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First record of *Limnocnida tanganjicae*, a freshwater medusa, from Caprivi, Namibia

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ABSTRACT

The freshwater medusa *Limnocnida tanganjicae* was collected during September in a small lake off the main stream of the Upper Zambezi River in Caprivi, Namibia. The transparent specimens ranged 5-28 mm in umbrella diameter while the number of tentacles and statocysts were 80-560 and 60-360 respectively. Gonads could not be clearly identified. No polyps were found on the vegetation in the lake. The medusae were confined to the central area in the lake, which was devoid of vegetation. A distinct diurnal vertical migration was recorded and described. A summary of the known distribution records of *L. tanganjicae* in Africa was compiled. The emerging trend indicates that it is restricted to isolated, still, clear water bodies far removed from each other. In big lakes it is confined, in most cases, to secluded parts. It is generally accepted that there is only one species of *Limnocnida* in Africa.

INTRODUCTION

The accidental discovery of freshwater medusae in London in 1880 *(Craspedacusta sowerbii* Lankester) stimulated interest in the subject. Soon afterwards the African genus *Limnocnida* was reported from Lake Tanganyika in 1883, Lake Victoria in 1893 (Gunther 1903) and the Niger River by Günther provided the first proper description of the species, which he named Limnocnida tanganjicae Günther (1894). *Since* then the systematic position of *Limnocnida* has remained a puzzle, marred by ambiguous reports from various localities in Africa. (e.g. Kramp 1954; Bouillon 1957; Pitman 1965; Goy 1977). The hydroid stage (misidentified *Hydra vulgaris* Palles and *Moerisia alberti* Leloup) is usually found on stems of aquatic plants at depths reaching 5 m. Bouillon (1955) observed the hydroid development from elongated larvae to mature polyps which bud small medusae. At a later stage, Beadle & Thomas (1957) and Beadle *et al.* (1960) provided information concerning sexual reproduction of *Limnocnida* under laboratory conditions. With the fertilization of the eggs shed by the medusae, a free-swimming larva is formed. At 20-23°C, it settles down to form an hydroid, approximately five days after fertilization. The medusae are found in a variety of water conditions and localities throughout Africa. Although they sometimes occur abundantly in flowing rivers, they are more likely to occur in still, clear lakes, small reservoirs and backwaters of rivers (Pitman 1965). Recorded sizes vary from a few millimetre to over 30 mm. All are transparent or whitish, whereas the hydroid stage is pale brown or yellow and opaque (Pitman 1965).

Bouillon (1957) compiled information concerning several reported species into a more concise framework. This approach indicated that there are three African species of the genus *Limnocnida* namely:

Limnocnida tanganjicae Gunther 1893; *Limnocnida victoriae* Gunther 1907 (= *Limnocnida rhodesiae* Boulenger 1912 and *Limnocnida cymodoce* Jordaan 1934); and *Limnocnida congoensis* Bouillon 1957. Nevertheless, Kramp (1954) stated emphatically that there is only one species of *Limnocnida* in African south of the Sahara, i.e. *L. tanganjicae* (Limnocnidae; Limnomedusae). More recent publications support Kramp's approach, substantiating it with distribution records and biometric data (Pitman 1965; Goy 1977). The confusion in identification is attributed mainly to artifacts of preservation, which altered taxonomic features, as well as to the examination of medusae and hydroids in many varying stages of growth (Kramp 1954; Pitman 1965; Goy 1977). Nevertheless, Limn*ocnida* populations sampled in different lakes and rivers all over Africa differ in certain characteristics such as number of tentacles and statocysts (Kramp 1954; Goy 1977).

In the light of new records of *Limnocnida* from a variety of lakes, rivers, reservoirs and isolated localities in Africa (Pitman 1963; Goy 1977), it is the purpose of this paper to summarise all available distribution records of *L. tanganjicae*. The medusa is described and some population features are dealt with, based on studies of a population in Lake Lisikele, Caprivi, Namibia.

MATERIAL AND METHODS

Medusa specimens were collected at Lake Lisikili (17°30'S; 24°50'E) during the course of two field expeditions to the Caprivi strip in September 1984 and 1985. A large hand net with a 1 mm mesh, was used to sample medusae while diving underwater by means of SCUBA. Specimens were fixed and preserved separately in 5% formalin and 70% ethanol respectively. Water quality measurements (pH, conductivity, temperature and light penetration) were monitored continuously for three days at four stations along the lake (Fig. 1). The wind regime was recorded and the pattern of vertical and horizontal medusa migration was followed by repeated diving (vertical) and surface observations (horizontal) every two hours.

Size distribution of the medusa population was determined by measuring umbrella diameter in a petri-dish with a calibrated millimetric grid under a dissecting microscope. Additional parameters (manubrium diameter, number of tentacles and number of statocysts) were measured similarly. The latter were used in the determination of biometric ratios facilitating comparisons to other African records (Goy 1977) as well as a general description of the medusa.

RESULTS

General description of *L. tanganjiciae* from Caprivi

All medusa specimens collected at Lisikili were transparent with whitish tentacles. Their size (umbrella diameter) ranged from 5 to 28 mm (Fig. 2). The manubrium is contracted in live specimens, and the mouth appears as a wide circular aperture (Fig. 3a). However, the mouth can close completely while regulating movement in the water. No gonads could be detected in any of the 347 specimens collected during September (1984 & 1985). The radial canals leading from the mouth towards the circumference are clearly visible in Figure 3a. The velum in the live specimens is horizontal and rather wide (Fig. 3a, b) while in the SEM preparation it contracted considerably (Fig. 3c).

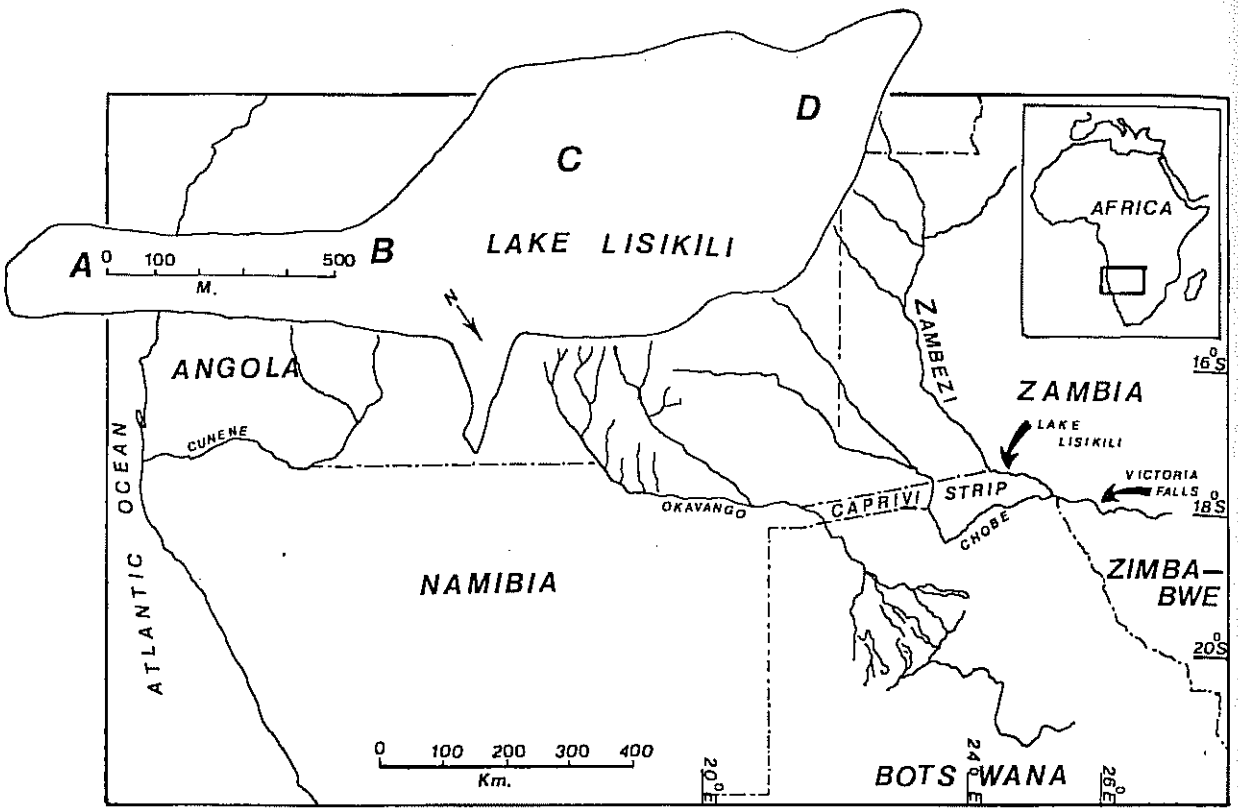

FIGURE 1: Lake Lisikili and its location in the Upper Zambezi System. Sampling stations are marked A to D.

The margin of the umbrella, known as the nettle ring is thickened and folded round the basis of the large tentacles in a manner resembling the tentacle-bulbs which occur in many craspedote medusae (Fig. 3c, d). The short tentacles, however, originate from the basis of these thickened structures (Fig. 3e). The number of tentacles in different sized individuals ranged from 80 to 560. They are arranged in series according to size, the interradial and adradial being the largest (Fig. 3a,b,c). The larger -tentacles have long narrow bases attached to the exumbrella surface of the bell (Fig. 3a,b,c). They are 16-18 mm long and covered by batteries of nematocysts (Figs. 3f & 4b). The short tentacles are more numerous and completely different in their surface texture (Fig. 3e & 4c,d). No nematocysts were found on any of the short tentacles. The number of statocysts correspond to the number and arrangement of tentacles. There are between 60 and 350 sense organs in the various size groups. They are situated at the tip of the thickened bulbs of the nettle ring in a single, double and triple mode. At the base of a large tentacle there are two or three statocyst openings, while only a single opening occurred at the thickenings of the small tentacles. The shortest tentacles did not have any openings at all. The diameter of a statocyst opening is 60 - 70 $\mu \pm$ SD 24 μm (Figs. 3e & 4a). The biometric ratios for various size - class specimens were: 0,50 - 0,85 manubrium/umbrella diameter; 0,64 - 0,70, number of statocysts/number of tentacles. Although all types of existing vegetation and other substrata were carefully examined under a dissecting microscope, no polyps were recovered.

Migration

During the period of sampling, the medusa population was confined exclusively to the vicinity of station B (Fig. 1). The substrate at this area was bare with fine sediment and no gravel. The rest of the lake floor was completely covered by vegetation.

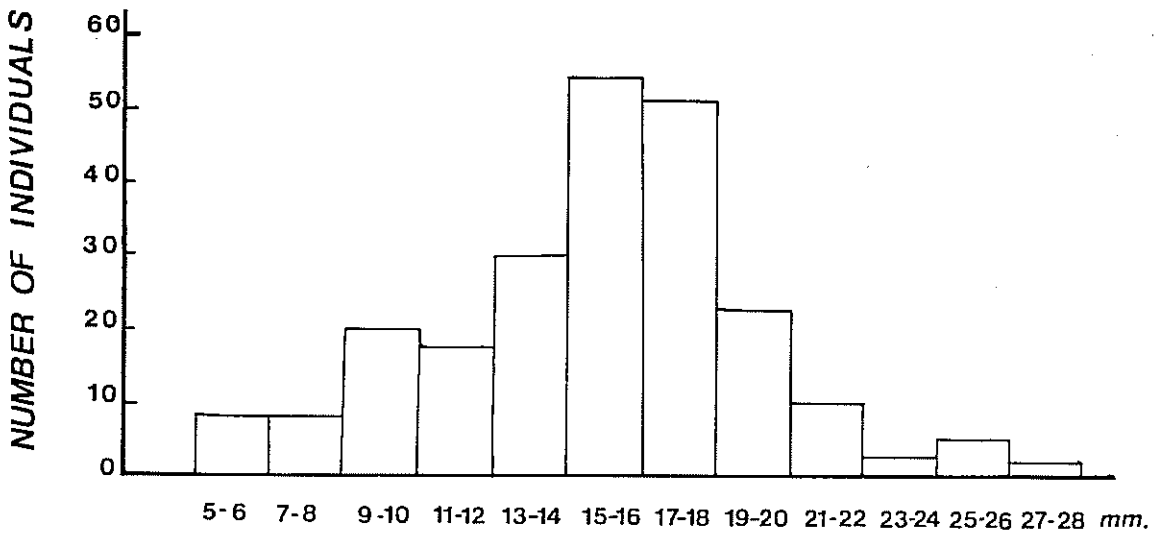

FIGURE 2: Size distribution of the *L. tanganjicae* population sampled during the month of September 1985

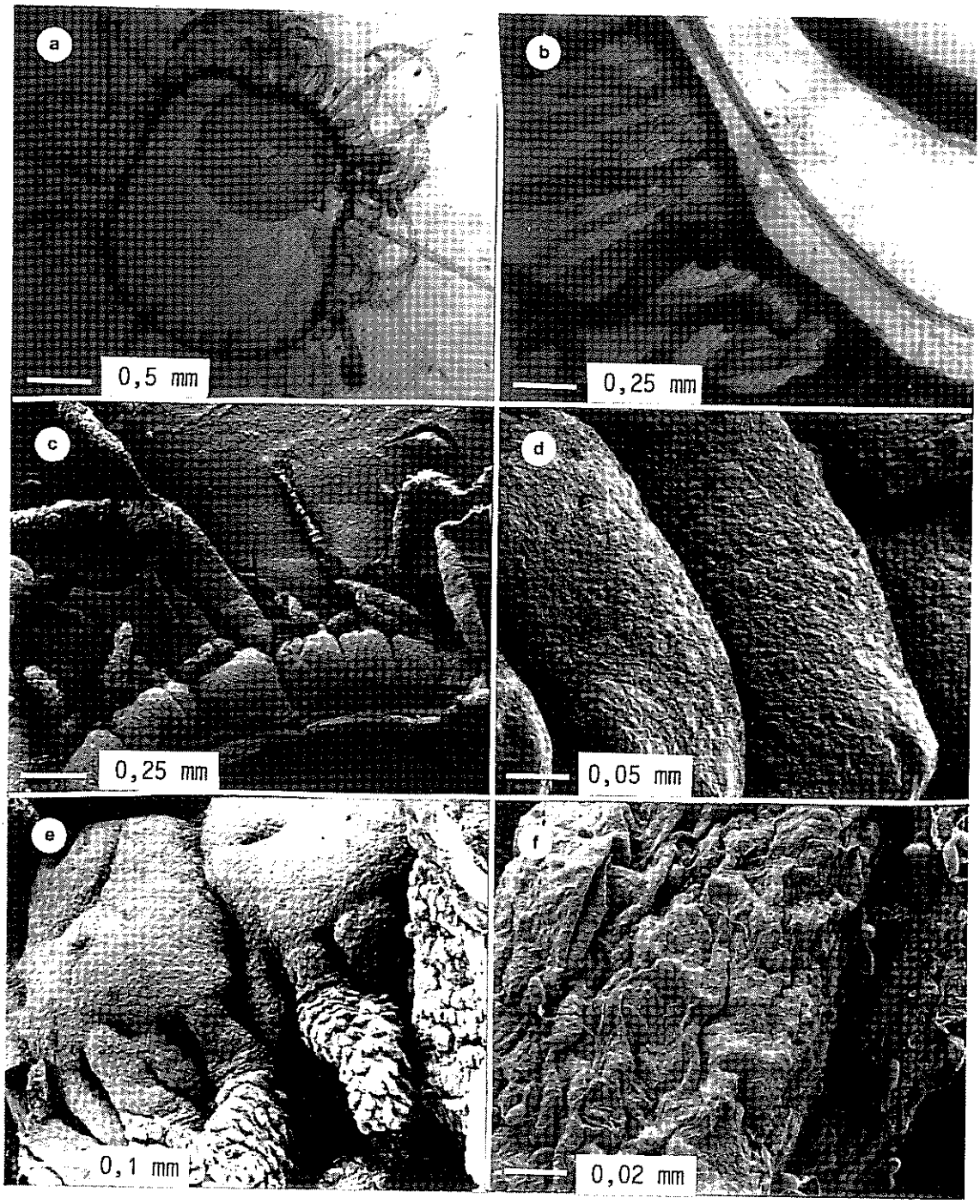

FIGURE 3: Some morphological characteristics of *L. tanganjicae* from Caprivi: a. swimming individual where the manubriu, mouth, radial canals, velum, nettle ring and tentacles are in full view (X6). b. a close-up of the nettle ring, velum and manubrium edge (X12). c. and d. the bulb-like structure of the nettle ring and the extension of the short tentacles from its base. e. the bases of the long tentacles and f. the surface texture of the long tentacles with the massive batteries of nematocysts (many of which were discharged)

Horizontal migration was restricted to a 100 m radius from the boundaries of station B. It took place during the day between 10h00 and 15h00 and in both instances, when it was recorded, the horizontal movement was in an opposite direction to the mild wind prevailing at the time. Since the medusa were 20-50 cm below the surface, the possible effect of the wind was negated. The vertical migration pattern was more closely related to the recorded water properties. Water conductivity was 112,8 $^{\pm}$SD 27,5 µS while conductivity ranged between 6,40 to 7,65 µS during early morning and late afternoon, respectively (at the various sampling stations). Surface water temperatures ranged from 22°C in the early morning, to 26,5°C during the early afternoon. Bottom temperatures, however, were more constant around 22°C and dropped to 21°C during the night (thermograph readings at station A). In the shallower stations (up to 2 m) visibility was clear down to the bottom throughout the day. Medusa started to appear on the subsurface at 07h30 in the morning and by 08h00 most of the population concentrated between 30 and 50 cm below the surface with very few specimens remaining close to the bottom. This situation prevailed until 14h00 15h00 daily. At about 15h00 most medusae were concentrated at midwater (1-2 m) and more individuals were observed closer to the bottom at a depth of 3 m. The thermocline at station B was at 2 m. Between 15h30 and 17hO0 more medusae went under the 2 m mark and many of them were seen with the umbrella touching the bottom. After sunset no medusae were seen at subsurface and mid-water level and the entire population was concentrated on the bottom at 2-3 m below the surface. This cycle repeated itself throughout the observation period.

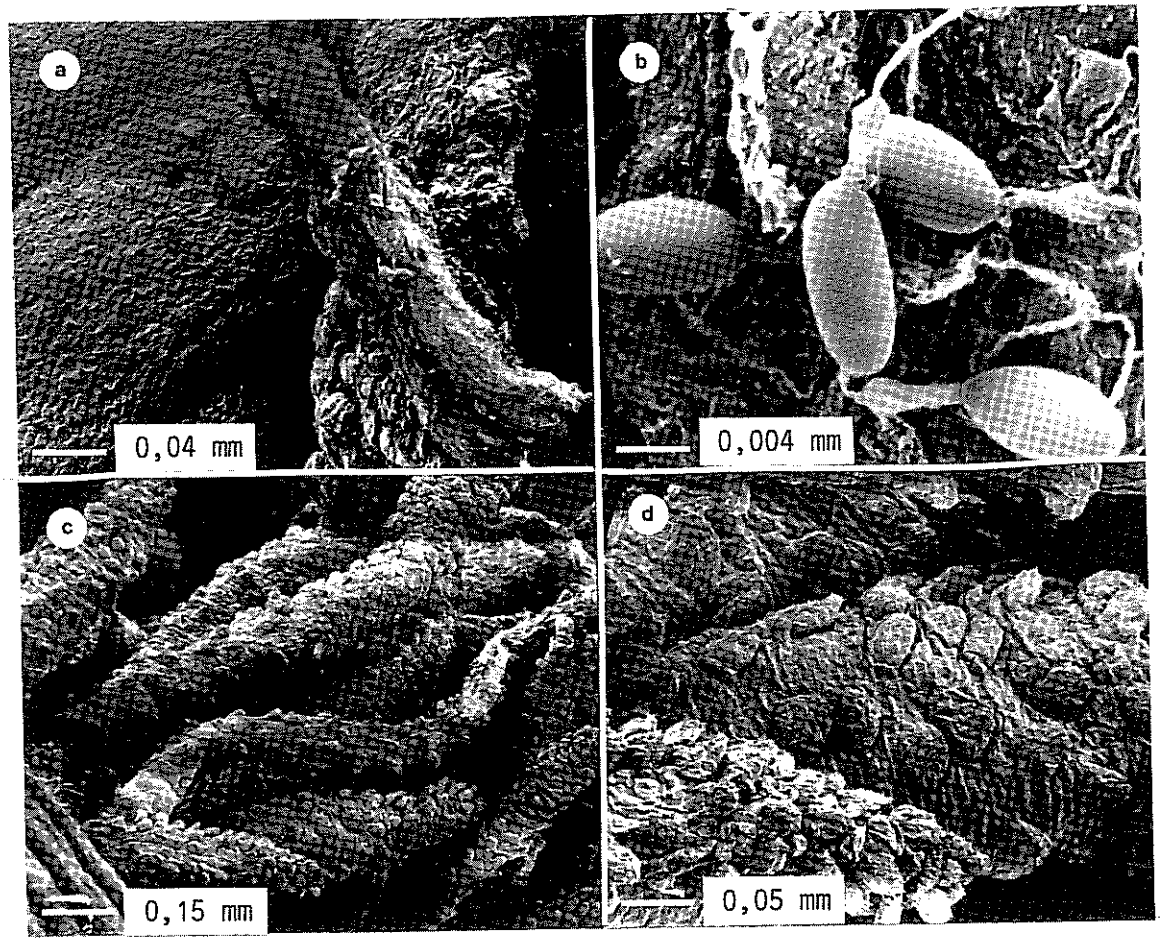

FIGURE 4: Some morphological characteristics of *L. tanganjicae* from Caprivi: a. a close-up of a statocysts opening. b. a close-up of discharged nematocysts on the surface of a long tentacle. c. and d. the surface texture of some short tentacles

Distribution of *L. tanganjicae* in Africa

All known records on the distribution of *L. tanganjicae* in Africa, in both small and large water bodies are shown in Table 1.

DISCUSSION

Although *L. tanganjicae* was collected at Lake Lisikili during the month of September only (1984 and 1985), integration of other African records facilitates a better understanding of its population ecology and behaviour. African records (Table 1), clearly indicate a seasonal occurrence of *L. tanganjicae*. In the Zambezi basin, the seasonal occurrence resumes annual bloom proportions during the latter months of the dry season, i.e. July to November (Edney 1939; Pitman 1965; Mills 1973). Mills (1973) reported a ninefold increase in numbers during a week in August at an estuary in Lake Kariba. The overall duration of the bloom lasted from July to September. He did not find gonads in any of the few thousand specimens examined, as was the case in the current study. Edney (1939) did not observe any gonads in his January specimens, while in some of the larger September specimens they were present, but poorly developed. The occurrence of very small individuals in September (Fig. 2 & Edney 1939) suggests that the breeding season is early spring. To date, the hydroid phase of the *Limnocnida* life cycle is yet to be discovered in the Zambezi and Limpopo basins. It is apparent that the time most suitable for searching is not during the reported medusae bloom. Bouillon (1955) did, however, discover and describe the polyp stages at Lake Tanganyika.

Ecologically, the medusa and hydroid phases of the *Limnocnida* life cycle occupy different habitats within their reported localities. At Lake Lisikili, the medusae were concentrated exclusively within the boundaries of the only site on the lake floor devoid of vegetation. Likewise, reports from the Lufupa and Kafue Rivers in Zambia, as well as from Lake Kariba and Lake Mohasi (Pitman 1965) show that medusa are found where there is no vegetation. In all cases where polyps were recovered they were found on the stems of aquatic plants at depths extending down 5 m below the surface (Pitman 1965). The preference by the medusae for bare patches can be related to their vertical migratory pattern. At Lake, Lisikili many medusae were found resting on the bottom during the late hours of the afternoon and evening. Edney (1939) reported the same behavioural pattern from aquaria observations.

Vertical migration differs in its diurnal cycle when in-shore, shallow populations are compared with open water, off-shore, populations. At Lake Lisikili, medusae started surfacing at 07h30 and by 08h00 most of the population concentrated at 30 - 50 cm under the surface. They remained there until 14h00 - 15h00 daily, after which most of the population concentrated at mid-water (13h00 - 14h00) and more individuals were seen closer to the bottom at 15h00. Between 15h30 17h00 most medusae were below the 2 m mark while after sunset no medusae were to be seen at the subsurface or mid-water levels. Similarly, medusae observed in the Chobe and Gwaai Rivers were active at the subsurface during the midday heat (Pitman 1965). Arnold & Boulenger (1915) suggested that Limnocnida prefers the cooler water and in the day remains 50 cm below the surface. Mills (1973) noted that medusae at Mwenda estuary, Lake Kariba, were at the bottom during the night while ascending to the subsurface on bright clear days. They were more numerous on the surface on overcast days. Contrary to these observations, vertical migration at Lake Tanganyika assumed the reverse diurnal pattern in the off-shore, open water populations (Pitman

TABLE 1: Distribution records of *L. tanganjicae* in Africa. First records were reported by Günther in 1880 (Niger River), 1883 (Lake Tanganyika) and 1893 (Lake Victoria).

Basin	Locality	Time of year	Depth (m)	Temperature °C	Occurence	Remarks	Reference
a. MEDUSAE							
Zambezi	Hubyani River	-	-	-	-	Thomas, 1908	In Arnold & Boulenger (1915)
	Chobe River	July	-	-	Plenty (disappeared after one day)	Slow running backwaters	Jordaan (1935)
	Prince Edward Dam	October	-	-	30	(=*L. rhodesiae*) Stewart, 1931	In Fantham & Porter (1933)
	Khami River	October	-	-	Vast numbers	Still waters	Pitman (1965)
	Lake MacIlwaine	September	10	20-30	Plenty	Still waters	Pitman (1965)
	Gwaai River	October	3-6	-	Common water	Slow flowing	Pitman (1965)
	Nanzhila River	-	-	-	-	-	Pitman (1965)
	Kafue river	Occur annualy	1-7	-	Extremely abundant at times	-	Pitman (1965)
	Chinanja Lagoon	October	-	-	Plenty	-	Pitman (1965)
	Lufupa River	Sept-Nov	-	-	Common	-	Pitman (1965)
	Mulungushi Dam	July	1	22-24	A few vast numbers	-	
		December	1-3	26			
	Luansanza Stream	October	-	-	1	Still water	Pitman (1965)
	Shishamba Stream	October	-	-	Common	-	Pitman (1965)
	Lake Kariba	February	Surface	30	2	Zwonge River	Pitman (1965)
		July			Plenty	Mouth	
	Lake Kariba	September	-	-	Widespread off-shore specimens to concentrations of a few hundreds	from a few	Pitman (1965)
	Lake Kariba	July	-	23-24	A few	Ngwena (near the dam wall)	Pitman (1965)
	Lake Kariba	Aug-Sep	3	22-25	1694	Nwenda River Mouth	Mills (1973)
	Zambezi River	September	-	-	Large numbers	Songwe river Mouth	Pitman (1965)
	Zambezi River	August	-	-	Vast numbers	At Katimo Mulilo	Pitman (1965)
Limpopo	Hartebeespoort Dam	-	-	-	A few	(=*L. cymodoce*)	Jordaan (1934)
	Crocodile River	March	-	-	3	(=*L. rhodesiae*)	Fantham & Porter (1933)
	A pool on Kirton farm (Bulawayo)	January & September	-	-	50	(=*L. rhodesiae*)	Edney (1939)
	Norquane River	January	-	-	-	(=*L. rhodesiae*)	Arnold & Boulenger (1915)
	Ncem Dam	November	sub-surface	-	Vast numbers	Drifting	Pitman (1965)
Congo	Stanly Pool	October	1-7	26	Common	(=*L. congoensis*)	Bouillon (1957)
	Lake Leopold II	-	-	-	-	Observed simming	Kramp (1954)
Nile	Lake Mohasi	January	4-5	-	Abundant	Curry-Lindahl, 1952	In Pitman (1965)
		-	-	-	29	Verhulst, 1939	In Kramp (1954)
	Lake Risale	-	-	-	-	-	Kramp (1954)
	Lake Sake	-	-	-	-	-	Kramp (1954)
	Lake Bilala	-	-	-	-	-	Kramp (1954)
	Lake Victoria	September	-	-	Plenty	Kavirondo gulf	Pitman (1965)
		August	-	-	Common	Kavirondo gulf	Pitman (1965)
		December	-	-	None	Kavirondo gulf	Pitman (1965)
		March	-	-	None	Kavirondo gulf	Pitman (1965)
Lake Tanganyika complex	Lake Tanganyika	May-October	-	-	Abundant	Open water Mayer, 1910	In Pitman (1965)
		May	6	-	24	Stappers, 1912 West Coast	In Kramp (1954)
		-	-	-	38	Van den Berge, 1933	In Kramp (1954)
	Lake Kivu	-	-	-	-	North East Coast	In Kramp (1954)
Niger	Largeau Swamps	-	-	-	-	Monad, 1940	In Pitman (1965)
	Tibesti	-	-	-	-	Rock pools	Pitman (1965)
	Ke-Macina Bamako	January	-	-	Abundant	In pools Daget, 1957	In Pitman (1965)
	Niger Delta	-	-	-	Scarce	Daget, 1957	In Pitman (1965)
	Sokoto River	Feb-April	surface	20	Abundant	Holden, 1957 in a pool	In Pitman (1965)
	Eileyele Reservoir	Jan-Dec	-	-	Swarms occasionally. Peak in June.	Woodward 1961	In Pitman (1965)
	Bouaflè	-	-	-	-	Monad, 1945	In Pitman (1965)
	Atar	-	-	-	1875	-	Goy (1977)
	Lake Chad	-	-	-	9	-	Goy (1977)

TABLE 1 cont.

Basin	Locality	Time of year	Depth (m)	Temperature °C	Occurence	Remarks	Reference
Senegal	Casamance Lagoon	-	-	-	-	Leloup, 1951	In Pitman (1965)
Northermost record	Atar Mauritania	-	-	-	-	Rock pool Monad, 1951 DeKeyser 1957	In Pitman (1965) In Goy (1977)
Southernmost record	Johannesburg South Africa	Feb-April	-	-	plenty	(= *L. cymodoce*) isolated cement pool	Jordaan (1934)
b. POLYP							
Nile	Lake Mokoto	-	5	23	Common	Altitude 1725m, Volcanic	Pitman (1965)
	Lake Mohasi	-	5	25	Rare	Altitude 1450m, drowned valley	Pitman (1965)
	Lake Tanganyika	-	5	27	Rare	Altitude 775m very deep	Bouillon (1955)
Congo	Lake Lungwe	-	5	17	Abundant	Altitude 2710m Glacial (no medusae)	Pitman (1965)

1965). Specimens were detected and collected at night from the surface of the water while during the day none were witnessed on or immediately under the surface of the water. This pattern corresponds with the diurnal, vertical migration of zooplankton.

Close examination of morphological and biometric features of *Limnocnida* from various localities in Africa, reveal some apparent differences with particular regard to a varying number of tentacles and statocysts (Kramp 1954; Goy 1977). These differences were the main factor contributing to the state of confusion concerning the systematical standing of this genus. At Lake Lisikili, specimens ranging 5 - 28 mm in umbrella diameter, had 80-560 tentacles and 60 - 360 statocysts (yielding biometric ratios of 0.50 - 0,85 and 0.64 - 0.70 for manubrium/umbrella diameter and number of statocysts/number of tentacles, respectively). These parameters are within the range reported from many different African localities by Goy (1977). Number of tentacles ranged 48 to 564 in specimens recovered from different places. Bouillon (1957) reported 800 tentacles for *L. congoensis*. Number of statocysts ranged between 32 - 384 whereas umbrella diameter has been recorded to be 0.5 - 11 mm (Goy 1977) to 30 mm (Pitman 1965). Biometrically, this variability is reflected by manubrium/umbrella and statocyst/tentacles ratios extending to 0.33 - 0.75 and 0.3 - 0.75, respectively (Goy 1977).

In view of this apparent infraspecific variability of some dominant morphological characteristics (Kramp 1954) the possibility of witnessing a process of speciation in *L. tanganjicae* merits some discussion. In this regard, the isolation of restricted populations in rock pools, small lakes, dams and other small water bodies (Table 1), seems a major factor contributing to the possible creation of races and subspecies of *L. tanganjicae*. Medusa populations inhabiting these big lakes (Table 1) are less likely to differentiate into races and subspecies in one and the same lake (Kramp 1954). Although they were found in restricted parts of some big lakes (Table 1) wind action can move them about over large distances as was the case in Lake Kariba during the 1972 bloom (Mills 1973) which is opposite to what was found during the present study. Accordingly, no infraspecific differences among *Limnocnida* populations sampled in any one of the big African lakes have been noted. The only report of *Limnocnida* from the Zambezi River in this area dates back to the late fifties and early sixties, where vast numbers were seen at Katima Mulilo (a few kilometres away from Lake Lisikili) (Pitman 1965). Since then the river has subsided to its current low level of late 1985, isolating in the process a few water bodies in the region, Lisikili among them. Similar isolation occurred in the Sokoto River (Niger basin) where specimens were abundant in a pool off the main stream following a marked drop in the level of the river (Pitman 1965).

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