Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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ABSTRACT
The arachnid fauna of Angola and Namibia is diverse and includes high levels of endemism, much of which is associated with the arid zone, especially the Namib Desert. The endemic arachnid fauna of the highlands and escarpments, including mountain ranges, plateaus and inselbergs, has received less attention. The study presented here is the first to compile existing distributional data for three arachnid orders – whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae Sundevall, 1833) – occurring in the highlands and escarpments of Angola and Namibia from published literature, online databases and natural history collections. Distribution maps were used, together with available data or expert knowledge of taxon habitat requirements, to prepare a list of described arachnid taxa considered endemic or near-endemic to the western highlands and escarpments of these two countries. In addition, arachnid endemism was assessed more broadly by scoring the presence of described and potential undescribed endemics in relevant highlands and escarpments, tallying the scores for each order, and ranking the highlands and escarpments based on the sum of all three ordinal tallies. These scores provide a rough index of the relative importance of highlands and escarpments in Angola and Namibia for prioritising decisions regarding conservation as well as further survey and inventory from the arachnid perspective. Although the highlands and escarpments of Angola and Namibia probably serve as refugia for taxa requiring cooler, more humid habitats than are available in the surrounding arid lowlands, including palaeoendemics, they appear to contain fewer endemic arachnid taxa than the lowlands. This may be because: (1) the highlands and escarpments of Angola and Namibia are relatively low, on average, providing few opportunities for insular speciation; (2) much arachnid endemism in the arid lowlands is associated with unique substrates that are absent in the highlands, including sand dunes, gravel plains and clays associated with drainage systems, all of which facilitate burrowing to escape the arid conditions and promote diversification; and (3) much of the taxonomy of the arachnids of both countries remains unresolved, and the distributions poorly understood, especially in Angola. More intensive surveys, with an emphasis on collecting genetic samples from disjunct populations across the distributions of each putative species, are needed to better understand arachnid diversity and endemism in the region.

Keywords: Amblypygi, Angola, Arachnida, endemism, escarpments, highlands, Namibia, Scorpiones, Solifugae

INTRODUCTION

Arachnids have inspired fear and fascination since antiquity, in part because they are predators and some, such as scorpions and spiders, are venomous. Few are considered medically important, however, and fewer still have been implicated in fatal or debilitating envenomation. Despite their fearsome appearance, most arachnids are harmless.

Arachnids are of particular interest to students of evolution because of the great age of their lineage. Fossil scorpions from the Silurian, 435 mya, present the first unequivocal evidence for terrestrialisation (Dunlop *et al*. 2008). The arachnid ground plan has changed little since the first scorpions colonised land: Palaeozoic arachnids closely resemble their modern descendants. Morphological conservatism, together with low vagility and stenotopic ecological requirements, make many arachnid taxa prone to vicariance and allopatric speciation (Prendini 2001b, Bryson *et al*. 2013, Loria & Prendini 2021, Schramm *et al*. 2021).

As elsewhere in southern Africa, the arachnid fauna of Angola and Namibia is diverse and includes high levels of endemism, much of which is associated with the arid zone, especially the Namib Desert (Lamoral 1979, Prendini 2005c, Prendini & Esposito 2010). The endemic arachnid fauna of the highlands and escarpments, including mountain ranges, plateaus and inselbergs, has received less attention, although the highlands probably serve as refugia for taxa requiring cooler, more humid habitats than are available in the surrounding arid lowlands, as in other parts of the world (Prendini 2003a, Bryson *et al*. 2013, Loria & Prendini 2021, Schramm *et al*. 2021). One reason is because knowledge of the taxonomy and distributions of arachnids in both countries, but especially in Angola, is limited, compared to other taxa such as vertebrates, flowering plants and even some terrestrial invertebrates.

The study presented here is the first to compile existing distributional data for three arachnid orders – whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae

Sundevall, 1833) – occurring in the highlands and escarpments of Angola and Namibia from published literature, online databases and natural history collections. Distribution maps were used, together with available data or expert knowledge of taxon habitat requirements, to prepare a list of described arachnid taxa considered endemic or near-endemic to the highlands and escarpments. In addition, arachnid endemism in the highlands and escarpments was assessed more broadly by scoring the presence of described and potential undescribed endemics in relevant highlands, tallying the scores for each order and ranking the highlands and escarpments based on the sum of all three ordinal tallies.

Although the picture may change when the taxonomy of each order is revised and the distributions are better understood, these data provide a baseline for prioritising decisions regarding conservation, as well as further survey and inventory, from the arachnid perspective. More intensive surveys, with an emphasis on collecting genetic samples from disjunct populations across the distributions of each putative species, are needed to better understand arachnid diversity and endemism in the region.

METHODS

Taxonomic and geographical constraints

The study presented here made use of the most recent published classifications for each arachnid order and relied on existing sources of distributional data (see below). Only valid, described infrageneric taxa (species and subspecies) were included in the assessment. Synonyms, *nomina dubia* and taxa, the validity of which was questioned in the most recent taxonomic treatments, were omitted. For example, *Solpugema aethiops* Lawrence, 1967 was excluded, despite having been described from the Brandberg (the only known locality for this species), as Wharton (1981) suggested that this species is almost certainly conspecific with the more widespread *Solpugista namibica* Kraus, 1956. Female solifuges are notoriously difficult to identify and, given that *S. aethiops* was described from a single female and the only known specimen, its validity must be re-evaluated.

Whereas the taxonomy of southern African whip spiders is fairly well resolved, the secretive nature and seasonal activity of these arachnids, and their need for a humid microhabitat, implies that their distributions, especially in the arid zone of Angola and Namibia, remain poorly documented.

The taxonomy of southern African scorpions has received much attention but continues to undergo active revision, and the distributions of scorpion taxa are fairly well documented due to the ease with which many (though by no means all) may be collected.

Compared to Amblypygi and Scorpiones, the knowledge of solifuges is much poorer in terms of taxonomy and distribution for the following reasons. Firstly, species-level taxonomy of Solifugae depends almost entirely on characters of adult males, which are highly seasonal and active for only a brief period annually. Secondly, the seasonality, habitat specificity and speed of most solifuges makes them difficult to collect and survey. Thirdly, there are few experts on the order, worldwide. The highland endemic status of solifuge species was therefore evaluated based on few specimens and locality records, often singletons. In addition, the precision of many historical records is unknown. This may influence whether a locality record falls on a highland or only in the vicinity thereof, which in turn affects decisions regarding whether or not a species may be endemic or near-endemic to the highland.

Given these constraints, understanding of the taxonomy, distributions, and endemism of all three arachnid orders in southern Africa lags far behind that of the vertebrates, flowering plants and even some terrestrial invertebrates, like butterflies and dragonflies. There is also a huge disparity between the knowledge of arachnids in Angola and Namibia. The fauna of Namibia has been subject to surveys, inventories and publications from the German colonial period to the present, with extensive collections deposited in natural history museums in Germany, South Africa and the National Museum of Namibia. In contrast, research on Angolan arachnids which began during the Portuguese colonial period, largely ceased during approximately three decades of war (1975–2002), a time in which no new collections were added to the Museo do Dundo. Arachnid collections from Angola represent a tiny fraction of those from Namibia and large swaths of the country have never been surveyed.

Georeferencing and mapping

A database of point locality records for mapping the distributions of arachnid taxa considered or suspected to be endemic to the highlands and escarpments of Angola and Namibia was assembled from published literature, online databases, e.g., iNaturalist (https://www.inaturalist.org), and material examined from the following natural history collections: Albany Museum, Grahamstown, South Africa; American Museum of Natural History, New York, USA; Ditsong National Museum of Natural History (former Transvaal Museum), Pretoria, South Africa; Iziko South African Museum, Cape Town, South Africa; KwaZulu-Natal Museum (former Natal Museum), Pietermaritzburg, South Africa; and National Museum of Namibia, Windhoek.

Records for which geographical coordinates were previously entered by the collector were checked for accuracy and the remaining records georeferenced

using the Geographic Names Server (https://geonames.nga.mil/geonames/GNSHome), the Fuzzy Gazetteer (https://isodp.hof-university.de/fuzzyg/query) and Google Earth (https://earth.google.com). Dubious or imprecise records were omitted. The final dataset comprised 209 point localities for 22 infrageneric taxa in 16 genera and ten families. Distribution maps were produced using QGIS 3.16.10 'Hannover' Long Term Release (QGIS Development Team 2021), by superimposing point locality records on datasets representing the political boundaries, topography (inselbergs and mountain ranges, plateaus, escarpments) and major rivers of Angola and Namibia.

Assessing highland endemism

Distribution maps were used, together with available data or expert knowledge of taxon habitat requirements, to prepare a list of described arachnid taxa considered endemic or near-endemic to the highlands and escarpments of Angola and Namibia. Consistent with other treatments in the present volume, the highlands and escarpments of Angola and Namibia comprise inselbergs and mountain ranges (free-standing hills or mountains that rise at least 200 m above the surrounding land); plateaus (broad areas of flat or hilly ground, at least 1,600 masl); and escarpments (narrow areas with steep slopes on the western margins of plateaus).

Relatively few taxa were considered *bona fide* highland endemics; i.e., those exclusively restricted to highlands and escarpments. The remaining taxa were considered highland endemics or near-endemics only if most of the known locality records were situated on or adjacent to highlands and escarpments, applying the metapopulation concept (Levins 1969), whereby disjunct populations occupying highland refugia may coalesce during periods of cooler, more humid climate. Hotter, drier lowlands represent barriers to dispersal for highland taxa inhabiting disjunct refugia. In contrast, taxa with one or a few records on highlands and escarpments, but an otherwise predominantly lowland distribution, even if occurring within valleys between highlands and escarpments, were not considered highland endemics. For these taxa, highlands and escarpments represent barriers to dispersal between disjunct lowlands.

In addition, arachnid endemism was assessed more broadly by scoring the presence of described and potential but undescribed endemics in the highlands and escarpments of Namibia and Angola, tallying the scores for each order, and ranking the various highlands and escarpments based on the sum of all three ordinal tallies (a relative score of the number of endemic arachnids in each highland). Although these scores may change when the taxonomy of each order is revised and the distributions are better understood, they provide a rough index of the relative importance of highlands and escarpments for prioritising decisions regarding conservation, as well as for further survey and inventory, from the arachnid perspective.

RESULTS AND DISCUSSION

Highland endemic whip spiders

Only two species of Amblypygi may be considered endemic to the highlands and escarpments of Angola and Namibia (Table 1). Both constitute monotypic genera, palaeoendemics which diverged from other phrynichid genera before the breakup of Gondwanaland (Weygoldt 1996), and occupy refugia in the highlands, escarpments and other areas with a higher humidity (e.g., wells and watercourses) than the surrounding arid lowlands.

Phrynichodamon scullyi (Purcell, 1902), of the family Phrynichidae Simon, 1892, has been recorded from only four localities in southwestern Namibia (Figure 1), each represented by a single individual, over the course of a century (Lawrence 1967, Weygoldt 1996). These localities are situated in the Hakosberge, the Tirasberge, Naukluft Mountains and the Aus Mountains. Most of the known records of *P. scullyi* occur further south, in the Kamiesberg, Bokkeveldberge and Cederberg of South Africa (Lawrence 1949, 1955, Weygoldt 1996, 1998), where the species has been encountered slightly more often. Given the large distances between the four disjunct populations of this species in Namibia, and between them and the two disjunct populations in South Africa, it would be important to compare them genetically to assess whether more than one species is involved and to determine the timing of divergence.

Xerophrynus machadoi (Fage, 1951), considered *incertae sedis* within superfamily Phrynoidea Blanchard, 1852 by Weygoldt (1996, 2000), is known from fewer than ten localities, two (the type locality and a second record near Omahua) in southwestern Angola (Lawrence 1949, Fage 1951) and the rest in northwestern Namibia (Figure 1). Most of the known localities (and specimens) were collected from valleys on the southern slopes of the Brandberg Massif (Weygoldt 1996, 1998). The other Namibian localities are associated with the Etendeka and Otjikondavirongo mountains, the Huab outliers and the Uis Mountains of Damaraland, an area in northwestern Namibia bordered to the north by the Kaokoveld, to the west and south by the Namib Desert, and to the east by the Kalahari Desert, and encompassing a distinctive semi-desert landscape comprising vast, arid, gravel or rocky plains intersected by towering granite outcrops. As with *P. scullyi*, the large distances between the disjunct populations of *X. machadoi* in Angola, and between

them and the disjunct Namibian populations in the Kaokoveld and Damaraland, emphasise the need for genetic comparison to assess whether more than one species is involved, as well as to determine the timing of divergence.

The difficulty of collecting these secretive lithophilous arachnids, which appear to retreat into deep rock crevices or exfoliations during the dry season, implies that collection efforts must be focused on the rainy season, and concentrated on areas with higher humidity, such as caves, wells and watercourses, for any possibility of success.

Damon gracilis Weygoldt, 1998, a third species of whip spider, endemic to southwestern Angola and northwestern Namibia, has been recorded from some highlands and escarpments, including the Serra da Neve in Angola and the Baynes–Otjihipa Mountains in Namibia (Weygoldt 1998, 1999, 2000). However, this species was not considered endemic or near-endemic to the highlands and escarpments as the majority of the known records are situated at low elevation, often in association with wells and watercourses. *Damon sylviae* Prendini *et al*., 2005, the fourth species of whip spider recorded in Namibia, has not been recorded from the highlands and escarpments (Prendini *et al*. 2005).

Table 1: *Described species and subspecies of whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae Sundevall, 1833) that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia, with countries and highlands of occurrence.*

Classification	**Species**	**Country: highlands and escarpments**
Amblypygi		
Phrynichidae	*Phrynichodamon scullyi* (Purcell, 1902)	Namibia: Hakosberge, Tirasberge, Naukluft Mountains and Aus Mountains; South Africa: Kamiesberg, Bokkeveldberge and Cederberg
	Xerophrynus machadoi (Fage, 1951)	Angola: lowlands; Namibia: Kaokoveld (Etendeka and Otjikondavirongo mountains), Huab outliers, and Brandberg Massif (valleys)
Scorpiones		
Bothriuridae	*Brandbergia haringtoni* Prendini, 2003	Namibia: Brandberg Massif (summit)
	Lisposoma josehermana Lamoral, 1979	Namibia: Otavi and Paresis mountains and Waterberg Plateau
Buthidae	*Uroplectes ngangelarum* Monard, 1930	Angola: southwestern highlands (e.g., Serra de Chela, Serra da Neve)
	Uroplectes tumidimanus Lamoral, 1979	Namibia: Erongo Mountains through central highlands (Khomas Hochland, Auas Mountains, Hakosberge and Gamsberg), Naukluft and Tsaris mountains, and Rooirand Plateau to Huib-Hoch Plateau and Hunsberge
Hormuridae	*Hadogenes lawrencei* Newlands, 1972	Namibia: Uri-Hauchab (inselberg, west of Awasibberge)
Scorpionidae	*Opistophthalmus scabrifrons* Hewitt, 1918	Namibia: Groot Karasberg
	Opistophthalmus schultzei Kraepelin, 1908	Namibia: Aus Mountains
	Opistophthalmus ugabensis Hewitt, 1934	Namibia: Brandberg Massif (valleys), Tafelkop and Huab outliers
Solifugae		
Ceromidae	*Ceromella focki* (Kraepelin, 1914)	Namibia: central highlands (Khomas Hochland)
Daesiidae	*Biton striatus bidentatus* Lawrence, 1955	Namibia: Kaokoveld (Etendeka Mountains) and Brandberg Massif (summit)
	Blossia angolensis (Lawrence, 1960)	Angola: highlands near Lubango
	Blossia falcifera quibensis Hewitt, 1934	Namibia: Rooirand Plateau and Huib-Hoch Plateau
	Blossia gaerdesi Lawrence, 1972	Namibia: Otavi Mountains, Waterberg Plateau, central highlands (Khomas Hochland) and Rooirand Plateau
	Hemiblossia machadoi Lawrence, 1960	Angola: Serra da Chela (highlands near Lubango)
Gylippidae	*Bdellophaga angulata* Wharton, 1981	Namibia: central highlands (Auas Mountains and Gamsberg)
	Trichotoma fusca (Roewer, 1941)	Namibia: Waterberg Plateau
Melanoblossiidae	*Melanoblossia ansie* Bird & Wharton, 2015	Namibia: Tsaukhaib (inselberg in Sperrgebiet)
Solpugidae	*Solpugista methueni* (Hewitt, 1914)	Namibia: Rooirand Plateau and Huib-Hoch Plateau
	Zeria glabricornis (Lawrence, 1928)	Namibia: Kaokoveld (Baynes–Otjihipa and Etendeka mountains) and Brandberg Massif (summit)
	Zeria schlechteri (Purcell, 1899)	Namibia: Rooirand Plateau; South Africa: Naroepberge

Highland endemic scorpions

Two genera and three species of the family Bothriuridae Simon, 1880 are endemic to Namibia. This monophyletic lineage of palaeoendemic taxa diverged from their relatives in South America and Australia when Africa separated from the rest of Gondwana ca. 140 million years ago (Prendini 2003a, 2005c). Two of the three species are highland endemics (Table 1), occupying refugia with higher humidity (e.g., wells and watercourses) than the surrounding arid lowlands.

Brandbergia haringtoni Prendini, 2003 is known from only two specimens collected at 1,650 masl in Goaseb (or Ga-Asab) gorge on the southern side of the Brandberg Massif in 1978 (Figure 1). Little is known about this species and several subsequent attempts to collect it at the type locality (including during the rainy season) were unsuccessful (Prendini 2005a). However, further attempts are considered a high priority as the male remains unknown and a genetic sample is needed for comparison with other bothriurid taxa in Namibia, South America and Australia.

Lisposoma josehermana Lamoral, 1979 is relatively common in the Otavi Mountains, where it is known from several inselbergs, and the Waterberg Plateau (Figure 1). This lapidicolous species may be found under stones and in caves on wooded, humid slopes (Lamoral 1979, Prendini 2003b, 2005a). It has also been recorded from the Paresis Mountains. Genetic comparison of the disjunct populations is needed to assess whether more than one species is involved and to test the timing of divergence from one another and from other Namibian bothriurids.

Lisposoma elegans Lawrence, 1928, the third species of endemic Namibian bothriurid, has been recorded from some highlands and escarpments (Prendini 2003b), including the Kaokoveld (Otjikondavirongo Mountains) and the Central Highlands (Khomas Hochland and Gamsberg). However, this species was not considered endemic or near-endemic to the highlands and escarpments as most of the known records are from low elevations. This lapidicolous species occurs under stones, often in humid microhabitats, such as along gulleys and episodic watercourses, in rather arid locations (Lawrence 1928, Prendini 2005a). As with *L. josehermana*, genetic comparison of the disjunct populations of *L. elegans* is needed to assess whether more than one species is involved and to determine the timing of divergence from one another and from other Namibian bothriurids. The diverse family Buthidae C.L. Koch, 1837 contains only two species considered near-endemic to the highlands and escarpments, one in southwestern Angola, and the other in central-southern Namibia (Table 1). Both are lapidicolous species of the exclusively Afrotropical genus *Uroplectes* Peters, 1861 and may be found under stones (Prendini 2001b). *Uroplectes ngangelarum* Monard, 1930 is near-endemic to the highlands and escarpments of southwestern Angola, most of the known localities having been recorded on the plateau in the vicinity of Lubango and Humpata (Figure 1). *Uroplectes tumidimanus* Lamoral, 1979 is near-endemic to the highlands and escarpments of Namibia, extending from the Erongo Mountains through the central highlands (Khomas Hochland, Auas Mountains, Hakos Mountains and Gamsberg) to the Rooirand Plateau, Huib-Hoch Plateau and Hunsberge (Figure 1). Both species appear to be closely related to the widespread *Uroplectes planimanus* (Karsch, 1879), distributed from southern Angola and northern Namibia, across Botswana and Zambia to Mozambique, Zimbabwe and the Limpopo Province of northern South Africa (Prendini 2005c), from which it appears they became isolated in the highlands and subsequently diverged. However, the timing of these events, as well as the limits of all three species, await further testing. Indeed, the taxonomy of *Uroplectes* is probably the least resolved of any group of southern African scorpions. Further collections and genetic analyses are needed to address species limits as several undescribed highland endemics are suspected.

One species of the lithophilous Afrotropical genus *Hadogenes* Kraepelin, 1894, in the family Hormuridae Laurie, 1896, is endemic to the highlands and escarpments of Namibia (Table 1). Like other species of the genus, *Hadogenes lawrencei* Newlands, 1972 inhabits the cracks and crevices of weathered rock outcrops (Prendini 2001b, 2005c). It appears to be restricted to the Uri-Hauchab, a relatively low elevation inselberg west of the Awasibberge (Figure 2), surrounded by sand dunes of the central Namib dune field, where it is presumed to have evolved in isolation since the inselberg was isolated from the escarpment in the Pliocene (Newlands 1972). This hypothesis awaits rigorous testing which will require the collection of genetic material from *H. lawrencei* and the nearest populations of *Hadogenes tityrus* (Simon, 1888) in the Awasibberge. The collection and analysis of genetic material from across the distribution of *H. tityrus* is considered an important priority for delimiting the species of this complex (Newlands & Cantrell 1985) and for better understanding distributions which suggest that some may be endemic to the highlands and escarpments of Namibia.

Another hormurid, *Hadogenes zumpti* Newlands & Cantrell, 1985, has been recorded from the Hunsberge of southern Namibia and the Richtersveld of South Africa (Newlands & Prendini 1997), but was not considered endemic or near-endemic to the highlands and escarpments of Namibia as most of the

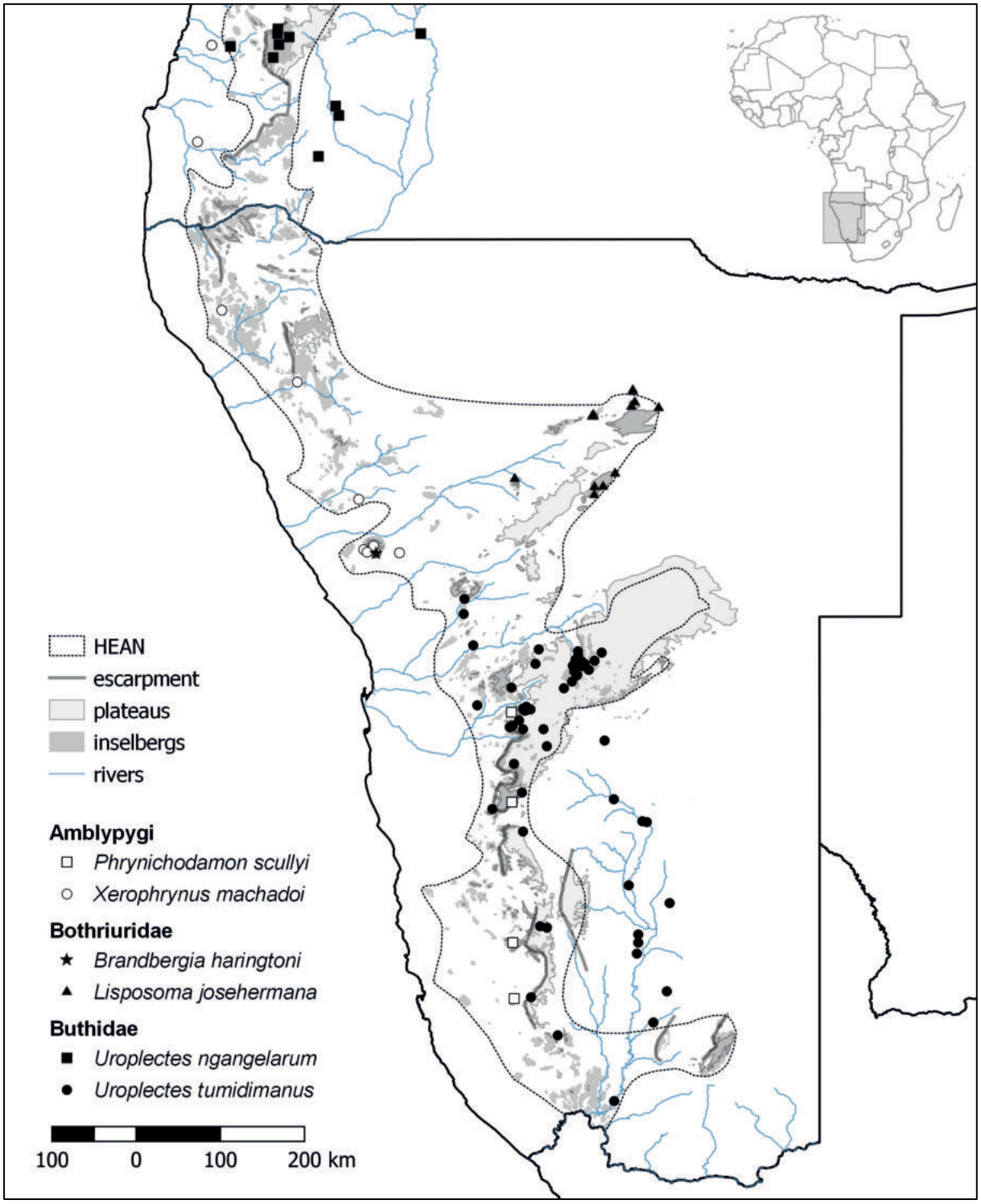

Figure 1: *Described species of whip spiders (Amblypygi Thorell, 1883) and scorpions (Scorpiones C.L. Koch, 1837) in the families Bothriuridae Simon, 1880 and Buthidae C.L. Koch, 1837 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Brandbergia haringtoni *Prendini, 2003;* Lisposoma josehermana *Lamoral, 1979;* Phrynichodamon scullyi *(Purcell, 1902);* Uroplectes ngangelarum *Monard, 1930;* Uroplectes tumidimanus *Lamoral, 1979; and* Xerophrynus machadoi *(Fage, 1951).*

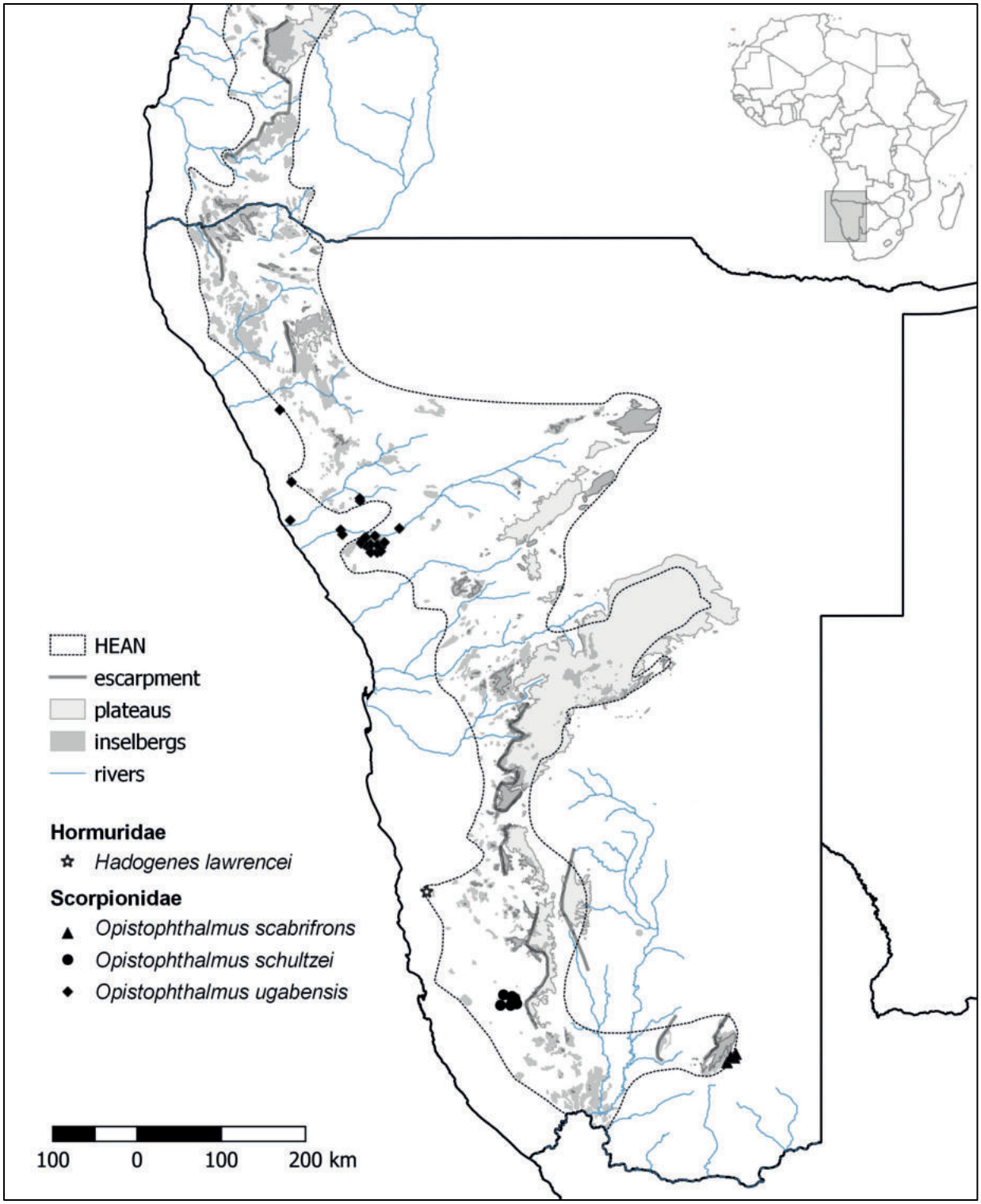

Figure 2: *Described species of scorpions (Scorpiones C.L. Koch, 1837) in the families Hormuridae Laurie, 1896 and Scorpionidae Latreille, 1802 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Hadogenes lawrencei *Newlands, 1972;* Opistophthalmus scabrifrons *Hewit, 1918;* Opistophthalmus schultzei *Kraepelin, 1908;* Opistophthalmus ugabensis *Hewitt, 1934.*

known records are at low elevations. The same proved true for two other hormurids recorded in Angola and Namibia, *Hadogenes hahni* (Peters, 1862) and *Hadogenes phyllodes* Thorell, 1876 (Prendini 2005b).

Three species of the fossorial Afrotropical genus *Opistophthalmus* C.L. Koch, 1837 in the family Scorpionidae Latreille, 1802 (Lamoral 1979, Prendini 2001a, 2005c, Prendini *et al*. 2003) were considered endemic or near-endemic to the highlands of Namibia (Table 1). *Opistophthalmus scabrifrons* Hewit, 1918, a pelophilous species that constructs burrows under stones in shaley clay, is restricted to valleys on the eastern side of the Groot Karasberg (Figure 2). *Opistophthalmus schultzei* Kraepelin, 1908, another pelophilous species which constructs burrows in open ground and under stones in granitic sandy loam, is restricted to the Aus Mountains (Figure 2). Finally, *Opistophthalmus ugabensis* Hewitt, 1934, a semi-lithophilous species that constructs shallow scrapes under stones in sandy loam, occurs in the valleys and lower slopes of the Brandberg Massif, as well as other inselbergs in Damaraland, including the Gobobosebberge (e.g., Tafelkop) and the Huab outliers (Figure 2). Although these three species are well characterised morphologically and genetically, many other widespread Namibian species of *Opistophthalmus* represent species complexes that are the subject of ongoing revision which, once completed, will increase the number of highland endemics and near-endemics in the country (Prendini & Loria 2020).

Highland endemic solifuges

Southern Africa has the world's highest diversity of Solifugae, much of which is concentrated in the arid west of the subcontinent. This diversity is almost certainly underestimated, however, particularly for Angola (Lawrence 1960). The distributions of many solifuge species appear to be highly restricted (Wharton 1981), especially in the fossorial, psammophilous Hexisopodidae Pocock, 1897 and the small, diurnal Melanoblossiidae Roewer, 1933. In addition, many highlands and escarpments are undersampled for solifuges. More extensive sampling with more precise locality data is expected to increase the list of highland endemic solifuges presented here.

The small family Ceromidae Roewer, 1933 contains a single highland endemic, *Ceromella focki* (Kraepelin, 1914), restricted to the central highlands (Khomas Hochland) of Namibia (Table 1). It is known from only two male specimens collected in Windhoek in 1911 (Kraepelin 1914) and 2009, respectively (Figure 3).

Five species of the diverse, probably paraphyletic (Bird *et al*. 2015), family Daesiidae Kraepelin, 1899 are endemic or near-endemic to the highlands and escarpments: two to southwestern Angola, one to northwestern Namibia, one to southwestern Namibia and one to central Namibia (Table 1). *Biton* (*Biton*) *striatus bidentatus* Lawrence, 1955 is known from four records in Namibia, mostly from the Kaokoveld, including the vicinity of the Etendeka Mountains, and one from the summit of the Brandberg Massif (Figure 3). It is uncertain whether this species is strictly endemic to the highlands and escarpments, as all known localities of this species were georeferenced *a posteriori*, and the precise coordinates of the original collection localities are unknown.

Blossia angolensis (Lawrence, 1960) is known from a single female collected at an altitude of 1,500 masl in the highlands near Lubango, southwestern Angola (Figure 3). Unfortunately, the male has never been collected, and little is known about this species. *Blossia falcifera quibensis* Hewitt, 1934, recorded from only two localities on plateaus in southwestern Namibia, appears to be a *bona fide* highland endemic (Figure 3). Its congener, *Blossia gaerdesi* Lawrence, 1972, is relatively widespread in the highlands and escarpments of Namibia, from the Otavi Mountains and the Waterberg Plateau, through the central highlands, to the Rooirand Plateau (Figure 3). Many locality records of *B. gaerdesi* are not actually situated in highlands, but in the near proximity, suggesting that highlands may serve as refugia. More material is needed for morphological and genetic analysis to determine whether these populations are conspecific.

Hemiblossia machadoi Lawrence, 1960 is known from a single female collected at 2,300 masl in the Serra da Chela near Lubango, southwestern Angola, in 1949 (Figure 3), and a juvenile female collected approximately 100 km to the southeast (Lawrence 1960). More collections are needed to verify whether this species is endemic or near-endemic to the highlands and escarpments. Its congener, *Hemiblossia lawrencei* Roewer, 1933, described from a single female collected in Windhoek, Namibia, was excluded from the list of highland endemics as it was inadequately characterised (Wharton 1981). Further comparison with females of different species in the *australis* group of *Hemiblossia* Kraepelin, 1899 are needed to assess the validity of this species.

The southern African species of the small family Gylippidae Roewer, 1933 are assigned to three genera in subfamily Liphophaginae Wharton, 1981. Two of the four lipophagine species occurring in Namibia are endemic or near-endemic to the highlands and escarpments (Table 1). Available data suggest that the monotypic *Bdellophaga angulata* Wharton, 1981 is restricted to the central highlands of Namibia (Figure 4). *Trichotoma fusca* (Roewer, 1941) is known only from the type locality, the Waterberg Plateau (Figure 4). Wharton (1981)

suggested that the latter may be conspecific with *Trichotoma brunnea* Lawrence, 1968, from which it is almost indistinguishable morphologically. As *T. brunnea* appears to be restricted to the Namib coast, however, *T. fusca* was assumed to be a valid species for the present assessment. A genetic comparison between material from the Namib and the Waterberg Plateau is needed to resolve this question.

The nominotypical subfamily Melanoblossinae Roewer, 1933, of the small family Melanoblossiidae, is also restricted to southern Africa. *Melanoblossia ansie* Bird and Wharton, 2015, a *bona fide* endemic, restricted to the Tsaukhaib Mountain of the Tsau ǁKhaeb (Sperrgebiet) National Park in southwestern Namibia (Bird & Wharton 2015; Figure 4), is the only highland endemic currently recognised in this family (Table 1). The melanoblossiid diversity of Namibia is probably vastly underestimated (Wharton 1981), however, due to the small size and cryptic morphology and behaviour of these solifuges. Many undescribed species are expected to be narrow endemics (Wharton 1981).

The family Solpugidae Leach, 1815 is probably the most conspicuous group of solifuges in southern Africa, on account of their size and the spectacular colour of some of the diurnal species. Based on current knowledge, three solpugid species appear to be endemic or near-endemic to the highlands and escarpments of Namibia (Table 1). *Solpugista methueni* (Hewitt, 1914) and *Zeria schlechteri* (Purcell, 1899) were both recorded from southwestern Namibia, and occur in sympatry on the Rooirand Plateau. Whereas *S. methueni* was recorded from a second locality in Namibia, the Huib-Hoch Plateau, *Z. schlechteri* is known from only a single locality in Namibia (Figure 4), but a record from the Naroep Mountains, south of the Orange River in South Africa, supports its recognition as a highland endemic.

Most of the known locality records of *Zeria glabricornis* (Lawrence, 1928) are situated in northwestern Namibia, extending across the Kaokoveld and Damaraland to the Brandberg Massif and vicinity (Figure 4). The southernmost outlier record of this species requires verification. Although many records of *Z. glabricornis* are not located on the highlands and escarpments per se, their occurrence in the foothills and lowlands associated with these highlands, suggests that this species may be near-endemic to the highlands, a hypothesis that merits further testing based on the collection of material for genetic analysis.

Relative importance of highlands

Whereas highland endemic or near-endemic arachnid taxa are distributed across the length of Namibia, within Angola they appear to be restricted to the southwest (Figures 1–4). Although this may be partly explained by the paucity of data for Angola, the pattern of endemism in Angola appears to match that of Namibia. As with Namibia, in which most of the highland endemics or near-endemics are associated with escarpments, plateaus and inselbergs in the arid west (the Namib and pro-Namib), the highland endemics and near-endemics of southwestern Angola occur in the most arid part of the country, containing the northern limit of the Namib.

Scoring the presence of described and potential undescribed endemics in relevant highlands and escarpments and tallying the scores for each order, revealed that some highlands and escarpments are more important areas of endemism for some arachnid taxa than others. The central highlands (especially the Gamsberg and to a lesser extent, the Khomas Hochland), the Hunsberge and the Brandberg Massif and Huab outliers, each contain four or more endemic scorpions. The central highlands (especially the Khomas Hochland) and the Rooirand Plateau each contain three or more endemic solifuges.

When considering the sum of all three ordinal tallies, the following areas stand out as priorities for conservation and for further survey and inventory: the central highlands (especially the Khomas Hochland, the Gamsberg and the Auas Mountains); the Brandberg Massif and Huab outliers; the Hunsberge; the mountains of the Kaokoveld (especially the Etendeka Mountains, the Baynes–Otjihipa Mountains and, to a lesser extent, the Otjikondavirongo Mountains); the Rooirand and the Huib-Hoch plateaus; the mountains of southwestern Angola (including the Serra de Chela and the Serra da Neve); the Naukluft Mountains; the Otavi Mountains; and the Waterberg Plateau. A complete ranking of the highlands according to the number of endemic arachnids in each, is provided in Table 2. Six of these highlands (i.e., the Auas Mountains, the Baynes–Otjihipa Mountains, the Brandberg Massif, the Gamsberg, the Khomas Hochland, the Naukluft Mountains and the Otavi Mountains) were among the 12 highest ranked mountains identified by Irish (2002) who used abiotic information (altitude, elevation, surface area and isolation) to infer and rank the 39 most prominent mountains or mountain ranges in Namibia for biodiversity potential.

CONCLUSIONS AND FUTURE DIRECTIONS

The arachnid fauna of Angola and Namibia is diverse and includes high levels of endemism, much of which is associated with the arid zone, especially the Namib Desert. Although highlands and escarpments may serve as refugia for taxa requiring cooler, more humid habitats than are available in the surrounding arid lowlands, fewer endemic arachnid taxa are present in the highlands than in the lowlands. This may be explained by several factors.

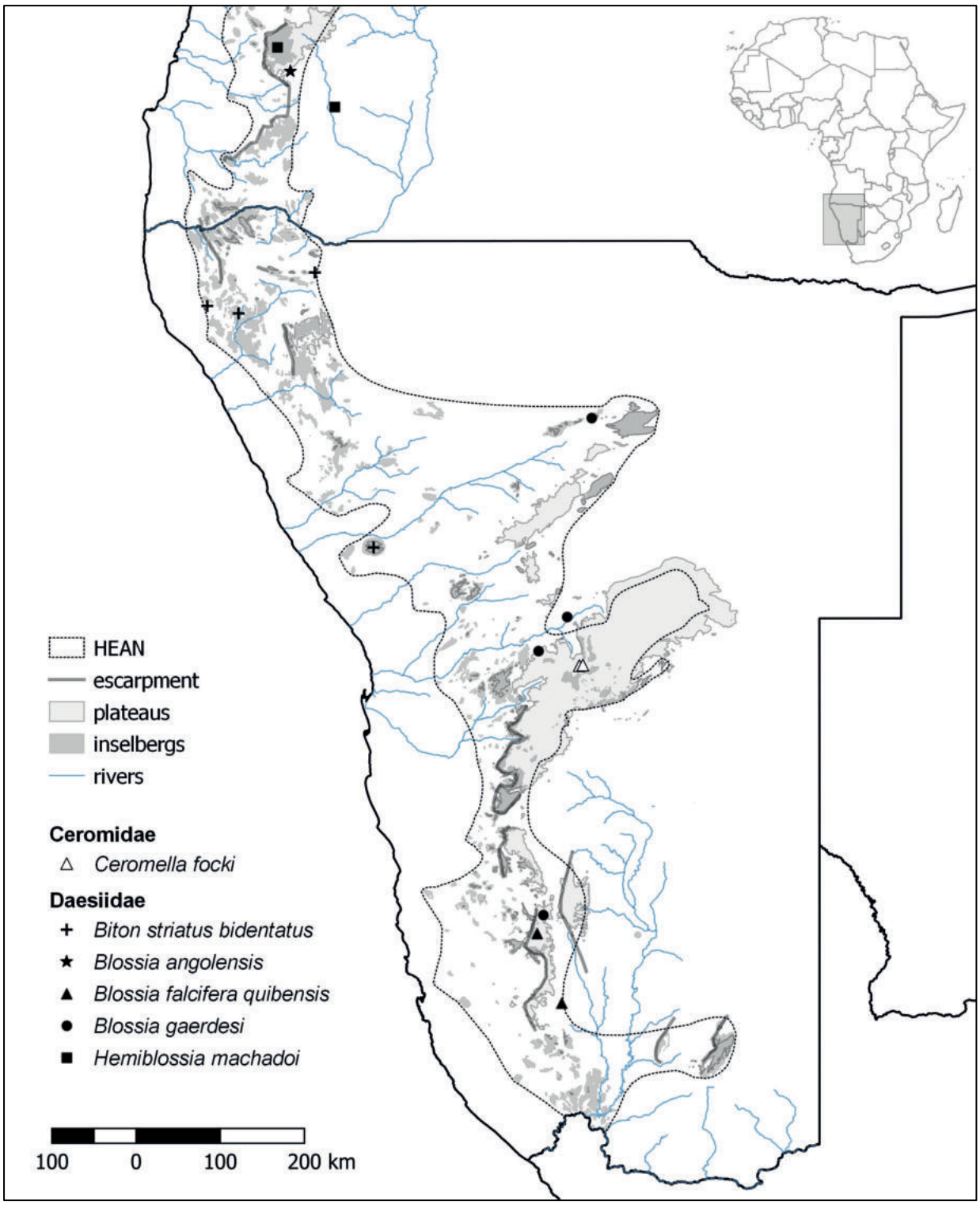

Figure 3: *Described species and subspecies of solifuges (Solifugae Sundevall, 1833) in the families Ceromidae Roewer, 1933 and Daesiidae Kraepelin, 1899 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Biton striatus bidentatus *Lawrence, 1955;* Blossia angolensis *(Lawrence, 1960);* Blossia falcifera quibensis *Hewitt, 1934;* Blossia gaerdesi *Lawrence, 1972;* Ceromella focki *(Kraepelin, 1914);* Hemiblossia machadoi *Lawrence, 1960.*

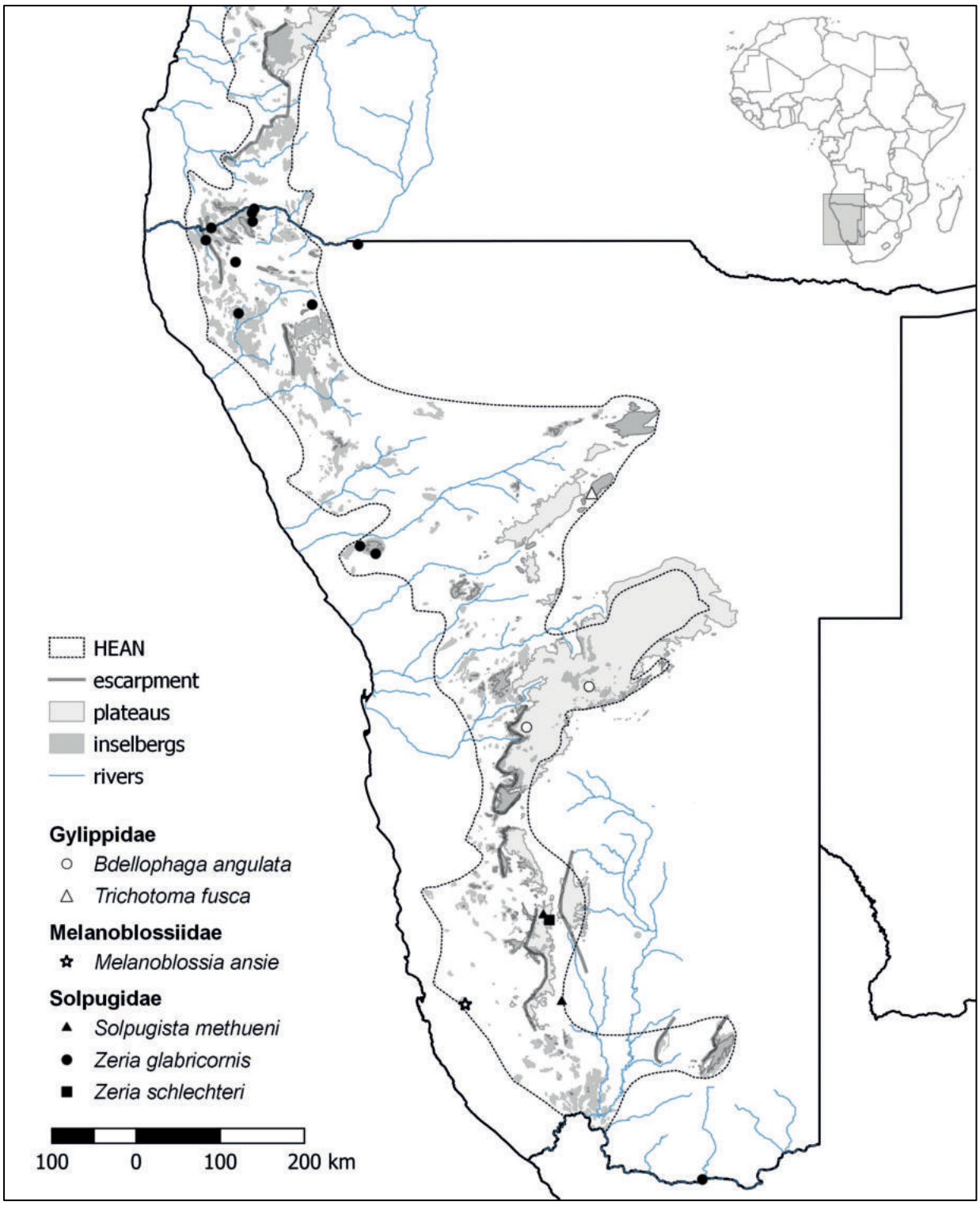

Figure 4: *Described species of solifuges (Solifugae Sundevall, 1833) in the families Gylippidae Roewer, 1933, Melanoblossiidae Roewer, 1933 and Solpugidae Leach, 1815 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Bdellophaga angulata *Wharton, 1981;* Melanoblossia ansie *Bird and Wharton, 2015;* Solpugista methueni *(Hewit, 1914);* Trichotoma fusca *(Roewer, 1941);* Zeria glabricornis *(Lawrence, 1928);* Zeria schlechteri *(Purcell, 1899).*

Firstly, the highlands and escarpments of Angola and Namibia are relatively low, on average, compared to the highlands and escarpments of other African countries, such as Ethiopia, Kenya and South Africa, providing fewer opportunities for insular speciation and/or a higher probability of extinction during unfavourable periods of increased aridity, e.g., during the Miocene and Pliocene. At 2,500 masl, the Brandberg Massif is the highest mountain in Namibia and, as might be expected, it contains several endemic or near-endemic arachnids. On the other hand, even small differences in elevation, e.g., low inselbergs 200 m above the surrounding plains, may have a profound effect on attracting precipitation in the hyperarid Namib, facilitating survival and diversification that might be impossible on the surrounding plains, as suggested by at least one endemic arachnid, the hormurid scorpion, *Hadogenes lawrencei*.

Secondly, much arachnid endemism in the arid lowlands is associated with unique substrates that are absent in the highlands and escarpments, including sand dunes, gravel plains, and clays associated with drainage systems, all of which facilitate burrowing to escape the arid conditions, and promote diversification (Prendini 2001b, 2005c).

Table 2: *Highlands and escarpments (including plateaus, mountain ranges and inselbergs) of Angola and Namibia with high levels of described and potential undescribed endemic whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae Sundevall, 1833), ranked in decreasing order of priority for conservation as well as further survey and inventory.*

Highland	**Amblypygi**	**Scorpiones**	**Solifugae**	**Total**
Khomas Hochland		4	4	8
Brandberg Massif	1	4	2	7
Gamsberg		6	1	7
Huab outliers	1	4	1	6
Hunsberge		6		6
Kaokoveld (Etendeka Mountains)	1	2	2	5
Rooirand Plateau		1	4	5
Angolan southwestern highlands (e.g., Serra de Chela, Serra da Neve)	1	1	2	4
Auas Mountains		2	2	4
Huib-Hoch Plateau		2	2	4
Kaokoveld (Baynes–Otjihipa Mountains)	1	1	1	3
Naukluft Mountains	1	2		3
Otavi Mountains		1	2	3
Waterberg Plateau		1	2	3
Aus Mountains		2		2
Awasibberge		2		2
Groot Karasberg		2		2
Hakosberge	1	1		2
Kaokoveld (Otjikondavirongo Mountains)	1	1		2
Sperrgebiet (Tshaukhaib Mountain)		1	1	2
Swakop–Khan (Scheifferberge)		2		2
Tirasberge	1	1		2
Erongo Mountains		1		1
Kaokoveld (Steilrand)			1	1
Klein Karasberg		1		1
Otjihaveraberge		1		1
Paresis Mountains		1		1
Sperrgebiet (Höhlenberg, Kirchberg, Sturmhaube)		1		1
Sperrgebiet (inselbergs between Teuffelkuppe and Agub Mountains)		1		1
Swakop–Khan (Bloedkoppie, Chuosberge, Langer-Heinrichberg and Rössing Mountain)		1		1
Tafelkop		1		1
Tsaris Mountains		1		1

Thirdly, the relatively low endemism of arachnids in the highlands and escarpments of Angola and Namibia is to some extent artefactual because much remains unknown. The arachnid fauna of Namibia has been far better surveyed and studied than that of Angola, yet, even in Namibia, much work remains to be done. Large areas have never been systematically surveyed in the optimal seasons or using techniques appropriate for collecting these secretive, seasonal taxa (e.g., pitfall trapping, ultraviolet-light detection). The use of genetic data has been sporadically applied to the systematics of arachnids in the region but is expected to reveal much cryptic diversity. More intensive surveys of the highlands and escarpments of Angola and Namibia, with an emphasis on collecting genetic samples from disjunct populations across the distributions of each putative species, are needed to better understand arachnid diversity and endemism in the region.

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REFERENCES

Bird TL, Wharton RA (2015) Description of a new solifuge *Melanoblossia ansie* sp. n. (Solifugae, Melanoblossiidae) with notes on the setiform flagellar complex of Melanoblossiinae Roewer, 1933. *African Invertebrates* 56(2): 515–525. https://doi.org/10.5733/afin.056.0218.

Bird TL, Wharton RA, Prendini L (2015) Cheliceral morphology in Solifugae (Arachnida): primary homology, terminology, and character survey. *Bulletin of the American Museum of Natural History* 394: 1–356. https://doi.org/10.1206/916.1.

Bryson RW, Riddle BR, Graham MR, Smith BT, Prendini L (2013) As old as the hills: montane scorpions in southwestern North America reveal ancient associations between biotic diversification and landscape history. *PLoS ONE* 8(1): e52822. https://doi.org/10.1371/journal.pone.0052822.

Dunlop JA, Erik Tetlie O, Prendini L (2008) Reinterpretation of the Silurian scorpion *Proscorpius osborni* (Whitfield): integrating data from Palaeozoic and Recent scorpions. *Palaeontology* 51(2): 303–320. https://doi.org/10.1111/j.1475-4983.2007.00749.x.

Fage L (1951) Pedipalpes (Amblypyges) récoltés en Angola par M. A. de Barros Machado. *Publicações culturais da Companhia de Diamantes de Angola, Lisboa* 13: 8–17.

Irish J (2002) *Namibian mountains: biodiversity potential based on topography*. Unpublished report: Mountain Working Group of the National Biodiversity Task Force, Windhoek. pp. 42.

Kraepelin K (1914) Skorpiones und Solifugae. In: W Michaelsen (ed) *Beiträge zur Kenntnis der Land- und Süßwasserfauna Deutsch-Südwestafrikas. Ergebnisse der Hamburger deutsch-südwestafrikanischen Studienreise 1911*. Volume 1: 107–137. Hamburg: L. Friederischen & Co.

Lamoral B (1979) The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum* 23(3): 497–784.

Lawrence R (1928) Contributions to a knowledge of the fauna of South-West Africa. VII. Arachnida (Part 2). *Annals of South African Museum* 25(2): 217–312.

Lawrence R (1949) Notes on the whip-scorpions (Pedipalpi) of South Africa. *Transactions of the Royal Society of South Africa* 32: 1–11.

Lawrence R (1955) Solifugae, scorpions and Pedipalpi, with checklist and keys to South African families, genera and species. In: Hanström B, Brinck P, Rudebeck G (eds) *South African animal life: results of the Lund University Expedition in 1950–1951*. 1. Almqvist & Wiksell, Stockholm.

Lawrence R (1960) The Solifugae (Arachnida) of Angola. *Publicações culturais da Companhia de Diamantes de Angola, Lisboa* 51: 109–127.

Lawrence R (1967) Additions to the fauna of South West Africa: solifuges, scorpions and Pedipalpi. *Scientific Papers of the Namib Desert Research Station* 34: 1–19.

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15(3): 237–240.

Loria SF, Prendini L (2021) Burrowing into the forest: phylogeny of the Asian forest scorpions (Scorpionidae: Heterometrinae) and the evolution of ecomorphotypes. *Cladistics* 37(2): 109–161. https://doi.org/10.1111/cla.12434.

Newlands G (1972) A description of *Hadogenes lawrencei* sp. nov. (Scorpiones) with a checklist and key to the South West African species of the genus *Hadogenes*. *Madoqua* 1: 133–140.

Newlands G, Cantrell A (1985) A re-appraisal of the rock scorpions (Scorpionidae: *Hadogenes*). *Koedoe* 28: 35–45.

Newlands G, Prendini L (1997) Redescription of *Hadogenes zumpti* (Scorpiones: Ischnuridae), an unusual rock scorpion from the Richtersveld, South Africa. *South African Journal of Zoology* 32(3): 76–81.

Prendini L (2001a) A review of synonyms and subspecies in the genus *Opistophthalmus* C.L. Koch (Scorpiones: Scorpionidae). *African Entomology* 9(1): 17–48.

Prendini L (2001b) Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited. In: Fet V, Selden P (eds) *Scorpions 2001. In Memoriam Gary A. Polis*. 113–138. British Arachnological Society, Burnham Beeches, Bucks, UK.

Prendini L (2003a) A new genus and species of bothriurid scorpion from the Brandberg Massif, Namibia, with a reanalysis of bothriurid phylogeny and a discussion of the phylogenetic position of *Lisposoma* Lawrence. *Systematic Entomology* 28(2): 149–172. https://doi.org/10.1046/j.1365-3113.2003.00207.x.

Prendini L (2003b) Revision of the genus *Lisposoma* Lawrence, 1928 (Scorpiones: Bothriuridae). *Insect Systematics & Evolution* 34(3): 241–264. https://doi.org/10.1163/187631203788964764.

Prendini L (2005a) New records and observations on the natural history of *Lisposoma elegans* and *L. josehermana* (Scorpiones: Bothriuridae). *American Museum Novitates* 3487: 1–11. https://doi.org/10.1206/0003-0082(2005)487[0001:NRAOOT]2.0.CO;2.

Prendini L (2005b) On *Hadogenes angolensis* Lourenço,

1999 syn. n. (Scorpiones, Liochelidae), with a redescription of *H. taeniurus* (Thorell, 1876). *Revue suisse de zoologie* 112(2): 371–399. https://doi.org/10.5962/bhl.part.80304.

Prendini L (2005c) Scorpion diversity and distribution in southern Africa: pattern and process. In: Huber B, Sinclair B, Lampe K-H (eds) *African biodiversity: molecules, organisms, ecosystems. Proceedings of the 5th International Symposium on Tropical Biology, Museum Alexander Koenig, Bonn*. 25–68. Springer US, Boston, MA. https://doi.org/10.1007/0-387-24320-8_2.

Prendini L, Crowe TM, Wheeler WC (2003) Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. *Invertebrate Systematics* 17(2): 185–259. https://doi.org/10.1071/IS02016.

Prendini L, Esposito LA (2010) A reanalysis of *Parabuthus* (Scorpiones: Buthidae) phylogeny with descriptions of two new *Parabuthus* species endemic to the Central Namib gravel plains, Namibia. *Zoological Journal of the Linnean Society* 159(3): 673–710. https://doi.org/10.1111/j.1096-3642.2009.00608.x.

Prendini L, Loria SF (2020) Systematic revision of the Asian forest scorpions (Heterometrinae Simon, 1879), revised suprageneric classification of Scorpionidae Latreille, 1802, and revalidation of Rugodentidae Bastawade et al., 2005. *Bulletin of the American Museum of Natural History* 442: 1–480. https://doi.org/10.1206/0003-0090.442.1.1.

Prendini L, Weygoldt P, Wheeler WC (2005) Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. *Organisms, Diversity & Evolution* 5(3): 203–236. https://doi.org/10.1016/j.ode.2004.12.004.

QGIS Development Team (2021) QGIS: A free and open-source Geographic Information System. Available online: http://qgis.osgeo.org.

Schramm FD, Valdez-Mondragón A, Prendini L (2021) Volcanism and palaeoclimate change drive diversification of the world's largest whip spider (Amblypygi). *Molecular Ecology* 30(12): 2872–2890. https://doi.org/10.1111/mec.15924.

Weygoldt P (1996) The relationships of the south-east African whip spiders *Hemiphrynus machadoi* Fage, 1951 and *Phrynichus scullyi* Purcell, 1901: introduction of the new generic names *Xerophrynus* and *Phrynichodamon* (Chelicerata: Amblypygi). *Zoologischer Anzeiger* 235: 117–130.

Weygoldt P (1998) Mating and spermatophore morphology in whip spiders (*Phrynichus scullyi* [Purcell, 1901], *Damon gracili*s nov. spec., *Damon variegatus* [Perty, 1834], and *Euphrynichus bacillifer* [Gerstaecker, 1873]) (Arachnida: Amblypygi: Phrynichidae). *Zoologischer Anzeiger* 236: 259–276.

Weygoldt P (1999) Revision of the genus *Damon* C. L. Koch, 1850 (Chelicerata: Amblypygi: Phrynichidae). *Zoologica Stuttgart* 150: 1–45.

Weygoldt P (2000) African whip spiders: synopsis of the Amblypygi reported from Africa. *Memorie della Societa Entomologica Italiana* 78(2): 339–359.

Wharton RA (1981) Namibian Solifugae (Arachnida). *Cimbebasia Memoir* 5: 3–87.