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HISTORICAL DECLINE OF THE MANGROVE GASTROPODS, *TELESCOPIUM* AND *TEREBRALIA* IN THE RYUKYU ISLANDS AND TAIWAN: EVIDENCE FROM SHELL MIDDENS

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Abstract

Present and past distributions of the mangrove gastropods, *Telescopium telescopium*, *Terebralia palustris* and *Terebralia sulcata* in the Ryukyu Islands and Taiwan were investigated by field surveys and analysis of excavation records of shell middens. Present populations of the three species are distributed in the Philippines and the south (<20°N), but not in Amami Island and the north (>28°N). Between these areas, empty shells of *T. sulcata* are found only where the living animals are distributed. *T. telescopium* and *T. palustris* are often seen in areas lacking conspecific living individuals, which indicates localized extinction of these species. Information from 157 shell middens formed after 6500 yBP suggests the following patterns: (1), The ranges of *T. telescopium*, *T. palustris* and *T. sulcata* have never extended north of Okinawa since 6000 yBP. (2), *T. telescopium* declined and disappeared after the 12th century AD in Okinawa and after the 17th century in Yaeyama and Taiwan. (3), *T. palustris* disappeared after the 17th century in Okinawa and Taiwan. (4), The historical distribution pattern of *T. sulcata* have been more constant than the other two species. Increasing human activity since the 17th century is one of the possible factors in the decline of *T. telescopium* and *T. palustris* in the Ryukyu Islands and Taiwan, in addition to natural factors such as topographic changes and climatic impacts proposed in previous studies.

Key words: *Telescopium*, *Terebralia*, Ryukyu Islands, Taiwan, shell middens, excavation records, localized extinction, human activity.

Introduction

Telescopium and *Terebralia* belong to the Potamididae and are distributed in mangals in tropical and subtropical regions of the Indian and western Pacific Oceans, and include four species, one in *Telescopium* and three in *Terebralia*. The Ryukyu Islands (24–27°N) and Taiwan (22–25°N) are near the northeastern limits of the geographical ranges of these genera, and either living animals or empty shells of the three species, i.e., *Telescopium telescopium* (Linnaeus), *Terebralia palustris* (Linnaeus) and *Terebralia sulcata* (Born) have been recorded from these areas (Houbrick 1991). Among the three species, living individuals of *T. telescopium* have never been found in the Ryukyu Islands and Taiwan despite the sporadic occurrence of empty shells. This implies the extinction of *T. telescopium* in these areas. The phenomenon has attracted attention by biologists, and hypotheses have been proposed for the causes of the disappearance of *T. telescopium* from these areas (Kuroda 1940; Ozawa *et al.* 1995).

On the other hand, empty shells of *Telescopium* and *Terebralia* in the mangals seem to be derived, at least partly, from shell middens, because in the Ryukyu Islands and Taiwan, they often contain abundant shells of these species (Nishimura *et al.* 1960; Kaneko 1978; Kaneko 1992). The Ryukyu Islands is an area where

archaeological sites have been investigated most intensively amongst the Pacific islands (Takamiya 1996), and the chronology of this region since ~6000 yBP has been examined in detail. This may enable us to trace historical changes in the distribution of *Telescopium* and *Terebralia* around the Ryukyu Islands, based on shell midden data.

Near the northwestern limits of the geographical ranges of *Telescopium* and *Terebralia*, i.e., the Arabian Gulf and the Red Sea, the range of *Terebralia palustris* is known to have contracted southwards within the past several millennia (Plaziat 1995; Glover 1998). In this report, we examine the records of shells of *Telescopium* and *Terebralia* from shell middens in the Ryukyu Islands and Taiwan, in order to reconstruct the historical distribution patterns of these genera. The results are compared with those obtained from other regions, and the causes of changes in these species are explored with reference to archaeological, geological and ecological information.

Study area and methods

Four areas, i.e., Amami Island, Okinawa Island, and the Yaeyama Islands in the Ryukyu Islands, and Taiwan were investigated (Fig. 1). These islands range from 22°N to 28°N to the east of the Asian Continent, and their flora is subtropical (Yasugi *et al.* 1996). Mangals develop in the river mouths and estuaries of these areas. The scale of the mangals decreases to the north, there being only one of >10 ha in Okinawa and another in Amami. The dominant mangrove species is *Kandelia candel* (Rhizophoraceae) in Amami, Okinawa and Taiwan, and *Rhizophora stylosa* (Rhizophoraceae) in Yaeyama.

We visited Amami eight times, Okinawa 23 times and Yaeyama 16 times, and searched for living animals and empty shells of *Telescopium* and *Terebralia* in the mangals of these areas over a period of 23 years from 1975 to 1998. Either of us resided in Okinawa from 1977 to 1983 and in Yaeyama from 1987 to 1990 and made occasional field observations also during these periods. The information on Taiwan was obtained from the literature.

We examined the records of the shells of *Telescopium* and *Terebralia* from 147 shell middens in Amami, Okinawa, Yaeyama and Taiwan. These data are presented in 102 reports of excavations executed by individual archaeologists, universities, and municipality or prefectural governments, which were published between 1960 to 1999. An additional four sites were examined for Miyako Island between Okinawa and Yaeyama (Fig. 1). Data on six sites in Yaeyama were added to by our observations. Research on Taiwan was limited to the southwest because shells of *Telescopium* and *Terebralia* have been excavated almost exclusively from this part of the island (Kaneko 1978). The ages of a total of 157 sites were determined from the reports of excavation and monographs on the general archaeology of each area. The prehistoric chronology of the Ryukyu Islands and Taiwan is sometimes controversial, especially for the early periods, and future modifications are likely. When there are discrepancies in chronology among the references, the data in the most recent paper was adopted. In the analysis of excavated shells, we used the maximum number of shells / site as an index, because it is more sensitive than the mean or minimum in detecting the presence of the species in a particular area and a period.

Results

Distribution of living animals and empty shells

Table 1 shows the presence or absence of living animals and empty shells of *Telescopium telescopium*, *Terebralia palustris* and *T. sulcata* in the present mangals of the five areas from the Philippines to Amami. Living animals of each of the three species occur in the Philippines, but not in Amami, where even dead shells are absent. Between these areas, the patterns are different among different species. Living individuals of *T. telescopium* are absent in Taiwan, Yaeyama and Okinawa, although empty shells are found in all these areas. Living populations of *T. palustris* occur only in Yaeyama, while empty shells are known from Taiwan and Okinawa. In Yaeyama, empty shells of *T. telescopium* and *T. palustris* are often found on sand or mud flats in the mangals

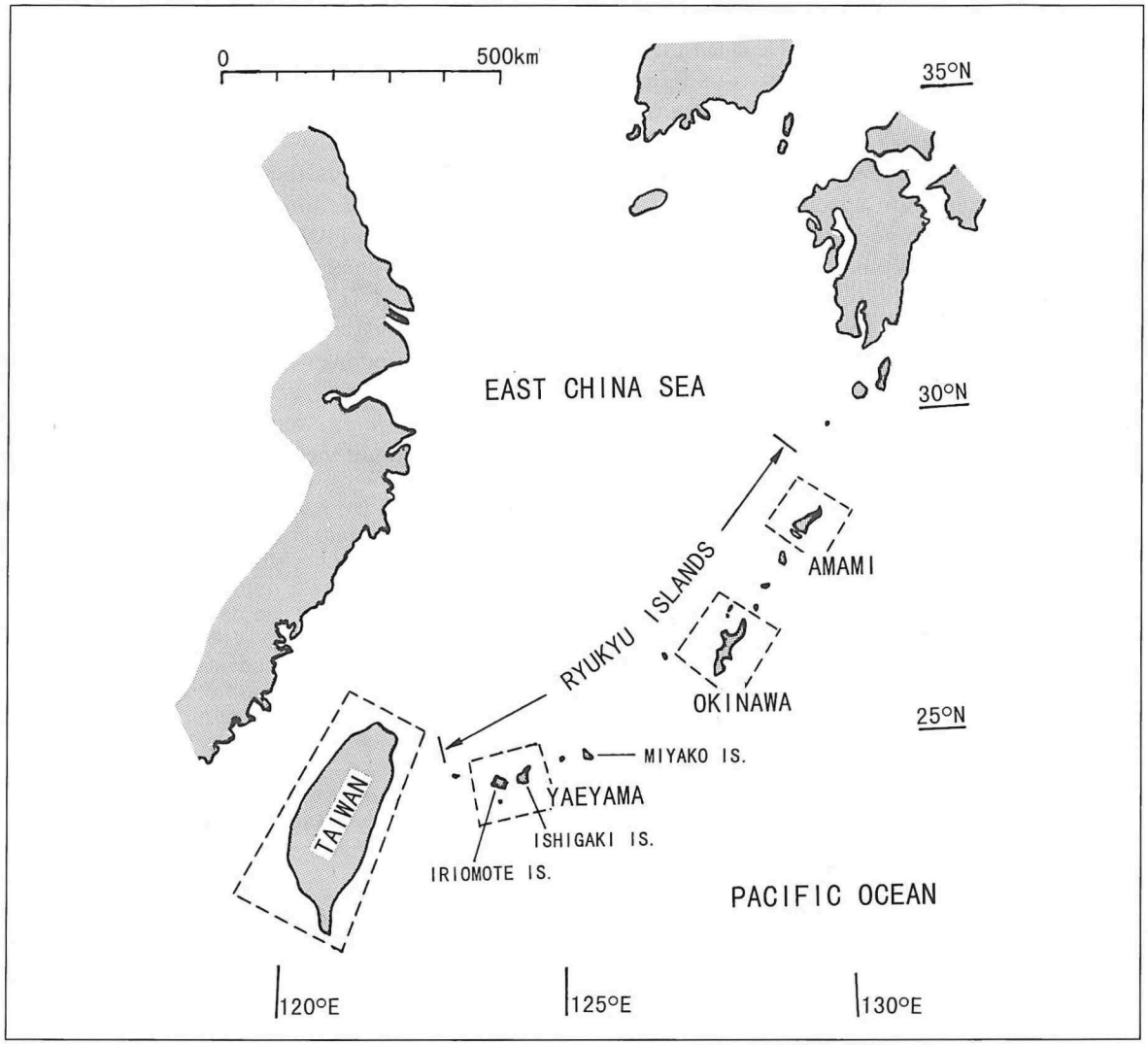

Fig. 1. Map of the Ryukyu Islands and Taiwan. The four study areas are surrounded by broken lines.

Table 1. Occurrences of living animals and empty shells of *Telescopium and Terebralia* in the present mangals among five areas from the Philippines to Amami. Information from shell middens is not included. +, existence of living animals; –, absence of living animals; (+), existence of dead shells; (–), absence of dead shells. Sources: the Philippines, Springsteen and Leobrera (1986); Taiwan, Kuroda (1941), Kaneko (1978) and Lai (1997); other areas, the present study.

	Philippines 6–19°N	**Taiwan 22–25°N**	**Yaeyama 24°N**	**Okinawa 26–27°N**	**Amami 28°N**
Telescopium telescopium	+ (+)	– (+)	– (+)	– (+)	– (–)
Terebralia palustris	+ (+)	– (+)	+ (+)	– (+)	– (–)
Terebralia sulcata	+ (+)	+ (+)	– (–)	+ (+)	– (–)

and, in most cases, are inhabited by hermit crabs such as *Clibanarius longitarsus* (De Haan). Living animals of *T. sulcata* are often found in the mangals of Okinawa, but never in Yaeyama where even empty shells are absent. Kuroda (1940) described *'Terebralia semistriata'* (= *Terebralia sulcata*) as a very rare species in Taiwan, and Kaneko (1978) found no living animals there but only empty shells. On the other hand, Lai (1997) included *T. sulcata* in a list of the modern Potamididae of Taiwan. These reports suggest that *T. sulcata* is rare in Taiwan, even if it is present. Thus in Okinawa, Yaeyama and Taiwan, empty shells of *T. telescopium* and *Terebralia palustris* are often found in areas where the living populations are absent, proving the disappearance of the two species from these areas in the past.

Analyses of excavation records

Table 2 summarizes the excavation records of *Telescopium* and *Terebralia* from archaeological sites dated after 4000–6500 yBP in Amami, Okinawa, Yaeyama, and Taiwan. The number of sites examined is comparatively few for the earliest and latest archaeological periods in each area. The total number of sites where each species occurred was 23 for *Terebralia palustris*, 36 for *Terebralia sulcata*, and 47 for *Telescopium telescopium* for all the areas and periods. None of

Table 2. Chronology of 153 archaeological sites in four study areas and the numbers of excavated shells of *Telescopium telescopium*, *Terebralia palustris*, and *Terebralia sulcata* in each area and period. yBP: years before present (=1950). Terminology for archaeological periods is shown in parentheses. 'No. sites' under the name of species is the number of sites where the shells of the species were found. 'Max. no.' is the maximum number of shells excavated at one site. ?: no data on the number of shells. SMP: Shell Midden Period of Okinawa. The period 3300–2500 yBP in Yaeyama is an 'archaeological blank', for which no archaeological sites have been discovered. References for chronology: Amami, Kawaguchi (1988); Okinawa, Okinawa Prefectural Board of Education (1982); Yaeyama, Kin (1994) and Ouhama (1996); Southwest Taiwan, Japan Society for Southeast Asian Archaeology (1994).

Years in yBP (Archaeological periods)		No. sites examined	*T. telescopium*		*T. palustris*		*T. sulcata*	
			No.sites	Max.no.	No.sites	Max.no.	No. sites	Max.no.
Amami								
6000–2200	(Jomon)	7	0	–	0	–	0	–
2200–1700	(Yayoi)	5	0	–	0	–	0	–
1700–1250	(Kofun)	3	0	–	0	–	0	–
1250–750	(Nara-Heian)	3	0	–	0	–	0	–
750–	(Recent)	0	0	–	0	–	0	–
Okinawa								
6500–3500	(Initial SMP)	4	2	28	2	72	0	–
3500–2500	(Early SMP)	16	5	4313	2	93000	4	10300
2500–2000	(Middle SMP)	11	3	?	3	217	3	5
2000–850	(Late SMP)	21	4	3	9	1118	7	112
850–350	(Gusuku)	25	0	–	3	47	3	3572
350–	(Recent)	7	1	3	0	–	2	608
Yaeyama								
4000–3300	(Shimotabaru)	3	0	–	0	–	0	–
2500–900	(Non-ceramic)	7	6	222	2	73	0	–
900–350	(Suku)	12	6	36	0	–	0	–
350–	(Recent)	4	4	7	0	–	0	–
SW Taiwan								
5000–3900	(Niu-chou)	3	0	–	0	–	1	?
3900–1900	(Ta-hu)	7	4	10	1	?	5	20
1900–350	(Niao-sung)	13	12	43	1	?	11	77
350–	(Recent)	2	0	–	0	–	0	–

the three species has been excavated from shell middens of any periods in Amami, those of 4000–3300 yBP in Yaeyama or the sites dated to after 350 yBP in Taiwan. However, sites lacking *Telescopium* and *Terebralia* often contain the shells of molluscs inhabiting mangals and estuaries, such as the potamidid snails *Batillaria zonalis* (Bruguière), *Cerithidea morchii* A.Adams and *Cerithideopsilla cingulata* (Gmelin) which are known from sites dated to 6000–2200 yBP and 2200–1700 yBP in Amami. A mangrove corbiculid, *Geloina coaxans* (Gmelin) has been recorded from the shell middens of all periods in the four areas except after 350 yBP in Amami and Taiwan. For Miyako Island (Fig. 1), excavation reports of four sites were examined, one dated to 2500–900 yBP and three to 900–350 yBP. The only record of *Telescopium* or *Terebralia* from this island is of 28 shells of *T. telescopium* from a site of 500–350 yBP. The patterns of occurrence of *Telescopium* and *Terebralia* in the shell middens in each study area except Amami are as follows.

Telescopium telescopium. In Okinawa, the maximum number of shells/site decreases markedly from the period before 2500 yBP to that after 2000 yBP. This species has been excavated from only one site dated to the period after 350 yBP (three shells) among the 32 sites dated to after 850 yBP. In Yaeyama, *Telescopium telescopium* has been recorded from the shell middens dated to after 2500 yBP, showing a decrease in the maximum number towards the later periods. In Taiwan, shells are known from 3900–350 yBP sites, but none from those formed either before or after this period.

Terebralia palustris. In Okinawa, shells have been excavated from sites dated to the period 6500–350 yBP but none from the seven sites dated to after 350 yBP. In Yaeyama, this species is known from two sites on Ishigaki Island (Fig. 1) and a nearby islet both dated to 2500–900 yBP, but it has never been recorded from the ten sites on Iriomote Island where living populations are common. In Taiwan, *Terebralia palustris* has been recorded from only two sites of 25. The numbers of shells from these sites are unknown but were estimated to be 'rare', whereas both *T. telescopium* and *Terebralia sulcata* were described as 'common' at the same sites (Kaneko 1978).

Terebralia sulcata. In Okinawa, the maximum number of shells/site is >100 for each archaeological period after 3500 yBP except 2500–2000 yBP. No shells have been excavated from Yaeyama. In Taiwan, *Terebralia sulcata* is known from all archaeological sites between 5000 to 350 yBP, but not from a few sites dated to after 350y BP.

Table 3 exhibits the frequency distributions of the number of excavated shells/site of the three species. The mean and variance of the numbers of shells are largest in *Terebralia palustris* and smallest in *Telescopium telescopium.* The mean number of shells of the former was 22 times larger than that of the latter (t-test after transformation to natural logarithms, $t = 1.94$, $P = 0.058$), and a significant difference was detected for the variance ($F = 501$, $P < 0.001$) between the two species. We selected the sites where both of these species occurred (n= 5, all in Okinawa) in order to exclude the supposed effect of differences in excavation efforts from site to site, and carried out a paired analysis. *Terebralia palustris* was always more abundant than *Telescopium telescopium* and the difference was significant (Sign-test using binomial distribution, $P = 0.031$).

Table 3. Numbers of sites with different numbers of excavated shells of *Telescopium* and *Terebralia* for all the areas and periods in Table 2, based on reports containing precise numbers.

No. shells/site	1	2–9	10–99	100–	1000–	10000–	Mean±SD (n)
Telescopium telescopium	9	12	6	1	1	0	164±785 (29)
Terebralia palustris	4	7	10	4	1	1	3554±17543 (27)
Terebralia sulcata	5	12	6	2	1	1	550±2028 (27)

Figure 2 shows the distribution of shells of *Telescopium* and *Terebralia* in the sites of two historical phases selected and of their living populations at present. In the sites dated between 2500–2000 yBP, *Telescopium telescopium* is known from Okinawa, Yaeyama and Taiwan, but limited to the areas southwest of Okinawa among the sites dated between 850–350 yBP. Living *T. telescopium* is absent in all the areas from Amami to Taiwan. *Terebralia palustris* also occurs widely from Okinawa to Taiwan in sites dated between 2500–2000 yBP, but are limited to Okinawa and Taiwan in those dated between 850–350 yBP. At present, *T. palustris* inhabits only Yaeyama where its shells are unknown from sites of between 850–350 yBP. The distribution patterns of *T. sulcata* are constant. It is known from Okinawa and Taiwan but not from Yaeyama through the two historical phases (2500–2000 yBP and 850–350 yBP) and the present.

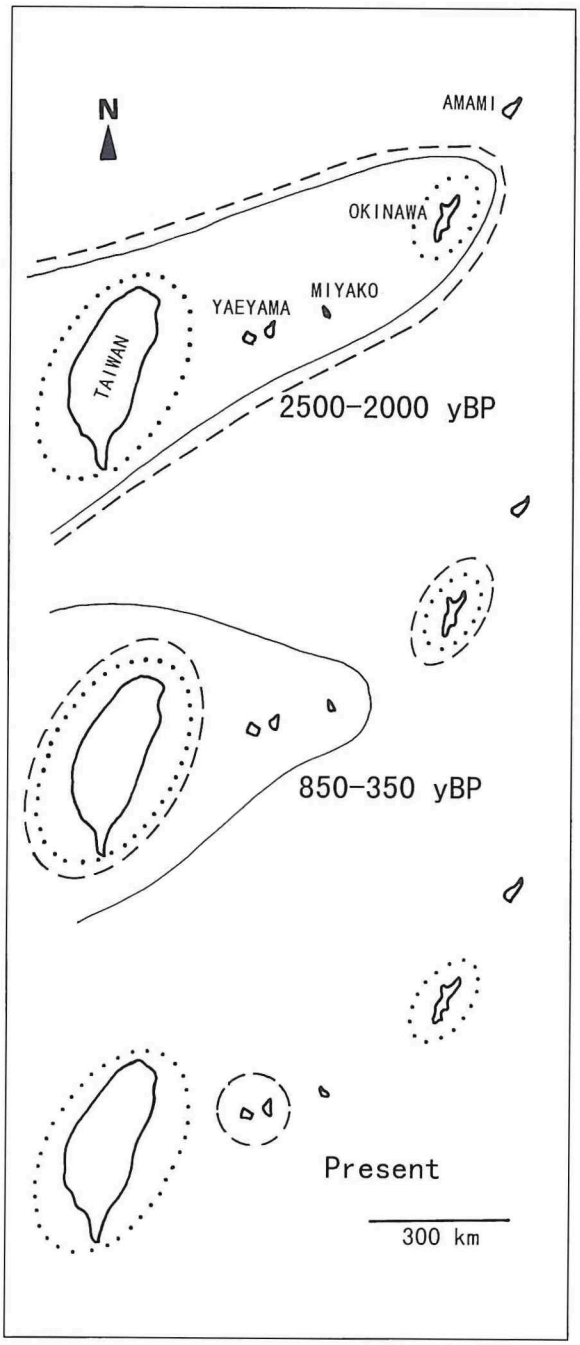

Fig. 2. Distribution patterns of the shells of *Telescopium* and *Terebralia* in shell middens dated to two historical periods (upper two figures) and of their living populations at present (bottom), based on Tables 1 and 2. Solid line, *Telescopium telescopium*; broken, *Terebralia palustris*; dotted, *Terebralia sulcata*.

Discussion

Interpretation of excavation records

There are several problems involved in the analysis of excavation records. Utilization of *Telescopium* and *Terebralia* as food by prehistoric people is obvious: their shells are often abundant in shell middens and most of the shells have a trace of artificial breakage at their apertures as shown in many photographs in excavation reports. Therefore, determination of shells of *Telescopium* or *Terebralia* shells from a shell midden basically means that there were living animals of the species near the site when it was formed. The possible exception to this is that of empty shells brought into the shell midden from mangals or nearby shell middens through transportation by prehistoric people, hermit crabs or other physical means, i.e., 'secondary deposition'. We often observed the shells of *Telescopium telescopium* and *Terebralia palustris* being carried by hermit crabs in the mangals. Such a problem of secondary deposition is critical especially when there are few excavated shells. On the other hand, if the shells occur at considerable numbers of sites dated to one historical period, sometimes abundantly, and yet

living animals of the species are absent at present, it can be concluded that the species has died out in the area between that particular period and the present.

Alternatively, the lack of a record of either *Telescopium* or *Terebralia* from a shell midden does not necessarily mean that the species did not live in the area. The shells may not have been picked up despite the existence of living animals, or further excavation could detect the species in the shell mound. However, the custom of gathering molluscs in mangals seems to have continued in the Ryukyu Islands and Taiwan since 4000 yBP, because the shells of mangrove molluscs such as *Geloina coaxans* have been excavated from sites dated to most of the archaeological periods in each area. The absence of living populations of *Telescopium* or *Terebralia* is therefore more likely, if the shells are lacking at a larger number of sites. The historical distribution patterns of these genera are discussed in the following sections with the above points in mind.

Historical patterns of the distributions

There are no traces of either *Telescopium* or *Terebralia* in Amami at present or in the past, so the species does not seem to have lived there, at least since 6000 yBP. In Okinawa, Yaeyama and Taiwan, empty shells and/or living animals of at least two of the three species have been recorded. Analysis of shell middens suggests that the range of *Telescopium telescopium* has contracted toward the southwest since 2500 yBP and the species disappeared from the Ryukyu Islands and Taiwan by the present time (Fig. 2). No shells of this species are known from the sites dated between 850–350 yBP in Okinawa, which suggests that *T. telescopium* had declined in this area either during or before this period. As for the record of this species from one site dated to after 350 yBP in Okinawa (Table 2), the possibility of secondary deposition cannot be excluded because of the small number of excavated shells at only one site. The shells of *T. telescopium* are often found in shell middens dated to after 350 yBP in Yaeyama (Table 2), and Ozawa *et al.* (1995) determined the radiocarbon date of an empty shell of this species from Yaeyama as 330±80 yBP. Thus, the decline of *T. telescopium* in Yaeyama might have occurred later than in Okinawa.

Terebralia palustris was distributed from Okinawa to Taiwan between 2500–2000 yBP but its range contracted afterwards (Fig. 2). In Okinawa, the shells of *T. palustris* are often found at sites dated between 850–350 yBP whereas no shells of *Telescopium telescopium* are known for the same period. This implies the later disappearance of *T. palustris* than *T. telescopium* in Okinawa, although further data are needed. The size of *T. palustris* from the shell middens in Okinawa is small, as compared with those of the present populations in other regions of the Indo-Pacific. Kurozumi (1987) examined the shells of *Terebralia palustris* from a shell midden in Okinawa dated between 3500–2500 yBP, and reported the shell length of 'adults', i.e., shells with a developed axial varix and thickened aperture, as <72mm (n=1571). On the other hand, sizes >130 mm are known from the present populations in Yaeyama (Nishihira 1983a), Thailand (Shokita *et al.* 1985), and Indonesia (Soemodiharjo and Kastoro 1997). Such a small size of *T palustris* is typical of a general trend for Okinawan shell middens (T. Kurozumi, personal observations), and thus dwarfs of this species seem to have once been distributed near the northern limit of its range. Shells of *T. palustris* occur in a fewer shell middens but more abundantly per site than those of *T. telescopium* (Table 3). It is unlikely that prehistoric people searched for *T. palustris* less widely but picked it up more eagerly once it was found than *T. telescopium*. Differences in natural distribution patterns are more probable, such as a more focussed distribution of *T. palustris* than *T. telescopium*.

The existence of living *Terebralia sulcata* in Okinawa but its absence in Yaeyama is well known to local biologists. The same pattern was detected in the present analysis of shell middens dated to after 6500 yBP (Table 2; Fig. 2). A reasonable explanation for this has not been proposed, but floral patterns might be concerned. Wells (1980) reported that *T. sulcata* and *T. palustris* were absent around *Rhizophora stylosa* stands in several mangals in Western Australia, and *R. stylosa* is dominant only in Yaeyama within

the region of the Ryukyu Islands and Taiwan.

Subfossil shells of *Telescopium telescopium* and *Terebralia palustris* are found in the innermost part of the Red Sea and along the coast of the Arabian Gulf where living animals of these species are absent (Houbrick, 1991; Plaziat 1995; Glover 1998). In the Red Sea, the shells of *T. palustris* were excavated from a site dated between 5300–6100 yBP and located ~2000 km north of its present habitat near the entrance to this sea (Plaziat 1995). Glover (1998) suggested that *T. palustris* has declined since about 2000 yBP and disappeared from the Arabian Gulf, based on the data from shell middens. Thus, a parallel phenomenon of southward contraction of the ranges of *T. telescopium* and *T. palustris* have occurred both at the northwestern and northeastern limits of their geographical ranges within the last several millennia.

Causes of decline

Shell middens in Taiwan often contain abundant shells of *Telescopium* and *Terebralia* (Kuroda 1940; Kaneko 1978) despite absence of the living animals in this area. Kuroda (1940) explained this as historical distributional changes due to progradation. Rin (1960) depicted coastlines as more complicated between 3100–1900 yBP than at present, based on information on the geology and distribution of shell middens in southwest Taiwan. He deduced prehistoric marine regression accompanied by land upheaval and sedimentation in this region. Such topographical changes can reduce the habitat of mangrove gastropods, i.e., sheltered bays and brackish areas. Sea-level decline and progradation are known to have caused a decrease in diversity and abundance of sheltered-bay molluscs in mainland Japan (Matsushima 1984), and contraction of a mangrove area in Australia (Allen 1996) since ~6000 yBP. Ozawa *et al.* (1995) found that *Telescopium telescopium* has declined in the Ryukyu Islands since the 'Climatic Optimum' with a mild climate around 6000 yBP, in parallel with the subsequent decrease in temperature, and perished in the 17–18 century AD in the midst of a cold climate. The period from the 16th to 19th centuries is regarded as a 'Little Ice Age' with a worldwide cold climate (Schwartzbach 1961; Lamb 1984), although whether this was actually the case within the subtropical eastern Asia still remains to be determined. On the other hand, the contraction in ranges of *T. telescopium* and *Terebralia palustris* around the Arabian Peninsula during the past several millennia have been explained by the degradation of mangroves due to either a decrease in precipitation and winter temperature or sea-level changes (Plaziat 1995; Glover 1998).

Besides the above-mentioned natural factors, we point to the effects of increasing human activity. Wheat and rice production became widespread during the 12–16th century AD in Okinawa (Okinawa Prefectural Board of Education 1982) and the number of archaeological sites dated to this period is 4–7 times more than in previous periods (Takamiya 1996). An extreme increase (~5 times) in human population is known to have occurred in Yaeyama in the 18th century (Tsubouchi 1982), when the Ryukyu Dynasty warned against the devastation of the forests on these islands (Kishaba 1954). These reports are consistent with the finding in the present study that *Telescopium telescopium* either declined or disappeared around the 12–16th century in Okinawa and after the 17th century in Yaeyama. Land development is one of the possible detrimental factors with regard to human activities for mangrove gastropods. Hirata (1991) observed that a farmland development around Nagura Estuary in Yaeyama caused the influx of soil into the mangal and damaged the benthic fauna. Over-exploitation of *Telescopium* and *Terebralia* by an increased human population is also probable, although evidence either for or against this has not been obtained so far.

Studies on *Telescopium telescopium* show that it is specialized to feed on microparticles including diatoms on the liquid mud surface (Alexander *et al.* 1979; Houbrick 1991) and is limited to the internal glades and landward fringe of mangals exposed to sunlight (Soemodiharjo and Kastoro 1977; Shokita *et al.* 1985; Budiman 1988). *Terebralia palustris* has a robust radula and buccal mass (Houbrick 1991) and ingests various food

items, e.g., leaves and other soft parts of mangrove plants, attached or stranded algae, and detritus (Plaziat 1977; Nishihira 1983b). This species is distributed wider in mangals than *T. telescopium* (Shokita *et al.* 1985; Houbrick 1991). *T. palustris* thus seems to be a more generalistic species and more tolerant of environmental stress than *T. telescopium*. This is consistent with the fact that *Terebralia palustris* is still alive in the Ryukyu Islands that have been developed over historical periods, after the extinction of *T. telescopium*. Information on *Terebralia sulcata* is comparatively scarce. Houbrick (1991) described this species as 'a hardy generalist', which occurs on various substrata, e.g., sand or rock in salt marshes and mangroves, and ingests various food items, e.g., algae, vascular plants and detritus. Such flexibility of *T. sulcata* might account for the historical consistency of its distribution pattern, including the survival in Okinawa where human activity has been increasing.

The exact causes of decline in *Telescopium telescopium* and *Terebralia palustris* in the Ryukyu Islands and Taiwan cannot be determined at present. A combination of natural and artificial factors, and different situations between areas, e.g., Taiwan versus the Ryukyus, or between species, e.g., *T. telescopium* versus *T. palustris*, should be considered. Several species, except *Telescopium* and *Terebralia*, are known almost exclusively as subfossil shells in the Ryukyu Islands and Taiwan (Kuroda 1940; Kaneko 1978; Yoshiba and Nobuhara 1997), and comparison with such species is promising also for the study of mangrove gastropods. Further excavation records of *Telescopium* and *Terebralia* and comprehensive analyses, including other species, will enable more detailed exploration of the subject.

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