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CNEMODESMUS RIPARIUS, N. SP., A RIPARIAN MILLIPED FROM THE NAMIB DESERT, AFRICA (POLYDESMIDA: PARADOXOSOMATIDAE)

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ABSTRACT

Cnemodesmus riparius, n. sp., the southernmost species of *Cnemodesmus* and the first generic record from Namibia, occurs in silt banks along the upper and middle Kuiseb River in the Namib Desert. A conspicuous part of the assemblage of flood-activated detritivores and carnivores, its aggregations are evident within days of brief surging flows ("floods") down the normally dry bed of the Kuiseb, and can remain for at least a month in sheltered bank habitats after such events. When exposed for 6 hrs to dry air in the laboratory, 30 adult females lost approximately 3.3% of their initial weight per hour. During a subsequent rehydration test, some continued to lose weight while others took up water, in part by rectal imbibition. Remaining on moist silt appears necessary for the survival of *C. riparius* in the hyper-arid Namib Desert.

The most diverse of the 115 families in the Class Diplopoda is the Paradoxosomatidae, order Polydesmida. Comprised of 3 subfamilies, 22 tribes, and 142 genera (Hoffman 1980), the family is indigenous to all the inhabited continents except North America. It appears to have originated in Asia, and faunal connections between the western part of the Oriental and the Ethiopian biogeographic regions suggest that desiccation of northern Africa and southwestern Asia was largely responsible for the isolation of the sub-Saharan fauna (Jeekel 1968). Paradoxosomatids are intolerant of arid conditions, and the African species primarily inhabit forests where the litter and humus provide shelter and protection from desiccation. A few paradoxosomatids occur in savannas, for example in Nigeria (Toye 1967; Lewis 1971, 1974), but the family is rarely encountered in harsh desert environments, where there is little moisture and little protection from the high summer temperatures.

In January and February 1994, summer in the southern hemisphere, the second author visited the Namib Desert in central Namibia to continue his research on riparian ecosystems in arid regions. The previous summer, Kathryn and Peter Jacobson, researchers at Gobabeb, site of the Desert Ecological Research Unit of Namibia, had discovered sizable populations of a paradoxosomatid in wet silt along the banks of the Kuiseb River, an otherwise dry, ephemeral river that floods occasionally when heavy summer rains fall in its upper catchment. This milliped is thus an unusual desert paradoxosomatid that is able to survive by inhabiting the moist banks of the stream itself. The species is referable to *Cnemodesmus* Cook (tribe

Cnemodesmini), otherwise known only from Zaire and Angola (Hoffman 1968, 1980; Jeekel 1968). We present a description of C. *riparius*, n. sp., along with a discussion of its habitat and water relations based on the second author's field and laboratory observations. Acronyms of repositories of the type material are as follows:

DERU - Desert Ecological Research Unit, Gobabeb, Namibia.
MSWB - Museum of Southwestern Biology, University of New Mexico, Albuquerque.
NCSM - North Carolina State Museum of Natural Sciences, Raleigh.
NMNH - National Museum of Natural History, Smithsonian Institution, Washington, D. C.
SMWN - State Museum, Windhoek, Namibia.
VMNH - Virginia Museum of Natural History, Martinsville.

Cnemodesmus riparius, new species
Figs. 1-2

Type specimens: Male holotype (NMNH) and 47 male and 6 female paratypes (DERU, MSWB, NCSM, NMNH, SMWN, VMNH) collected by C. S. Crawford, 30 January 1994, near Namib Desert Research Station at Gobabeb, 235 km (148 mi) WSW Windhoek and 85 km (53 mi) ESE Walvis Bay, along the Kuiseb River in the Namib Desert, Namibia. Paratypes apportioned as follows: DERU (9M, F), MSWB (19M, 2F), NCSM (3M), NMNH (3M, 2F), SMWN (10M, F), VMNH (3M).

Diagnosis: Characterized by combination of following acropodal features: process A long, generally upright but curving gently proximad; process B short and broad, sublaminate; postfemoral elements arising distomediad on femur, in form of broad loops, solenomere situated mediad to tibiotarsus, coiling over medial surface of process A, terminating lateral to base of latter, tibiotarsus curving broadly over distal extremity of process A, terminating just beyond latter, with short, laminate projection near midlength of inner margin.

Color in life: Dorsum and epicranium dark brown, pigment fading in interantennal and genal regions, bases of mandibles and sides of metazonites light brown, becoming progressively lighter ventrad on sternites and legs; anterior one-third of paranota/peritremata dark brown, concolorous with middorsum, caudal two-thirds white, latter color extending mediad onto caudal halves of metazonites.

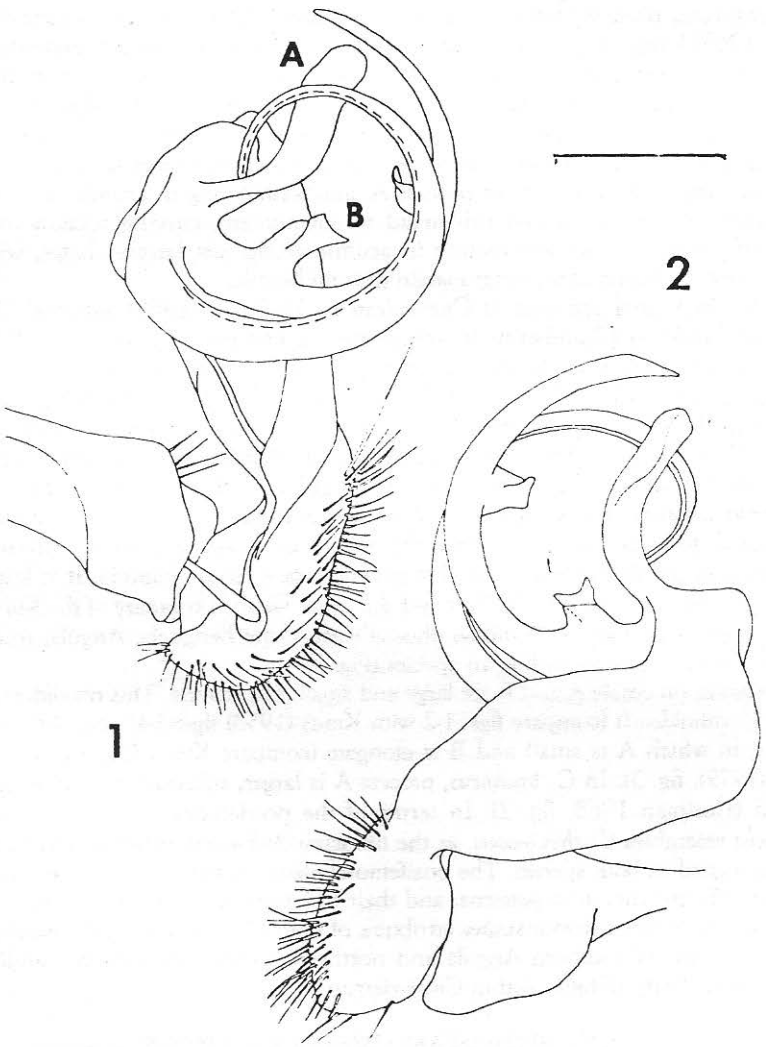
Description: Males ca. 15.6 mm long and 1.4 mm wide, females slightly larger, all specimens with heads tightly curled, impossible to unroll without fragmentation. Body essentially parallel-sided throughout most of length, narrowing on caudalmost segments.

Head of normal appearance, slightly punctate. Epicranial suture distinct, terminating just above interantennal region. Antennae relatively long and slender, reaching back to midlength of 3rd tergite, becoming progressively more hirsute distad, with 4 terminal sensory cones and a microsensillum on outer distal margins of both 5th and 6th articles, relative lengths of antennomeres 2>3>4>5>6>1>7. Genae narrowly margined laterad, ends broadly rounded and extending slightly beyond adjacent cranial margins, without impressions. Facial setae as follows: epicranial absent; supra-antennal in two series of 1-1 each; interantennal 2-2; subantennal in two series of 1-1 each; frontal region with numerous setae, becoming denser in lower frons next to clypeus; genae with numerous setae scattered irregularly over surface; clypeal about 14-14; labral about 20-20.

Terga generally smooth and polished or lightly punctate; metaterga with transverse grooves characteristic of family bissected by faint, short, longitudinal grooves. Collum broad, ends terminating well above those of succeeding tergites. Paranota narrow, poorly developed, noticeable only on segments 2-4, strongly declined, imparting arched or vaulted appearance to

dorsum, paranota of 2nd segment with corners squared, those of segments 3-4 extending slightly caudad; paranota of remaining segments essentially reduced to widths of peritremata, latter strong, well defined, caudolateral corners extending slightly caudad, ozopores located just anterior to caudolateral corners, opening sublaterad. Epiproct strongly extended, apically blunt.

Sides of metazonites lightly punctate, with distinct supracoxal ridges running entire lengths on segments 1-14, stronger and higher on anteriormost segments, becoming progressively lower, more rounded, and less conspicuous around midlength. Strictures distinct. Pregonopodal sterna essentially glabrous, with at most only 1-2 fine setae adjacent to coxae, unmodified except for strong, broad, plate-like projection between anterior legs of segment 4 (4th legs), directed anteriad in midline, extending over prozonite to 3rd sternum.



Figs. 1-2. *Cnemodesmus riparius*. 1, left gonopod of holotype, medial view. 2, the same lateral view. Scale line = 1: 00 mm for both figs.

Postgonopodal sterna glabrous and unmodified, with at best only faint transverse impressions originating between leg pairs, caudal margins gently curved. Podomeres without projections or modifications, tarsal claws short, faintly curved. Hypoproct moderate-size, slightly extended in midline; paraprocts with two submarginal setae apiece as diagnostic for family, margins slightly thickened.

Gonopodal aperture moderately broad, anterior margin strongly indented anteriad in midline, sides and caudal margin elevated above metazonal surface. Gonopods *in situ* with femoral regions diverging slightly, extending over anterior margins of aperture and overhanging prozonum, distal regions of acropodite directed mediad, coiling around each other and intertwining in midline. Gonopod structure (Figs. 1-2): Coxae with four setae arising from ventral surface. Prefemur short and broad, densely setose, with distinct ledge arising distad and extending along medial surface of femur. Femoral region set off from prefemur by distinct cingulum, relatively long and broad, expanding distad; process A (terminology of Hoffman, 1968) long, upright but slightly curved proximal to midlength, expanding distad with narrow, thickened flange on lateral surface, apically blunt; process B short and broad, sublaminate, folded on medial side. Postfemoral region abruptly narrower than femur, arising from distomedial surface of latter, looping dorsad toward coxa then ventrad and anteriad, divided basally into two branches, solenomere located mediad to tibiotarsus, coiling inside loop of latter, over medial surface of process A, and terminating in acuminate tip lateral to base of latter; tibiotarsus located sublaterad to solenomere, curving broadly over distal extremity of process A and terminating in acuminate tip just beyond latter, with short, folded, laminate projection along inner margin near midlength.

Remarks: In a brief synopsis of *Cnemodesmus*, Hoffman (1968) assigned *Dysthymus* Attems and *Lundacus* Chamberlin to synonymy; he had earlier (Hoffman 1953) placed *Lundacus* under *Dysthymus*. In the earlier paper, Hoffman recognized three species: C. *thysanopus* (Cook & Collins), the type species, from Cubal da Ganda, Benguela District, Angola, and "Bas Congo," probably near Matadi, Zaire; C. *brunneus* (Attems), from N'Gombe, Kasai Province, Zaire, and Dundo, near Portugalia, Angola; and C. *calundensis* Kraus, from Calunda Lake, Bihe District, Angola. Hoffman (1980) reiterated that *Cnemodesmus* consists of three species in Zaire and Angola. To the best of our knowledge, no additional records exist for either the genus or a species, so C. *riparius* is the southernmost cnemodesmine and the first generic report from Namibia. It is known only from the upper and middle Kuiseb River and the lower Gaub, a tributary of the Kuiseb, these sites being some 1,088 km (680 mi) south-southeast of the Benguela, Angola, record of C. *thysanopus*, the most proximate known species (Fig. 3).

In C. *riparius* processes A and B are large and small, respectively. This condition is similar to that in C. *calundensis* (compare figs. 1-2 with Kraus (1958) figs. 3-4) and distinct from C. *thysanopus*, in which A is small and B is elongate (compare Kraus (1958), figs. 1-2, with Hoffman (1979), fig. 3). In C. *brunneus*, process A is larger, subequal to B in length, and is subdivided (Hoffman 1968, fig. 2). In terms of the postfemoral curvature, however, C. *riparius* most resembles C. *thysanopus*, as the tibiotarsi and solenomeres coil in broad loops and are attenuated in both species. The postfemoral elements in C. *brunneus* and *calundensis* conform to different curvature patterns, and their tibiotarsi are broader and expand distad. Consequently, C. *riparius* demonstrates attributes of both C. *thysanopus* and *calundensis*. The intervening regions of southern Angola and northern Namibia may harbor undiscovered species that may clarify affinities within *Cnemodesmus*.

DISTRIBUTION AND WATER RELATIONS

During January and February 1994, C. *riparius* was recorded along the drainage of the ephemeral Kuiseb River from the Us Pass Bridge (longitude 16°20'79"E, latitude 23°

01'43"S) and the Gaub Bridge (longitude 14°45'51"E, latitude 23°28'92"S) to 3 km below the weir (longitude 14°57'50"E, latitude 23°29'05"S), downstream from the settlement of

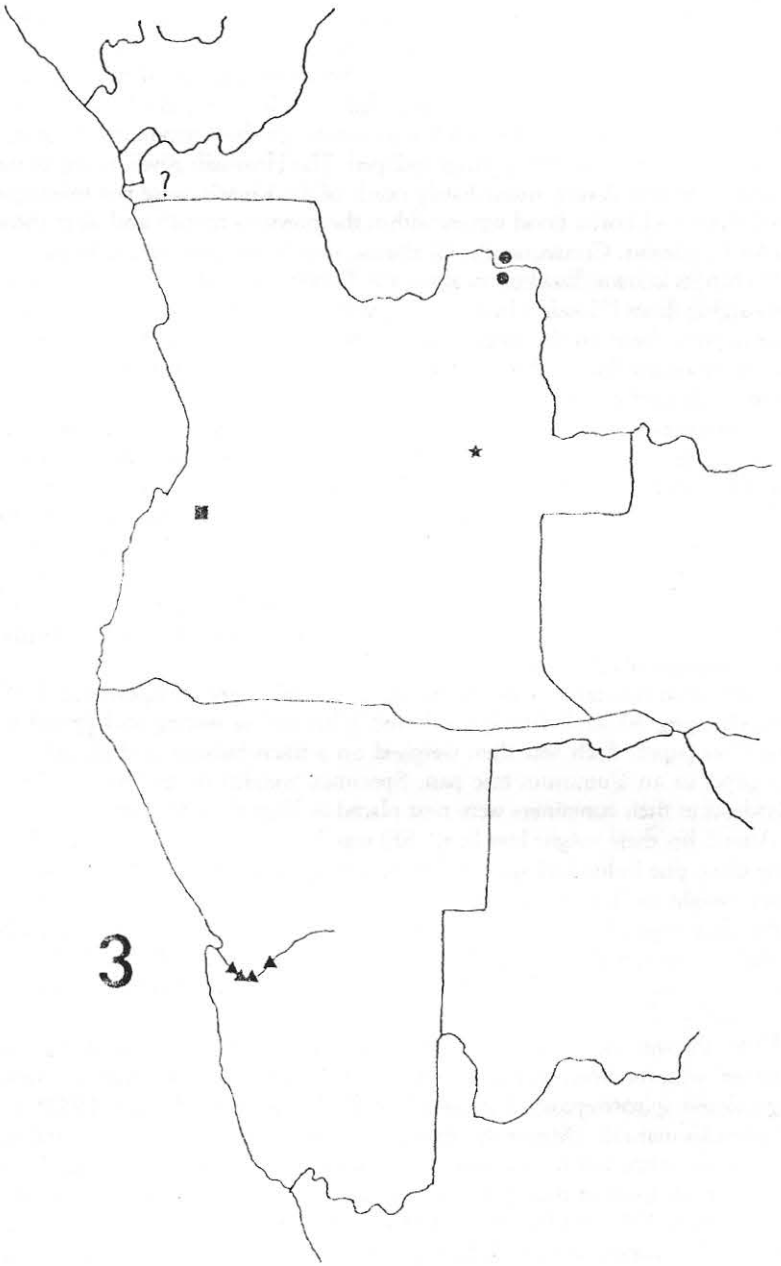


Fig. 3. Distribution of *Cnemodesmus*. Dots, *C. brunneus*; star, *C. calundensis*; square, *C. thysanopus*; triangles, *C. riparius*. The question mark denotes the type locality in "Bas Congo" of *C. thysanopus*, which Hoffman (1968) speculated was near Matadi. The approximate course of the Kuiseb River is indicated in central Namibia.

Khomabes. However, above the escarpment that bounds the Namib Desert to the east, no individuals were recorded after a 3-hr search along the banks of the Gaub River, the main tributary of the Kuiseb, at Weissenfels Guest Farm (longitude 16°27'06"E, latitude 23° 18'92"S). Several days of rainstorms preceded the search at Weissenfels, during which other millipeds--including another species of polydesmid--were noted. In addition, a preliminary, 6-day search along the banks of sections of five other ephemeral rivers north of Gobabeb - the Omaruru (ca. 190 km to the north), Ugab (ca. 300 km), Huab (ca. 340 km), Uniab (ca. 430 km), and Hoanib (ca. 490 km), and several of their tributaries (Fig. 4) - revealed no specimens of C. *riparius* or any other milliped. The Hoarusib River, north of the Hoanib, and the Khan/Swakop Rivers, immediately north of the Kuiseb, were not investigated. All of the visited rivers had borne flood waters within the previous month and were therefore plausible sites for C. *riparius*. Consequently, C. *riparius* may be endemic to the Kuiseb drainage.

Within its known distribution along the Kuiseb and Gaub Rivers, C. *riparius* responds to brief surging flows ("floods") by emerging, within one or two days, from presumed sites deep in silt deposits beneath the river's banks. Once on the surface, individuals aggregate on silt exposed by recent flows, often on patches of green cyanobacteria. On cool, foggy mornings, they move along the base of sharply incised banks and occasionally into the dry river channel. As a conspicuous component of an assemblage of flood-activated arthropod detritivores and carnivores, this species can be found for the next month or so beneath deep, flood-formed piles of leaf and wood litter, and under flood-transported logs at or below the strand line.

The apparent spatial and temporal distribution of C. *riparius* suggests that it is a poorly-adapted desert animal, even though its habitat lies within the borders of one of the most arid regions on earth. This thought was explored by testing the capacity of the species to resist and recover from desiccation, which it would have to do in order to survive prolonged transport to new and distant locations by wind, birds, and other non-anthropogenic agents of dispersal.

Desiccation-resistance was examined in a laboratory (temperature 22°C to 27°C) at Gobabeb using 30 adult females collected 3 hrs before testing and placed immediately on moist filter paper. Each was then weighed on a microbalance and placed on a circle of dry filter paper in an aluminum tare pan. Specimen weights ranged from 0.0320g to 0.0475g. Individuals in their containers were next placed in large glass desiccators containing dried silica gel. After 1 hr, their weight loss (x +/- SE) was 3.10 +/- 0.14% of their original weight. After 6 hrs, when one individual appeared to be dying, the remaining 29 had lost 19.23 +/- 0.56% of their weight, or 3.31 +/- 0.09% per hour. None defecated during that time. The water loss results are comparable to those recorded by Perttunen (1953) (cited in Crawford [1972]) for the slightly larger, widespread paradoxosomatid, *Oxidus gracilis* (C. L. Koch). Loss rates for O. *gracilis* averaged from 3.50%/hr to 4.67%/hr for 12 hours; length and width values for the species are listed in Blower (1985).

Following the last weighing, all filter papers were moistened with distilled water and each container, with its desiccated specimen, was placed in a humid chamber overnight. As with certain desert spirostreptoids (Crawford 1972, Crawford & McClain 1983) and alpine julids and chordeumatoids (Meyer & Eisenbeis 1985), some individuals imbibed rectally, a behavior also observed on the moist silt banks. Twenty hours later, the 15 specimens that had not crawled out of their pans (four drowned in wet spots) were weighed again. Six had lost between 0.36% and 66.39%, while nine had regained between 2.92% and 47.81%, of their post-desiccation weights. These greatly varying responses are difficult to explain; they varied far less in the larger and more dessication-resistent Namib Desert harpagophorid, *Harpagophora nigra* Attems, following a 54-hr period of drying (Crawford & McClain, 1983).

Clearly, C. *riparius* is able to survive in the hyper-arid Namib Desert only by inhabiting moist environments, in this case moisture-conserving silt along an ephemeral river. How its life history has adjusted to the Kuiseb's erratic flooding regime, and whether the species

occurs along other ephemeral rivers in the region are questions warranting further investigation.

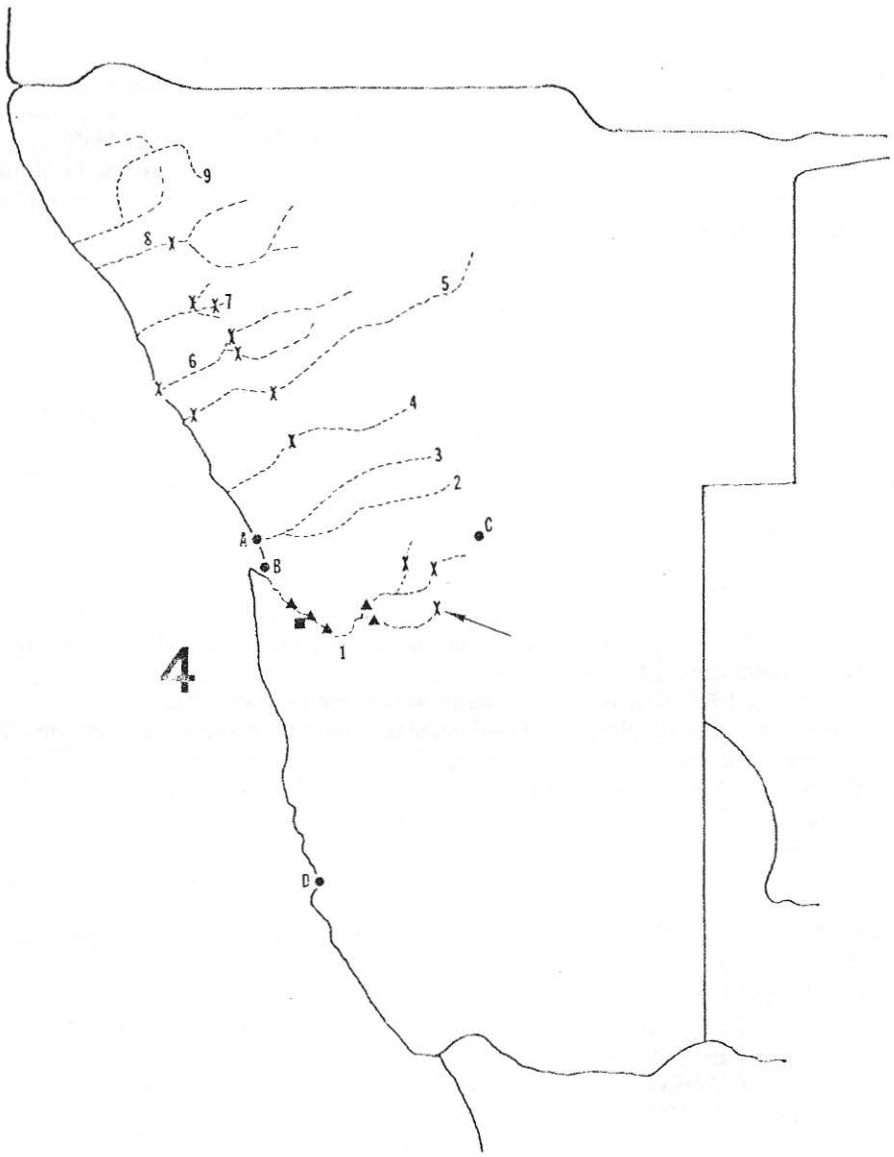


Fig. 4. Extent of investigations by the second author to discover additional populations of C. *riparius*. Triangles, known sites of C. *riparius*; X's, sites of unsuccessful explorations; square, location of Gobabeb, site of the DERU; dotes, cities - (A, Swakopmund; B, Walvis Bay; C, Windhoek; D, Luderitz). Ephemeral rivers numbered as follows: 1, Gaub, tributary of the Kuiseb; 2, Swakop; 3, Khan; 4, Omaruru; 5, Ugab; 6, Huab; 7, Uniab; 8, Hoanib; 9, Hoarusib. The arrow points to the location of Weissenfels Guest Farm, on the Gaub River.

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