Phylogeny of *Parabuthus* (Scorpiones, Buthidae)

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A cladistic analysis of the 20 southern African species of *Parabuthus* Pocock, 1890 (Scorpiones, Buthidae) and five of the eight north-eastern African and Arabian species is presented, based on 53 characters, mostly of the adult morphology. The resultant topology is largely congruent with Lamoral's (1978) unpublished topology for 14 Namibian species. Monophyly of the genus *Parabuthus* is supported, but monophyly of the disjunct southern African vs. north-eastern African and Arabian species is unsupported. The implications of the cladogram for understanding ecological specialization in *Parabuthus*, Afrotropical arid biogeography and *Parabuthus* envenomation are discussed.

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Introduction

Parabuthus Pocock, 1890 is the fifth largest genus in the diverse, cosmopolitan scorpion family Buthidae (Fet & Lowe 2000). The genus includes the world's largest buthid scorpions, e.g. *Parabuthus villosus* (Peters, 1862), *Parabuthus transvaalicus* Purcell, 1899 and *Parabuthus schlechteri* Purcell, 1899, which can reach a length of 140 mm and a mass of 14 g (Newlands 1974a, 1978a). The genus also includes the world's only known diurnal buthid, *P. villosus* (Newlands 1974a; Harington 1982).

Species of *Parabuthus* (with one exception) are unique among scorpions in possessing a stridulatory region, composed of fine to coarse granules, sometimes forming transverse ridges, on the dorsal surfaces of tergite VII, metasomal segments I, II and, to a lesser extent, III (Newlands 1974a, 1978a; Lamoral 1977, 1979, 1980). This stridulatory region is used to make an audible sound, known as 'stridulation', when the scorpion is alarmed, by repeatedly scraping the aculeus (sting) across the granules or ridges (Hewitt 1913, 1918; Lawrence 1928; Alexander 1958; Dumortier 1964; Newlands 1974a, 1978a; McCormick & Polis 1990).

Parabuthus displays a classic 'arid corridor' pattern of distribution (Balinsky 1962), occurring in two disjunct geographical regions — arid south-western Africa, and arid north-eastern Africa and the Arabian Peninsula (Fig. 1). During past periods of increased aridity, such as the Pliocene and the Upper Pleistocene (Tankard & Rogers 1978; Lancaster 1981, 1984; Ward *et al*. 1983), these two areas were contiguous, allowing dispersal or range expansion of arid-adapted taxa between them. As evidence for their arid requirements, the southern African species of *Parabuthus* are today restricted to areas receiving less than 600 mm of rainfall per annum (Newlands 1978a,b).

In addition to their dependence on aridity, many *Parabuthus* species are also specialized for life on particular substrata. Several species (e.g. *Parabuthus distridor* Lamoral, 1980, *Parabuthus kuanyamarum* Monard, 1937 and *Parabuthus kalaharicus* Lamoral, 1977) are restricted to the sand dune systems of the Namib and Kalahari deserts, and exhibit ecomorphological adaptations to facilitate locomotion and burrowing in the soft sand (Lamoral 1977, 1979, 1980). There are also some species that seem to be partially specialized for living in rocky areas.

All species of *Parabuthus* are adapted for a burrowing existence (Newlands 1974b, 1978a,b). Burrows are constructed in open ground, at the base of shrubs or under stones (Newlands 1974b, 1978a,b; Eastwood 1977, 1978b; Lamoral 1979; Newlands & Martindale 1980; Harington 1984; Prendini 2000a). The evolution of burrowing behaviour, and the specialized ecomorphological adaptations associated with it, may explain why the genus *Parabuthus* is so speciose. 'Adaptive radiation' in *Parabuthus* can be explained by the 'effect hypothesis of macroevolution' (Vrba 1980), where repeated allopatric speciation is the predicted outcome of vicariance, promoted by stenotopic habitat requirements, in this case 'substratum specialization' (Prendini, in press).

The dependence of *Parabuthus* species on aridity has some fortunate implications for the geographical distribution of scorpionism in southern Africa. *Parabuthus* includes some of the

Fig. 1 Map of Africa and the Arabian Peninsula, showing approximate distributional range of *Parabuthus* (shaded), countries from which *Parabuthus* species have been recorded and the numbers of species recorded in each.

world's most dangerously venomous scorpions, envenomation by which is a significant cause of morbidity and, in some instances, mortality in the sparsely populated arid to semi-arid western regions of southern Africa (Müller 1993; Bergman 1997a,b). However, since the more densely populated eastern regions, which receive higher rainfall, are devoid of *Parabuthus* (Prendini 1995), the incidence of scorpion envenomation in southern Africa is lower than expected.

The medical importance of *Parabuthus* has received increasing attention during the past 25 years (Newlands 1974a, 1978a; Newlands & Martindale 1980; Petersen 1987; Hill 1990; Saunders & Morar 1990; Lee 1991; Müller 1993; FitzPatrick 1994; Bergman 1995, 1997a,b; Swerts *et al.* 1997; Debont *et al.* 1998; Tytgat *et al.* 1998). *Parabuthus granulatus* (Ehrenberg, 1831) has been identified as the species responsible for the highest incidence of scorpion envenomation in southern Africa (Müller 1993). Mortalities attributed to envenomation by this species have been reported from Botswana (Petersen 1987) and the Western Cape Province of South Africa (Müller 1993). *Parabuthus mossambicensis* (Peters, 1861) and *P. transvaalicus* have also been implicated in severe cases of envenomation, sometimes resulting in mortality, in Zimbabwe (Bergman 1995, 1997a,b). Among the north-eastern African and Arabian species, *Parabuthus leiosoma* (Ehrenberg, 1828) has been implicated in serious envenomations (Cilli & Corazzi 1946; Goyffon & Vachon 1979).

Due to their medical importance, renewed interest has developed in the systematics of these scorpions, largely neglected since Lamoral (1979) revised the species occurring in Namibia. Recently, FitzPatrick (1994) reviewed the species occurring in Zimbabwe and Prendini (2000a) described a new species from Namibia. Prendini (in press) subsequently reviewed the southern African species, and provided an illustrated key to their identification. *Parabuthus* currently includes 28 species, 20 of which are endemic to the southern African subregion (Fet & Lowe 2000). In contrast with the southern African species, the eight north-eastern African and Arabian species of *Parabuthus* remain poorly known, albeit extensively catalogued (e.g. Birula 1915; Vachon 1966, 1979; Pérez 1974; Lamoral & Reynders 1975; El-Hennawy 1992; Fet & Lowe 2000).

Knowledge of the phylogenetic relationships among species of *Parabuthus* is limited to an unpublished cladogram by Lamoral (1978), based on a manual cladistic analysis of 19 morphological characters scored for the 14 Namibian species recognized at the time (Fig. 2). Renewed attention to *Parabuthus* systematics has culminated in a re-investigation of *Parabuthus* phylogeny. In the present contribution, the results of a cladistic analysis of the 20 southern African species and five of the eight north-eastern African and Arabian species, including the type species, *P. leiosoma*, are presented. This analysis is based on 53 characters, mostly of adult morphology, including characters from Lamoral's (1978) unpublished data matrix (Table 1). The aims of this study were to test the monophyly of *Parabuthus*; to investigate whether the southern African vs. north-eastern African and Arabian species are monophyletic clades; to investigate the evolution of psammophily in the genus; and to identify species that are closely related to the dangerously venomous species, especially *P. granulatus*.

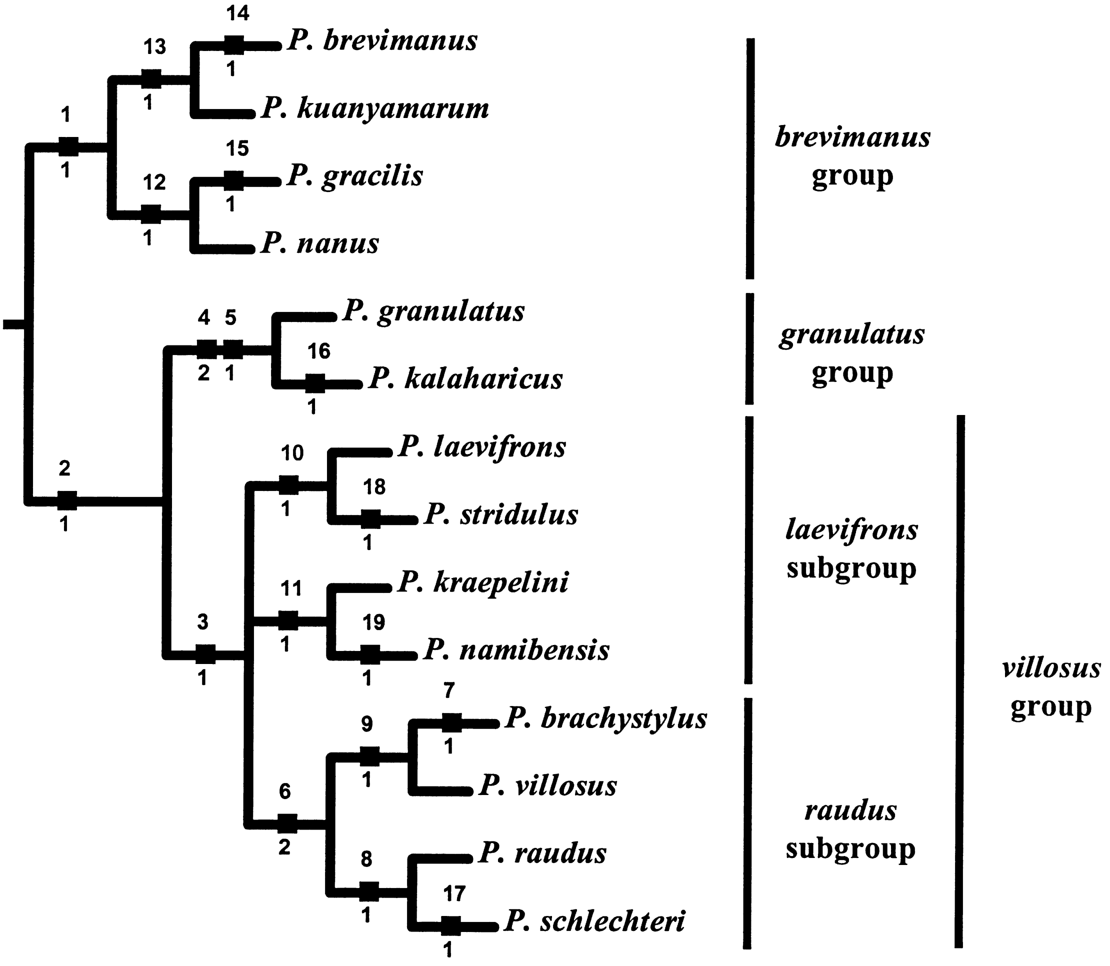

Fig. 2 Lamoral's (1978: fig 5.3) unpublished cladogram for the 14 Namibian species of *Parabuthus* recognized at the time. *Parabuthus brachystylus* Lawrence, 1928 has since been synonymized with *P. villosus* (Prendini, in press). This tree was produced by hand from a matrix of 19 characters (Table 1). Characters were polarized *a priori* using outgroup comparison, the 'common is primitive' criterion and the 'structurally complex or ecologically specialized is advanced' criterion (Lamoral 1978: 269–270, 276–278). Solid bars indicate apomorphic character states, hypothesized by Lamoral. The figure above each character bar gives the character number, whereas the figure below gives the character state.

Table 1 Lamoral's (1978: table 5.2) unpublished character matrix and character list for the 14 species of *Parabuthus* recognized from Namibia at the time. *P. brachystylus* has since been synonymized with *P. villosus* (Prendini, in press). Characters were polarized *a priori* using outgroup comparison, the 'common is primitive' criterion, and the 'structurally complex or ecologically specialized is advanced' criterion (Lamoral 1978: 269–270, 276–278), such that the state in the hypothetical outgroup is plesiomorphic in each case. Three multistate characters were treated as ordered (additive). Terminology follows Lamoral (1978, 1979), τ denotes trichobothrium and lmf/lhb denotes length movable finger/length handback.

Outgroup	00000	00000	00000	0100
P. brachystylus	01100	21010	10000	0100
P. brevimanus	10120	01001	10111	0200
P. gracilis	10120	01001	11001	0001
P. granulatus	01021	00000	10010	0000
P. kalaharicus	01021	00000	10001	1001
P. kraepelini	01100	11000	10010	1200
P. kuanyamarum	10120	01001	00101	0001
P. laevifrons	01110	11001	00011	0000
P. namibensis	01100	11000	10110	0201
P. nanus	10020	01001	11000	0001
P. raudus	01100	20100	10000	1000
P. schlechteri	01100	20100	10000	0200
P. stridulus	01110	11001	00001	0011
P. villosus	01100	20010	10000	0100

1 Cauda IV, ventral and lateral keels: present (0); absent (1).

2 Adult general size: small (0); large (1).

3 Sexual dimorphism in shape of proximal middle lamella of pectines in adults: virtually absent (0); present and distinct (1).

4 Cauda IV, median lateral keel: present, well developed and distinct (0); present but poorly developed (1); absent to posteriorly [*sic*, this should read 'proximally'] obsolete (2). [additive]

5 Telson vesicle: not reduced in size (0); reduced in size (1).

6 Cauda V, accessory dorsal crest in adult male: absent (0); present, poorly developed with blunt tubercles (1); present, always distinct and with spiniform tubercles (2). [additive]

7 Cauda II, dorsal stridulatory area: not reaching posterior margin (0); reaching posterior margin (1).

8 Caudal segments width: cauda I wider than IV (0); cauda I narrower than IV (1).

9 Cauda I–V and telson: sparsely pilose (0); densely pilose (1).

10 Pedipalp tibia, τ esb_2: distinctly distal to esb_1 (0); level with or slightly distal to esb_1 (1).

11 Cauda IV–V, lateral intercarinal surfaces: smooth (0); granular (1).

12 Sternites: smooth (0); punctate (1).

13 Pedipalp femur, τ e_1: level with or distal to τ d_5 (0); almost halfway between trichobothria d_4 and d_5 (1).

14 Cauda V, distal half of ventrolateral keels: with spinose processes (0); with lobate processes (1).

15 Pedipalp hand movable finger length of female: long (lmf/lhb ±2.00) (0); short (lmf/lhb ±1.50) (1).

16 Tergites I–VI, median keels: present (0); absent (1).

17 Cauda V, ventrolateral keels: converging distally (0); subparallel distally (1); diverging distally (2). [additive]

18 Telson vesicle dorsoproximal surface: deeply excavated along longitudinal half (0); very shallowly excavated (1).

19 Legs IV length: moderately long (0); very long (1).

Materials and methods

Lamoral's data reanalysed

Lamoral's (1978) data matrix (Table 1) was reanalysed computationally before embarking on the new analysis with additional taxa and characters. This reanalysis was undertaken by scoring a hypothetical outgroup for the states originally postulated to be plesiomorphic by Lamoral, according to outgroup comparison, the 'common is primitive' criterion and the 'structurally complex or ecologically specialized is advanced' criterion (Lamoral 1978: 269–270, 276–278). As in Lamoral's original manual analysis, characters were weighted equally, and the three multistate characters were ordered, i.e. treated additively (Farris 1970).

Taxa

All 20 southern African species of *Parabuthus* and five of the eight north-eastern African and Arabian species were included in the new analysis (Table 2). The following three north-eastern African and Arabian species were omitted from the analysis, as specimens could not be obtained for examination: *Parabuthus maximus* Werner, 1913, from Tanzania; *Parabuthus mixtus* Borelli, 1925, from Somalia; *Parabuthus zavattarii* Caporiacco, 1939, also from Somalia. The taxonomic status of these three species is presently unknown. The remaining five species (including the type species of *Parabuthus*) were considered sufficiently representative of the north-eastern African and Arabian species to test the monophyly of the southern African species and of the genus as a whole.

In an effort to ensure consistent treatment and repeatability, characters used in the analysis were critically examined in actual specimens, excepting the male of *Parabuthus calvus* Purcell, 1898, for which character entries were obtained from Purcell's (1898) original description. *P. calvus* is presently known from only a few female specimens. The holotype male, formerly in the South African Museum (SAMC, Cape Town, South Africa) collection, is lost (M. Cochrane, personal communication).

Contingent upon the availability of specimens, an attempt was made to assess the extent of intraspecific variation in characters by including specimens from populations with known polymorphisms in the sample, and by including specimens from extremes of the geographical ranges of widespread species.

Characters were polarized by means of outgroup comparison (Watrous & Wheeler 1981; Farris 1982; Nixon & Carpenter 1993). Two Afrotropical buthid genera, *Grosphus* Simon, 1888, from Madagascar, and *Uroplectes* Peters, 1861, from southern and central Africa, were included as outgroup taxa. These genera have been considered to be closely related to *Parabuthus* since Pocock (1890) noted the similarity between the lobate proximal median lamella of the pectines

Table 2 Material examined for cladistic analysis of the genus *Parabuthus*. Depositories for specimens are abbreviated as follows: AMNH, American Museum of Natural History (New York, NY, USA); BMNH, The Natural History Museum (London, UK); NMSA, Natal Museum (Pietermaritzburg, South Africa); NMNW, National Museum of Namibia (Windhoek, Namibia); SAMC, South African Museum (Cape Town, South Africa); TMSA, Transvaal Museum (Pretoria, South Africa); USNM, National Museum of Natural History, Smithsonian Institution (Washington DC, USA).

Outgroups
Grosphus madagascariensis (Gervais, 1843): 3 ♂, ♀ (AMNH)
Uroplectes triangulifer (Thorell, 1876): ♂, ♀ (SAMC B8227); ♂ (SAMC C3754); 4 ♀ (AMNH)

North-eastern African and Arabian *Parabuthus*
P. granimanus Pocock, 1895: ♂, ♀ syntypes (BMNH 1893.1.11.48–54); 2 ♀ (BMNH 1895.6.1.45); juv. ♀ (BMNH 1893.1.11.48–54)
P. heterurus Pocock, 1899: ♂, ♀ syntypes (BMNH 1897.11.10.9–10); ♂ (BMNH 1949.12.19.5); ♀ (BMNH 1939.3.16.17–18)
P. hunteri Pocock, 1895: ♂ syntype (BMNH 1892.12.22.1); ♂ syntype (BMNH 1894.11.2.41–50); ♂, ♀ syntypes (BMNH 1894.11.2.52–60)
P. leiosoma (Ehrenberg, 1828): ♂, ♀ (AMNH); ♂, ♀, juv. ♂ (SAMC 409.60); ♂, ♀ (SAMC 4060); ♀, juv. ♂, juv. ♀ (SAMC 6343); subad. ♀, 3 juv. ♂, 6 juv. ♀ (USNM)
P. pallidus Pocock, 1895: ♂, ♀ syntypes (BMNH 1890.3.15.10–11); 2 ♀ (BMNH); 3 ♀ (AMNH)

Southern African *Parabuthus*
P. brevimanus (Thorell, 1876): 3 ♂, ♀, juv. ♀ (NMSA 10442); 20 ♂, 5 ♀, 2 subad. ♂, 2 juv. ♂, 8 juv. ♀ (NMSA 10819)
P. calvus Purcell, 1898: ♀ (AMNH); ♀ (SAMC 2228); ♀ (SAMC C4615)
P. capensis (Ehrenberg, 1831): ♂ (NMNW 1509); 2 ♂, 3 ♀, 4 subad. ♂, 2 subad. ♀, 3 juv. ♂, 2 juv. ♀ (NMSA 10358); 5 ♂, 2 ♀, 2 juv. ♀ (SAMC 12010); ♀, juv. ♂ (SAMC C1618); ♂, 2 subad. ♀, subad. ♂ [black form] (SAMC C74)
P. distridor Lamoral, 1980: 12 ♂, 2 ♀, juv. ♂, juv. ♀ paratypes (NMSA 11305); ♂ paratype (NMSA 11436); ♀ paratype (NMSA 11435); 2 ♂, ♀ (SAMC C4604)
P. gracilis Lamoral, 1979: 5 ♂, 2 ♀, 5 juv. paratypes (NMSA 10848); 3 ♂, ♀, 4 juv. ♂ paratypes (NMSA 10859)
P. granulatus (Ehrenberg, 1831): 9 ♂, 2 ♀, juv. ♂, juv. ♀ (NMSA 10731); 4 ♂, 2 ♀, 3 subad. ♀, 9 juv. (NMSA 10836)
P. kalaharicus Lamoral, 1977: 9 ♂ paratypes (NMSA 10947); 3 ♂ paratypes (SAMC C213); 2 ♀ paratypes (NMSA 10946)
P. kraepelini Werner, 1902: 2 ♂, 2 ♀ (SAMC C4605); 2 ♀ (NMSA 10019); ♀ (NMSA 10022); subad. ♂ (NMSA 10850)
P. kuanyamarum Monard, 1937: 13 ♂, ♀, 7 juv. (NMSA 10813); 3 ♀ (NMSA 13972)
P. laevifrons (Simon, 1888): 2 ♂, ♀, juv. ♀ (NMSA 10509); ♂, 4 ♀, 2 subad. ♀, 3 juv. ♂, 3 juv. ♀ (NMSA 10521)
P. mossambicensis (Peters, 1861): ♂ (NMSA 10088); ♂ (SAMC C4606); 3 ♂ (SAMC C4607); 3 ♀ (SAMC C4608)
P. muelleri Prendini, 2000: ♀ holotype (NMNW 1854); ♀ paratype (SAMC C4514)
P. namibensis Lamoral, 1979: ♀ holotype, ♂ paratype (NMSA 2184); ♂ (NMNW 896); ♀, juv. ♂ (NMNW 845)
P. nanus Lamoral, 1979: ♂ paratype (NMSA 10703); ♂, ♀ paratypes (NMSA 10772); ♂, ♀ paratypes (NMSA 11304)
P. planicauda (Pocock, 1889): ♀ syntype (BMNH 1870.26); ♂, ♀ (TMSA 8520); 4 ♂, 6 ♀, 2 subad. ♂, juv. ♀ (SAMC 1734); 15 ♂, 28 ♀ (SAMC 12008); 6 ♀ (SAMC B1748)
P. raudus (Simon, 1888): 8 ♂, 5 ♀, subad. ♀, 3 juv. ♂, juv. ♀ (NMSA 10817); 3 ♂, 2 ♀ (NMSA 10924); ♀, 2 subad. ♂ (NMSA 10931)
P. schlechteri Purcell, 1899: ♂, ♀ (SAMC C4609); ♂ (SAMC C4610); ♂, ♀ (NMSA 11406); ♀, subad. ♂, subad. ♀ (NMSA 10730)
P. stridulus Hewitt, 1913: ♂ holotype (TMSA 1868); ♂, subad. ♂ (NMSA 10501); ♂ (NMSA 10904); ♂, ♀ (SAMC C4611); ♂, 2 ♀ (NMSA 10573); ♀ (NMSA 10907)
P. transvaalicus Purcell, 1899: 2 ♀ syntypes (SAMC 3003); ♂, ♀ (SAMC 4612); ♂ (SAMC C4613); ♀ (NMSA 11449); ♀ (NMSA 13899)
P. villosus (Peters, 1862): 2 ♂ (SAMC C4614); ♂, 3 ♀ (NMSA 10805); ♀ (NMSA 10738); ♀ (NMSA 10833); subad. ♂ (NMSA 10913)

in most adult female *Parabuthus* and the enlarged basal pectinal tooth in adult female *Grosphus* and *Uroplectes*, e.g. see Kraepelin (1908a) and Werner (1934). Pocock (1890: 125) stated: 'This dilatation, although it appears to belong to the shaft of the pecten, results, I am now inclined to think, from the fusion of the enlarged basal tooth with the sclerite that supported it. If this be so, the character can be directly derived from what is seen in *Grosphus*, where the tooth is enlarged but still free, and it unmistakably points *Grosphus* as the ancestor of *Parabuthus*.' In Pocock's (1890: 128) hypothetical tree diagram, *Grosphus*, *Uroplectes*, *Lepreus* — a junior synonym of *Uroplectes* (Karsch 1879) — and *Parabuthus* were placed in the following arrangement: (*Parabuthus* (*Grosphus* (*Uroplectes Lepreus*))). Recent investigations of scorpion higher phylogeny, based on molecular data (L. Prendini & W.C. Wheeler, in preparation), have similarly placed *Grosphus* and *Uroplectes* as the closest relatives of *Parabuthus*. *Grosphus madagascariensis* (Gervais, 1843) and *Uroplectes triangulifer* (Thorell, 1876) were scored as exemplars for these genera (Table 2).

Characters

Fifty-one characters of the adult morphology and two behavioural characters were scored across the 27 species for the cladistic analysis (Tables 3 and 4). Eighteen of these characters were adopted from Lamoral's (1978) unpublished data matrix (Table 1), whereas the remaining characters are new or were collated from the literature (Appendix 1).

Examination of specimens necessitated a reinterpretation of putative homologies in a few cases. Ten of Lamoral's (1978) characters were corrected or otherwise modified, based on new information for the 12 additional species, or reinterpretation, and Lamoral's character 16, which could not be scored unambiguously, was omitted (Appendix 1). Eight characters remain unaltered. Trichobothrial terminology follows Vachon (1974). All other terminology follows Sissom (1990),

Table 3 Characters and character states used for cladistic analysis of the genus *Parabuthus*. Character states were scored 0–2, ? (unknown), – (inapplicable) or * (polymorphic). Multistate characters were treated as unordered (nonadditive). Three autapomorphies, indicated by †, were excluded from all analyses. Refer to Table 4 for data matrix and Appendix 1 for character descriptions.

General

1 Adult general size: large, carapace length 6.5–17.0 mm (0); small, carapace length 2.5–5.0 mm (1)
2 Colour of carapace, mesosoma and metasoma: pale yellow to light brown (0); dark brown to black (pedipalps and legs may be dark or pale) (1); polymorphic (*)
3 Colour pattern of metasoma: metasomal segments I–V and telson uniformly coloured (0); metasomal segments III–V and telson infuscated (i.e. darker than segments I–II) (1); polymorphic (*)

Carapace

4 †Carapace dorsoventrally compressed: absent (0); present (1)
5 Granulation of median ocular tubercle (male, female) and surrounding surfaces (female): entire (0); smooth areas (1)

Pedipalps

6 Pedipalps, setation: setose (0); smooth (1)
7 Chela manus, surface: smooth (0); granular (1)
8 Chela movable finger, length compared with length of manus (measured along ventroexternal carina), in female: long (length finger/length carina: 1.70–2.00) (0); short (length finger/length carina: ±1.50) (1)
9 Chela manus, shape in adult male, compared with adult female: similar (0); sexually dimorphic (1); unknown (?)
10 Chela fixed finger, shape in adult male: straight or slightly curved dorsally, such that proximal dentate margin linear when fingers are closed (0); strongly curved dorsally, proximal dentate margin distinctly emarginate when fingers are closed (1); unknown (?)
11 Chela movable finger, shape in adult male: straight, proximal dentate margin linear when fingers are closed (0); curved ventrally, proximal dentate margin distinctly emarginate when fingers are closed (1); unknown (?)
12 Chela fixed and movable fingers with basal lobe in adult male: absent (0); present (1); unknown (?)

Trichobothria

13 Pedipalp femur, position of e_1: level with or distal to d_5 (0); almost halfway between d_4 and d_5 (1)
14 Pedipalp patella, position of esb_2: distinctly distal to esb_1 (0); level with or slightly distal to esb_1 (1)
15 Chela fixed finger, position of *dt*: in line with or distal to *et* (0); proximal to *et* (1)

Pectines

16 Proximal median lamella of pectines, in female: arcuate (0); enlarged and lobate (dilate) (1)
17 Proximal median lamella of pectines, in male: subrectangular (0); weakly lobate (dilate) (1); strongly lobate (dilate) (2); unknown (?)

Legs

18 Legs IV, length: moderately long, not reaching to posterior edge of metasomal segment III (0); very long, reaching past posterior edge of metasomal segment III (1)
19 Basitarsi of legs I–II, macrosetal combs: absent (0); weakly developed (1); strongly developed (2)
20 Basitarsi of legs I–II, laterally expanded: absent (0); present (1)
21 †Basitarsi of legs III–IV, prolateral surfaces with dense macrosetae: absent (0); present (1)
22 Telotarsal ungues, relative length: equal (0); subequal (1)

Hemispermatophore

23 Hemispermatophore, *pars recta*: parallel to axis (0); S-shaped (1); unknown (?)

Mesosoma

24 Sternites, surface: smooth (0); punctate (1)
25 Sternite III, 'pit' organ at proximal apex: absent (0); present (1)
26 Sternite VII, carinae: present (0); absent (1)

Metasoma

27 Metasomal segments I–V and telson, setation: virtually asetose (0); sparsely to moderately setose (1); very densely setose (2)
28 Metasomal segments, width relative to length: much narrower (length IV/width IV: 1.7–2.11) (0); slightly narrower (length IV/width IV: 1.2–1.5) (1)
29 Metasomal segments, width from I–IV: becoming narrower distally, metasomal segment I wider than segment IV (0); becoming wider distally, metasomal segment I narrower than segment IV (1)
30 Metasomal segments I–III, stridulatory region on dorsal surface: absent from I–III (0); strongly developed on I–III (1); strongly developed on I–II, weakly developed to absent on III (2)
31 Metasomal segment I, shape of stridulatory region (if present) in dorsal aspect: narrow, parallel-sided (0); broad, rounded anteriorly, with posterior constriction (1); inapplicable (–)
32 Metasomal segment I and, to a lesser extent, II, shape of stridulatory region (if present) in lateral aspect: truncated at anterodorsal edge of segment (0); rounded, extended beyond anterodorsal edge of segment (1); inapplicable (–)
33 Metasomal segment I, extent of stridulatory region (if present) in dorsal aspect: terminating at anterodorsal edge of segment (0); extended forwards in V-shape onto anterior surface (1); inapplicable (–)
34 Metasomal segment II, extent of stridulatory region (if present) in dorsal aspect: reaching posterodorsal margin (0); not reaching posterodorsal margin (1); inapplicable (–); polymorphic (*)
35 Metasomal segment II, nature of stridulatory region (if present): fine to coarse granules (0); horizontal ridges (1); inapplicable (–)

Table 3 *Continued*

36 Metasomal segments II–III, posterodorsal edge: straight (0); anteromedially curved in a V-shape (1)
37 Metasomal segments IV–V, lateral intercarinal surfaces: granular (0); smooth (1)
38 Metasomal segments I–IV, dorsosubmedian carinae: present (0); absent (1)
39 Metasomal segment IV, dorsosubmedian carinae (if present): continuous (0); discontinuous (1); inapplicable (–)
40 Metasomal segments II–IV, distal spiniform granules of dorsosubmedian carinae (if present), size relative to preceding granules: equally developed (0); noticeably more pronounced (1); inapplicable (–)
41 Metasomal segment IV, ventrosubmedian and ventrolateral carinae: present and continuous to edge of segment (0); present but ventrosubmedian carinae becoming obsolete distally (1); absent (2)
42 Metasomal segment IV, median lateral carina: absent to proximally obsolete (0); continuous but poorly developed (1); continuous and distinct (2)
43 Metasomal segment V, dorsosubmedian carinae: absent (0); present, poorly developed with blunt, rounded granules (1); present, distinct with sharp, spiniform granules (2)
44 Metasomal segment V, dorsolateral carinae: absent, except for a few proximal granules (0); distally obsolete (1); continuous to distal edge of segment (2)
45 Metasomal segment V, ventrolateral carinae: converging distally (0); subparallel to diverging distally (1)
46 Metasomal segment V, distal half of ventrolateral carinae: with spinose processes (0); with lobate processes (1)
47 Metasomal segment V, ventrosubmedian carinae: absent or indistinct from surrounding granules (0); distinct (1)
48 Metasomal segment V, ventromedian carina: present (may be indistinct) (0); absent (1)

Telson

49 Telson vesicle, width relative to width of metasomal segment V: approximately equal (0); considerably narrower (1)
50 †Telson vesicle, dorsoproximal surface: very shallowly excavated along longitudinal half (0); deeply excavated (1)
51 Telson aculeus, shape: gently curved (0); abruptly bent (1)

Behaviour

52 Diurnal retreat: hides under rocks (0); burrows under rocks (1); burrows in open ground (2); unknown (?); polymorphic (*)
53 Foraging strategy: sit-and-wait (0); errant (1); unknown (?)

Table 4 Distribution of 53 characters among 25 species of the genus *Parabuthus*. The first two taxa are outgroups. Refer to Table 3 for character list and Appendix 1 for character descriptions. Character states are scored 0–2, ? (unknown), - (inapplicable) or * (polymorphic). Characters derived from Lamoral's (1978: table 5.2) list (Table 1) are indicated below by their corresponding numbers, with changes underlined in the matrix.

G. madagascariensis	01000	10001	00000	00000	00000	00000	- - - - -	00000	00000	00000	000
U. triangulifer	10000	00000	00000	00000	00000	01000	- - - - -	00000	00000	00100	000
P. granimanus	01100	01010	01000	10020	00001	01112	00000	00000	12110	01000	1??
P. heterurus	00100	00010	00000	10020	00001	01112	00000	00000	12110	11000	1??
P. hunteri	00100	01010	01000	10020	00001	01112	00000	00000	12110	01000	1??
P. leiosoma	00100	00010	00000	10020	00001	01111	00000	00000	12110	11000	1??
P. pallidus	00000	00000	00000	11010	00000	01111	00000	00011	12110	10000	1??
P. brevimanus	10001	00110	00111	10121	00000	01001	10000	00001	20001	10100	020
P. calvus	00001	10000	00000	12010	10?00	00101	11000	01011	20110	10100	1??
P. capensis	0**00	00010	00000	10020	00000	01111	11000	10011	12210	10000	1*0
P. distridor	10001	00110	00111	10121	01000	11000	- - - - -	011 - -	20000	00100	020
P. gracilis	10000	01110	00011	10121	00110	11001	10000	001 - -	20000	00100	020
P. granulatus	01000	10011	10000	00121	00000	00101	10010	00000	10010	10010	021
P. kalaharicus	01000	10111	10011	00121	01000	00101	10010	00000	10010	00110	021
P. kraepelini	00000	00011	00000	10020	00000	01111	10100	00001	12221	10000	120
P. kuanyamarum	10001	00111	10111	10121	01000	10001	10000	011 - -	20000	00100	020
P. laevifrons	00101	10111	10011	10121	00000	00002	11000	01000	11000	11000	021
P. mossambicensis	00000	00010	00000	10020	00000	01111	11101	00001	12220	10000	120
P. muelleri	00100	001??	??000	1?020	00?00	01101	11000	10011	12210	10000	110
P. namibensis	00101	00011	10110	10120	00000	01002	11000	00000	11110	11000	021
P. nanus	10000	01000	00011	10121	00110	11001	10000	001 - -	20000	00100	020
P. planicauda	00000	00000	00000	11010	00000	01101	110*0	00011	12110	10000	110
P. raudus	0**00	00011	00000	10020	00000	01111	10110	00011	12220	00000	120
P. schlechteri	0*000	00011	00000	10020	00000	01111	10110	00011	12221	00000	120
P. stridulus	00*01	10111	10010	10121	00000	00002	11001	01000	11000	01001	021
P. transvaalicus	01000	00011	00000	10020	00000	01111	10100	00011	12221	00000	110
P. villosus	01010	00011	00000	10020	00000	02101	111*0	00011	12221	00000	111
Lamoral's (1978)	2	1	11	3 1	1	9 8	7	1	146 1	1 5	1
character numbers		5	30	9	2			1	7	4	8

except for pedipalp carinae (Stahnke 1970), metasomal carinae (Prendini 2000a) and tarsi (Couzijn 1976; Lamoral 1979).

Although four characters (2, 3, 34, 52) displayed intraspecific polymorphism in a few species, state assignment was unambiguous in the remaining species. Characters of the adult male (9–12, 17, 23) were scored unknown in *P. muelleri*, the male of which has not yet been discovered, whereas behavioural characters (52, 53) were scored unknown in *P. calvus* and the north-eastern African and Arabian species, for which observational data were unavailable.

Characters were not weighted *a priori*. Nine characters were coded into multistates and 44 were coded into binary states (Appendix 1). Multistate characters were treated as unordered, i.e. nonadditive (Fitch 1971).

Cladistic analysis

Character data were edited and cladograms prepared using WinClada, Ver. 0.9.9+ (Nixon 1999). Three autapomorphies (characters 4, 21 and 50) were excluded from all analyses; hence tree statistics are calculated from phylogenetically informative characters only (Bryant 1995).

Analyses with equal weights were conducted using NONA Ver. 1.6 (Goloboff 1997), Hennig86 Ver. 1.5 (Farris 1988) and PAUP Ver. 3.1.1 (Swofford 1991). In Hennig86, the heuristic branch breaking routine (command sequence: 'mh*; bb*;') was used. In PAUP, heuristic tree bisection-reconnection (TBR) branch swapping (Swofford 1991) was conducted on 100 random addition replicates, with MULPARS in effect and maxtrees set to 1000. In NONA, the heuristic analysis was run with the following command sequence: 'hold1000; hold/100; mult*100;' (hold 1000 trees in memory; hold 100 starting trees in memory; perform 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 sequence: 'jump50;') was performed to help the swapper move between multiple 'islands' of trees (Goloboff 1997). Trees found with the jump command were again swapped. All trees obtained with Hennig86 and NONA were submitted to TBR branch swapping in PAUP and vice versa.

The relative degree of support for each node in the tree obtained with equal weights was assessed with branch support indices (Bremer 1994). The branch support or decay index for a given node in the shortest unconstrained tree is the number of extra steps required in the shortest trees that are inconsistent with that node, i.e. the number of steps required to collapse the node. Branch support indices up to 100 extra steps (setting the maximum number of trees held in memory to 1000) were calculated with NONA, by means of the command sequence: 'h1000; bsupport 100;'.

Successive approximations character weighting (Farris 1969) and implied character weighting (Goloboff 1993a, 1995) were conducted to assess the effects of weighting against homoplasious characters and the resultant topology was compared with the topology obtained by analysis with equal weights (see Prendini 2000b). The effects of successive weighting were explored with Hennig86, using the command sequence: 'xs w; mh*; bb*;'. Pee-Wee version 2.5.1 (Goloboff 1993b) was used for analyses with implied weights applying the command sequence: 'hold1000; hold/100; mult*100; jump50;'. Analyses with implied weights investigated the use of six values for the concavity constant, *k*, spanning the input range permitted by Pee-Wee (command: 'conc N;').

Alternative hypotheses of the relationship were investigated in NONA (commands: 'force +N; max/;', 'ref;' and 'cmp;') by constraining clades, proposed by Lamoral (1978, 1979, 1980), on the topology of the tree located by the analysis with equal weights, swapping on the other terminals and calculating the difference in length and fit.

Results

Lamoral's data reanalysed

Reanalysis of Lamoral's (1978) data matrix (Table 1) located a single most parsimonious tree with a length of 46 steps, a consistency index (CI) of 46 and a retention index (RI) of 67 (Fig. 3). Most of the groupings hypothesized by Lamoral (1978) were retrieved and the monophyly of *Parabuthus* was supported.

Contrary to Lamoral's (1978: 278) topology (Fig. 2), the '*granulatus*' group was paraphyletic and formed a sister group of the '*brevimanus*' group, rather than the '*villosus*' group. In addition, the '*villosus*' group, comprising the '*laevifrons*' and '*raudus*' subgroups, was rendered paraphyletic by placement of two members of the '*laevifrons*' subgroup (*P. laevifrons* and *P. stridulus*) in a monophyletic clade with the '*brevimanus*' group. Kraepelin (1908b) was the first to suggest a close relationship between *P. brevimanus* and *P. laevifrons*.

New analysis: equal weights

Equal weights analysis of the 50 informative characters in the new data matrix located a single most parsimonious tree with a length of 130 steps, a CI of 45 and an RI of 74 (Fig. 4). The ci and ri values of characters are presented in Table 5. The monophyly of *Parabuthus* was supported by eight unambiguous synapomorphies, and received a high branch support value. The two major clades of the basal dichotomy (nodes 3 and 12), each supported by three unambiguous synapomorphies, also received high branch support values. Lower branch support values were obtained for the remaining nodes, with the exception of nodes 4, 7, 9 and 13, which also received strong support.

The first major clade of the basal dichotomy (node 3) comprises species endemic to the desert and semi-desert regions

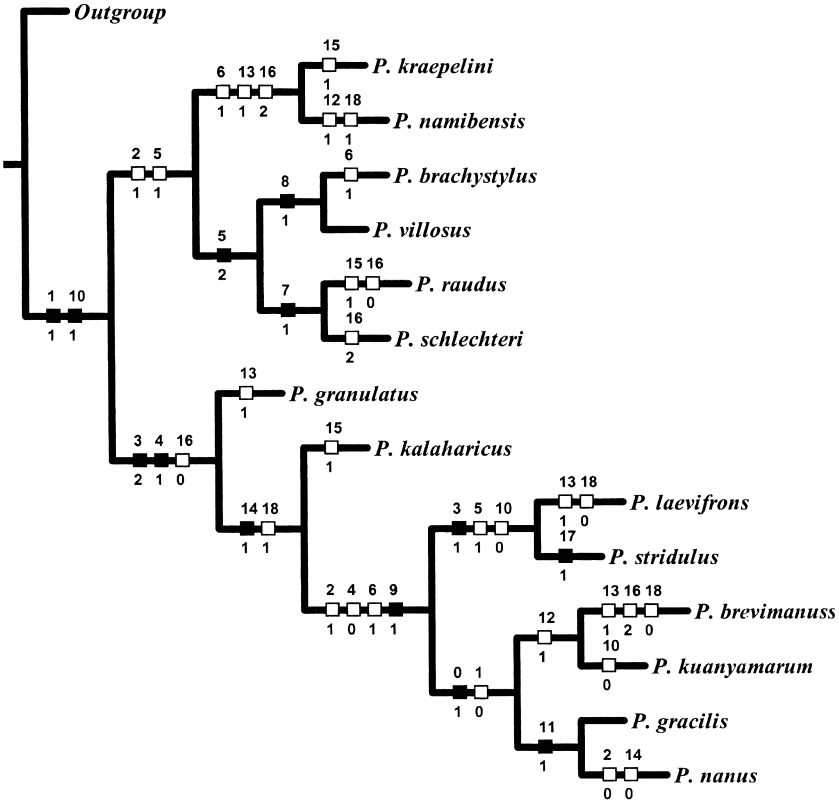

Fig. 3 The single most parsimonious tree (length, 46; CI, 46; RI, 67) obtained by computational reanalysis of Lamoral's (1978: table 5.2) unpublished data matrix (Table 1), rooting on a hypothetical outgroup. Solid bars indicate uniquely derived apomorphic character states, whereas empty bars indicate parallel derivations of apomorphic states under ACCTRAN optimization. The figure above each character bar gives the character number, whereas the figure below gives the character state.

of southern Africa, including the Namib and Kalahari. All except two of the species in this clade (*P. brevimanus* and *P. namibensis*) inhabit sand dune habitats, and display ecomorphological adaptations for locomotion and burrowing in loose sand. This clade is divided into two subclades, one of which (node 4) comprises the five small species of the genus. The other subclade (node 8) includes five of the six *Parabuthus* species with an 'errant' foraging strategy, one of which is the dangerously venomous *P. granulatus*.

The second major clade (node 12) comprises mostly semi-psammophilous species, which inhabit harder substrata, including species that are restricted to rocky areas, from arid fynbos through semi-desert to arid savanna regions in southern Africa, and semi-desert to arid savanna regions in north-eastern Africa and the Arabian peninsula. This clade is divided into three subclades, the first of which (node 13) comprises four of the five north-eastern African and Arabian species represented in this analysis, including the type species of *Parabuthus*.

The second subclade (node 17) includes four species endemic to the fynbos, succulent Karoo (semi-desert) and Nama Karoo regions of the Northern, Western and Eastern Cape Provinces of South Africa, and southern Namibia, but also includes the north-eastern African species, *P. pallidus*. *P. capensis* is a psammophilous species, inhabiting littoral sands along the west coast of South Africa, but the remaining southern African species inhabit hard sandy-loam to clay soils, and at least two species (*P. muelleri* and *P. planicauda*) burrow under stones.

The third subclade (node 21) comprises mostly arid savanna species from the eastern (*P. mossambicensis* and *P. transvaalicus*), central (*P. raudus*) and western (*P. kraepelini*, *P. schlechteri* and *P. villosus*) regions of southern Africa. Unlike the other four species, *P. schlechteri* occurs predominantly in succulent Karoo and Nama Karoo regions of the Northern Cape Province of South Africa and southern Namibia, whereas *P. villosus*, distributed from the Northern Cape Province to Angola, inhabits Karoo, Namib desert and arid savanna. *P. raudus*, which occurs in the Kalahari sand system, is the only psammophilous species in this subclade, all other species inhabiting areas with consolidated sand to sandy-loam substrata. *P. transvaalicus* and *P. villosus* are restricted to rocky areas.

New analysis: topological comparisons

The following groups, proposed in Lamoral's (1978) original topology (Fig. 2) and in the topology obtained by reanalysis of Lamoral's matrix (Fig. 3), were recovered in the new analysis (Fig. 4): (*P. brevimanus P. kuanyamarum* (*P. gracilis* +

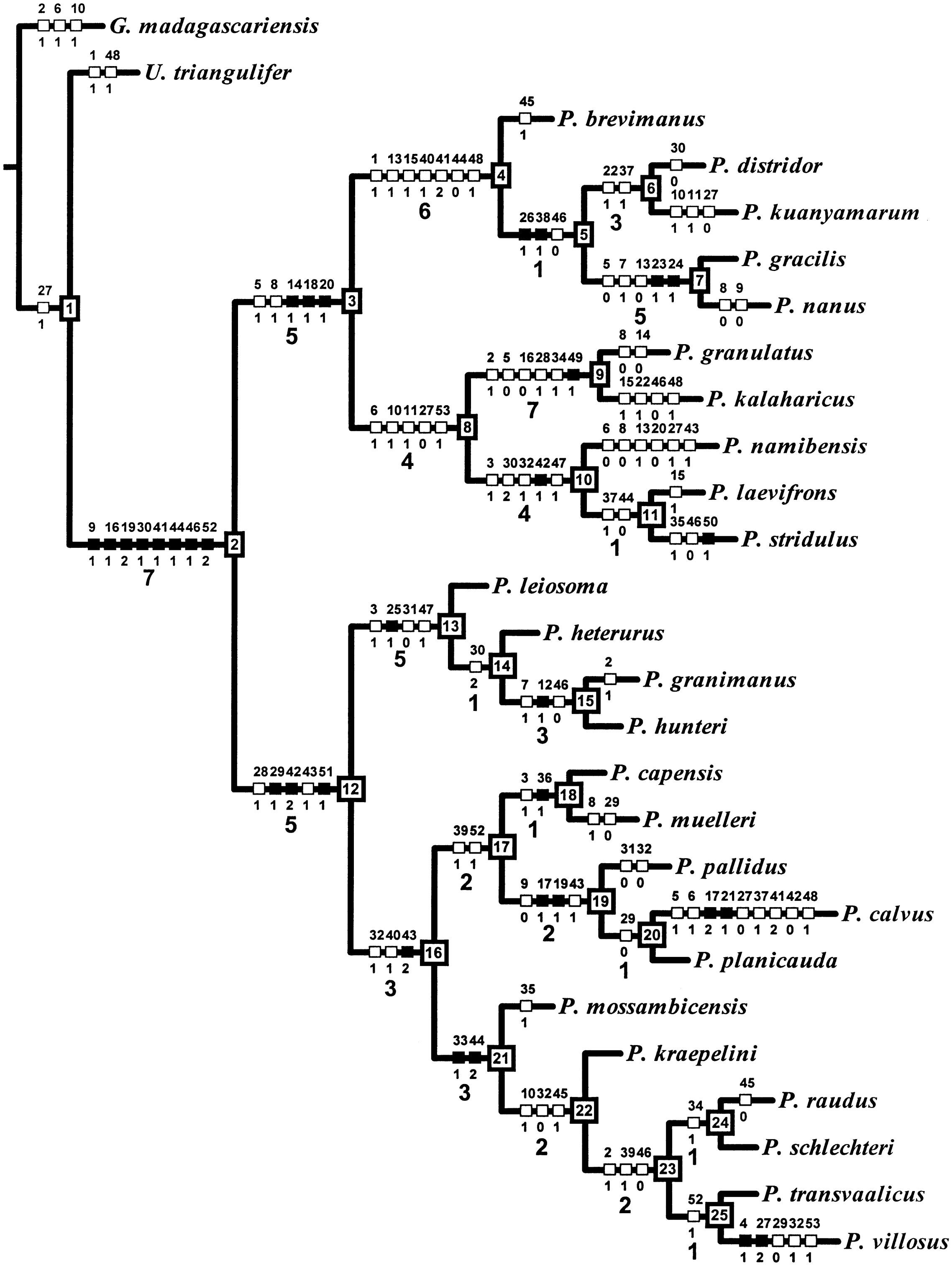

Fig. 4 Cladogram for 25 species of *Parabuthus*. A single most parsimonious tree (length, 130; CI, 45; RI, 74) derived from the character matrix in Table 4 by analysis with equal weights. Solid bars indicate uniquely derived apomorphic character states, whereas empty bars indicate parallel derivations of apomorphic states under ACCTRAN optimization. The figure above each character bar gives the character number, whereas the figure below gives the character state. Branch support values of nodes are provided below branches, whereas node numbers are provided at nodes.

Table 5 Length (steps), consistency indices (ci) and retention indices (ri) of 50 informative characters scored among 25 species of the genus *Parabuthus*. Numbers in parentheses indicate changes in steps, ci and ri values of four characters (underlined) as a result of successive weighting. Final weights (SW) are also reported.

Char	Steps	ci	ri	SW	Char	Steps	ci	ri	SW
1	2	50	80	4	28	2	50	88	4
2	4	25	40	1	29	4	25	70	1
3	3	33	66	2	30	4	50	71	3
5	4	25	50	1	31	2	50	75	3
6	4	25	40	1	32	5	20	50	1
7	2	50	66	3	33	1	100	100	10
8	5	20	42	0	34	2	50	66	3
9	3	33	60	2	35	2	50	0	0
10	4 (5)	25 (20)	72 (63)	1	36	1	100	100	10
11	2	50	80	4	37	3	33	50	1
12	1	100	100	10	38	1	100	100	10
13	3	33	33	1	39	2	50	87	4
14	2	50	87	4	40	2	50	90	4
15	3	33	66	2	41	3	66	83	5
16	2	50	66	3	42	3	66	90	5
17	2	100	100	10	43	4 (3)	50 (66)	85 (92)	6
18	1	100	100	10	44	4	50	84	4
19	2	100	100	10	45	3 (4)	33 (25)	50 (25)	0
20	2	50	87	4	46	6 (7)	16 (14)	58 (50)	0
22	2	50	50	2	47	2	50	83	4
23	1	100	100	10	48	4	25	57	1
24	1	100	100	10	49	1	100	100	10
25	1	100	100	10	51	1	100	100	10
26	1	100	100	10	52	3	66	75	5
27	6	33	33	1	53	2	50	80	4

P. nanus)); (*P. laevifrons* + *P. stridulus*); (*P. villosus* (*P. raudus* + *P. schlechteri*)). Lamoral's (*P. granulatus* + *P. kalaharicus*) sister group (Fig. 2), although unsupported by his data (Fig. 3), was also recovered (Fig. 4). Lamoral's (*P. brevimanus* + *P. kuanyamarum*) and (*P. kraepelini* + *P. namibensis*) sister groups were falsified. *P. kuanyamarum* forms part of a clade that includes *P. brevimanus*, but *P. kraepelini* is more closely related to Lamoral's '*raudus*' subgroup than to the remaining three species of his '*laevifrons*' subgroup. Three extra steps (loss in fitness of 5.4) were required to force the monophyly of (*P. brevimanus* + *P. kuanyamarum*), and 18 extra steps (loss in fitness of 25.1) were required to force the monophyly of (*P. kraepelini* + *P. namibensis*). The current placement of *P. kraepelini* recalls the opinions of Kraepelin (1908b, 1914), Werner (1916) and Hewitt (1918), who considered *P. kraepelini* to be closely related to *P. mossambicensis*. Kraepelin (1908b) placed *P. kraepelini* in synonymy with the latter, but subsequently retracted this view (Kraepelin 1914).

Compared with Lamoral's (1978) original topology, the present analysis (Fig. 4) was congruent with the topology obtained by reanalysis of Lamoral's matrix (Fig. 3), as regards the placement of the '*brevimanus*' group in a clade with the '*laevifrons*' subgroup (*P. kraepelini* excluded). However, inclusion of the (*P. granulatus* + *P. kalaharicus*) clade, as sister group of the (*P. namibensis* (*P. laevifrons* + *P. stridulus*)) clade, within this larger monophyletic group (node 8) is novel. A total of 26 extra steps (loss in fitness of 35.1) was required to constrain these clades according to the topology presented by Lamoral (1978), compared with three extra steps (loss in fitness of 4.3) to constrain only the (*P. granulatus* + *P. kalaharicus*) clade to be basal in *Parabuthus*.

The placement of *P. distridor* as the sister species of *P. kuanyamarum* falsifies Lamoral's (1980) hypothesis that *P. distridor* is most closely related to the (*P. gracilis* + *P. nanus*) sister group. Two extra steps (loss in fitness of 2.5) were required to force *P. distridor* to be monophyletic with these species. Prendini's (2000a) suggestion that *P. muelleri* is the sister species of *P. capensis*, on the basis of character 36, was supported in the present analysis.

Placement of the five north-eastern African and Arabian species in the new topology is of particular interest for two reasons. First, the position of these species rendered the southern African species paraphyletic. Second, although four of these species formed a well-supported monophyletic group, the fifth species, *P. pallidus*, was more closely related to two species from southern Africa. The grouping of *P. pallidus* with *P. calvus* and *P. planicauda* was supported by two unambiguous synapomorphies (Fig. 4), and three extra steps (loss in fitness of 5.7) were required to force this species to be monophyletic with the remaining north-eastern African and Arabian species. A total of six extra steps (loss in fitness of 11.2) was required to force the southern African species, and the north-eastern African and Arabian species, to be monophyletic sister clades.

New analysis: **a posteriori** *weights*

The successive weighting routine located a single tree that was two steps longer (unweighted length) than the topology obtained by analysis with equal weights (Table 6), with a CI of 68 and an RI of 88. This tree differed from the topology in Fig. 4 only as regards the arrangement of species in one of the major clades (node 16): ((*P. pallidus* (*P. calvus* + *P. planicauda*)) ((*P. capensis* + *P. muelleri*) ((*P. transvaalicus* + *P. villosus*) ((*P. mossambicensis* + *P. kraepelini*) (*P. raudus* + *P. schlechteri*))))). Relative to the analysis with equal weights, the ci and ri values of three characters decreased, whereas one increased, as a result of successive weighting (Table 5).

Analyses with implied weights located the same topology as the analysis with equal weights when values for the concavity constant were mild to medium (*k* = 3–6). However, under strong concavity (*k* = 1–2), analyses with implied weights located two most parsimonious trees, each three steps longer and 4–11% less fit than the topology obtained by analysis with equal weights (Table 6). These trees differed from the topology in Fig. 4 with respect to the same species (node 16),

Table 6 Summary of statistical and topological differences among the most parsimonious trees (MPTs) obtained by analysis with equal weights (EW), successive weights (SW) and implied weights (IW) with six values for the concavity constant (*k*), arranged in order of decreasing fitness. Unweighted length is reported for the SW tree. Letters A–C refer to alternative topologies for node 16 (listed below).

	MPTs	Steps	Fit (F_i)	Rescaled fit	A	B	C
IW: *k* = 6	1	130	413.5	62	×		
IW: *k* = 5	1	130	402.0	60	×		
IW: *k* = 4	1	130	387.0	58	×		
IW: *k* = 3	1	130	365.3	55	×		
EW	1	130	365.3	55	×		
SW	1	132	364.6	55		×	
IW: *k* = 2	2	133	330.9	51			×
IW: *k* = 1	2	133	275.0	44			×

A: (((*P. capensis* + *P. muelleri*) (*P. pallidus* (*P. calvus* + *P. planicauda*))) (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) (*P. transvaalicus* + *P. villosus*))))).

B: ((*P. pallidus* (*P. calvus* + *P. planicauda*)) ((*P. capensis* + *P. muelleri*) ((*P. transvaalicus* + *P. villosus*) ((*P. mossambicensis* + *P. kraepelini*) (*P. raudus* + *P. schlechteri*))))).

C: (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) (*P. transvaalicus* *P. villosus* ((*P. capensis* + *P. muelleri*) (*P. calvus P. pallidus P. planicauda*)))))).

for which the arrangement in the strict consensus was as follows: (*P. mossambicensis* (*P. kraepelini* ((*P. raudus* + *P. schlechteri*) (*P. transvaalicus P. villosus* ((*P. capensis* + *P. muelleri*) (*P. calvus P. pallidus P. planicauda*)))))).

Discussion and conclusions

Ecological specialization

All species of *Parabuthus* are characterized by the ability to construct burrows in the substratum (Newlands 1974b, 1978a,b; Newlands & Martindale 1980). The thickened metasoma, especially the processes on the ventrolateral carinae of segment V, are used to initially loosen the soil in tail-scraping operations (Eastwood 1977, 1978b), whereas the first two pairs of legs are used to subsequently scrape and rake soil out of the burrow (Eastwood 1977, 1978b; Lamoral 1979).

Most species of *Parabuthus* inhabit regions of sandy-loam or consolidated sand substrata, and can be regarded as semi-psammophilous (Eastwood 1977, 1978b; Lamoral 1977, 1978, 1979, 1980; Newlands & Martindale 1980). All species of *Parabuthus* display a row of macrosetae on the retrolateral margins of the tibia and basitarsi of the first and second pairs of legs, to enhance burrowing efficiency in these substrata. However, several *Parabuthus* species inhabit unconsolidated sand dunes, and display additional ecomorphological adaptations to increase locomotor and burrowing efficiency in loose sand. These psammophilous and ultra-psammophilous species are characterized by dorsoventral compression of the basitarsi of legs I–II, with comb-like rows of long macrosetae ('sand combs') on the retrolateral margins (e.g. *P. laevifrons*, *P. stridulus*), elongated, often subequal telotarsal ungues (e.g. *P. distridor*, *P. kalaharicus* and *P. kuanyamarum*) and a streamlined metasoma and telson, often lacking carinae (e.g. *P. distridor*).

Such psammophilous scorpions are stenotopes, maladapted to life outside their sandy environments and unable to burrow in harder substrata, over which they have limited dispersal abilities (Polis 1990; Fet *et al.* 1998). Speciation in such psammophilous clades may have been enhanced during past periods of increased aridity from the Pliocene (Van Zinderen Bakker 1975) to the Upper Pleistocene (Lancaster 1981), when pockets of sand were often isolated from major sand systems by wind action. This process of 'adaptive radiation' in stenotopic clades is predicted by the 'effect hypothesis of macroevolution' (Vrba 1980), and supported by the cladogram for *Parabuthus*. Eight of the 10 species recorded from sand dune habitats belong to the same major clade (node 3): *P. distridor*, *P. gracilis*, *P. granulatus*, *P. kalaharicus*, *P. kuanyamarum*, *P. laevifrons*, *P. nanus*, *P. stridulus*. Several of these pairs of sister species occupy allopatric sand dune systems (e.g. *P. distridor* and *P. kuanyamarum*), suggesting that speciation occurred by the translocation of psammophilous fauna, away from major sand systems, on aeolian sand dunes (Endrödy-Younga 1982). Specialization to sand dune habitats, though not as marked as in these latter species, evolved independently in *P. capensis* and *P. raudus*.

In comparison with the above-mentioned sand specialists, adaptation to life on relatively harder substrata appears to have also evolved on at least one occasion in *Parabuthus*. The macrosetal combs on basitarsi I–II are weakly developed in three species — *P. calvus*, *P. pallidus* and *P. planicauda* — a condition hypothesized to be synapomorphic (Appendix 1). The presence of weakly developed combs in these species may be associated with their occurrence in regions of hard, compacted soil (Eastwood 1977). However, this has not yet been verified in *P. pallidus*.

Another ecological trend evident from the cladogram is the association with rocky habitats in related species, e.g. *P. transvaalicus* and *P. villosus*, and also *P. muelleri* and *P. planicauda* (Appendix 1). The ecological requirement for rock cover appears to be essential for these species, which are restricted to rocky areas (Newlands 1974b, 1978a,b; Lamoral 1979; Newlands & Martindale 1980; Harington 1984; Prendini 2000a). *P. villosus*, in particular, displays at least one ecomorphological adaptation to its rocky environment, in the form of a dorsoventrally compressed carapace (Appendix 1), which presumably reduces scratching of the median ocelli when the scorpion creeps under stones. The elongated pedipalps of *P. planicauda* are also characteristic of the lithophilous ecomorphotype (Eastwood 1978b; Bradley 1988; Polis 1990).

Afrotropical arid biogeography

Several authors (e.g. Balinsky 1962; Werger 1978; Kingdon 1990; Poynton 1995) have noted marked similarities between the fauna and flora of the arid south-western and north-eastern regions of Africa. A zone of arid country still connects the two areas through western Tanzania and, particularly during dry phases of the Quaternary, a substantial 'drought corridor' or 'arid corridor' probably existed, allowing xerophilous faunal and floral interchange between the south-west and north-east (Van Zinderen Bakker 1962).

The distribution of *Parabuthus* provides yet another example of the 'arid corridor' pattern of distribution. *Parabuthus* is endemic to the Afrotropical faunal region. All the extant species, with the exception of *P. leiosoma* and *P. granimanus* (which also occur in Arabia), are confined to sub-Saharan Africa, with the exclusion of Congo, and all regions west of it, and west of Sudan (Fig. 1). On the basis of this distributional pattern, Lamoral (1978) inferred that the ancestral elements of *Parabuthus* evolved in north-eastern Africa during Eocene or post-Eocene times. At this time, Africa had virtually acquired its present shape, most of central Africa was tropical to subtropical, the northern parts of the continent were more mesic than during the Quaternary and some semi-desert to arid savanna had arisen in parts of north-eastern Africa (Van Zinderen Bakker 1962; Lamoral 1978).

Lamoral (1978) surmised that the Namibian species, on which his cladogram (Fig. 2) was based, were more closely related to species from the Northern Cape Province of South Africa than to species from north-eastern Africa. Accordingly, Lamoral concluded that the Namibian species evolved from ancestral elements that dispersed from north-eastern to southern Africa after the Kalahari sand system had begun to form, and had to bypass the Kalahari in a southerly direction, to migrate into Namibia (and ultimately Angola) during Miocene or post-Miocene times. This scenario, in turn, required two hypotheses to account for the distribution of semi-psammophilous vs. psammophilous and ultrapsammophilous species of *Parabuthus*. Lamoral invoked westward expansion of the Kalahari sand dune system up to the eastern 1500 m contour of the Namibian Central Highlands, during Pliocene times, to account for the allopatric distributions of semi-psammophilous species (for which the Kalahari sand system would have constituted a barrier to dispersal) to the north and south of the highlands. Post-Pliocene adaptation to sandy substrata was invoked to account for the emergence of psammophilous and ultrapsammophilous species of *Parabuthus* in the Namib and Kalahari sand dune systems.

Lamoral recognized the limitations of his cladogram, particularly the omission of extralimital species from southern and north-eastern Africa. His hypotheses can now be re-evaluated in the light of the present cladistic analysis, wherein these taxa were included. Lamoral's scenario leads to the following predictions: the north-eastern African and Arabian species should be relatively basal to the southern African species, and should be monophyletic or paraphyletic with respect to the latter; the southern African species should be monophyletic, and relatively distal; the psammophilous and ultrapsammophilous southern African species should be relatively distal to the semi-psammophilous southern African species.

The finding that neither the southern African species nor the north-eastern African and Arabian species form monophyletic groups falsifies the first two predictions, but supports geological evidence for several periods of aridity from the Pliocene through to the Upper Pleistocene (Tankard & Rogers 1978; Lancaster 1981, 1984; Ward *et al.* 1983).

Lamoral's hypothesis of a north-eastern African origin for *Parabuthus* is similarly falsified by the finding that the north-eastern African species are not basal to the southern African species. The cladogram clearly indicates a southern African origin for *Parabuthus*. Range expansion to north-eastern Africa appears to have occurred during at least two separate periods of aridity, followed by vicariance during wetter periods, that promoted speciation of the scorpion populations isolated to the north-east and south-west. Evidence for this scenario can be seen in the disjunct distributions of *P. pallidus* in north-eastern Africa, and its most closely related species, *P. calvus* and *P. planicauda*, in south-western Africa.

Lamoral's hypothesis that psammophilous and ultrapsammophilous species of *Parabuthus* evolved later, and are thus more derived than semi-psammophilous species of the genus, is also falsified. Although psammophily has evolved on at least two occasions within the semi-psammophilous clade (*P. capensis* and *P. raudus*), most of the psammophilous and ultrapsammophilous species form a sister clade to the semi-psammophilous species. This suggests that the ancestors of *Parabuthus* diverged into unconsolidated sand dune habitats, as well as consolidated sand and sandy-loam habitats, contemporaneously. The occurrence of reversals to the semi-psammophilous habitus in two members of the psammophilous clade (*P. brevimanus* and *P. namibensis*) indicates that this process can evolve in either direction, and is comparatively plastic. The evidence supports Lamoral's hypothesis that the major sand systems of southern Africa must have formed significant barriers to range expansion by semi-psammophilous species in the past, such as the common ancestor of *P. transvaalicus* and *P. villosus*, sister species inhabiting rocky habitats on the eastern and western sides of the Kalahari, respectively.

Parabuthus *envenomation*

The present cladistic analysis of *Parabuthus* species leads to some important conclusions about envenomation by these scorpions. For example, it is noteworthy that the four species thus far conclusively implicated in envenomations — *P. granulatus* (Petersen 1987; Müller 1993; FitzPatrick 1994; Bergman 1995, 1997a,b), *P. leiosoma* (Cilli & Corazzi 1946; Goyffon & Vachon 1979), *P. mossambicensis* (Bergman 1995, 1997a,b) and *P. transvaalicus* (FitzPatrick 1994; Bergman 1995, 1997a,b) — do not form a monophyletic group. A single fatality, ascribed to *P. capensis* (Hill 1990; Lee 1991), could not be satisfactorily verified (Müller 1993).

The fact that these species represent three different clades in the genus suggests that envenomation by most species of *Parabuthus* has the potential to induce severe, and perhaps fatal, systemic symptoms and signs. Only the '*brevimanus*' group, comprising the five small species of the genus, is not represented by a species thus far implicated in envenomation. The small size of species in this group suggests that envenomation by these scorpions will be less severe, if for no other reason than that a smaller quantity of venom can be injected, compared with larger species such as *P. granulatus* and *P. transvaalicus*.

The cladogram also leads to the prediction that the unusually potent venom of *P. granulatus* (G. J. Müller, personal communication), implicated in the greatest number of fatalities compared with the other species (Müller 1993), should be present in its sister species, *P. kalaharicus*, and perhaps also in the closely related '*laevifrons*' group. *P. kalaharicus*, *P. laevifrons*, *P. namibensis* and *P. stridulus* have thus far never been implicated in incidents of scorpionism in southern Africa, presumably because these species occur in sparsely populated sand dune regions of the Namib and Kalahari deserts. However, with intensified ecotourism in these areas, the possibilities for envenomations by these species, perhaps with symptoms as severe as those induced by *P. granulatus* envenomation, become increasingly likely. Current research on the venoms of *Parabuthus* species should focus more attention on these species, especially *P. kalaharicus*. It may be advisable to include venoms from these species in the production of a polyvalent antivenom.

Finally, it is noteworthy that *P. granulatus*, the species of *Parabuthus* that has been implicated in the greatest number of serious envenomations, is also one of only six species that display the 'errant' foraging strategy (character 53). The errant strategy may be the cause of *P. granulatus* coming into more frequent contact with humans, thereby resulting in the prevalence of envenomation by this species, compared with species which adopt the 'sit-and-wait' strategy. Four of the remaining six species observed to forage in this manner — namely *P. kalaharicus*, *P. laevifrons*, *P. namibensis* and *P. stridulus* — are all closely related to *P. granulatus*.

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Appendix 1

Character descriptions and analysis

Characters corresponding to Lamoral's (1978: table 5.2) list (Table 1) are noted. Refer to Table 3 for character states, Table 4 for data matrix and Fig. 4 for node numbers. The ci and ri values of characters are provided in Table 5.

General

1 Adult general size. Lamoral's (1978) character 2, in which small adult size was considered to be plesiomorphic on the basis of outgroup comparison. This hypothesis was falsified in the present analysis, according to which small adult size is synapomorphic for the five species of *Parabuthus* comprising node 4 (Hewitt 1918; Lamoral 1978, 1979, 1980). Small adult size is hypothesized to be independently derived in *Uroplectes*.

2 Colour of carapace, mesosoma and metasoma. Although most species of *Parabuthus* are pale yellow to light brown in colour, several species are dark brown to black (Pocock 1895; Purcell 1898, 1899, 1901; Kraepelin 1899, 1908b; Hewitt 1918; Lawrence 1955; Eastwood 1977; Lamoral 1977, 1979; Newlands & Martindale 1980; Harington 1984). In some of these dark coloured species (e.g. *P. schlechteri* and *P. villosus*), the legs and pedipalps may be pale yellow, contrasting with the dark carapace, mesosoma and metasoma, although this character is polymorphic in *P. villosus* (Purcell 1901; Kraepelin 1908b; Harington 1984). The dark brown or black colour is considered to be apomorphic in *Parabuthus*, and to have evolved independently in node 9, node 23 and *P. granimanus*. *P. capensis*, *P. raudus* and *P. schlechteri* are polymorphic for this character (Purcell 1901; Eastwood 1977; Lamoral 1979). The dark brown colour of *G. madagascariensis* is considered to have evolved independently.

3 Colour pattern of metasoma. Infuscation of metasomal segments III, V and telson occurs in several species of *Parabuthus* (Pocock 1895, 1899a; Kraepelin 1899, 1908b; Purcell 1901; Werner 1916; Probst 1973; Eastwood 1977; Lamoral 1979; Vachon 1979; Sissom 1994; Prendini 2000a), but is absent in the outgroup, and hence is considered to be apomorphic. Usually, metasomal segments III–V and telson are all darker than segments I–II, but *P. heterurus* is unusual in that segment IV is the same pale colour as segments I–II, whereas segments III, IV and telson are infuscated (Pocock 1899a). Weak infuscation of segment IV only also occurs in some specimens of *P. capensis* and *P. mossambicensis*, but this is fairly uncommon. Infuscation is hypothesized to have evolved independently in nodes 10, 13, 18 and *P. raudus*, *P. capensis*, *P. stridulus* and *P. raudus* are polymorphic for this character (Hewitt 1915; Eastwood 1977; Lamoral 1979; Newlands & Martindale 1980).

Carapace

4 Carapace dorsoventrally compressed. Purcell (1901: 159) first remarked that the carapace of *P. villosus* is 'more depressed and relatively wider than in other species of the genus.' Dorsoventral compression of the carapace is autapomorphic for *P. villosus*, and presumed to be an adaptation to the semi-lithophilous existence of this species.

5 Granulation of median ocular tubercle (male, female) and surrounding surfaces (female). The carapace of the adult male and female is entirely granular in *Grosphus*, *Uroplectes* and all except seven species of *Parabuthus*, in which the median ocular tubercle is smooth in the male and female, and there are smooth areas on the carapace of the female. The entirely granular condition is thus considered to be plesiomorphic. The smooth condition is considered to be synapomorphic for node 3 (Kraepelin 1899, 1908b; Hewitt 1912, 1913, 1918; Lawrence 1955; Lamoral 1979), with a reversal to the entirely granular condition in node 9 (Lamoral 1979, 1980). It is hypothesized to be independently derived in *P. calvus* (Purcell 1898, 1901; Kraepelin 1908b).

Pedipalps

Characters 9–12 were scored unknown in *P. muelleri*, the adult male of which has not been discovered.

6 Pedipalps, setation. The pedipalps of *Uroplectes* and all except five species of *Parabuthus* are densely covered in fine setae (Kraepelin 1899; Purcell 1901; Lamoral 1979); hence this condition is considered to be plesiomorphic. The smooth condition is hypothesized to be synapomorphic for node 8 with a reversal to the setose condition in *P. namibensis* (Purcell 1901; Lamoral 1977, 1979). It is considered to be independently derived in *P. calvus* and in *G. madagascariensis*.

7 Chela manus, surface. The absence of granulation on the chela manus of *Grosphus*, *Uroplectes* and all except four species of *Parabuthus* (Pocock 1895, 1899a; Kraepelin 1899; Purcell 1901; Lamoral 1979) is considered to be plesiomorphic. Granulation is hypothesized to be synapomorphic for node 7 (Lamoral 1979) and for node 15 (Pocock 1895, 1899a; Kraepelin 1899). Pocock (1895, 1899a) stated that the manus of *P. hunteri* is smooth but, in the specimens of *P. hunteri* examined for the present study, the manus was only slightly less granular than that of *P. granimanus*.

8 Chela movable finger, length compared with length of manus (measured along ventroexternal carina), in female. Lamoral's (1978) character 15, in which short fingers were considered to be apomorphic on the basis of outgroup comparison. According to the present analysis, short fingers are synapomorphic for node 3 (Kraepelin 1899, 1908b; Purcell 1901; Hewitt 1918; Lamoral 1979, 1980), with reversals to long fingers occurring in *P. granulatus*, *P. namibensis* and *P. nanus* (Lamoral 1977, 1979). Short fingers are hypothesized to have evolved independently in *P. muelleri* (Prendini 2000a).

9 Chela manus, shape in adult male, compared with adult female. Most species of *Parabuthus* are sexually dimorphic with respect to the shape of the chela manus. The manus of adult males is noticeably incrassate (bulbous or swollen), compared with that of adult females, which is slender (Pocock 1889, 1890, 1902; Purcell 1898, 1899, 1901; Kraepelin 1899, 1908b; Hewitt 1913, 1915, 1918; Werner 1916; Eastwood 1977; Lamoral 1977, 1979, 1980; Newlands & Martindale 1980). Based on outgroup comparison with *Uroplectes*, in which the manus is slender in both sexes, and *Grosphus*, in which the manus is incrassate in both sexes, the occurrence of this sexual dimorphism is considered to be synapomorphic for *Parabuthus* (node 2). However, reversals to the plesiomorphic state (slender manus in both male and female) occur in node 19 and, independently, in *P. nanus* (Pocock 1890, 1902; Purcell 1898, 1901; Kraepelin 1908b; Hewitt 1918; Lamoral 1979).

10 Chela fixed finger, shape in adult male. The adult males of many buthids, including most species of *Parabuthus*, display a slight dorsal curvature of the fixed finger (Pocock 1889; Kraepelin 1899, 1908a; Werner 1934). This curvature is usually not pronounced, and the fingers close together without a 'gap'. However, in certain species of *Parabuthus*, pronounced dorsal curvature of the fixed finger creates a proximal gap with the movable finger, when the fingers are closed. Lamoral (1977, 1979) described the absence or presence of this gap, respectively, as the 'linear' or 'emarginate' condition of the proximal dentate margin. The linear condition is considered to be apomorphic in *Parabuthus*, based on outgroup comparison with *Uroplectes*, in which the fixed finger is almost straight and no gap is evident. Pronounced curvature, with an emarginate proximal dentate margin, is hypothesized to have evolved independently in node 8, node 22 and *P. kuanyamarum*. Pronounced curvature is also hypothesized to have evolved independently in *G. madagascariensis*. The ci and ri values of this character decreased with successive weighting (Table 5).

11 Chela movable finger, shape in adult male. Ventral curvature of the movable finger, with an emarginate proximal dentate margin, is similarly considered to be apomorphic in *Parabuthus*, but occurs in fewer species. It is hypothesized to have evolved independently in node 8 and in *P. kuanyamarum* (Lamoral 1977, 1979).

12 Chela fixed and movable fingers with basal lobe in adult male. The presence, in adult males, of a lobe at the base of both the fixed and movable fingers of the chela is uniquely synapomorphic for node 15 (Pocock 1895, 1899a; Kraepelin 1899).

Trichobothria

13 Pedipalp femur, position of e_1. Lamoral's (1978) character 13, in which e_1 located level with or distal to d_5 was considered to be plesiomorphic according to the common is primitive criterion. In the present analysis, the alternative condition is hypothesized to be synapomorphic for node 4, with a reversal in node 7, and independently derived in *P. namibensis* (Lamoral 1978, 1979, 1980).

14 Pedipalp patella, position of esb_2. Lamoral's (1978) character 10, with the entries for *P. kalaharicus* and *P. namibensis* corrected (esb_2 is level with or slightly distal to esb_1 in these species). Lamoral surmised that the distinctly distal position of esb_2 was plesiomorphic, based on the common is primitive criterion. This hypothesis was confirmed in the present analysis. The distal position is synapomorphic for node 3

(Lamoral 1977, 1978, 1979, 1980). The occurrence of the plesiomorphic state in *P. granulatus* (Lamoral 1979) is interpreted as a reversal.

15 Chela fixed finger, position of *dt*. The distal position of *dt* is hypothesized to be plesiomorphic, based on its occurrence in the outgroups and all except seven species of *Parabuthus* (Lamoral 1977, 1979, 1980; Vachon 1979; Sissom 1994). The proximal position is hypothesized to be synapomorphic for node 4 and independently derived in *P. kalaharicus* and *P. laevifrons*.

Pectines

16 Proximal median lamella of pectines, in female. Lamoral's (1978) character 3, with the entry for *P. nanus* corrected (the lobate condition is clearly evident in the female of *P. nanus*). The occurrence of an enlarged, lobate proximal median lamella of the pectines in females has been regarded as a diagnostic character for *Parabuthus* since Pocock (1890) created the genus (e.g. Purcell 1901; Pocock 1902; Kraepelin 1908a; Hewitt 1918; Werner 1934; Lawrence 1955; Eastwood 1977; Lamoral 1979; Sissom 1994). Lamoral (1978) considered the lobate condition to be apomorphic, based on outgroup comparison and the structural complexity criterion. This hypothesis was confirmed in the present analysis, since the lobate condition is absent in both of the outgroups. The lobate condition is synapomorphic for *Parabuthus* (node 2), with a reversal to the arcuate condition in node 9 (Purcell 1901; Pocock 1902; Kraepelin 1908b; Lamoral 1977, 1979).

17 Proximal median lamella of pectines, in male. The presence, in males, of a lobate proximal median lamella of the pectines is uniquely synapomorphic for node 19. According to Purcell (1898), the lobate condition is unusually well developed in *P. calvus*, and this is considered to be autapomorphic for the species. This character is scored unknown in *P. muelleri*, the male of which has not been discovered.

Legs

18 Legs IV, length. Lamoral's (1978) character 19, with the entries for *P. brevimanus*, *P. granulatus* and *P. laevifrons* corrected (these species also have very long hind legs). Lamoral considered long hind legs to be apomorphic on the criteria of outgroup comparison and ecological specialization (psammophily). In the present analysis, long hind legs are hypothesized to be synapomorphic for node 3 (Lamoral 1977, 1979, 1980).

19 Basitarsi of legs I–II, macrosetal combs. The occurrence of strongly developed macrosetal combs on the basitarsi of legs I–II, an adaptation to burrowing in sandy substrata, is considered to be synapomorphic for *Parabuthus* (Lamoral 1977, 1979, 1980; Newlands & Martindale 1980). The macrosetal combs are weakly developed in the species comprising node 19, a condition hypothesized to be synapomorphic. The reason for the weakly developed combs in these species is unclear, but may be associated with their occurrence in regions of hard, compacted soil (Eastwood 1977; verified in *P. calvus* and *P. planicauda*, but not in *P. pallidus*).

20 Basitarsi of legs I–II, laterally expanded. Dorsoventral compression of the basitarsi of I–II is a psammophilous adaptation, hypothesized to be synapomorphic for node 3. The occurrence of the plesiomorphic state in *P. namibensis* is interpreted as a reversal.

21 Basitarsi of legs III–IV, prolateral surfaces with dense macrosetae. The occurrence of dense macrosetae on the prolateral surfaces of basitarsi III–IV is autapomorphic for *P. calvus*.

22 Telotarsal ungues, relative length. Subequal telotarsal ungues are a psammophilous adaptation, hypothesized to be synapomorphic for node 6 (Lamoral 1979, 1980) and independently derived in *P. kalaharicus* (Lamoral 1977, 1979).

Hemispermatophore

23 Hemispermatophore, *pars recta*. Lamoral (1978, 1979) noted the distinctive S-shape of the *pars recta* of *P. gracilis* and *P. nanus*, which is considered synapomorphic for these species (node 7). This character is scored unknown in *P. muelleri*, the adult male of which has not been discovered, and in *P. calvus*, in which the hemispermatophore of the lost holotype could not be examined.

Mesosoma

Lamoral's (1978) character 16 — in which the absence of a median carina on tergites I–VI was considered to be apomorphic in *P. kalaharicus*, *P. kraepelini* and *P. raudus* on the criteria of outgroup comparison and common equals primitive — was omitted from the present analysis. Examination of specimens of *P. kalaharicus*, *P. kraepelini* and *P. raudus* revealed the presence of a median carina on the tergites, not noticeably different from that in other species of *Parabuthus*.

24 Sternites, surface. Lamoral's (1978) character 12, in which the smooth condition was hypothesized to be plesiomorphic according to the common is primitive criterion. The punctate condition is considered to be synapomorphic for node 7 (Lamoral 1979).

25 Sternite III, 'pit' organ at proximal apex. The presence of a distinctive organ at the proximal apex of sternite III, visible externally as a horizontal 'pit', is synapomorphic for the north-eastern African and Arabian species (node 13). Sissom (1994: 24), who noted a 'conspicuous anteromedian pit bordered posteriorly by prominent boss' in *P. leiosoma*, appears to be the first to have mentioned this structure.

26 Sternite VII, carinae. The absence of carinae on sternite VII is uniquely synapomorphic for node 5 (Lamoral 1979, 1980).

Metasoma

Characters 31–35 are inapplicable to the outgroups and to *P. distridor*, which lack a stridulatory region, whereas characters

39–40 are inapplicable to the four species in which dorsosubmedian carinae are absent (node 5).

27 Metasomal segments I–V and telson, setation. Lamoral's (1978) character 9, with the addition of a new state for the virtually asetose condition in *Grosphus*, *P. granulatus*, *P. kalaharicus*, *P. kuanyamarum*, *P. laevifrons* and *P. stridulus*. Lamoral surmised that the sparsely to moderately setose condition was plesiomorphic and the densely setose condition synapomorphic for *P. brachystylus* and *P. villosus* (Pocock 1889; Kraepelin 1899, 1908b; Purcell 1901; Werner 1916; Hewitt 1918; Lawrence 1955; Lamoral 1979; Harington 1984) on the criteria of common equals primitive and structural complexity. Since *P. brachystylus* is synonymous with *P. villosus* (Prendini, in press), the densely setose condition is autapomorphic for the latter. Based on outgroup comparison with *Grosphus*, the sparsely to moderately setose condition is hypothesized to be synapomorphic for *Uroplectes* and *Parabuthus* (node 1), with independent reversals to the virtually asetose condition in node 8 (Purcell 1901; Hewitt 1918; Lamoral 1977, 1979) and *P. kuanyamarum* (Lamoral 1979; FitzPatrick 1994). The sparsely to moderately setose condition of *P. namibensis* (Lamoral 1979) is interpreted as a reversal to the plesiomorphic condition for *Parabuthus*.

28 Metasomal segments, width relative to length. Slender segments are restricted to the five small species (node 4) and the species comprising node 10 (Kraepelin 1899; Purcell 1901; Hewitt 1918; Lamoral 1979, 1980; FitzPatrick 1994). However, the relatively broad metasomal segments of most *Parabuthus* species are considered to be apomorphic, compared with *Grosphus* and *Uroplectes*. Broad segments are hypothesized to have evolved independently in node 9 and node 12.

29 Metasomal segments, width from I–IV. Lamoral's (1978) character 8, with the entry for *P. kraepelini* corrected (segment I is narrower than segment IV in this species). Lamoral considered distal narrowing to be plesiomorphic, according to the common is primitive criterion. Since distal narrowing occurs in *Grosphus* and *Uroplectes*, this hypothesis was supported in the present analysis. Distal widening is considered to be synapomorphic for node 12 (Purcell 1901; Kraepelin 1908b; Hewitt 1912, 1918; Eastwood 1977). Reversals to distal narrowing are hypothesized to have evolved independently in node 20, in *P. muelleri* and in *P. villosus* (Pocock 1889; Purcell 1898, 1899, 1901; Kraepelin 1908b; Hewitt 1915, 1918; Harington 1984).

30 Metasomal segments I–III, stridulatory region on dorsal surface. The presence of a stridulatory region on the dorsal surface of metasomal segments I–III has been used as a diagnostic character for *Parabuthus* since Pocock (1890) created the genus (e.g. Pocock 1899b; Kraepelin 1908b; Hewitt 1918; Lawrence 1955; Newlands 1974a, 1978a; Lamoral 1977, 1979; Newlands & Martindale 1980; Sissom 1990; FitzPatrick 1994). It was only recently that Lamoral (1980) described *P. distridor*, in which the stridulatory region is completely absent. However, *P. distridor* can be placed unequivocally within *Parabuthus* on the basis of numerous other characters. The absence of a stridulatory region is autapomorphic for this species, and interpreted as a reversal. Although the stridulatory region occurs on segments I–III in most species of *Parabuthus*, it is weakly developed to absent on III in six species. This condition is hypothesized to be apomorphic, relative to the occurrence of a strongly developed stridulatory region on segments I–III, and to have evolved independently in node 10 (Hewitt 1913, 1918) and node 14 (Pocock 1895; Kraepelin 1899).

31 Metasomal segment I, shape of stridulatory region (if present) in dorsal aspect. The five north-eastern African and Arabian species are characterized by a narrow, parallel-sided stridulatory region, compared with the stridulatory region of the southern African species, which is broad and rounded anteriorly, becoming constricted posteriorly, before widening again at the posterior edge of the segment (Kraepelin 1899, 1908b; Purcell 1901). The narrow condition is hypothesized to be apomorphic and, according to the present analysis, to have evolved independently in node 13 and *P. pallidus*. The stridulatory region of *P. mossambicensis* has been described as 'confined to a rather narrow channel' (Hewitt 1918: 114). However, the basic shape of the region, including the posterior constriction, is evidently homologous with that of the other southern African species.

32 Metasomal segment I and, to a lesser extent, II, shape of stridulatory region (if present) in lateral aspect. The stridulatory region is truncated at the anterodorsal edge of segments I–II in most species of *Parabuthus*. However, nine species are characterized by a rounded extension of the stridulatory region, beyond the anterodorsal edge, giving a step-like appearance in lateral aspect (Purcell 1898, 1901; Kraepelin 1908b; Hewitt 1913, 1918; Lamoral 1979). This condition is hypothesized to be synapomorphic, but independently derived in node 10, node 16 and *P. villosus*. Reversals are hypothesized for node 22 and *P. pallidus*.

33 Metasomal segment I, extent of stridulatory region (if present) in dorsal aspect. The stridulatory region is confined to the dorsal surface of the metasomal segment in all except six species of *Parabuthus*, in which it extends onto the anterior surface in a short V-shape, regardless of whether the surface is truncated or extended anterodorsally (character 32). This V-shaped extension of the stridulatory region onto the anterior surface is considered to be synapomorphic for node 21.

34 Metasomal segment II, extent of stridulatory region (if present) in dorsal aspect. Lamoral's (1978) character 7, with the entry for *P. villosus* corrected to account for polymorphism. Newlands & Martindale (1980) questioned the utility of this character. Harington (1984) demonstrated that this character was unreliable for separating *P. brachystylus* from *P. villosus* (Lawrence 1928, 1955; Lamoral 1979), and Prendini (in press) subsequently synonymized *P. brachystylus*. Similar rationale was used to synonymize *Parabuthis planicauda frenchi* (Purcell, 1901) with *P. planicauda* (Prendini, in press). Lamoral (1978) regarded the posterodorsal extension of the stridulatory region on segment II to be apomorphic on the basis of structural complexity and outgroup comparison. However, this hypothesis was falsified in the present analysis, in which the posterodorsal extension was demonstrated to be plesiomorphic. Absence of a posterodorsal extension is considered to be synapomorphic, but independently derived in nodes 9 and 24 (Kraepelin 1908b; Hewitt 1915, 1918; Lawrence 1955; Lamoral 1977, 1979; Newlands & Martindale 1980; FitzPatrick 1994). This character is polymorphic in *P. planicauda* and *P. villosus*.

35 Metasomal segment II, nature of stridulatory region (if present). The stridulatory region of segment II is composed of fine to coarse granules in all except two species of *Parabuthus*, *P. mossambicensis* (Pocock 1899b, 1901a,b; Kraepelin 1908b; Hirst 1911; Hewitt 1912, 1914, 1918; Lawrence 1955; Newlands & Martindale 1980; FitzPatrick 1994) and *P. stridulus* (Hewitt 1913, 1918; Lawrence 1955; Lamoral 1979), in which it comprises horizontal ridges. Whereas the stridulatory region of *P. mossambicensis* also comprises horizontal ridges on segment I, the corresponding region of *P. stridulus* comprises fine granules, suggesting that the ridges have evolved independently in the two species, a hypothesis supported by the present analysis.

36 Metasomal segments II–III, posterodorsal edge. The V-shaped anteromedian curvature of the posterodorsal edge of segments II–III, long recognized as a diagnostic character for *P. capensis* (Purcell 1899, 1901; Kraepelin 1908b; Werner 1916; Hewitt 1918; Lawrence 1955; Eastwood 1977), also occurs in the recently described *P. muelleri* (Prendini 2000a), and is therefore considered to be synapomorphic for these species (node 18).

37 Metasomal segments IV–V, lateral intercarinal surfaces. Lamoral's (1978) character 11, in which granular lateral intercarinal surfaces were hypothesized to be apomorphic on the basis of outgroup comparison and structural complexity. This hypothesis was falsified in the present analysis. Smooth lateral intercarinal surfaces are apomorphic, and considered to have evolved independently in node 6 (Lamoral 1979, 1980; FitzPatrick 1994), node 11 (Hewitt 1913, 1918; Lamoral 1979) and *P. calvus* (Purcell 1898, 1901; Kraepelin 1908b).

38 Metasomal segments I–IV, dorsosubmedian carinae. The absence of dorsosubmedian carinae on metasomal segments I–IV is unique to four species of *Parabuthus* (node 5), for which it is considered to be synapomorphic (Lamoral 1979, 1980; FitzPatrick 1994).

39 Metasomal segment IV, dorsosubmedian carinae (if present). In the outgroup taxa and most species of *Parabuthus*, the dorsosubmedian carinae of metasomal segment IV comprise a continuous row of granules. However, in nine species of *Parabuthus*, this row is medially discontinuous — referred to by Purcell (1901: 163) as 'dislocated or … distinctly doubled in the middle' — a condition hypothesized to be apomorphic. This apomorphic condition has evolved independently in node 17 (Purcell 1901; Kraepelin 1908b; Lamoral 1979) and node 23.

40 Metasomal segments II–IV, distal spiniform granules of dorsosubmedian carinae (if present), size relative to preceding granules. In *Grosphus* and *Uroplectes*, the distal spiniform granules on the dorsosubmedian carinae are not noticeably more pronounced than the preceding granules, suggesting that this condition is plesiomorphic. Pronounced distal spiniform granules, which occur in 12 species of *Parabuthus* (Pocock 1889; Purcell 1901; Eastwood 1977; Lamoral 1979; Prendini 2000a), are considered to be synapomorphic for node 16, but independently derived in *P. brevimanus*.

41 Metasomal segment IV, ventrosubmedian and ventrolateral carinae. Lamoral's (1978) character 1, with the addition of a state for the outgroups, *Grosphus* and *Uroplectes*, in which the ventrosubmedian and ventrolateral carinae are present and continuous to the distal edge of metasomal segment IV, and which is considered to be plesiomorphic. In most species of *Parabuthus*, the ventrolateral carinae are present and distinct, but the ventrosubmedian carinae become obsolete distally (Pocock 1890, 1899a; Harington 1984), a condition hypothesized to be synapomorphic for *Parabuthus*. The condition is particularly marked in *P. kalaharicus*, in which the ventrosubmedian carinae are reduced to the proximal third of their length (Lamoral 1977, 1979). Complete absence of ventrosubmedian and ventrolateral carinae on metasomal segment IV occurs in only six species of the genus (Pocock 1890, 1901a,b; Purcell 1898, 1901; Kraepelin 1899, 1908b; Hewitt 1918; Lawrence 1955; Lamoral 1979, 1980; FitzPatrick 1994). It is considered to be synapomorphic for node 4, but independently derived in *P. calvus*.

42 Metasomal segment IV, median lateral carina. Lamoral's (1978) character 4, with the entry for *P. namibensis* corrected (the median lateral carina is continuous but poorly developed in this species). Lamoral (1978) postulated an ordered transformation series for this character on the basis of outgroup comparison: continuous and distinct was considered to be plesiomorphic, whereas sequentially, continuous but poorly developed was considered to be derived, and absent or proximally obsolete even more derived. This character was treated unordered in the present analysis, and Lamoral's transformation series was falsified. The absent to proximally obsolete condition is hypothesized to be plesiomorphic in nodes 4 and 9 (Kraepelin 1899, 1908b; Purcell 1901; Hewitt

1918; Lawrence 1955; Lamoral 1979; FitzPatrick 1994), due to occurrence in the outgroups, and the two apomorphic states are considered independently derived. The continuous but poorly developed condition is synapomorphic for node 10 (Kraepelin 1899, 1908b; Purcell 1901; Pocock 1902; Hewitt 1913, 1918; Lawrence 1955; Lamoral 1979), whereas the continuous and distinct condition is synapomorphic for node 12 (Pocock 1890, 1902; Kraepelin 1899, 1908b; Purcell 1901; Hewitt 1913, 1918; Lawrence 1955; Lamoral 1979; FitzPatrick 1994). The absence of median lateral carinae in *P. calvus* (Purcell 1898, 1901; Kraepelin 1908b) is interpreted as a reversal.

43 Metasomal segment V, dorsosubmedian carinae. Lamoral's (1978) character 6, with the entries for *P. kraepelini*, *P. laevifrons* and *P. stridulus* corrected — dorsosubmedian carinae are absent in *P. laevifrons* and *P. stridulus*, but display sharp spiniform granules in *P. kraepelini* (Kraepelin 1899, 1908b). Lamoral (1978) postulated an ordered transformation series for this character, on the basis of outgroup comparison: absence was considered to be plesiomorphic, poorly developed was considered to be derived and distinct sequentially more derived. This character was treated unordered in the present analysis, but Lamoral's transformation series was supported. The absence of dorsosubmedian carinae is plesiomorphic whereas poorly developed dorsomedian carinae, with rounded granules, are synapomorphic for node 12 (Purcell 1901; Kraepelin 1908b; Hewitt 1918; Lawrence 1955; Lamoral 1979). Distinct dorsosubmedian carinae, with spiniform granules, are synapomorphic for node 16, with a reversal to poorly developed dorsosubmedian carinae hypothesized for node 19 (Pocock 1889; Purcell 1899, 1901; Kraepelin 1908b; Hewitt 1915, 1918; Werner 1916; Lawrence 1955; Eastwood 1977; Lamoral 1979; Newlands & Martindale 1980; FitzPatrick 1994). Poorly developed dorsosubmedian carinae are considered to have evolved independently in *P. namibensis* (Lamoral 1979). The ci and ri values of this character increased with successive weighting (Table 5).

44 Metasomal segment V, dorsolateral carinae. Dorsolateral carinae are absent in *Grosphus* and *Uroplectes*; hence the presence of distally obsolete dorsolateral carinae is considered to be synapomorphic for node 2 (Purcell 1899, 1901; Kraepelin 1908b; Hewitt 1918; Lawrence 1955; Eastwood 1977; Lamoral 1979; Prendini 2000a). A reversal to plesiomorphic absence is hypothesized for node 4 (Lamoral 1979, 1980). Continuous dorsolateral carinae are considered to be relatively derived from distally obsolete carinae, and synapomorphic for node 21 (Purcell 1901; Kraepelin 1908b; Hewitt 1918; Lawrence 1955; Lamoral 1979; Newlands & Martindale 1980).

45 Metasomal segment V, ventrolateral carinae. Lamoral's (1978) character 17, with the entry for *P. namibensis* corrected (the ventrolateral carinae were observed to converge distally in the specimens examined). On the basis of outgroup comparison, ecological specialization and the 'correlation of applied criteria', Lamoral (1978: 277) hypothesized that subparallel carinae were plesiomorphic, whereas distally diverging and distally converging carinae were oppositely derived states. In the present investigation, the separate state recognized by Lamoral in *P. villosus* (and *P. brachystylus*) for subparallel carinae was merged with the state for diverging carinae, since these conditions were impossible to distinguish in the specimens examined. Lamoral's hypothesis was nonetheless falsified, since distally converging carinae occur in the outgroup taxa. Subparallel to diverging carinae are hypothesized to be synapomorphic for node 22, with a reversal to the converging condition in *P. raudus* (Lamoral 1979). Distally diverging carinae are considered to be independently derived in *P. brevimanus* (Lamoral 1979). The ci and ri values of this character decreased with successive weighting (Table 5).

46 Metasomal segment V, distal half of ventrolateral carinae. Lamoral's (1978) character 14. All species of *Parabuthus* are characterized by the presence of distinctive processes in the distal half of the ventrolateral carinae on metasomal segment V (Pocock 1895; Purcell 1901; Lamoral 1977, 1979; Newlands & Martindale 1980). These processes, used to loosen soil in the initial stages of burrowing (Eastwood 1977), are considered to be synapomorphic for *Parabuthus*. Although the exact shape and number of these processes are species specific, they can be grouped into two types: spinose processes are narrow, conical or flattened, and tapering towards the apex, whereas lobate processes are broad and, unlike spinose processes, always present a flat surface at the apex. Lamoral (1978) considered spinose processes to be plesiomorphic and lobate processes to be apomorphic, according to the structural complexity and common is primitive criteria. This hypothesis was falsified in the present analysis. Spinose processes are relatively apomorphic within *Parabuthus*, and are hypothesized to have evolved independently in nodes 5, 15, 23 and *P. stridulus*. The ci and ri values of this character decreased with successive weighting (Table 5).

47 Metasomal segment V, ventrosubmedian carinae. Ventrosubmedian carinae on metasomal segment V are absent, or indistinct from the surrounding granules on the ventral surface, in many buthid scorpions, including the outgroups for this analysis, *Grosphus* and *Uroplectes* (Pocock 1890). However, the ventrosubmedian carinae are distinct, although distally obsolete, in seven species of *Parabuthus*. This condition is hypothesized to be independently derived in nodes 10 and 13.

48 Metasomal segment V, ventromedian carina. Although the ventromedian carina of metasomal segment V is present in most species of *Parabuthus*, it may be difficult to discern from surrounding granules on the ventral surface in some species (e.g. *P. villosus*). The presence of a ventromedian carina is considered to be plesiomorphic in *Parabuthus* on the basis of its occurrence in *Grosphus*. Absence of the ventromedian carina is hypothesized to have evolved independently in *Uroplectes*, and in node 4, *P. kalaharicus* and *P. calvus* (Purcell 1898; Lamoral 1977, 1979, 1980).

Telson

49 Telson vesicle, width relative to width of metasomal segment V. Lamoral's (1978) character 5, in which the reduced, narrow vesicle of *P. granulatus* and *P. kalaharicus* (Purcell 1901; Hewitt 1918; Newlands 1974a, 1978a; Lamoral 1977, 1979; FitzPatrick 1994) was considered to be synapomorphic on the basis of outgroup comparison. This hypothesis was confirmed in the present study (node 9).

50 Telson vesicle, dorsoproximal surface. Lamoral's (1978) character 18, in which the deep longitudinal excavation of the vesicle of *P. stridulus* (Hewitt 1913, 1918; Lamoral 1979) was considered to be apomorphic, and the shallow excavation plesiomorphic, on the basis of the common is primitive criterion. This character is autapomorphic for *P. stridulus*.

51 Telson aculeus, shape. Pocock (1895: 316) first noted the 'curiously curved aculeus' of *P. villosus*. The abrupt curvature of the aculeus is most distinctive in *P. kraepelini*, *P. transvaalicus* and *P. villosus*. However, it is also evident in the remaining species of node 12, for which it is considered to be synapomorphic.

Behaviour

The following behavioural characters are based on observations of *Parabuthus* species personally recorded in the field and laboratory with the aid of UV detection methods, as well as information from Newlands (1974b, 1978b), Eastwood (1977, 1978b), Lamoral (1977, 1978, 1979, 1980) and Newlands & Martindale (1980). Observations are unavailable for the north-eastern African and Arabian species and for *P. calvus*, and are scored unknown in these species.

52 Diurnal retreat. All species of *Parabuthus* are obligate burrowers, compared with many other buthids, including the outgroups, that merely hide under stones or other available cover without constructing a burrow (Newlands 1974b, 1978a,b; Eastwood 1978a; Newlands & Martindale 1980). Evidence for this burrowing existence can be seen in the following characters: thickened metasoma with well-developed metasomal carinae, and spinose or lobate processes on ventrolateral carinae of metasomal segment V, used to loosen soil in tail-scraping operations (Eastwood 1977, 1978b); macrosetal combs on basitarsi of legs I–II, used to scrape and rake soil out of the burrow (Eastwood 1977, 1978b; Lamoral 1979). The ability to burrow is considered to be synapomorphic for *Parabuthus* (node 2). Most species of *Parabuthus* construct burrows in open ground, the entrances of which are then subsequently filled with sand from below. However, several species (e.g. *P. muelleri*, *P. planicauda*, *P. transvaalicus* and *P. villosus*) construct burrows under stones (Newlands 1974b, 1978a,b; Eastwood 1978b; Lamoral 1979; Newlands & Martindale 1980; Harington 1984; Prendini 2000a). The requirement for rocks appears to be obligate in these species, which are restricted to rocky habitats, in contrast to other species of *Parabuthus* that can be found in any area of suitable substratum, regardless of the presence of rocks and stones. The dependence on rock is considered to be synapomorphic for node 17 and independently derived in node 25. It should be noted that, although the dependence on rock has been confirmed in numerous individuals of *P. planicauda*, *P. transvaalicus* and *P. villosus*, $n = 2$ for *P. muelleri*. *P. capensis* is polymorphic for this character.

53 Foraging strategy. Six species of *Parabuthus* are unusual because they consistently display an 'errant' mode of foraging (Bradley 1988; Polis 1990), i.e. they hunt actively, rather than adopting a 'sit-and-wait' strategy, as in most species of *Parabuthus* and the outgroups, *Grosphus* and *Uroplectes*. This errant strategy is hypothesized to be synapomorphic for node 8 and independently derived in *P. villosus*. The latter species is unusual in foraging actively by day or night (Newlands 1974a; Harington 1982).