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The advertisement call, breeding biology, description of the tadpole and taxonomic status of *Bufo dombensis*, a little-known dwarf toad from southern Africa

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Males of *Bufo dombensis* were observed calling late at night at Ongongo Waterfall in north-western Namibia. The analyzed advertisement calls differ distinctly from those of *B. vertebralis*, *B. hoeschi* and *B. fenoulheti*, indicating that all these taxa are separate valid species. Tadpoles raised from a breeding pair found at Ongongo showed the typical oral characters of southern African *Bufo* (1:1+1/3 keratodont formula, broad mental gap in oral papillae) but differed by some characters from tadpoles of other sympatric *Bufo* species.

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Bufo dombensis was described from Dombe in Angola (Bocage 1895), but little has been discovered of its natural history and taxonomic status in the last century. It has been recognized either as a distinct species (Mertens 1971, Tandy & Keith 1972) or as a part of the *Bufo vertebralis* group (Poynton 1964). Poynton (1964) placed it in the vertebralis group of dwarf toads on the basis of small size, lack of a tarsal fold, and indistinct parotid glands. Taxa such as *Bufo fenoulheti* and *Bufo hoeschi* from Namibia have at times been placed as junior synonyms of *Bufo dombensis* (Tandy & Keith 1972).

The taxon appears to inhabit the fringes of the Namib desert from southern Angola to northern Namibia, and inland in arid areas (Channing & Griffin 1963). Tandy & Keith (1972) remarked on the camouflage displayed in this species. The Namib desert is a harsh environment for an amphibian, and further studies are required to investigate how it continues to be successful in this extremely arid area. Data on breeding biology, vocalizations, and tadpole morphology of this toad are unknown.

In most amphibians inhabiting arid regions, adults can only be found during a short breeding season following precipitation. In contrast, tadpoles can generally be found during longer periods, and are much more easily surveyed. However, very few African *Bufo* tadpoles have been adequately described. Tadpole keratodont formulae, which in many anuran genera differ between species, are very uniform in African *Bufo* (e.g. Wager 1965). Comparison of recent descriptions (e.g. Channing & Drewes 1997) shows that there are a number of characters, especially those from internal buccal anatomy, which can probably be considered as diagnostic at the species level. A complete revision and re-description of African tadpoles, including *Bufo* tadpoles, as well as studies on intraspecific geographic variation in tadpole morphology, are required to allow tadpoles to be used as reliable indicators for distribution of anuran species.

In the present article, we describe the tadpole of *Bufo dombensis*, and record the first description of its breeding behaviour. We also describe the advertisement call of the species, and discuss its taxonomic status based on the bioacoustic data.

Materials and methods

Field observations were made at Ongongo Waterfall (19°08'S, 13°47'E), east of Sesfontein, Namibia. Material is deposited in the Museum Alexander Koenig in Bonn, Germany (ZFMK), or the Port Elizabeth Museum, South Africa (PEM). Duplicate material will be deposited in the State Museum, Windhoek, Namibia.

Vocalizations were recorded in the field with a Sony DC 66 Professional Walkman and an external microphone (Vivanco EM 238). Tapes (Maxell UR 90) were analyzed with the ME-DAV sound analyzing system Spektro 3.2.

Eggs were collected from a breeding pair at Ongongo, and raised. A developmental series was preserved in 10% formalin (specimens not individually labeled): ZFMK 66757 (sample of freshly laid eggs); ZFMK 66758 (three tadpoles preserved on 11 January 1998, ca. 48 hours after egg-laying); ZFMK 66759 (five tadpoles preserved on 14 January 1998, ca. 120 h after egg-laying); ZFMK 66760 (four tadpoles preserved on 16 January 1998, seven days after egg-laying); ZFMK 66761 (four tadpoles preserved on 18 January 1998, nine days after egg laying; ZFMK 66762 (four tadpoles preserved on 24 January 1998, 15 days after egg-laying); PEM A6982 (four tadpoles raised to stage 34).

Tadpoles were measured using a binocular microscope with a micrometer to the nearest 0.1 mm. Tadpole developmental stages are given according to Gosner (1960). Descriptive characters follow Van Dijk (1966). The keratodont formula is set out according to the recommendations of Dubois (1995), and the internal buccal anatomy is described using the terminology of Wassersug (1976, 1980).

Natural history

All the observations were made along a small stream fed by a permanent spring. The stream habitat consists of a rocky bottom, with shallow water. The stream drops some 20 metres in altitude over a 200 m stretch, producing one large waterfall, from which the site (Ongongo Waterfall) gets its name, with a number of smaller rapids. The weather in early January was dry. It had rained previously, judging from the emergence of new grass in places.

Active adult specimens could be observed in late afternoon along the stream. Most, however, were hiding during the day under small piles of rocks and stones at the water's edge. They emerged in large numbers, congregating along a 10 m section of stream, in the late evening (20:00–21:00). First calling was noted at about 22:00, but regular mating calls were only heard from 23:00 on. Highest calling intensity was reached between 01:00 and 03:00. The inflated vocal sac of calling males had a typical shape, being slightly conical and directed anteriorly. This shape was especially distinct during the climax of each expiration phase of the call (Figure 1).

Figure 1 Calling male of *Bufo dombensis*, Ongongo, 8 January 1998, ca. 23:00

Egg strings belonging to *Bufo dombensis* were found in the stream at the reproduction site. As they were exposed to the current, they collected in small depressions and between river stones (Figure 2). Two couples in axillary amplexus (Figure 3) were found on 9.1.1998 at about 01:00. In a plastic bag, one couple (male 40 mm SVL, female 48 mm SVL) deposited in the same night a string of 900 uniformly black eggs measuring 1.6–1.8 mm in diameter. A captive-raised tadpole from this egg string is shown in Figure 4. The second couple deposited 400 eggs under the same conditions, but this female probably still contained a rather large number of mature oocytes which were not laid, possibly due to the artificial conditions.

Figure 2 Egg string of *Bufo dombensis*. Ongongo, 9 January 1998

Other amphibian species found syntopically with *Bufo dombensis* at the Ongongo Waterfall site were *Bufo maculatus*, *Tomopterna tandyi*, *Tomopterna tuberculosa*, *Phrynobatrachus natalensis*, *Phrynomantis annectens* and *Xenopus laevis*.

Vocalizations

Vocalizations were recorded on 8 and 9 January 1998 from 23:00–02:00 at 22.0°C air temperature (specimens sitting at the water edge but outside water). Two call types were noted.

A presumed territorial call was heard at the beginning of the evening's vocalization, mainly from within refuges, and is an irregular repetition of a series of short notes. It is similar to the release call as known for many *Bufo* species, and possibly

Figure 3 Couple of *Bufo dombensis* in amplexus. Ongongo, 9 January 1998

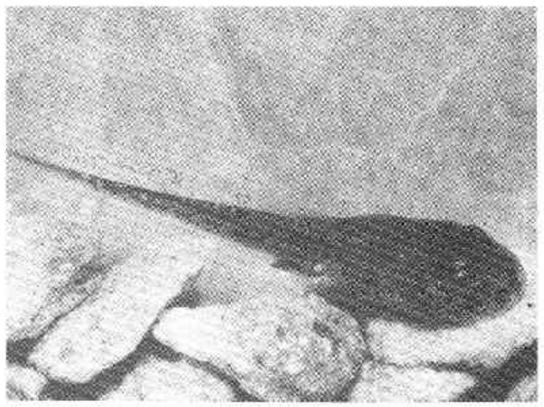

Figure 4 Captive raised tadpole of *Bufo dombensis*, 24 January 1998

was given in a territorial context within the refuges. Sonagram and oscillogram of part of a territorial call are shown in Figure 5. Five analyzed calls, given consecutively by one specimen, consist of 6, 4, 2, 2 and 4 notes, respectively. The first note of the four-note and six-note calls has a very low intensity and is only faintly recognizable on the sonagram. Temporal call parameters (in milliseconds) given as range followed by mean ± standard deviation and sample size (number of individuals) in parentheses are as follows: note duration 15–49 (31±7, n=16); duration of intervals between notes 74–124 (99±16, n=11). The frequency ranges from 1700–2500 Hz, dominant frequency maximum was at 1800 Hz. Notes are rapidly pulsed, but single pulses could mostly not be resolved on the oscillogram. In one note, four distinct pulses could be seen at the beginning of the call (pulse rate about 180/s), indicating that pulse rate increases towards the end of the call.

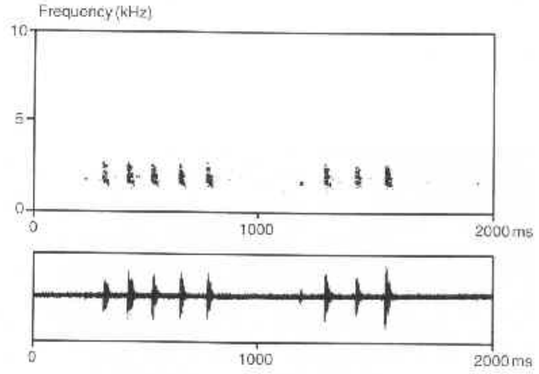

Figure 5 Sonagram and oscillogram of a presumed territorial call of *Bufo dombensis*, recorded on 8 January 1998 at 22.0°C air temperature

The advertisement call is produced by males, mostly from outside refuges. Sonagram and oscillogram of part of an advertisement call are shown in Figures 6–7. The following data refer to calls from one male. Calls consist of a series of a varying number (up to 50) of pulsed notes. Note repetition rate is 2.5/s. One note consists of 22–31 (n=5) individual pulses. Pulse rate increases towards the end of the note, and in the final note section no pulses can be distinguished, giving the impression of one very long pulse. In one analysed note, pulse rate is 118/s for pulses 1–4, 250/s for pulses 7–12, and 272/s for pulses 15–20.

Temporal call parameters (in milliseconds) are as follows: note duration 113–162 (139±14, n=23); duration of intervals between notes 170–422 (279±66, n=21). The frequency ranges from 2300–3400 Hz, dominant frequency from 2650–3100 Hz, with intensity maxima at 3100 Hz and 2800 Hz. Each note corresponds to one expiration. The vocal sac was greatly extended during each note, and remained partly inflated between notes.

Tadpole description

The following description of the tadpole is from a specimen

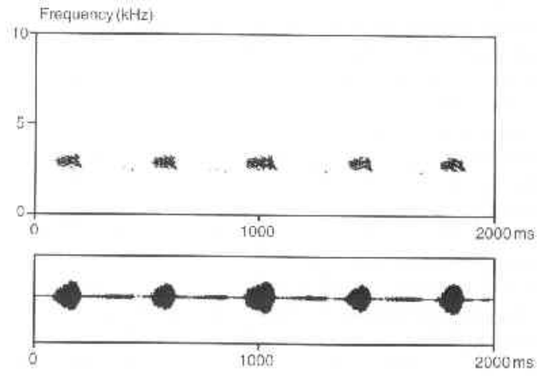

Figure 6 Sonagram and oscillogram of five notes of an advertisement call of *Bufo dombensis*, recorded on 8 January 1998 at 22.0°C air temperature

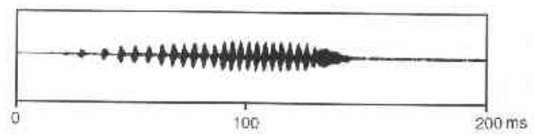

Figure 7 Oscillogram of one note (first note as shown in Figure 6) of an advertisement call of *Bufo dombensis*, recorded on 8 January 1998 at 22.0°C air temperature, showing detailed arrangement of pulses

in batch PEM A6982, and compared to three other specimens raised at the same time. The internal features (buccal roof and buccal floor) are described from a second tadpole in the same batch, lightly stained with bromocresol green.

External features

The individual is a tadpole at stage 34 of 24.3 mm total length (Figure 8). The tail length is 67% of total length. The maximum tail height is slightly greater than trunk height. The maximum height of the dorsal fin occurs 40% posteriorly along the trunk. The tail is euthyoural with the extrapolated axis passing above the eye. The height of the caudal muscles at the trunk is 45% of the maximum body height. The nostrils are large, oval, with a pale raised margin, and situated one nostril length forward of the corner of the eye. The nostril passages are visible dorso-laterally. The ratio of the relative nostril size (nostril width/internarial distance) is 0.3. The small pineal spot is visible slightly behind a line joining the front of the eyes. No orbitonasal line is present. The position of the nostrils from the snout, as a ratio of the rostronasal distance (measured between closest margins) or orbitonasal distance is 2.2. The eyes are dorsolateral, with an extra-ocular proportion, which is a measure of the lateral position of the eyes (head width minus distance between the lateral limits of the eyes/distance between the lateral limits of the eyes), of 0.72. The spiracle is sinistral, with the opening visible dorsally and laterally, and situated 62% along the body. The vent is medial, continuous with the ventral margin of the fin.

Figure 8 Tadpole of *Bufo dombensis* 24.3 mm

Oral disc

The oral disc is not visible dorsally, and is 70% of the width of the head at the level of the disc. The mental gap in the oral papillae is 47% of the disc width. The oral papillae are present as a single row, with extra papillae in the angle of the mouth. The rostrodonts are finely serrated, with the outer half black. The keratodont formula is 1:1+1/1+1:2 in this specimen, although typically 1:1+1/3 in the batch examined.

Colour in preservative

Dorsally the tadpole is stippled black, solidly pigmented over the head and body. The ventral surface is lightly stippled, with a clear mid-ventral band. The tail muscle is lightly pigmented, except for a narrow strip along the ventral margin. The dorsal fin is lightly mottled, while the ventral fin is transparent.

Measurements

The measurements of the tadpole (all in mm) are listed with the range of measurements from the batch of four tadpoles in parentheses. Total length 24.3 (21.5–24.3); head and trunk 8.6 (7.3–8.6); trunk height 4.2 (3.4–4.2); tail height 4.8 (3.2–4.8); caudal muscle height at trunk 1.9 (1.5–2.1); nostrils start 1.1 from snout (0.7–1.1); eye starts 2.0 from snout (1.0–2.0); spiracle starts 5.4 from snout (4.1–5.4); maximum trunk width 5.5 (4.5–5.5); head width at level of eyes 5.0 (3.9–5.0); distance between lateral limits of eyes 2.9 (2.7–3.1); nostril width (vertical) 0.3 (0.2–0.5); distance between nostrils 0.9 (0.9–1.1); head width at disc 2.7 (2.3–2.9); disc width 1.9 (1.9–2.3); mental gap 0.9 (0.9–1.5).

Buccal roof

The internal nares converge anteriorly, at an angle of 45° to the midline. Two small pustulations are found near the midline anterior to the internal nares. Two flattened postnarial papillae are found anterior to the median ridge. The ridge is defined by a large central papillae and two elongated simple papillae on each side. The buccal roof arena possesses more than 20 small pustulations, with three long simple papillae on each side, posteriorly.

Buccal floor

The anterior lingual pad has six to eight small papillae. The arena is nearly devoid of pustulations, but is flanked posteriorly by seven papillae, of which the middle three are large.

Variation during development

Hatchlings (stage 20; ZFMK 66758) have small external gills (ca. 0.3 mm), which are arranged in two main branches on

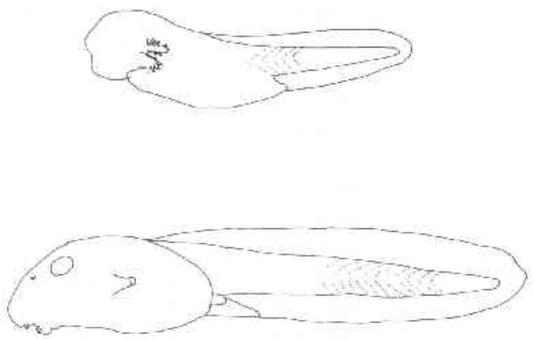

Figure 9 Outline drawings of two tadpoles in earlier developmental stages: ZFMK 66758 (1), above, stage 20; ZFMK 66759 (2), below, stage 27. Scale: 2 mm

either side (Figure 9). The final number of keratodont rows (two on the upper lip and three on the lower lip) is already present after 5 days (in stage 27; ZFMK 66759). In all specimens studied in stages 27, number of keratodont rows and arrangement of keratodont rows on the upper lip (one external undivided and one internal divided row; formula 1:1+1) is constant. In contrast, we observed a rather large variability in keratodont row arrangement on the lower lip. Most specimens, however, show three undivided rows, and we therefore consider this arrangement (and thus the complete formula 1:1+1/3) as typical for *Bufo dombensis*). Tadpoles in early stages (27–29) have a nearly entirely unpigmented belly. During further development, pigment cells seem to increasingly cover the belly from the flanks; in stages 31–33, only the central half of the belly remains unpigmented, whereas in late stages (35–36) the unpigmented part is reduced to a narrow central area, forming a light stripe as described above. Mean relative tail length (calculated from data in Table 1) increased from 35% of total length in stage 20 to 60% in stages 27–29 (Figure 9), 63% in stages 31–33, and 64% in stages 34–36.

Colour in life

Several tadpoles photographed in later stages were dorsally light brown. The tail was laterally dark brown with a variable amount of light brown to bronze markings. On the flanks, too, there were some areas with a dark brown ground colour with distinct small bronze dotting. The belly was whitish. Some black pigment is visible on the dorsal fin while the ventral fin is unpigmented.

Discussion

The taxonomy of southern African dwarf toads is not satisfactorily resolved. Based on their large phenetic similarity, it may be hypothesized that they constitute a monophyletic group of closely related species, although no phylogenetic study has so far addressed this question. In Graybeal's (1997) molecular study, *Bufo vertebralis* clustered in a lineage comprising four other African taxa, that is *Bufo gariepensis*, *Bufo taitanus*, *Bufo garmani* and *Bufo mauritanicus*, whereas the remaining African species included, that is *Bufo kisoloensis*,

Table 1 Measurements (in mm) and keratodont formulae of *Bufo dombensis* tadpoles in different developmental stages. TL = total length; BL = head and body length; TaH = maximum tail height; CM = height of caudal musculature at trunk

Tadpole number	Stage	TL	BL	TaH	CM	Keratodont formula
ZFMK 66758 (1)	20	5.1	3.3	1.1	0.5	–
ZFMK 66758 (2)	20	5.1	3.3	1.0	0.5	–
ZFMK 66758 (3)	20	5.1	3.4	0.9	0.5	
ZFMK 66759 (1)	28	10.4	4.3	2.0	0.7	1:1+1/3
ZFMK 66759 (2)	27	8.7	3.3	1.7	0.7	1:1+1/3
ZFMK 66759 (3)	28	10.5	4.3	2.0	0.9	1:1+1/3
ZFMK 66759 (4)	27	8.8	3.4	1.5	0.6	1:1+1/3
ZFMK 66759 (5)	27	9.8	3.8	1.8	0.9	1:1+1/1+1:2
ZFMK 66760 (1)	29	14.7	6.1	2.3	1.1	1:1+1/1+1+1:2
ZFMK 66760 (2)	28	12.3	4.9	2.1	0.9	1:1+1/1+1:2
ZFMK 66760 (3)	28	13.7	5.5	2.3	1.0	1:1+1/1+1:2
ZFMK 66760 (4)	28	12.3	5.0	2.1	0.9	1:1+1/3+3
ZFMK 66761 (1)	33	19.5	7.7	3.4	1.3	1:1+1/1+1+1:1
ZFMK 66761 (2)	31	15.9	6.2	3.1	1.2	1:1+1/1+1:2
ZFMK 66761 (3)	30	16.0	6.0	2.9	1.1	1:1+1/1+1:2
ZFMK 66761 (4)	30	17.5	6.6	2.9	1.3	1:1+1/1+1:2
ZFMK 66762 (1)	36	22.0	7.9	4.0	2.0	1:1+1/3
ZFMK 66762 (2)	35	21.6	8.1	3.8	2.0	1:1+1/3
ZFMK 66762 (3)	34	20.8	7.9	3.3	1.7	1:1+1/3
ZFMK 66762 (4)	33	18.0	6.6	3.2	1.5	1:1+1/3

Bufo maculatus, *Bufo steindachneri* and *Schismaderma carens* formed a second, rather distant lineage. Poynton & Broadley (1988) argue that in Namibia there are at least four taxa of dwarf toads recognizable on external features of adults:

1. *Bufo dombensis* Bocage, 1895, occurring in north-western Namibia and characterized by a very clearly shown tympanum, a lack of spines on the head, and a lacking or poorly developed dark interorbital bar.
2. *Bufo damaranus* Mertens 1954, from the Kaokoveld/ Waterberg area, differing by a concealed tympanum, spines on the head and different colour pattern.
3. *Bufo hoeschi* Ahl, 1934, occurring south of the range of *damaranus*, and including the taxon *jordani* Parker, 1936.
4. *Bufo kavangensis* Poynton & Broadley, 1988, described from Zimbabwe and also recorded from extreme northern Namibia, with a more granular skin and a light vertebral line. Based on the smooth skin, absence of spines on the head, 'squat' general appearance, well visible tympanum and absence of a light vertebral line, our specimens can clearly be referred to the taxon *dombensis*.

Observed specimens of *Bufo dombensis* started calling late at night, reaching a peak of calling activity around 01:00. This is in contrast to the other dwarf toads of Namibia, which, as far as is known, commence calling after sundown. According to the sonagrams presented in Passmore & Carruthers (1995), the calls of *Bufo vertebralis* (much higher note repetition rate of ca. 11/s, pulses recognizable on sonagram) and of *Bufo fenoulheti* (much longer note duration of ca. 500 ms) differ considerably from those of *Bufo dombensis*. The call of *Bufo hoeschi* is a series of short chirps (Channing, in press). Presently the calls of *Bufo jordani* and *Bufo damaranus* (if distinct) are unknown.

The shape of the inflated vocal sac of *Bufo dombensis* differs from that of other, large *Bufo* species observed in Namibia, such as *Bufo maculatus* and *Bufo gutturalis*; these species had a regularly rounded vocal sac, without an anteriorly conical shape during the call. The vocal sac of *Bufo fenoulheti* is an even more exaggerated cone. Vocal sac shape may be another feature characterizing the species of the *Bufo vertebralis* group, but has so far not been described for the other species of the group.

The eggs of *Bufo dombensis* are laid in strings that soon collect as a cup-sized accumulation in small depressions and between river stones. In other dwarf toads, it has been observed that eggs were laid in long strings along sandy edges (*Bufo fenoulheti* Matetsi, Zimbabwe; *Bufo hoeschi* Channing [1976] Blutkoppie, Namibia). Egg strings of *Bufo vertebralis* were observed thickly entangled amongst stones and bits of grass in a temporary shallow pool (Wager 1965).

The tadpole of *B. dombensis* has the broad mental gap in the row of oral papillae typical for southern African bufonids (Van Dijk 1971) which allows an immediate distinction from most ranid and hyperoliid tadpoles. Tadpole keratodont formulae are, as far as is known, the same in all southern African *Bufo* species (e.g. Wager 1965), but the *B. dombensis* tadpole

can be separated from the other tadpoles of *Bufo* in the area. It can be distinguished from that of *Bufo maculatus* which has an internarial ratio of 0.09–0.12, an extra-ocular proportion of 0.4, and an unpigmented dorsal fin (Channing 1972, as *Bufo pusillus*). At the moment it is not known if the tadpoles of *Bufo fenoulheti*, *B. hoeschi* and *B. damaranus* can be distinguished (Van Dijk 1971). Larval differences between all these dwarf toad species may be found in internal buccal characters which seem to be useful to distinguish between tadpoles of closely related taxa.

Described in 1895, *Bufo dombensis* is one of the early species in the *Bufo vertebralis* group. Data presented herein provide some clarification on the status of several taxa in the group. Advertisement call differences to *Bufo vertebralis* Smith, 1848, demonstrate the validity of *Bufo dombensis*. Since advertisement calls of *Bufo hoeschi* Ahl, 1934 and *Bufo fenoulheti* Hewitt & Methuen, 1913 differ from those of *Bufo dombensis* and *Bufo vertebralis*, these, too, are clearly to be regarded as valid species. *Bufo hoeschi* is not a junior synonym of *Bufo dombensis* as hypothesized by Tandy & Keith (1972). On the other hand, the status of the taxa *jordani* Parker, 1936 and *damaranus* Mertens, 1954 still remain unresolved.

Only incomplete information on ecology and biology of most Namibian dwarf toad species has been published, although distributional and ecological information for *Bufo hoeschi* is available (Channing 1976, Channing & Stuart 1976). The arid areas may yet prove to be unexpected centers of frog speciation. *Bufo robinsoni* was recently described from the southern border of Namibia (Branch & Braack 1995) and apparently is found only in this area of Namaqualand.

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