Western Indian Ocean J. Mar. Sci. Vol. 3, No. 2, pp. 189–197, 2004

Distribution and Abundance of *Candacia* Dana, 1846 and *Paracandacia* Grice, 1963 (Copepoda, Calanoida, Candaciidae) off the Kenya Coast

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Key words: *Candacia, Paracandacia*, systematics, distribution and abundance, monsoon, Kenya

Abstract—The distribution and abundance of copepods belonging to the genera *Candacia* and *Paracandacia* (family Candaciidae) within the inshore, shelf and offshore waters of the Kenya coast are presented. The copepod species are widely distributed, at low abundances (9 to 240 ind.100/m^3) within the inshore waters, which increases to a maximum (40 to 360 ind.100/m^3) within the shelf waters and decreases again to minimum (10 to 40 ind.100/m^3) in the open ocean. They are more abundant during the southeast monsoon period and less so during the northeast monsoon. Abundance decreases with increasing depth, from a maximum of 880 ind.100/m^3 at the surface to a minimum of 10 ind.100/m^3 in the deep layers. The Candaciidae are least abundant at the depths ranging of 400 to 800 m, where oxygen concentration is minimum.

In this study, *Candacia bradyi* A. Scott, 1902; *C. bipinnata* Giesbrecht, 1889; *C. curta* (Dana, 1849); *C. tuberculata* Wolfenden, 1905 and *C. ethiopica* (Dana, 1849) are reported as new records for the Kenyan coast.

INTRODUCTION

The copepod family Candaciidae Giesbrecht, 1892 is one of the most widely distributed in the Indian Ocean (Grice & Hulsemann, 1967; Lawson, 1977; Rao, 1979). It comprises two genera of carnivorous copepods, *Candacia* Dana, 1846 and *Paracandacia* Grice, 1963.

The current systematics of Candaciidae has remained stable since the revision by Grice (1963) and was recently further reinforced by a study of character phylogenies in this group (von Vaupel Klein & Gassmann 1998). There are currently 31 species ascribed to genus *Candacia* and four to *Paracandacia* (Mauchline, 1998). However, the literature, including unpublished reports, indicates that there may be about 80 species and subspecies of these genera worldwide. Apart from the Indian Ocean, where they are most common, the Candaciidae are also found in the Atlantic and Pacific Oceans. They are also represented in restricted localities such as the Mediterranean Sea, Red Sea, Antarctic, etc., where some of the species are considered endemic.

Grice & Hulsemann (1967), Lawson (1977) and Rao (1973, 1979) compiled much of the information on the family Candaciidae and its zoogeography in the Indian Ocean. The information was primarily based on the samples collected during the International Indian Ocean Expedition (IIOE 1960–1965) and the various atlases, handbooks and other publications compiled thereafter (IOBC, 1968; Stephen *et al.*, 1992; Desai, 1992). Since IIOE, there have also been a

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number of other expeditions in the western Indian Ocean organized by the former Soviet Union (with documentation mainly in Russian and therefore previously inaccessible) whose results, obtained between 1973 and 1990, are just emerging (Mishonov & Williams, 1998). During the past decade, there has been concerted effort in oceanographic research in the Indian Ocean by the regional leaders in oceanography i.e. India, Pakistan, South Africa and Australia mainly in collaboration with counterparts in France, Germany, Japan, the Netherlands, United Kingdom and the USA notably within the framework of the World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Study (JGOFS). Unfortunately, most of these initiatives and sampling cruises did not extend their sampling transects further inshore to sample coastal waters along the East African shoreline. This was only achieved during the Netherlands Indian Ocean Programme (NIOP) conducted during the 1992–1995 TYRO Expedition to the western Indian Ocean, when both the inshore and offshore waters of Kenya, including the exclusive economic zone (EEZ), were sampled.

Earlier, Kenya participated in long-term bilateral initiatives on zooplankton studies in the creeks and bays along the coast. Two important initiatives during that period were the Kenya–Belgium Project in Marine Sciences (KBP) from 1985 to 1995 and the Kenya–Netherlands Wetland Project for Conservation of Biodiversity (KNWP) from 1996 to 1997.

The study by Lawson (1977) is widely believed to be the most thorough IIOE-based species-level work on *Candacia* and *Paracandacia*, which were collected within the upper 200 m of mainly the oceanic provinces of the Indian Ocean. The study described and distinguished the niches of these copepods and proposed possible evolutionary explanations. Because the two genera are morphologically similar and of about the same size, they are potentially strong competitors, so they occupy different niches.

The objective of the study reported in this article was to identify the common Candaciidae of the inshore, neritic and oceanic waters of Kenya and describe their distribution.

MATERIALS AND METHODS

Study area

Specimens of Candaciidae were sorted from zooplankton sampled during the two NIOP cruises off the Kenya coast, as well as samples collected in the framework of the KBP and the KNWP. Sampling locations along the Kenya coast from where specimens were obtained during the KBP and KNWP projects are indicated in Fig. 1. The specific locations sampled were Gazi Bay (GB), Diani Lagoon (DL), Makupa Creek (MkC), Tudor Creek (TC), Mombasa Marine Park & Reserve Lagoon (MML), Mtwapa Creek (MtC), Kilifi Creek (KlC) and Mida Creek (MdC). The location of transects and the sampling stations from where the specimens were obtained during the TYRO expedition (NIOP 1992–1995) are also shown in Fig. 1. The sampling transects were Gazi (off Gazi Bay), Sabaki (off Malindi) and Kiwayu (northeast of Lamu).

Field sampling and laboratory analyses

Standard methods for zooplankton sampling (Omori & Ikeda, 1984; Greene, 1990), fixation and preservation (Steedman, 1976) were employed. Inshore and near-shore waters in bays, creeks and lagoons were sampled for zooplankton using a 1.5-m-long Bongo net with mouth radius of 45 cm and a mesh size of 335 μm.

Offshore sampling was conducted on board the R/V Tyro using a HydroBios Multinet zooplankton sampler with 200 μm mesh size plankton nets. Depth stratified sampling was done by horizontally towing the sampler at various depths. For shallow stations (0–50 m) only one shallow cast was made. For deeper stations (500–2000 m) three to four deep casts were made at various depth strata. A deck pump was used to collect surface (0–3 m) zooplankton at each station. Mwaluma (2000) provides further information regarding exact sampling dates, specific depths and the time and duration of each haul.

Some 400 zooplankton samples were analysed. All individuals of *Candacia* and *Paracandacia* were identified and quantitatively isolated from the

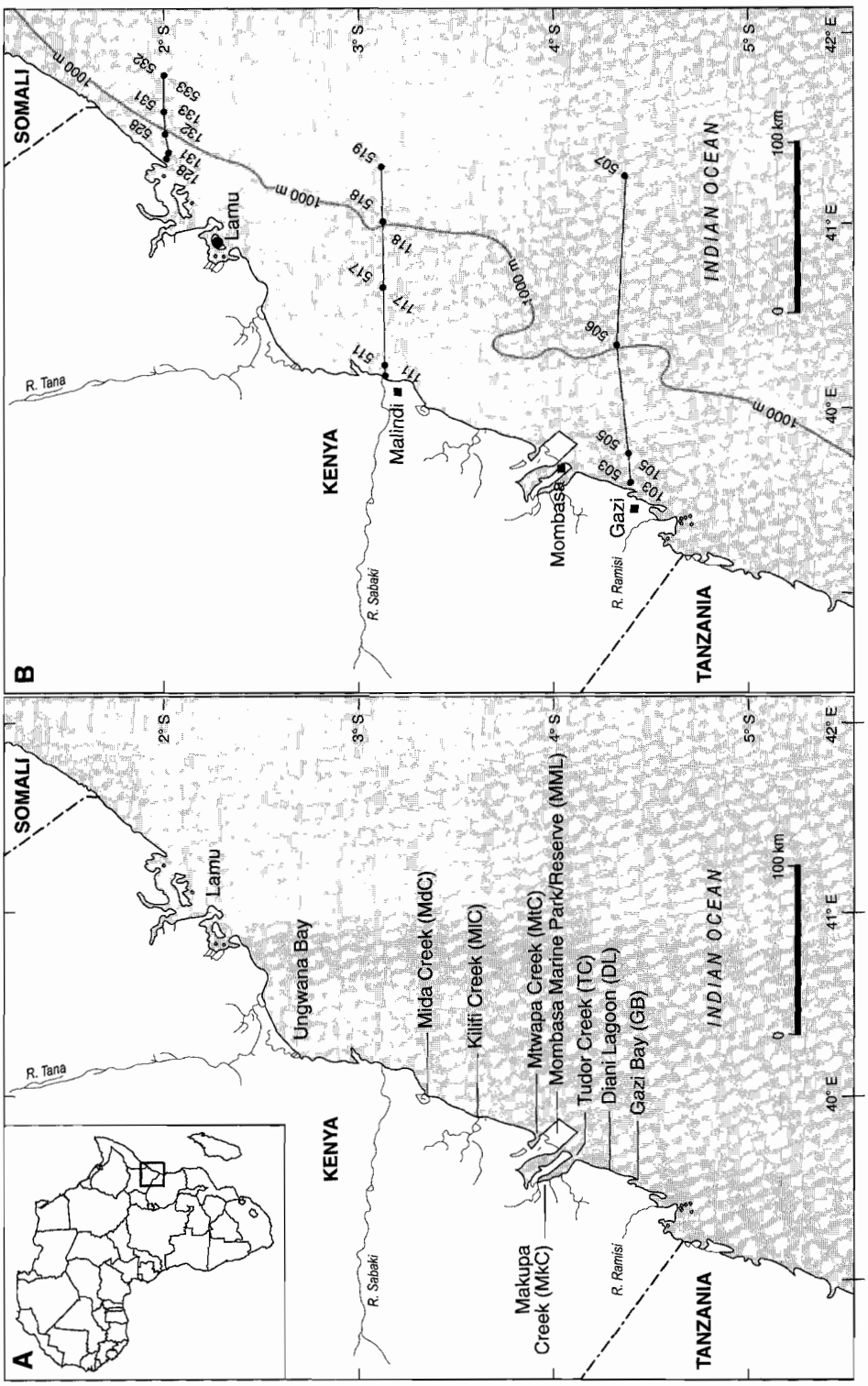

Fig. 1, The coastline of Kenya showing (a) the sampling sites during KBP & KNWP; and (b) transects and sampling stations during the TYRO expedition (NIOP 1992/1995)

samples. The identification keys used were obtained from Farran (1948), Fleminger & Bowman (1956), Grice (1961, 1962, 1963, 1981), Grice & Jones (1960), Pillai (1967), Tseng (1970), Lawson (1973), Grice & Lawson (1978) and Das et al. (1982). Individuals were counted and densities determined as numbers per cubic metre of water filtering through the sampling net.

From the 400 zooplankton samples, we studied in detail a total of 219 Candaciidae specimens from localities along the coast of Kenya as well as from collections down to 1000 m deep and as far as 200 km off the Kenya coast (Figs. 1).

RESULTS

Table 1 gives some indication of frequency of citation for species of Candaciidae, excluding copepodites, in the literature. Based on taxonomic literature search, the most frequently cited species of the Candaciidae were *C. pachydactyla*, *C. bipinnata*, *C. bradyi*, *C. curta* and *C. longimana* in that order. The results obtained from identifying and counting Candaciidae in our samples indicated that these species are also commonly encountered off the Kenya coast and, according to Lawson (1977), they are also common in the rest of the western Indian Ocean.

Inshore and nearshore distribution

Table 2 shows the densities of Candaciidae that were recorded at the various inshore sampling locations during the different months, including creeks, bays and lagoons. Where Candaciidae were present, their monthly abundance ranged from 0.09 to 2.40 ind./m^3 (i.e. 9 to 240 ind.100/m^3). Inshore water in sheltered systems such as creeks and bays recorded a somewhat lower abundance range (0.09–2.40 ind./m^3) than the lagoon systems adjacent to the open ocean (0.20–2.11 ind./m^3).

There was no apparent seasonality of abundance detected for Candaciidae in the creeks, bays and lagoons sampled. The common species encountered in the creeks and bays were *C. catula*, *C. magna* and *C. tuberculata*. However, a few individuals of other species such as *C. bipinnata*, *C. bradyi*, *C. discaudata*, *C. tenuimana* and *C. varicans* were found in Mombasa Marine Park lagoon (MML) and Diani lagoon (DL). Occasionally, *P. truncata* was also observed in samples obtained from these lagoons.

Table 1: The most commonly cited species of *Candacia* and *Paracandacia* in the literature (Fleminger & Bowman, 1956; Brodsky, 1962; Grice, 1962, 1963; Mori, 1964; Vervoort, 1965; Sazhina, 1982; Hure & Krsinic, 1998; Mauchline, 1998).

> 40 citations	31–40 citations	21–30 citations	11–20 citations
C. pachydactyla	*C. bradyi*	*C. catula*	*C. varicans*
C. bipinnata	*C. curta*	*C. armata*	*C. elongata*
	C. longimana		*C. norvegica*
			C. tenuimana
			C. ethiopica
			C. cheirura
			C. columbiae
			P. bispinosa
			P. simplex

Table 2: Maximum densities (ind./m^3) of Candaciidae obtained in zooplankton samples collected monthly from various localities (creeks, bays, lagoons) comprising the inshore waters of the Kenya coast.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GB	0	0	0.51	0	0.48	0.54	0	0	0	0	0	0
DL	0	0	0.24	0.8	0.2	0.4	0	0.8	0	0	0.92	0
MkC	0	0	0	0.63	0	0	0	0	0.52	0	0	0.67
TC	0.43	0	0.18	0	0	0	0	0.21	0	0	0	0
MML	1.9	0	nd	nd	3.0	0.5	0.5	0.43	0.32	0.90	0	2.11
MtC	0	0.22	0	0	0	0	0.21	0	0.19	0	0	0
KlC	0.11	.09	0	0	0	0	0	0	0	0.20	0.1	0
MdC	0.3	2.4	0	0.3	0	0	0.24	0.23	0	0	0	0

GB= Gazi Bay, DL= Diani Lagoon, MkC=Makupa Creek, TC=Tudor Creek, MML = Mombasa Marine Park Lagoon, MtC=Mtwapa Creek, KlC=Kilifi Creek, MdC= Mida Creek, 0 = no Candaciidae, nd = Not sampled.

Off shore distribution during the SE monsoon

The offshore distribution of the copepod species during SE monsoon period is presented in Table 3a. From the results, it appears that during the SE Monsoon period members of Candaciidae were less abundant in the upper layers of the near shore waters compared to similar layers offshore. At each station, abundance reduced as the sampling depth increased, until a certain minimum depth stratum and thereafter increased again. This depth stratum (about 200–600 m) of minimum abundance of Candaciidae coincided with the layer of minimum oxygen concentration recorded by Heip et al. (1995) at the time of sampling.

Table 3 (a). Abundance of Candaciidae in the various depth strata along the Kenya coast during the SE monsoon June/July 1992

Transect/ Stn	Depth (m)	Depth interval	Ind./100m^3
GAZI			
Gazi (103)	50	0–45	40
Gazi (105)	500	0–50	360
		50–150	120
		150–250	40
		250–450	560
SABAKI			
Sabaki (111)	50	0–40	58
Sabaki (117)	500	0–100	208
		100–200	32
		200–300	0
		300–450	26
Sabaki (118)	1000	0–200	31
		200–400	0
		400–600	66
		600–800	7
KIWAYU			
Kiwayu (128)	50	0–45	60
Kiwayu (131)	500	0–100	880
		100–200	80
		200–300	20
		300–425	20
Kiwayu (132)	1000	0–200	200
		200–400	5
		400–600	0
		600–800	3
Kiwayu (133)	2000	0–200	40
		200–400	0
		400–600	4
		600–800	4

Table 3 (b) Abundance of Candaciidae in the various depth strata along the Kenya coast during the NE monsoon November/December 1992

Transect/ Stn	Depth (m)	Depth interval	Ind./100m^3
GAZI			
Gazi (503)	50	0–40	130
Gazi (505)	500	0–136	80
		136–300	40
		300–450	0
Gazi (506)	1000	0–200	40
		200–400	30
		400–600	10
Gazi (507)	2000	0–400	10
		400–800	0
		800–1000	20
SABAKI			
Sabaki (511)	50	0–45	260
Sabaki (517)	500	0–200	50
		200–300	0
		300–450	14
Sabaki (518)	1000	0–200	20
		200–400	40
		400–800	22
Sabaki (519)	2000	0–400	40
		400–800	13
		800–1000	0
KIWAYU			
Kiwayu (528)	50	0–45	100
Kiwayu (531)	500	0–200	0
		200–300	0
		300–450	3
Kiwayu (532)	1000	0–200	25
		200–400	10
		400–800	0
Kiwayu (533)	2000	0–200	30
		200–400	13
		400–800	11

Table 3 (c) *t*-Test results for abundance of Candaciidae during southeast Monsoon (SE M) & northeast Monsoon (NE M) seasons

Transect Depth Strata	Abundance SE M	NE M
GAZI (50m)		
0-45m	40	130
GAZI (500m)		
0-50m	360	80
50-150m SE &136-300m NE	120	40
150-250m SE & 300-450 m NE	40	0
250-450 m SE	560	0
SABAKI (50m)		
0-40m	58	260
SABAKI (500m)		
0-200m	208	50
300-450 m	26	14
SABAKI (1000m)		
0-200m	31	20
200-400m	0	40
KIWAYU (50m)		
0-45	60	100
KIWAYU (500m)		
0-200m	880	0
300-450m	20	3
KIWAYU (1000m)		
0-200m	200	25
200-400m	5	10
KIWAYU (2000m)		
0-200m	40	30
200-400m	0	13

Summary Data

	SEM	NEM	Total
n	17	17	34
$-\sum X$	2648	815	3463
$-X^2$	1329090	108999	1438089
SS	916625.06	69926.94	1085372.26
mean	155.76	47.94	101.85

$Mean_{SEM} - Mean_{NEM}$	t	df	P
107.8235	1.71	16	0.053292

Offshore distribution during the NE monsoon

The offshore distribution of the copepod species during NE monsoon period is presented in Table 3b. Unlike during the SE monsoon, the upper layers (0–45 m) in the nearshore stations recorded a substantially higher abundance of Candaciidae than the offshore stations of similar depth strata during the NE Monsoon. Similar to the SE Monsoon period, abundance decreased with increasing depth except at Stn Kiwayu 531, which did not record any Candaciidae in the upper 0–300 m. Also, at Stn Sabaki 518 more Candaciidae were recorded in the deeper strata compared to the shallower layers. The stratum of minimum abundance observed during SE Monsoon was still present during the NE Monsoon period but had shifted deeper (to layers of about 200–800 m).

To compare the two monsoon periods, abundance of Candaciidae for similar depth strata (Tables 3a and b) during both the SE and NE Monsoon periods were considered. Results in Table 3c shows that from the statistical analysis, abundance of Candaciidae was significantly higher ($t = 1.71$, $df = 16$, $p = 0.05$) during the SE monsoon period.

Species composition of Candaciidae in the inshore and offshore waters of Kenya

During previous taxonomic studies of copepods and zooplankton in the creeks and bays off the Kenya coast (Okemwa, 1990; Osore, 1994), the eight commonly observed species of Candaciidae were *C. catula*, *C. longimana*, *C. magna*, *C. pachydactyla*, *C. tenuimana*, *P. bispinosa*, *P. simplex* and *P. truncata*. Following analysis of copepods from zooplankton samples collected in the shelf and deep waters of Kenya during NIOP 1992/93 TYRO expedition (Mwaluma, 2000; Osore et al., 1995), all the species mentioned above were also commonly encountered. However, *C. bradyi* is a new record for Kenya.

In the present study, *C. bipinnata*, *C. curta*, *C. tuberculata* and *C. ethiopica* were also identified as new records for Kenya. These species were previously unknown to occur in the inshore and

Table 4. List of Candaciidae sampled from the Kenya coast and their approximate range of distribution and abundance. Data were obtained from the present study and others

Species	Distribution	Abundance (ind.100/m^3)	Ref[+]
Candacia bipinnata	near shore (0–100 m)	50–800	1,5
C. bradyi	near shore	100–500	1,3,4
C. catula	lagoon, near shore	200–900	1,2,5
C. curta	off shore (deep 200–400 m)	50–800	1,3,4,5
C. discaudata	near shore	76–225	1,5
C. ethiopica	off shore, rare	1–15	1
C. guggenheimi	off shore (0–200 m)	26–75	1,5
C. longimana	off shore (deep 500 m)	1–75	1,2,3,4,5
C. magna	mouth of creek, lagoon	40–300	1,2,6
C. pachydactyla	off shore (surface 0–50 m)	70–2,000	1,2,3,4,5
C. tenuimana	near shore (deep 0–100 m)	10–100	1,2,5
C. tuberculata	mouths of creek, bay	10–40	1
C. varicans	near shore surface (0–50 m)	10–75	1,5
Paracandacia bispinosa	off shore (deep 400–800 m)	20–60	1,2,5
P. simplex	offshore (surface 0–200 m)	76–225	1,2,5,
P. truncata	near shore, off shore	200–2,000	1,2,3,5

[+]1, Present study; 2, Okemwa (1990); 3, Osore (1994); 4, Mwaluma (2000); 5, Lawson (1977); 6, Sewell (1932)

nearshore waters of Kenya. Lawson (1977) found them in offshore samples (working on IIOE 1960–1965) within the 0–200 m depth. Table 4 shows the updated list of all the Candaciidae identified in the Kenya coast and their horizontal and vertical distribution.

DISCUSSION AND CONCLUSION

This study has established that 16 species of the family Candaciidae occur along the coast of Kenya. Thirteen species of *Candacia* and three of *Paracandacia* appear to be characteristic of the shelf waters of the Kenya coast and were commonly found in the epipelagic zone and, to a lesser extent, at depths of down to 1,000 m. Close to the shores and in the inshore waters the abundance was low (9– 240 ind.100/m^3) whereas in the shelf waters it was high (40–360 ind.100/m^3). Offshore, abundance was quite low (10–40 ind.100/m^3) both in the surface layers and in the deep bottom layers. Quite often, the abundance in the mesopelagic zone (400–800 m) reduced substantially; this was most probably in response to the minimum oxygen concentration at these depths. Most copepod species are known to avoid water with oxygen content below 0.1–0.2 ml/l (Longhurst, 1967; Judkins, 1980; Sameoto, 1986; Sameoto et al. 1987). At the time of sampling offshore Kenya, low oxygen levels (0.1–1.5 ml/l) were recorded, especially at depths of 400–800 m (Heip et al., 1995). It has also been shown by Vinogradov & Voronina (1962) that the Arabian Sea in the neighbouring northern Indian Ocean region similarly experiences zones of low oxygen concentration at depths of 150 to 1,500 m, which influences zooplankton biomass distribution and informs species composition in the area.

The monsoonal currents in the Kenya coast created by the yearly reversing SE and NE monsoons affected abundance and distribution of Candaciidae in the offshore zone and deep waters. Abundance was higher during the SE monsoon and the Candaciidae were more concentrated in the offshore areas. During the NE monsoon, more Candaciidae occurred towards the shore. The minimum oxygen layer also had shifted deeper. Therefore, the reverse in the flow of the monsoon winds seems to have also influenced the abundance and distribution of Candaciidae.

The wet and dry seasonal regime at the coastal strip is responsible for the distribution of Candaciidae and other copepods within the creeks, bays and nearshore waters. Climatic changes and other environmental variables play a key role in the abundance, diversity and distribution of

zooplankton (of which Candaciidae are a part) of the inshore waters of Kenya (Okemwa, 1990; Osore, 1994; Mwaluma, 2000). During the wet season, Kenya's two main rivers, R. Tana and R. Galana/Sabaki, discharge over 5,000 m^3/s to the near shore and this causes pronounced changes in salinity, nutrient type and concentration, primary productivity and the general hydrography of the nearshore waters.

From this study, the Candaciidae may be geographically distributed off the Kenya coast in the following pattern: *C. catula*, *C. magna* and *C. tuberculata* in creeks, bays, lagoons and inshore waters, and *C. bipinnata*, *C. bradyi*, *C. discaudata*, *C. tenuimana*, *C. varicans* and *P. truncata* in nearshore waters above the continental shelf. The remaining ones, including *C. curta*, *C. ethiopica*, *C. guggenheimi*, *C. longimana*, *C. pachydactyla*, *P. bispinosa* and *P. simplex*, inhabit the offshore zone or even deep-water layers. However, these are not strict boundaries, and Candaciidae are known to occupy wide geographical regions in the Indian Ocean.

This study represents the first attempt to describe the distribution of family Candaciidae from the shelf waters of Kenya and deep offshore localities.

Acknowledgements—We are grateful to the KBP, KNWP and NIOP Research Projects, the Government of Belgium and the Free University of Brussels Advice Council for Development Cooperation (VUBAROS) for funding this research. We thank KMFRI, Mombasa and the RBIN in Brussels for kindly providing laboratory space and field equipment. We appreciate the reviewers' comments, which improved the quality of the manuscript.

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