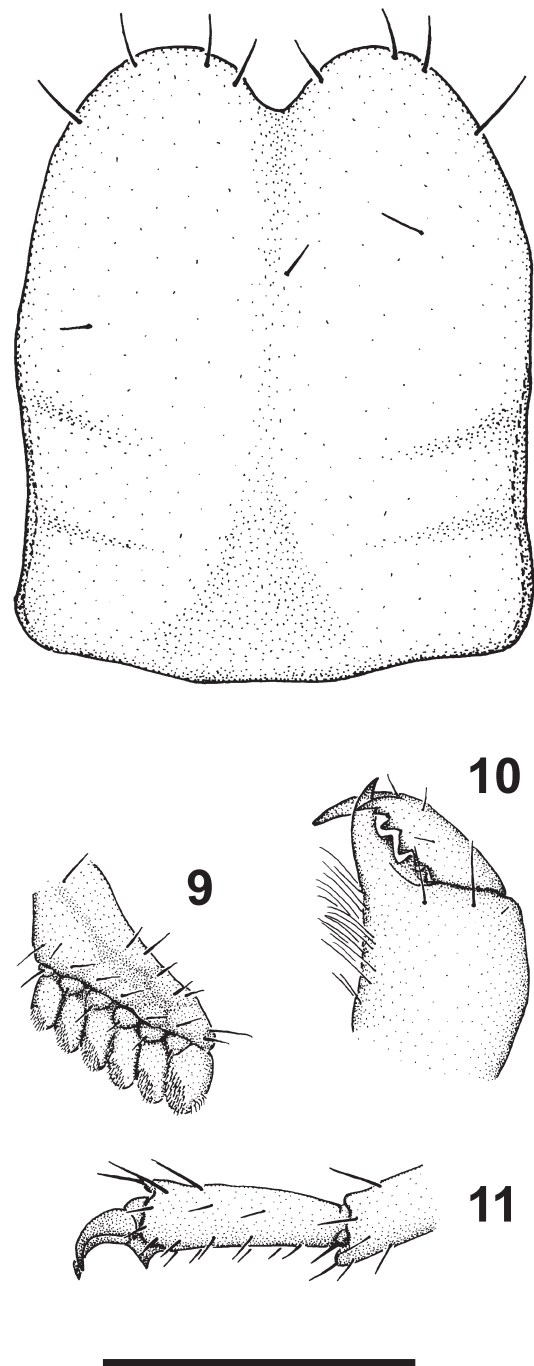
Suboval, genital opercula (♀) fused.

Female reproductive anatomy and male hemispermaphore

Unknown.

Embryonic development

Unknown, probably katoikogenic.



Figs 8–11. *Aops oncodactylus*, gen. et sp. nov. (holotype), diagnostic characters. 8, Carapace, dorsal aspect; 9, right pecten, ventral aspect; 10, right chelicera, dorsal aspect; 11, right telotarsus IV, prolateral aspect. Scale bar = 1 mm.

Distribution

Known only from the type locality, Ledge Cave on Barrow Island, off the north-western coast of Western Australia (Fig. 1).

Table 5. Meristic data for holotype of *Aops oncodactylus*, gen. et sp. nov.

Measurements (mm) following Stahnke (1970) and Sissom *et al.* (1990)

Carapace	Anterior width	1.87
	Posterior width	1.88
	Total length	2.31
	Length to median notch	2.04
Mesosoma	Total length (tergites)	6.06
Sternite VII	Width	2.06
	Length	1.58
Metasoma I	Maximum width	0.93
	Maximum height	0.77
	Length	0.96
Metasoma II	Maximum width	1.00
	Maximum height	0.64
	Length	1.25
Metasoma III	Maximum width	0.80
	Maximum height	0.62
	Length	1.34
Metasoma IV	Maximum width	0.76
	Maximum height	0.52
	Length	1.44
Metasoma V	Maximum width	0.68
	Maximum height	0.61
	Length	2.38
Telson	Maximum width	0.81
	Maximum height	0.58
	Aculeus length	0.77
	Total length	2.27
Metasoma	Total length ^A	9.61
Total length	Prosoma + mesosoma + metasoma	17.98
Femur	Maximum width	0.83
	Maximum height	1.00
	Length	2.55
Patella	Maximum width	0.90
	Maximum height	0.91
	Length	2.87
Chela	Maximum width	1.36
	Maximum height	1.16
	Length ^B	5.90
	Length of ventroexternal carina	2.34
	Length of fixed finger	2.55
	Length of movable finger	2.88
Pedipalp	Total length (trochanter–chela)	11.32
Pectines	Total length	1.02
	Length along dentate margin	0.80
	Tooth count (left/right)	6/5
Telotarsi I	Macrosetal count prolateral row (left/right)	5/5
	Macrosetal count retrolateral row (left/right)	6/6
Telotarsi II	Macrosetal count prolateral row (left/right)	5/5
	Macrosetal count retrolateral row (left/right)	6/6
Telotarsi III	Macrosetal count prolateral row (left/right)	5/6
	Macrosetal count retrolateral row (left/right)	6/7
Telotarsi IV	Macrosetal count prolateral row (left/right)	6/6
	Macrosetal count retrolateral row (left/right)	7/7

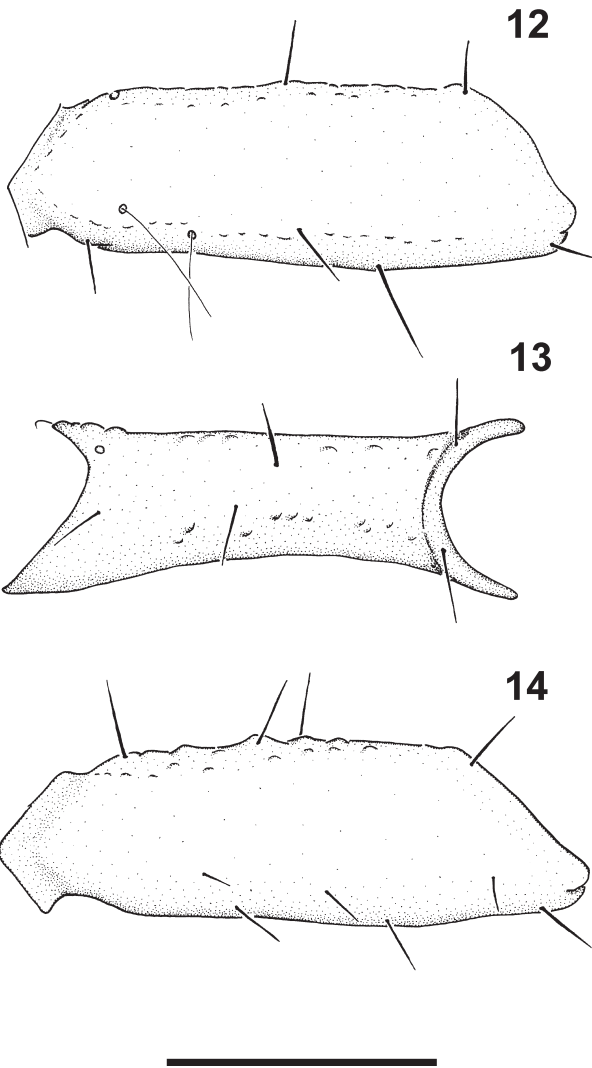
^ASum of metasomal segments I–V and telson.
^BMeasured from base of condyle to tip of fixed finger.

Ecology

On the basis of tarsal morphology, elongation of the legs and pedipalps, and limited dorsoventral compression, the new species appears to be lapidicolous, sheltering under stones or in crevices (Prendini 2001a). Unlike *Urodacus*, *Aops* is probably unable to burrow for it lacks the typical rows of spiniform or subspiniform macrosetae along the retrolateral margins of the tibiae and basitarsi of legs I and II, as well as the characteristic dorsoventral compression of these leg segments, that are observed in most *Urodacus*. The slender subspiniform macrosetae on the telotarsi, which differ from the stout spiniform macrosetae observed in most *Urodacus*, also appear unsuited for burrowing.

Conservation

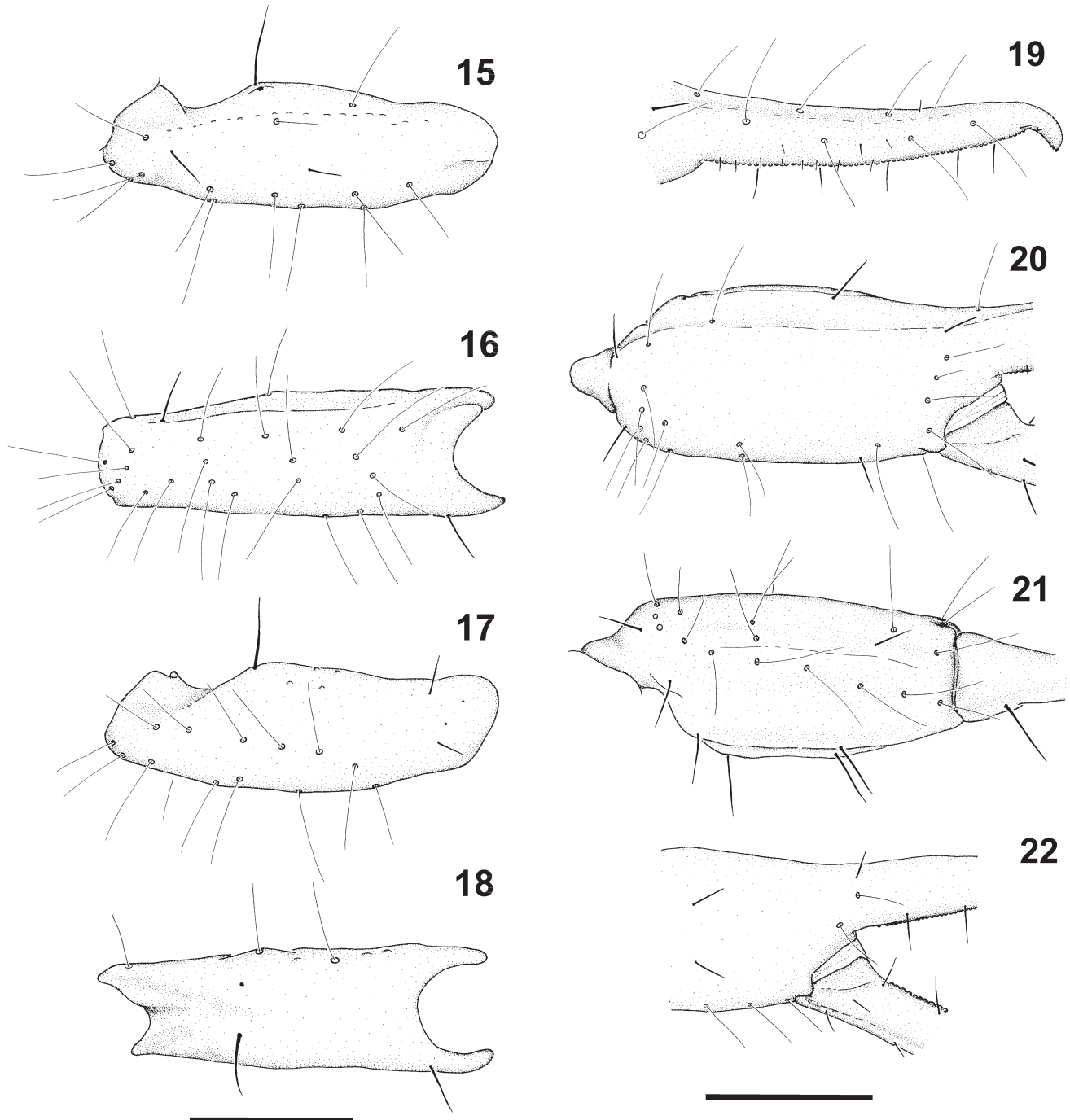
As the only known troglobitic scorpion from continental Australia, the only known troglobitic urodacid, and apparently



Figs 12–14. *Aops oncodactylus*, gen. et sp. nov. (holotype), right pedipalp femur. 12, Dorsal aspect; 13, internal aspect; 14, ventral aspect. Scale bar = 1 mm.

the most basal member of the family Urodacidae, *A. oncodactylus* is an important element of Australian biodiversity and one in need of protection. The species is known only from Barrow Island, much of which is currently exploited for oil (Humphreys 2001). Further development to process natural gas is underway. Barrow Island is an 'A class' reserve, receiving the highest 'protection' status available in Western Australia; however, this has

not prevented exploitation of the island for fossil fuels, a land-use practice that could threaten the future existence of this unique species and its cave habitat. We recommend that *A. oncodactylus* be assigned to the Critically Endangered category of the IUCN (2001) Red List, based on the following criteria: B1ab(i,ii,iii,iv)+2ab(i,ii,iii,iv). It is known to exist only at a single locality, the extent of occurrence is less than 100 km², and



Figs 15–18. *Aops oncodactylus*, gen. et sp. nov. (holotype), right pedipalp patella. 15, Dorsal aspect; 16, external aspect; 17, ventral aspect; 18, internal aspect. Scale bar = 1 mm.

Figs 19–22. *Aops oncodactylus*, gen. et sp. nov. (holotype), right pedipalp chela. 19, Fixed finger, external aspect; 20, chela manus, external aspect; 21, chela manus, ventral aspect; 22, chela manus, internal aspect. Scale bars = 1 mm.

the area of occupancy less than 10 km². A continuing decline is observed, inferred and projected in the extent of occurrence, the area of occupancy, the area, extent and quality of habitat, and the number of localities. We hope that this recommendation will draw the attention of relevant conservation authorities to the importance of conserving *A. oncodactylus* and, by implication, its cave habitat on Barrow Island.

Etymology

The specific name is derived from the Greek words *onkos* [hook], and *daktylos* [finger] (Brown 1956), and describes the markedly hooked distal ends of the pedipalp chela fixed fingers (Fig. 19).

Discussion

Defining troglobitism and troglomorphy

Troglobites are generally defined as organisms that are restricted to deep cave environments (Howarth 1972, 1983; Humphreys 2000a). Troglobites are thus defined strictly by their habitat and the term troglobitic may be regarded as synonymous with cavernicolous. Troglobites also exhibit pronounced troglomorphies, specific ecomorphological adaptations to cavernicolous habitats that include the loss (or reduction) of eyes and

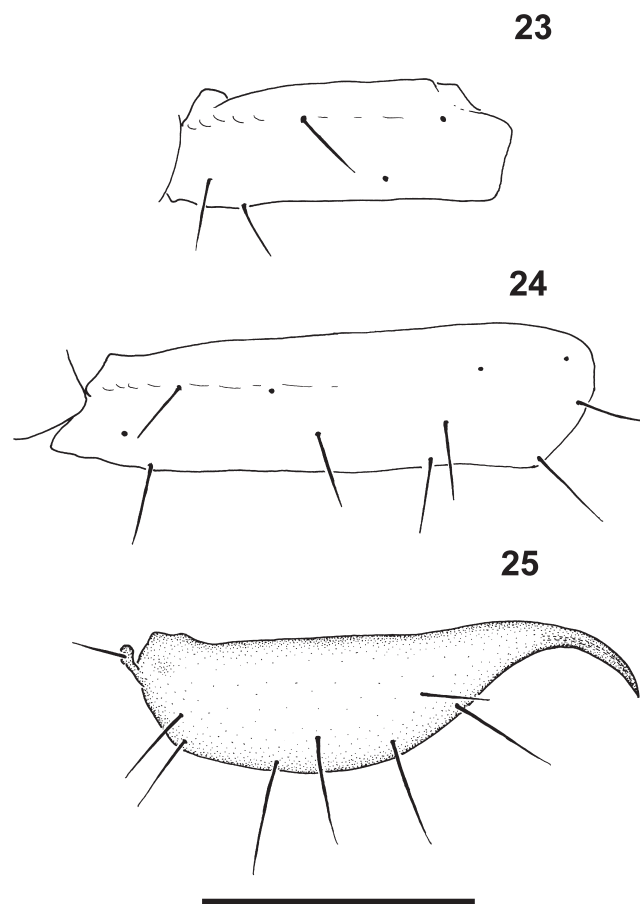
pigmentation, attenuation of the appendages, and thinning of the cuticle (Poulson 1963; Hamilton-Smith 1967; Barr 1968; Howarth 1982, 1983, 1993; Barr and Holsinger 1985; Humphreys 2000a). The evolution of troglomorphies has been largely attributed to the unusual characteristics of cave environments: extremely stable temperature, very high humidity, absolute and continuous darkness, and limited energy (food) availability (Barr 1968; Poulson and White 1969; Howarth 1982, 1983; 1993, Parzefall 1985). Cavernicolous environments select for the loss of characters that are both unnecessary and costly to produce or maintain (e.g. eyes, pigmentation, thickened cuticle), and the accentuation of characters that assist in resource-location or compensate for the unnecessary characters that have been lost (e.g. attenuated appendages, reduced metabolic rate).

Troglobitic scorpions exhibit various troglomorphies, particularly reduction or loss of median ocelli, lateral ocelli, pigmentation and sclerotisation, attenuation of the appendages, and loss of the pro- and retrolateral pedal spurs, respectively observed in 20 (95%), 17 (81%), 20 (95%), 20 (95%), 4 (19%) and 11 (52%) of the 21 unequivocally troglobitic species listed in Table 1. Another troglomorphy, uniquely observed in 12 (57%) of these species, is the enlargement of the telson vesicle. Volschenk *et al.* (2001) noted that the vesicle of *L. polisorum* Volschenk *et al.* was significantly larger, in proportion to its body size, than that of other *Liocheles* Sundevall species, and suggested that the increased size might be caused by enlargement of the venom glands for maximising prey capture-efficiency in a resource-limited environment.

Troglobitic versus troglomorphic scorpions

We believe it is important to draw a distinction between scorpions that are cavernicolous and scorpions that are troglomorphic, and to restrict the definition of troglobitic scorpions to those species that are both restricted to cavernicolous habitats and exhibit pronounced troglomorphies. At least three highly troglomorphic scorpion species have not been recorded from cavernicolous habitats *per se*. *Belisarius xambeui*, endemic to the Pyrenees of France and Spain, is eyeless and partially depigmented, displays a weakly sclerotised cuticle, and an enlarged telson vesicle. This species inhabits limestone caves and leaf litter in montane forests (Jeannel and Racovitza 1912, 1914, 1918; Jeannel 1926; Auber 1959). *Typhlochactas mitchelli* and *T. sylvestris*, endemic to leaf litter in the montane forests of Oaxaca, south-eastern México (Mitchell and Peck 1977; Sissom 1988), are eyeless, completely depigmented, and weakly sclerotised. These endogean *Typhlochactas* Mitchell species are morphologically similar to their hypogean counterparts, known from caves in eastern México (Mitchell 1968, 1971; Francke 1982, 1986; Sissom and Cokendolpher 1998). *Belisarius* Simon and the *Typhlochactas* species demonstrate that the presence of troglomorphies does not necessarily predict the occurrence in cavernicolous habitats.

Several scorpion species, recorded only from caves, do not possess pronounced troglomorphies (Table 1). Either these species have only recently been isolated in cavernicolous habitats and have not yet evolved troglomorphies, or they are troglophiles for which epigean records are presently absent. For example, *Tityus demangei*, recorded from the transitional zone



Figs 23–25. *Aops oncodactylus*, gen. et sp. nov. (holotype), diagnostic characters. 23, Metasoma I, lateral aspect; 24, metasoma V, lateral aspect; 25, telson, lateral aspect. Scale bar = 1 mm.

(cave entrance) to the deep cave zone of the Los Tayos Caves, Ecuador, possesses no troglomorphies whatsoever (Lourenço 1981). *Troglotityobuthus gracilis*, known only from the holotype collected in Grotte de Fanihys (Cave de la Chauve Souris), Madagascar, is weakly pigmented and possesses attenuated appendages. Although Lourenço (2000) based his diagnosis of this genus on these characters, together with its occurrence in a cavernicolous habitat, more data on its ecology are required to verify that it is an obligate cavernicole. Many epigeal buthids possess attenuated appendages and pale pigmentation, e.g. *Isometrus maculatus* (DeGeer) and *Uroplectes schlechteri* Purcell. Such characters, in isolation, cannot be regarded as evidence of troglomorphism.

Other similar examples of scorpions that have been deemed troglobitic, but that fail to meet one or both of the abovementioned criteria (i.e. they are not restricted to cavernicolous habitats and/or they do not exhibit pronounced troglomorphies), are listed in Table 1. Only 21 species, in 14 genera and nine families, worldwide, meet both criteria and can be considered unequivocally troglobitic (Table 1).

Taxonomic and geographical distribution of troglobitic scorpions

The majority of instances of troglomorphism in scorpions represent isolated evolutionary events within families or genera. Fewer than five troglobites are recorded from each of the following 'non-buthid' families (Coddington *et al.* 2004), and represent a small fraction of the species contained in them: Chaerilidae Pocock (10%), Diplocentridae Karsch (4%), Euscorpidae Laurie (14%), Liochelidae Fet and Bechly (2%), Urodacidae Pocock (5%), and Vaejovidae Thorell (2%; Table 1). Superstitioniidae Stahnke, composed predominantly of troglobitic species (67%), is a notable exception. A single troglobitic species is contained in each of two recently proposed non-buthid families of uncertain validity – the monotypic Akravidae Levy and Troglotayosidae Lourenço, comprising two species. The three troglobitic diplocentrids occur in the genus *Diplocentrus* Peters. Several diverse non-buthid families, e.g. Bothriuridae Simon, Iuridae Thorell and Scorpionidae Latreille, contain no troglobitic species.

The paucity of troglobites in Buthidae C. L. Koch, accounting for approximately half of all scorpion species (Fet and Lowe 2000; Coddington *et al.* 2004), is remarkable. Three buthids, representing less than 1% of the species in this diverse family, are alleged to be troglobitic (Table 1). Only one of those, *Troglorhopalurus* Lourenço, exhibits unequivocal troglomorphies, however.

The geographical distribution of troglobitic scorpions is also extremely asymmetrical. Sixteen (76%) troglobitic scorpions occur in the New World, thirteen (62%) of which are endemic to México. Old World troglobites occur in the Middle East, south-east Asia, and Australasia. No troglobitic (or troglomorphic) scorpions have been recorded from Africa.

The reasons for the observed asymmetries in the taxonomic and geographical distribution of troglobitic scorpions can only be speculated about. Some lineages appear to be preadapted for a hypogean existence whereas others do not. Broad differences in lifestyle or habitat requirements may explain why there are few troglobites in the Buthidae, a family that occurs worldwide

and accounts for approximately half of all scorpion species, compared with the non-buthid families, also collectively distributed worldwide, and making up the other half of scorpion diversity.

Evolution of troglobitic scorpions

Historical differences, e.g. extinction, may also account for the observed asymmetries, especially for explaining the diverse Mexican troglobite scorpion fauna. The evolution of troglobites is often considered unidirectional: reversal, i.e. the recolonisation of endogean habitats by hypogean taxa, is prevented through competitive exclusion by species already occupying, and better adapted to those habitats (Conway Morris 1995). Humphreys (2000b) proposed that hypogean species may be able to recolonise epigeal and endogean habitats when all potential competitors are removed, and speculated about the existence of epigeal and endogean species with hypogean ancestry in the Caribbean region. Epigeal and endogean competitors from southern North America, Central America, and northern South America would have been largely eliminated by the thermal pulse following the Chicxulub impact in the Yucatán Peninsula (Hilderbrand 1993) at the end of the Cretaceous (c. 65 Mya BP). Some deep cave habitats would probably have been spared the widespread destruction of surface habitats, providing a refuge for taxa that may have had epigeal and/or endogean relatives before the impact. The unique troglobitic scorpion fauna of México, including four endemic genera (*Alacran* Francke, *Sotanochoctas* Francke, *Troglacormus* Francke and *Typhlochoctas*) that are distantly related to most of the epigeal scorpion fauna (thought to be the result of relatively recent radiations) of the region, may represent hypogean relicts of formerly epigeal and/or endogean lineages that survived the Chicxulub impact.

According to such a scenario, the endogean *T. mitchelli* and *T. sylvestris* may, in turn, be examples of the recolonisation of endogean environments by hypogean taxa. Both endogean *Typhlochoctas* species are morphologically similar to their hypogean counterparts, being eyeless, completely depigmented, and weakly sclerotised, yet they inhabit montane forest litter, not caves (Mitchell and Peck 1977). Mitchell and Peck (1977) suggested that the troglomorphies of *T. sylvestris* developed in association with its humicolous habitat, but preadapted it for cave life, leading to the subsequent colonisation of cavernicolous habitats and the evolution of troglobitic *Typhlochoctas* species. With the exception of *B. xambeui*, all other humicolous scorpions are pigmented and possess well developed ocelli (Lamoral 1976; Lourenço 1998a, 1998b, 2003). It therefore seems more plausible that the ancestors of *T. mitchelli* and *T. sylvestris* were troglobites that recolonised the endogean environment. This hypothesis awaits rigorous testing using modern cladistic methods, a complete taxon sample of *Typhlochoctas* and additional characters. It is, however, supported in part by the terminal placement of *T. sylvestris*, relative to *Alacran*, *Sotanochoctas*, and two of the troglobitic species of *Typhlochoctas* (*T. reddelli* and *T. rhodesi*), in Francke's (1982) manually generated cladogram of the species and characters known at the time. A basal placement for the endogean species would be required to support the hypothesis of Mitchell and Peck (1977).

Belisarius xambeui is the only other eyeless humicolous scorpion but its evolution is more difficult to explain, for several reasons. Unlike *T. mitchelli* and *T. sylvestris*, *Belisarius* is recorded from both endogean and hypogean environments (Auber 1959). Furthermore, it is monotypic and its phylogenetic placement within the chactoid lineage remains contestable (Stockwell 1989; Lourenço 1998a; Sissom and Cokendolpher 1998; Fet and Sissom 2000; Sologlad and Sissom 2001; Sologlad and Fet 2003b; Coddington *et al.* 2004).

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Appendix 1. Material examined

Specimens deposited in the following collections: American Museum of Natural History (AMNH), New York, including Alexis Harington (AH) Collection and Lorenzo Prendini (LP) Collection; California Academy of Sciences (CAS), San Francisco; Erich S. Volschenk (ESV) personal collection, Brisbane, Australia; Field Museum of Natural History (FMNH), Chicago; Matt. E. Braunwalder (MEB) personal collection, Zurich, Switzerland; Museum National d'Histoire Naturelle (MNHN), Paris; Naturhistoriska Riksmuseet (NHRM), Stockholm; Queensland Museum (QM), Brisbane, Australia; Colección Nacional de Acaros y Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), México City; United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC; Western Australian Museum (WAM), Perth; W. David Sissom (WDS) personal collection, Canyon, TX; Zoologisches Museum der Humboldt-Universität, Berlin (ZMB); Zoologisches Institut und Museum der Universität Hamburg (ZMH).

Bothriuridae Simon, 1880

Lisposoma josehermana Lamoral, 1979: Namibia: 16 ♂ 54 ♀ (AMNH), Farm Varianto on Elandschoek 771, 19°22.773'S 17°44.456'E, Tsumeb District, Oshikoto Region, 4.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins; 5 ♂ 7 ♀ 5 subad. ♂ 5 subad. ♀ (AMNH), Farm Uisib 427, 15 km NW of Otavi, 19°33.132'S 17°14.124'E, Grootfontein District, Otjozondjupa Region, 2.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins.

Chactidae Pocock, 1893

Belisarius xambeui Simon, 1879: 1 ♂ [dissected by M. Vachon, no hemispermatophore] (MNHN RS 0790); 1 ♀ (MNHN RS 7748), Malhomme; 1 subad. ♀, 2 juv. ♂ (MNHN RS 0797), 18.xii.1949; 1 subad. ♂ (MNHN RS 0793), Amélie, les Bains, France, iv.1900; 1 ♀ (AMNH LP 2904), 1 juv. (AMNH LP 2851), East Pyrenees, c. 3 km above Prats de Mollo, 42°23.707'N 2°28.546'E, France, 10.vi.2003, S. Huber, 2725 ft, under leaf litter, scree and boulders (drainage); 2 juv. ♂, 1 juv. ♀ (MNHN RS 0789), Fr. De Montbolo, Pyrenees Orientales, France, 17.iv.1946, Coiffat; 1 juv. ♀ (MNHN RS 0794), Grotte pres de la metairie d'en Briscot a La Preste, commun d'Arles-sur-Tech, Pyrenees Orientales, France, 6.iv.1929, J. R. Denis & P. Remy, in cave, 40 m from entrance in total darkness; 1 subad. ♀, 4 juv. (MNHN RS 0792), La Preste, Pyrenees Orientales, France, Nadar; 1 subad. ♀ (MNHN RS 4708), Prats de Mollo, Pyrenees Orientales, France, 23.iv.1935, G. Colas; 2 ♀ (MNHN RS 0795), Pyrenees Orientales, France; 1 juv. (MNHN RS 0796), Pyrenees Orientales, France; 1 juv. (AMNH LP 1891), Pyrenees Orientales, Mts between La Preste and Prats de Mollo, France, 2001, L. Monod; 1 ♀ (MNHN RS 0791), Vernet les Bains, France, Bolivar; 1 ♀ (MNHN), Cav Petit Terrades (Alt Empordà), Spain, 13.iv.1979, X. Bellés & J. Comas; 1 ♀ (MNHN RS 0798), Cav del Ciri, San Lorenzo Muga, Spain, vi.1944, Espanol; 2 ♀, 1 juv. ♀ (MNHN RS 7743), Mataro, Spain, 31.viii.1948, J. Nègre; 1 ♂ (MNHN), Av. Toni (S of Barcelona), Spain, 9.v.1976, O. Escolá; 1 ♀, 1 juv. (MNHN RS 0802), San Bartolo me. Vidra, P Barcelona, Spain, 12.x.1950, J. Mateu, en foret du Fagus sous les cailloux; 1 juv. (AMNH LP 2325), Montseny, 41°45'45"N 2°21'53"W, Prov. de Barcelona, Spain, 17.vii.2002, G. Giribet, E. Mateos & N. Lopez, 820 m; 1 subad. ♀, 1 juv. ♂ (MNHN), Av. Taleixà, Girona, Spain, 1.xi.1970, E. Vives; 1 juv. ♂ (MNHN RS 0799), Avenc de Taleiczà, Terradas, Girona, Spain, 6.vi.1954, Heurob; 2 ♀ (MNHN RS 0801), Camprodon, Girona, Spain, ix.1954, J. Mateu; 2 ♀ (MNHN RS 0800), Camprodon, Girona, Spain, 17.x.1946, Espanol; 1 ♀ (MNHN RS 3230), Camprodon, Girona, Spain, J. Mateu; 1 ♀, 1 subad. ♀, 1 juv. ♀ (MNHN RS 4582), Camprodon, Forêt de Hêtres, Girona, Spain, viii.1963, J. Mateu; 2 juv. (MNHN RS 0803), Cueva Vera Major, Terrades, Girona, Spain, 23.vi.1944, Espanol; 1 ♀ (AMNH LP 1629), Fajeda d'en Jordà, Girona, Spain, 5.xi.1993, G. Giribet & C. Ribera; 2 ♂ (MNHN), Les Guilleriers, Girona, Spain, 24.v.1981, E. Vives; 1 ♀ (MNHN), Puig Sacalin, Girona, Spain, 30.v.1982, E. Vives; 1 juv. (MNHN RS 4554), San Juan de las Abadesas, Girona, Spain, 3.xi.1962, H. C.; 2 ♀ (MNHN), Santigosa, Girona, Spain, 21.viii.1969, E. Vives; 2 ♀ (MNHN), Santigosa, Girona, Spain, 3.viii.1976, E. Vives; 1 juv. ♀ (MNHN), Vall de Vianya, Fageda, Girona, Spain, 30.iv.1978, Espadaler, 800 m; 2 ♂ (MEB 002), Engracia near Amélie-les-Bains, Pyrenees, France, 16.vi.1983, M. E. Braunwalder; 1 ♀ (MEB 080), Engracia near Amélie-les-Bains, Pyrenees, France, 5.vi.1984, M. E. Braunwalder; 1 ♀ (MEB 081) Banat, near Prat-de-Mollo, Pyrenees, France, M. E. Braunwalder, 6.vi.1984; 2 ♂ (MEB 823), Ravin d'En, Sant Magi near Taulis, Roussillon-Pyrénées, France, 26.v.1995, M. E. Braunwalder; 1 ♂ (MEB 824), Coste de Galy near Marsal, Roussillon, Pyrenees, France, 26.v.1995, M. E. Braunwalder; 1 ♂ (MEB 961), Rivière de Caillan, between Conat and Ria-Sirach Urbanya, Pyrenees, France, 19.v.1997, M. E. Braunwalder; 1 juv. (MEB 964), Roubrio, Riuferrer, Vallée de Bonabosc, Pyrenees, France, 21.v.1997, M. E. Braunwalder; 1 ♀ and 1 juv. (AMNH), Pyrenees, Uaut Vellespir, D54 nach Montferrer, kleine Geröllhalde, France, 1305 ft, 42°27.120'N 2°36.191'E, 5.vi.2003, S. Huber.

Chaerilidae Pocock, 1893

Chaerilus chapmani Vachon & Lourenço, 1985: 1 ♂ (AMNH), Clearwater III Cave, S. Mulu NP, Sarawak, Gunong Api, Kalimantan (Borneo) Island, Malaysia, v.1984.

Diplocentridae Karsch, 1880

Diplocentrus anophthalmus Francke, 1977: Holotype ♀, paratype ♀ (AMNH), Actun Chukum, Yucatán, México, 29.xi.1974, J. Reddell, D. McKenzie, R. Mitchell & S. Wiley.

Diplocentrus cueva Francke, 1978: Holotype ♂ (AMNH), Cueva Desapareciendo, 2 km W Acatlan, Oaxaca, México, 3.i.1976, A. Grubbs.

Diplocentrus mitchelli Francke, 1977: Holotype juv. ♂ (AMNH), Actun Halmensura, Campeche, México, 31.x.1974, J. Reddell, S. Wiley & D. McKenzie.

Nebo hierichonticus (Simon, 1872): 1 ♀ (ZMB 31133), Tabgha, Palestine, 28.ii.1919, P. E. Schmitz; 1 ♀ (ZMB 8229), Palestine, Schluter; 2 subad. ♂, 1 juv. ♂, 1 juv. ♀ (ZMB 31134), Red Sea, Wadi Ghuwer, Palestine, 1912, Dr Brühl; 1 ♀ (NHRM [JF 54]), Nazaret, Israel, iii.1995, J. Ferrer; 5 ♂ 2 ♀ (FMNH), Afule, Palestine, 25.ix.1934, Dr F. R. S. Shaw; 1 juv. ♂ (CAS), Mt Carmel, Israel, 12.xi.1960, Dr M. R. Warburg; 1 subad. ♂ (CAS), Mt Carmel, Israel, 20.vii.1960, Dr M. R. Warburg; 1 ♂ (AMNH [AH 573]), En Gedi, Israel, 2.ii.1978, P. Amitai; 1 ♂ (AMNH [AH 573]), Arad, 7 km E, Judean Desert, Israel, 15.ix.1984, G. Swager.

Euscorpidae Laurie, 1896

Troglocormus ciego Francke, 1981: Holotype ♂ (AMNH), Cueva de Elias, 13 km N Agua Buena, San Luis Potosí, México, 3.viii.1975, D. McKenzie.

Troglocormus willis Francke, 1981: México: Tamaulipas: Holotype ♂ (AMNH), Cueva del Brinco (entrance passage), 3.v.1978, P. Sprouse. Paratypes: 1 ♀ (AMNH), Cueva de Esperanza, Yerbabuena, Tamaulipas, México, 20.xi.1979, P. Sprouse; 1 juv. (AMNH), Cueva del Brinco, vi.1978, P. Sprouse; 1 juv. (AMNH), Cueva de la Onza, 300 m N Conrado Castillo, 21.iii.1982, G. Atkins. Additional material: 1 subad. (AMNH LP 2461), Cueva Allarines, Conrado Castillo, 25.xi.2003, A. Gluesenkamp; 1 subad. (AMNH LP 2460), Cueva Cuchilla, Conrado Castillo, 28.xi.2003, A. Gluesenkamp; 1 subad. (AMNH LP 2743), P-2 Cave, Conrado Castillo, 3.iv.2004, B. Shade.

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Appendix 1. (continued)

Hemiscorpiidae Pocock, 1893

Hemiscorpius lepturus Peters, 1861: 1 ♂ syntype (ZMH 2321 ex ZMB), 1 ♀ syntype (ZMH 2322 ex ZMB), Baghdad, Iraq, 1893, Peters; 2 ♂, 2 ♀ syntypes (ZMB 43), Mendeli, near Baghdad, Iraq, Petermann. Additional material: 2 ♀ (ZMB 2322), Baghdad, Iraq; 2 ♂ (ZMB 7550); 1 ♂, 2 ♀ (USNM), Gach Saran, 35 km E, Khuzistan Prov., Iran, 6.ii.1964, J. Neal; 1 ♂, 2 ♀ (FMNH), Mandali, Iraq, Y. Lazar, 16.xii.1934; 1 ♀ (AMNH LP 4342), Baghmalek, Khuzestan Prov., Iran, v.2005, H. R. Goodarzi; 1 ♂, 1 ♀ (AMNH LP 4343), Andimeshk, Khuzestan Prov., Iran, v.2005, H. R. Goodarzi.

Heteroscorpionidae Kraepelin, 1905

Heteroscorpion opisthacanthoides (Kraepelin, 1896): Madagascar: Holotype ♀, 1 ♂, 1 juv. ♂ syntypes (ZMH), Nossi Comba, Nossibe, 27.ix.1895, P. Frey; 1 ♀, 4 juv. ♂ syntypes (ZMH), Nossi Comba, 3.x.1896, P. Frey. Additional material: 1 subad. ♂ (ZMB 7809 ex ZMH), Nossi Comba, iii.1896, P. Frey; 2 ♀, 1 subad. ♂, 1 subad. ♀, 1 juv. ♂, 3 (MNHN RS 4813), Nossi Komba, 1945, Millot; 1 ♂, 1 ♀ (MNHN RS 4813), Nossi Bé, Komba, 1945, Millot; 1 juv. ♀ (MNHN RS 3536), Nossi Komba, flanc nord, Prov. Diège Suarez, A. Robinson; 2 ♂, 3 ♀, 2 subad. ♂, 8 juv. ♂ (ZMH A26/03), Lokobé Reserve, Nossi Be I., 6–9.ii.1983, W. R. Lourenço; 1 ♀ (MNHN RS 5046), Sakavalana, 1901, Alluaud; 1 ♀ (MNHN RS 0557), Ambilobe, Waterlot; 1 juv. ♂ (MNHN RS 4473), Forêt de Mahory, Prov. Diège Suarez, 16.i.1966, Betsch & J. J. Petter.

Liochelidae Fet & Bechly, 2001

Opisthacanthus validus Thorell, 1876: South Africa: Eastern Cape Province: 1 ♀, 1 juv. ♀ (AMNH LP 2763 [JV 7482, 7483]), Rietvlei, Witmos, Bedford District, 32°32'S 25°44'E, 13.vi.2003, J. Visser; 1 subad. ♀ (AMNH LP 2766 [JV 7726]), Farm Rea's, c. 7 km E Ramaphosa Village, Hankey District, 19.i.2003, J. Visser; 1 juv. (AMNH LP 2761 [JV 7701]), Swart River, Humansdorp District, 34°04'S 24°54'E, 24.v.2003, J. Visser; 1 subad. ♂, 2 juv. (AMNH LP 2762 [JV 7668, 7669, 7671]), Elands River, at old bridge, Humansdorp District, 33°59'S 24°05'E, 20.i.2003, J. Visser; 1 ♂ (AMNH LP 2764 [JV 7827]), Farm Uitvlugt 194, Humansdorp District, 33°53'S 24°36'E, 7.ix.2003, J. Visser; 3 ♀ (AMNH LP 2765 [JV 7834–7836]), Rietvlei, Humansdorp District, 33°55'S 24°35'E, 7.ix.2003, J. Visser; 1 ♀ (AMNH LP 2767 [JV 7876]), Jeffreys Bay, Humansdorp District, 34°03'S 24°55'E, 13.ix.2003, J. Visser.

Scorpionidae Latreille, 1802

Scorpio maurus mogadorensis Birula, 1910: 1 ♀ (AMNH LP 3497), 8 km after Tagmoute, on road to Tanalt, NW of Tafraoute, Morocco, 29°44'05.5"N 09°09'55.9"W, 14.ix.2004, V. Vignoli; 1 ♂, 2 juv. (AMNH), Tafraoute, 500 m from village (camping), Morocco, 1008 m, 29°43'19.2"N 08°58'46.6"W, 10.ix.2004, V. Vignoli; 1 ♀, 1 juv. (AMNH), Tafraoute, 500 m from village (camping), Morocco, 1008 m, 29°43'19.2"N 08°58'46.6"W, 14.ix.2004, V. Vignoli; 4 juv. (AMNH), Asni, 4 km before, on road Marrakech-Asni, Morocco, 1082 m, 31°16'55.7"N 07°57'35"W, 22.ix.2004, V. Vignoli; 1 ♂, 2 ♀, 2 subad. ♂ (AMNH), Arbalou (Ourika), Marrakech Prov., Morocco, 1000 m, 14–18.v.1975, B. Malkin.

Superstitioniidae Stahnke, 1940

Alacran tartarus Francke, 1982: México: Oaxaca: Holotype ♀ (AMNH), Sótano de San Agustín, 720 m below surface, San Agustín, 5 km SE Huautla de Jiménez, San Agustín Expedition (Huautla Project), Spring 1979. Paratypes: 1 ♀ (MNHN RS 7439), Cueva del Escorpión, San Miguel Dolina, San Miguel, i.1978, R. Jameson & P. Mothes; 1 ♀ (AMNH), Sótano Li Nita, Huautla de Jiménez, 1.iv.1981, M. Minton, L. Wilk & R. Simmons; 1 juv., Sótano Li Nita, Huautla de Jiménez, 22.iii.1981, M. Minton. Additional material: 2 ♀ (WDS), Sótano de San Agustín Section, Sistema Huautla, 5 km SE Huautla de Jiménez, v.1985, A. G. Grubbs, J. H. Smith & F. Holliday; 1 ♀ (AMNH LP 3499), Cueva del Escorpión, 18.1065°N 96.7982°W, Municipio San Miguel, 18.ix.2004, A. Gluesenkamp, P. Sprouse & C. Savvas, 1561 m.

Sotanochactas elliotti (Mitchell, 1971): Holotype subad. ♂ (AMNH), Sótano de Yerbaniz, c. 12 km N Ciudad Valles, San Luis Potosí, México, 31.vii.1969, W. R. Elliott; 1 paratype ♂ (WDS), same locality data as holotype, R. W. Mitchell, 4.vii.1970; 1 juv. paratype (MNHN RS 5376), same locality data as holotype, 28.iii.1970, W. Elliott.

Typhlochactas cavicola Francke, 1986: Holotype ♂ (AMNH), Cueva del Vandalismo, 1 km SE Rancho Nuevo, Tamaulipas, México, 15.iii.1982, D. Honae.

Typhlochactas granulosus Sissom & Cokendolpher, 1998: Holotype ♂ (AMNH), Sótano de Poncho, Municipio Tlaquilpa, Veracruz, México, 22.iii.1995, P. Sprouse.

Typhlochactas mitchelli Sissomi, 1988: Holotype ♂, 1 ♂ 1 subad. ♀ paratypes (AMNH), Cerro Ocote, 5 mi S Tenango, Oaxaca, México, iv.1987, A. Grubbs, A. Cressler & P. Smith.

Typhlochactas reddelli Mitchell, 1986: Holotype ♀ (AMNH), Cueva del Ojo de Agua de Tililapan, Tililapan, Veracruz, México, 4.viii.1967, J. Reddell, J. Fish & T. R. Evans.

Typhlochactas rhodesi Mitchell, 1968: Holotype ♀ (AMNH), Cueva de la Mina, Rancho del Cielo, Tamaulipas, México, 29.iii.1967, R. Mitchell, R. Mitchell, V. Colvin, D. Falls & K. Pittard. Paratypes: 1 juv. ♀ (MNHN RS 4760), Cueva de la Mina, Rancho El Cielo, Tamaulipas, México, 29.viii.1967, R. Mitchell, F. Abernathy & W. Rhodes; 1 juv. ♀ (AMNH), Cueva de la Mina, 6 mi NW Gómez Farias, Tamaulipas, México, 1.vii.1969, S. J. Peck & R. Norton.

Typhlochactas sylvestris Mitchell & Peck, 1977: Holotype ♀ (AMNH), 15 mi S Valle Nacional, Oaxaca, México, 21.v.1971, S. Peck.

Urodacidae Pocock, 1893

Urodacus macrurus Pocock, 1899: 1 ♀ (ZMH), Australia, 26.iii.1897; 1 ♂ (QM S58508), Carnarvon NP, Mt Moffat Section, Queensland, Australia, 24°58'43"S 147°55'17"E, 31.i.–9.ii.2000, C. Eddie; 1 ♂ (ESV 4424), Carnarvon NP, Mt Moffat Section, Queensland, Australia, 25°01'15"S 147°55'57"E, 13–19.iv.1999, C. Eddie; 1 ♂ (ESV 6020), Carnarvon NP, Mt Moffat Section, Queensland, Australia, 25°04'18"S 147°52'43"E, 20.i.1999, C. Eddie, R. Johnston, & A. Young; 1 ♂ (AMNH LP 2341), Carnarvon NP, Mt Moffat section, SE side of road between mailboxes and homestead, Queensland, Australia, 25°02'37"S 147°54'39"E, 14.x.2002, C. Eddie; 1 ♂ (AMNH LP 2879), Carnarvon NP, Mt Moffat section, SE side of road between mailboxes and homestead, Queensland, Australia, 25°02'37"S 147°54'39"E, 13.x.2002, C. Eddie; 1 ♀ (ESV 6021), Carnarvon NP, Mt Moffat Section, Queensland, Australia, 25°06'51"S 147°51'36"E, 30.iii.–8.iv.1998, C. Eddie & A. Dudley.

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Appendix 1. (continued)

Urodacus manicatus (Thorell, 1876): 1 ♂, 1 ♀ (ESV 6022), Grampians Ranges, Victoria, Australia, 37°01'02"S 142°25'28"E, 5.xii.1998, E. S. Volschenk & J. Tregear; 1 ♂ (AMNH LP 938, 939), 1 ♂, 1 juv. (AMNH LP 941), 1 ♀ (AMNH LP 940), Canberra, Australian Capital Territory, Australia, xii.1997, H. Wilson; 1 ♀ (AMNH LP 1537), 1 ♀ (AMNH LP 1657), Overland corner, South Australia, Australia, 25.ix.1997, E. S. Volschenk; 1 ♂ (AMNH LP 1538), Rocky River, Kangaroo I., Australia, 1986, N. A. Locket; 3 ♂, 5 ♀, 2 subad. ♀ (CAS), Black Mtn, ACT, Australia, 760 m, 9.xii.1962, E. S. Ross & D. Q. Cavagnaro.

Urodacus mckenziei Volschenk, Smith & Harvey, 2000: Paratype ♀ (WAM 98/1592), Peron Homestead, Shark Bay, Western Australia, Australia, iv.1998, T. Tischler; 2 ♂ (WAM 99/1128, 99/1147), Francois Peron NP, Western Australia, Australia, 25°52'31"S 113°32'59"E, 17.i–25.v.1995, M. S. Harvey, *et al.*; 1 ♀ (AMNH LP 2689), Peron Homestead, 100 m W of Visitor's Centre, Western Australia, Australia, 25°50'S 113°33'E, iv.1996, T. Tischler.

Urodacus megamastigus L. E. Koch, 1977: 1 ♂ (WAM), Roy Hill, Western Australia, Australia, 18.v.1982, A. M. Douglas; 1 ♂ (WAM), Millstream, Western Australia, Australia, 8.v. 1986, D. King, *et al.*; 1 ♂ (WAM 99/1212), Mt Brockman Station, Western Australia, Australia, 22°18'27"S 117°15'27"E, 11.v. 1999, P. J. West; 1 ♂ (WAM T40692), Mt Brockman (Namuldi mine, Hamersley Iron) Western Australia, Australia, 22°18'38"S 117°47'47"E, Anstee.

Urodacus novaehollandiae Peters, 1861: Australia: 2 ♂, 1 ♀, 1 subad. ♂, 1 juv. ♂ (ZMH), Lion Mill, near Perth, 22.v.1905, Michaelsen; 1 ♂ (ZMH), Karrakatta, near Perth, 28.v.1905, Michaelsen; 1 ♂, 1 subad. ♂, 1 juv. ♂ (ZMH), Wooroloo, near Perth, 29.v.1905, Michaelsen; 1 ♂, 1 subad. ♀, 4 juv. ♂ (ZMH), York, 11.viii.1905, Michaelsen; 1 ♂ (AMNH LP 1540), 1 ♂ (AMNH LP 1658), Jarrahdale, Western Australia, Australia, 25.ii.1998, E. S. Volschenk; 1 ♀ (AMNH LP 2121), Perth Hills (Darling Escarpment), Western Australia, Australia, i.2002.

Urodacus planimanus Pocock, 1893: 1 ♂, 1 ♀, 1 juv. ♀ (ZMH), Jarrahdale, near Perth, Australia, 1905, Michaelsen; 1 ♂ ESV6023, Jarrahdale, Western Australia, 20.iii. 1998, E. S. Volschenk; 1 ♂, 3 ♀ (WAM 69/1/4), Roleystone, Western Australia, Australia, 1968, S. Stevans; 1 ♂, 1 juv. (WAM 97/2662, 97/2663), Mt Cooke (nr Summit), Western Australia, Australia, 32.255°S 116.18°E, 7.viii. 1990, M. Harvey, J. Waldock & M. Peterson; 1 ♀ (WAM 68/298), Mt Cooke, Western Australia, Australia, 26.vii.1967, M. Parking & M. Porter; 1 ♂ (AMNH LP 1539), 1 ♂ (AMNH LP 1661), Jarrahdale, Western Australia, Australia, 25.ii.1998, E. S. Volschenk; 1 ♂, 1 subad. ♀ (AMNH LP 2123), Jarrahdale, Western Australia, Australia, 32°17'35"S 116°10'39"E, 2.vi.2001, E. S. Volschenk; 1 ♂ (WAM 68–297), Mt Cooke, Western Australia, Australia, 26.vii.1967, M. Parkin & M. Porter.

Urodacus varians Glauert, 1963: 3 ♂ (WAM T51161, T41169, T41163), Meridian (Wildcat oilwell), 30 mi. E of Willara Hill, Western Australia, Australia, 19°03'S 122°22'E, 25.v.1982, A.M. Douglas.

Urodacus yaschenkoi (Birula, 1903): 1 ♂ (AMNH LP 1541), 1 subad. ♀ (AMNH LP 1659), Berri, South Australia, Australia, 24.ix.1997, N. A. Locket & E. S. Volschenk; 1 ♀ (AMNH LP 2120), Berri, South Australia, Australia, 34°12'40.5"S 140°12'42.4"E, 10.xii.1998, E. S. Volschenk.

Vaejovidae Thorell, 1876

Uroctonus grahami Gertsch & Soleglad 1972: Holotype ♀ (AMNH), Samwell cave (main entrance), Shasta County, California, USA, 27.vi.1960, R. E. Graham. Additional material: 1 juv. (AMNH), same locality data as holotype, 5.vi.1957, R. de Saussure.

Vaejovis gracilis Gertsch & Soleglad, 1972: México: Veracruz: Holotype juv. (AMNH), Cueva de Atoyac, Atoyac, 6.viii.1969, S. & J. P. Peck. Additional material: 1 ♂ (AMNH), Sótano de las Golondrinas, near Potrero, 8.i.1977, A. Grubbs; 2 ad. (UNAM), Paraje Nuevo, Cueva del Ojo de Agua de Tlilapan, Tlilapan.

Appendix 2. Characters and character states employed in cladistic analysis of nine species of Urodacidae Pocock, 1893 and six outgroup taxa
 Character states are scored 0–3, * (polymorphic); ? (unknown); and – (inapplicable). Eight uninformative characters, indicated by †, were excluded from all analyses. Unknown states in *Aops oncodactylus*, gen. et sp. nov. are attributed to the fact that the adults are presently unknown. Previous character numbers as follows (author/number): P00 = Prendini (2000), P03 = Prendini (2003), PCW03 = Prendini *et al.* (2003).

- (1) *Cheliceral movable finger, distal external and distal internal teeth*: unequal, with distal external tooth considerably smaller than distal internal tooth, aligned longitudinally and not opposable (0); unequal, with distal external tooth noticeably smaller than distal internal tooth, and opposable, i.e. forming a bicuspid (1); subequal, with distal external tooth only slightly smaller than distal internal tooth, and opposable, i.e. forming a bicuspid (2). Previous characters: P00/11, P03/10, PCW03/2.
- (†2) *Cheliceral movable finger, number of subdistal teeth*: two (0); one (1). Previous characters: P00/10, P03/9.
- (3) *Cheliceral fingers, secondary serrations*: absent (0); present (1). Previous characters: P00/12.
- (4) *Carapace, median notch in anterior margin*: absent (0); shallow (1); strongly excavated (2). Previous characters: P00/3, P03/3, PCW03/5.
- (5) *Carapace, lateral ocelli, number of pairs*: three (0); two (1); none (2). Previous characters: P00/1, P03/1.
- (6) *Carapace, median longitudinal furrow*: broad, shallow, without suture (0); narrow, suturiform (1). Previous characters: P00/4, P03/4.
- (7) *Carapace, median ocular tubercle*: raised (0); shallow (1); none (2). Previous characters: P00/2, P03/2.
- (8) *Carapace, posterior sutures*: absent (0); present (1). Previous characters: P00/7, P03/6.
- (9) *Prosoma, mesosoma, metasoma and legs, nongranular surfaces*: smooth (0); distinctly punctate (1). Previous characters: P00/8, P03/7.
- (10) *Pedipalp chela fingers, terminal teeth interlocking when closed*: unevenly, with movable finger displaced to exterior, with notch near tip of fixed finger (0); evenly, movable finger not displaced to exterior (1). Previous characters: PCW03/23 [merged states 1 and 2].
- (11) *Pedipalp chela fingers, dentate margins*: entire (0); markedly scalloped (1). Previous characters: P00/34, P03/28.
- (12) *Pedipalp chela fingers, number of rows of primary denticles*: single (0); double along entire length, but often fused basally (1); multiple (more than two), at least basally, sometimes becoming single or double distally (2). Previous characters: P00/33, P03/27.
- (13) *Pedipalp chela movable finger, lobe (♂)*: absent or at most weakly developed, close to base of movable finger and lacking an obvious notch in fixed finger (0); well developed, almost midway along movable finger (if dentate margin markedly scalloped, second lobe more strongly developed than other lobes on the movable finger), with a distinct notch in fixed finger, lobe rounded dorsally and lacking a sharp conical tooth (1); unknown (?). Previous characters: P00/35, P03/29, PCW03/25 (part) [corrected state in *Nebo*].
- (14) *Pedipalp chela manus, dorsal secondary carina*: obsolete (0); distinct (1). Previous characters: P00/22, P03/18.
- (†15) *Pedipalp chela manus, ventroexternal carina*: oblique to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards (almost connecting) internal movable finger condyle (0); parallel to longitudinal axis of chela, distal edge disconnected from external movable finger condyle and directed towards a point between external and internal movable finger condyles, but closer to external condyle (1). Previous characters: P00/27, P03/21.
- (16) *Pedipalp chela manus, ventrointernal carina*: equally developed as internomedian carina (0); more strongly developed than internomedian carina, which may be obsolete (1). Previous characters: P00/29, P03/23, PCW03/36.
- (17) *Pedipalp patella, anterior process*: absent (0); present (1). Previous characters: P00/18, P03/14.
- (18) *Pedipalp patella, dorso-external carina*: distinct (0); obsolete (1). Previous characters: P00/16, P03/12 [corrected state in *U. yaschenko*].
- (19) *Pedipalp chela, position trichobothrium* it: manus or base of fixed finger (0); midway (*Hemiscorpius*) to distal (*Nebo*) along fixed finger (1). Previous characters: P00/47, P03/38.
- (†20) *Pedipalp chela, position trichobothrium dsb*: below *db–dst* axis (0); in line with *db–dst* axis (1). Previous characters: P00/60, P03/50.
- (21) *Pedipalp chela, position trichobothrium db*: dorsal surface (0); internal surface (1). Previous characters: P00/59, P03/49.
- (22) *Pedipalp chela, position trichobothrium esb*: manus, behind point of articulation between fixed and movable fingers and below *eb–est–et* axis (0); midway along fixed finger, in line with *eb–est–et* axis (1). Previous characters: P00/62, P03/52.
- (23) *Pedipalp chela, external surface with accessory trichobothria*: absent (0); present (1). Previous characters: P00/53, P03/44.
- (24) *Pedipalp chela, position trichobothrium Dt*: manus, at basal end (0); manus, mid-length or slightly less than mid-length (1); manus, distal half, near base of fixed finger (2); proximal end of fixed finger (3). Previous characters: P00/52, P03/43.
- (25) *Pedipalp chela, position trichobothrium Db*: external surface (0); dorsal surface (1). Previous characters: P00/51, P03/42.
- (26) *Pedipalp chela, number V trichobothria*: 4 (0); 6 or more (1). Previous characters: P00/49, P03/40, PCW03/51.
- (†27) *Pedipalp chela, position trichobothria V₁–V₃*: evenly spaced, distance *V₁–V₂* similar to distance *V₂–V₃* (0); unevenly spaced, distance *V₁–V₂* much less than distance *V₂–V₃* (1); inapplicable (–). Previous characters: P00/50, P03/41.
- (28) *Pedipalp chela, position trichobothria V₂–V₄*: evenly spaced, distance *V₃–V₄* similar to distance *V₂–V₃* (0); unevenly spaced, distance *V₃–V₄* much less than distance *V₂–V₃* (1); inapplicable (–). Previous characters: P00/50, P03/41, PCW03/52.
- (29) *Pedipalp patella, number e trichobothria*: 13 (0); 15 or more (1). Previous characters: P00/45, P03/36, PCW03/54 (part).
- (30) *Pedipalp patella, number v trichobothria*: single row of 3 (0); single row of 4–10 (1). Previous characters: P00/43, P03/34, PCW03/55.
- (31) *Legs I and II, basitarsi, retrolateral margins, setation*: no macrosetae (0); row of three or more spiniform macrosetae (1); comb-like row of three or more setiform macrosetae that may or may not be interspersed with slender spiniform macrosetae (2). Previous characters: PCW03/67 (merged P00/72, P00/73 and P03/59).
- (32) *Legs, telotarsi, ventrosubmedian setae type*: stout, spiniform (0); slender, subspiniform (1). Previous characters: P00/70, P03/58.
- (†33) *Legs IV, telotarsi, prolateral row of ventrosubmedian spiniform setae*: present (0); absent (1). Previous characters: P00/71, PCW03/71 (part).
- (34) *Legs, telotarsi, well developed ventromedian row of setae*: setiform (0); spiniform (1); absent (2). Previous characters: P00/68, P03/56.
- (35) *Legs, telotarsi, laterodistal lobes*: truncated, base of median dorsal lobe flush (0); rounded, notches at base of median dorsal lobe (1). Previous characters: P00/65, P03/54.
- (†36) *Embryonic development*: apoikogenic (0); katoikogenic (1); unknown (?). Previous characters: P00/77, P03/62.
- (37) *Hemispermaphore, sclerotised mating plug*: absent (0); present (1); unknown (?). Previous characters: P00/92, P03/75.
- (38) *Metasomal segments (♂)*: similar to or slightly longer than ♀ (0); much longer than ♀ (1); unknown (?).

(continued next page)

Appendix 2. (continued)

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- (39) *Metasomal segments I–IV, dorsolateral carinae*: present and distinct on at least some segments (0); absent or obsolete on all segments (1).
- (40) *Metasomal segment V, dorsolateral carinae*: present and distinct (0); absent or obsolete (1). Previous characters: PCW03/77.
- (41) *Metasomal segment I, median lateral carinae* (♂): present and distinct (0); absent or obsolete (1); unknown (?).
- (42) *Metasomal segment I, median lateral carinae* (♀): present and distinct (0); absent or obsolete (1).
- (43) *Metasomal segment V, median lateral carinae*: present and distinct (0); absent or obsolete (1).
- (†44) *Metasomal segment V, ventrolateral carinae*: present and distinct (0); absent or obsolete (1). [corrected entries in *L. josehermana*].
- (45) *Metasomal segments I–IV, ventral carinae*: absent on all segments (0); present and distinct on at least some segments (1). Previous characters: P00/95, PCW03/80 (part).
- (46) *Metasomal segments I–IV, ventral carinae*: paired ventrosubmedian carinae (0); single ventromedian carina (1); inapplicable (–). Previous characters: P00/95, P03/77.
- (†47) *Metasomal segment V, ventromedian carina*: present and distinct (0); absent or obsolete (1). [corrected entries in *L. josehermana*].
- (48) *Metasomal segment V, ventromedian carina distal portion*: straight (0); breaking up into numerous granules (1); bifurcating (2); inapplicable (–). Previous characters: P00/99, P03/81, PCW03/86 [corrected entries in *L. josehermana*].
- (49) *Telson vesicle, shape* (♂): unmodified (0); elongated, with pair of distal lobes (1); elongated, without pair of distal lobes (2); unknown (?). Previous characters: P00/109, P03/89.
- (50) *Telson vesicle, shape* (♀): unmodified (0); laterally compressed (1); unknown (?). Previous characters: P00/107, P03/87.
- (51) *Telson vesicle, shape* (♀): unmodified (0); laterally compressed (1). Previous characters: P00/108, P03/88.
- (52) *Telson vesicle, anterodorsal lateral lobes*: present (0); absent (1). Previous characters: P00/110, P03/90.
- (53) *Telson vesicle, surface macrosculpture*: entirely smooth (0); longitudinal rows of granules on ventral and lateral surfaces (1); 2 or more longitudinal rows of granules on all or part of ventral surface only (2). Previous characters: P00/111 (modified), P03/91, PCW03/89.
- (54) *Telson, venom glands*: complex (0); simple (1). Previous characters: P00/113, P03/93.
- (55) *Telson, aculeus*: long, shallowly curved (0); very short, sharply curved (1). Previous characters: P00/105, P03/85.
- (56) *Burrows constructed*: absent (0); present (1); unknown (?). Previous characters: PCW03/104, PCW03/105 (modified).
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