

Notes about the parallels in evolution of the Pleistocene cervids from Greece (Crete, Kassos and Karpathos), Japan (the Ryukyu-islands) and Philippines (Masbate)*

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ABSTRACT: The phenomena of the shortening of the legs of Pleistocene cervids from Crete (Greece), the Ryukyu Islands (Japan) and Masbate (Philippines) are compared. There is concluded that in this aspect they follow a parallel path of evolution.

Key-words: *Endemic, unbalanced, island-faunas, metacarpals.*

ΠΕΡΙΛΗΨΗ: Συγκρίνονται τα φαινόμενα του περιορισμού του μήκους των ποδιών των πλειστοκαινικών cervids από την Κρήτη (Ελλάδα), τα νησιά Ryukyu (Ιαπωνία) και Masbate (Φιλιππίνες) και συνάγεται το συμπέρασμα ότι αυτά ακολουθούν μια παράλληλη πορεία εξέλιξης.

Λέξεις-κλειδιά: *ενδημική, μη-ισοροπημένη, νησιωτική πανίδα, μετακάρπια.*

INTRODUCTION

It is not new when I state that Paul was interested in ‘Island Evolution’. In the late sixties and seventies he came up with his ‘Island model’. In that model he proposed that the mammals reached the island by swimming or drifting (SONDAAR & BOEKSCHOTEN, 1967; DERMITZAKIS & SONDAAR, 1978). Once they settled on the island they underwent changes, adapting to the island conditions (SONDAAR, 1977). Paul was the first who recognized that the changes are adaptations and not degeneration’s, which opinion was common in those days (AZZAROLI, 1953, 1961, 1977). As only a restricted group of mammal species could reach the islands, an unbalanced endemic island fauna was formed (SONDAAR, 1971, 1977). The endemic unbalanced fauna points to isolation of the islands during a particular period (SONDAAR, 1971, 1977).

Paul took me to Crete in 1972 and gave me for my PhD study the endemic cervids of Crete. Paul distinguished already several morphotypes in those cervids. After I became curator at Naturalis, we still worked together and had the opportunity to go to Indonesia and visit the islands Flores, Sulawesi with their endemic island faunas, and Java. In Java was Fachroel Aziz who worked together with Japanese scientists and we became involved in their project. Paul knew already Hiroyuki Otsuka, who visited Utrecht in the early seventies. When the Japanese invited us in 1995 and 1996 to visit Japan, we visited Otsuka at Kagoshima

University. Paul was very enthusiastic about the Ryukyu Islands. We had the opportunity to see and study the cervid material of those Islands. I was measuring and Paul was writing down the measurements. We had big plans to do something with it, but we never could find the time. Further on that trip Paul convinced Otsuka to organize a congress about the islands, especially the Ryukyu Islands. This congress took place in November 1998, and was called “The Ryukyu islands; the arena of adaptive radiation and extinction of island fauna”. In 1988 at the Sardinian Congress Paul had invited Angel Bautista, from the National Museum of Manila. In 2001 we had the opportunity to visit the Philippines and do excavations in Cabarruyan Island and Cagayan Valley (Luzon). Again Paul was very enthusiastic about the endemic island fauna.

In memory of Paul I will make some notes about the parallels in evolution of the island cervids from Greece (Crete, Kassos and Karpathos), Japan (Ryukyu Islands) and Philippines (Masbate).

MATERIAL

The material from the Ryukyu Islands is stored in the Kagoshima University. The material from Crete is stored partly in the Natuurmuseum, Rotterdam, The Netherlands, partly in the Geological Museum of the University of Athens, Greece. The material of Masbate is stored in

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Naturalis, Leiden, The Netherlands.

The recent material of *Axis porcinus*, *Axis axis*, *Blastocercus campestris*, *Mazama zetta*, *Mazama rufa* and *Capreolus capreolus* is stored in the Natural History Museum, London, England. *Axis axis* is coming from the Kanha National Park, Mandla district, India. Collector G. Schaller. *Mazama zetta*, is coming from Medellin, Antioquia, Colombia. The origin of the other species is unknown.

The Pleistocene material of *Rangifer tarandus*, *Megaloceros giganteus* and *Cervus elaphus* is stored in Naturalis, Leiden, The Netherlands.

Rusa marianna, or *Rusa philippinensis*, is stored in the National Museum of Manila, Philippines, in the osteo collection under number 879. Date of collecting was October/December, 1983 by de Vera and Ramos in Pelablanca, Cagayan, Luzon.

The measurements of the Cretan material, *Capra* sp., *Dama dama*, *Rusa* sp., *Rucervus duvauceli*, *Moschus* sp., are taken from DE VOS (1979; table 11).

The measurements of *Candiacervus cerigensis* are taken from KUSS (1975b: table III).

The measurements were taken with vernier calipers. All measurements are given in 0,1 mm. For the measurements of the parameters, the method of HEINTZ (1970) was followed. The measurements of the individual specimens are given in appendix 1. Size ranges and massivity indices are given in appendix 2.

CRETE, KASSOS AND KARPATOS (GREECE)

Crete

Pleistocene mammals of Crete (Fig. 1) are known since the eighteenth century (POCOCK, 1745). Description of the fossils started early in the twentieth century (BATE, 1905, 1907; SIMONELLI, 1907, 1908). In the last two decades a lot of new localities have become known and monographs on the mammals, to wit cervids (KUSS, 1965, 1975b; DE VOS, 1979, 1984; CAPASSO BARBATO & PETRONIO, 1986;

CAPASSO BARBATO, 1989, 1990, 1992 a and b), hippos (BOEKSCHOTEN & SONDAAR, 1966; KUSS, 1975a), murids (KUSS & MISONNE, 1968; MAYHEW, 1977), shrews (REUMER, 1986; REUMER & PAYNE, 1986), elephants (KUSS, 1965, 1966, 1973), an otter (SYMEONIDIS & SONDAAR, 1975; WILLEMSEN, 1980) have appeared, and further of birds (WEESIE, 1982, 1987) and reptiles (BACHMAYER *et al.*, 1975).

From the list above it is clear that the fauna of Crete only contains cervids, hippos, murids, shrews, elephants, birds and reptiles, while large carnivores, with the exception of the otter, are lacking. It is clear that we are dealing here with an endemic unbalanced island fauna (SONDAAR, 1971, 1977).

The cervid material from Crete is coming from several Caves deposits and fissure fillings.

The cervid material is described independently for each cave deposit or fissure filling by DE VOS (1979, 1984). DE VOS (1979) distinguished six size groups. Appendix 2 shows only 5 size groups, but in combination with the metatarsal, which length is running from 110,0 mm till 406 mm, six size groups could be distinguished. The variation in size of the metacarpals is running from 88,4 mm till 284,0 mm. The percentage of maximum to minimum metacarpal size exceeds 321 and is far much more than in the subspecies *Cervus nippon centralis* that has a percentage of 117,6 (N=25; MATSUMOTO & OTSUKA). This means that we are dealing with more than one population.

Within the variation of the five groups, two groups can be distinguished, size group 1,2,3 with a massivity of 0.20 and more and size group 4 and 5 with a massivity less than 0.20 (appendix 2).

In the continental cervids the massivity, i.e. the length/Dt dist. ratio of the metacarpals, is below the 0.20 (appendix 2), with the exception of *Rangifer tarandus* and *Megaloceros giganteus*. However, *Rangifer tarandus* has the distal condyles more or less spread, that is why it gives the suggestion that the massivity is large.

The massivity index of the metacarpals of size 1 and 2 is like those of *Capra* (Appendix 2). Further, appendix 2

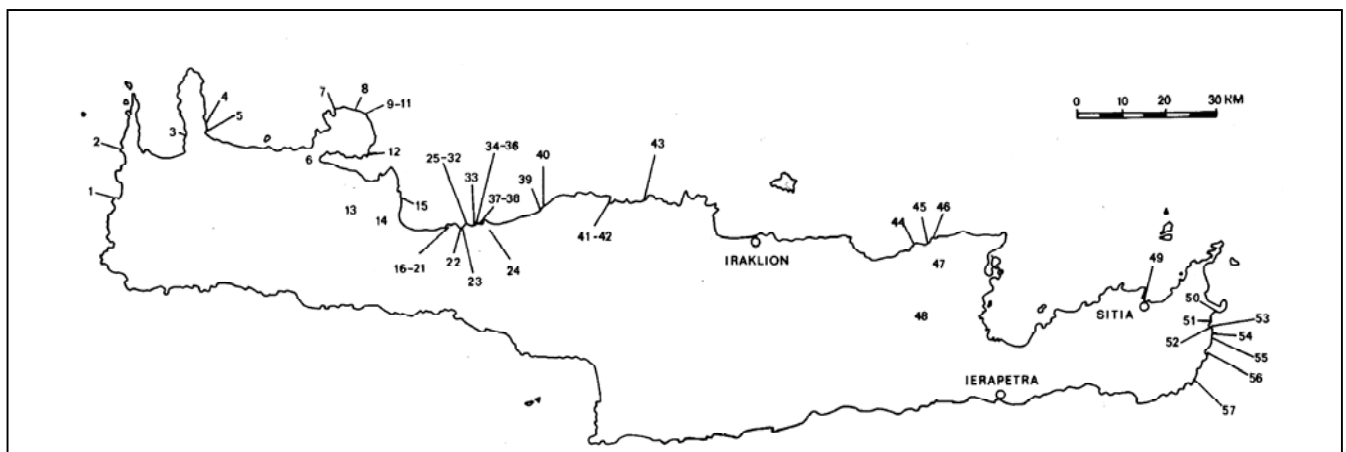


Fig. 1. Sites of Crete with fossil mammals (taken from DE Vos, 1979).

shows clearly that in the Cretan material the massivity of the metacarpals declines when the length of the metacarpals becomes larger; this means that the metacarpals become more slender. However, this doesn't mean that the massivity is related to size. *Mazama zetta*, which size is at the outer limit of size 2, is clearly slender than size group 2. At *Mazama rufa* which length falls within the length of *Candiacervus* size 2, the massivity is smaller. The metacarpals of smaller size show a greater degree of robustness than the other postcranial bones (DE VOS, 1979).

A lot of caves are known, but in most cases the different sizes are found in the same cave next to each other in the same level (like Mavro Mouri Cave with the sizes 1, 2, 3 and 4), which means that they are contemporaneous. The larger sizes are extremely rare (Appendix 2).

Karpathos

KUSS (1967) mentioned a small cervid from Karpathos, which was similar to *Cervus cretensis* from Crete. In 1975 (b) KUSS distinguished in Karpathos 2 species: *Candiacervus cerigensis* and *Candiacervus pigadiensis*. *Candiacervus cerigensis* has the size of *Candiacervus cretensis* (size 1 and 2 of DE VOS, 1979; see appendix 1 and 2), but the front legs are shorter and more powerful, while the hind legs are more slender than *Cervus cretensis*. The metacarpals of *Candiacervus cerigensis* have a massivity (mean 0,26), which is larger than size 1 and 2 of Crete. *Candiacervus pigadiensis* has the size of *Candiacervus rethymnensis*. Pities enough there are no metacarpals reported, but the antlers are different in morphology from *Candiacervus rethymnensis*.

Kassos

KUSS (1969) described cervid material from Kassos, which he attributed to *Candiacervus cretensis* from Crete. In 1975, after describing the material from Karpathos, in which KUSS (1975b) distinguished two species, he attributed the material from Kassos to *Candiacervus cerigensis*, which he had described from Karpathos. Probably the cervid material from Kassos is a species on its own and different from *Candiacervus cerigensis* from Karpathos (KUSS, 1975b).

The Ryu-Kyu islands (Japan)

In the Ruykyu islands (Figs 2, 3) cervid material attributed to *Cervus astylodon*, is reported from Okinawa (MATSUMOTO, 1926; MATSUMOTO & OTSUKA, 2000), Ishigaki (OTSUKA & HASEGAWA, 1973), Ie-jima (HASEGAWA *et al.*, 1978), Kume and Tokunoshima (OTSUKA *et al.*, 1980, 1990; MATSUMOTO & OTSUKA, 2000). The faunas of these islands, almost only consisting of cervids, can be considered as unbalanced endemic island faunas, in which the

mammals reached the islands by swimming. However, Japanese colleagues (KIMURA, 2000; OTSUKA & TAKAHASHI, 2000) still holds the opinion that the mammals reached the islands by land bridges.

Three sites of Okinawa (Kita-Nakagusku= Kita, U-site, Chinen) will treat here in more detail. We (Paul SONDAAR



Fig. 2. Map of the Ryukyu Islands taken from MOTOKAWA (2000).

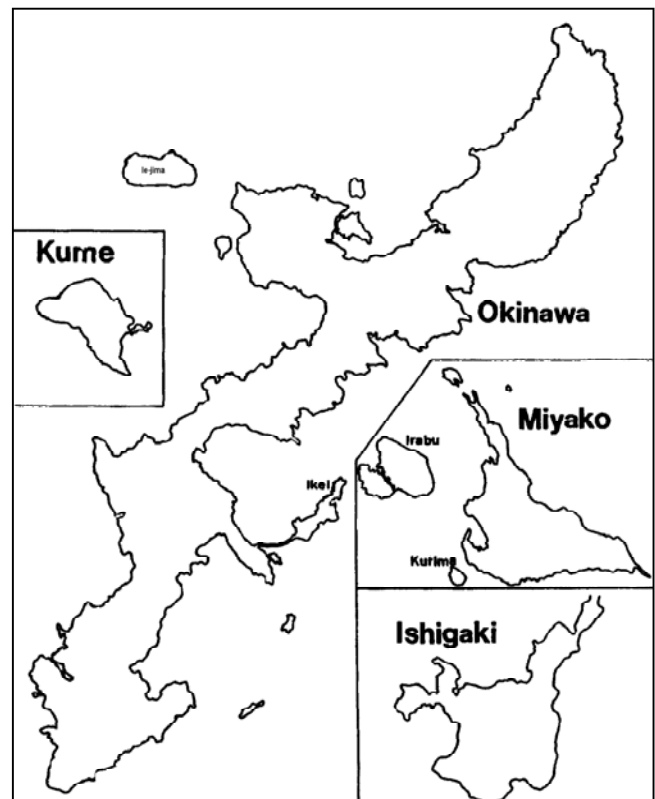


Fig. 3. Map of Okinawa, Kume and Ie-jima after OSHIRI & NOHARA (1998).

and the author) measured material from Kita-Nakagusku, U-site, Chinen and Kume Island. The data from the Gohezu-cave and Iejima are taken from HASEGAWA *et al.* (1978). MATSUMOTO & OTSUKA (2000) stated that each island has his own morphotype.

I. Kume-island

The fossils are coming from a cave in which they are found disarticulated (MATSUMOTO & OTSUKA, 2000) and the authors distinguished four morphotypes in *Cervus astylodon*, which are characterized by different body-sizes and proportions of teeth and limb bones. At least two morphotypes in the metacarpals can be distinguished:

1) morphotype-A = the morphology of the proximal articulation facet of the metacarpal has the morphology as in “*Muntiacus*”

2) morphotype-B = the morphology of the proximal articulation facet of the metacarpal has the morphology as in “*Metacervulus (=Cervus) astylodon*”.

Although the material is scanty, within the metacarpal material, in an optimistic way, at least 6 or 7 size-groups can be distinguished: two size-groups in morphotype-A and 4 or 5 size-groups in morphotype-B (Fig. 4).

The length of the metacarpals varies from 44,4 till 141,6 (Appendix 2). The percentage of maximum to minimum metacarpal size exceeds 318 and is far much more than in the subspecies *Cervus nippon centralis* that has a percentage of 117,6 (N=25; MATSUMOTO & OTSUKA, 2000).

If size-group 1 and 2 of morphotype-A represents males and females is not clear. The same holds true for size-groups 3 and 4 of morphotype-B.

Appendix 2 shows the massivity indices (DT dist/length) of the Kume material. All morphotypes, with the exception of Kume morph 7 have a massivity of the metacarpals above 0.20. From the appendix 2 we can observe that size 1 and 2 of morphotype A are the most shortened. Kume morph B size 3 and 4 are more slender, but still more massive than the sizes 1 and 2 from Crete, Greece.

In general we can observe, as within the Cretan material, that when the metacarpals became larger in length, they become more slender.

II. Okinawa

Also here, in the three sites of Okinawa, the two morphotypes A and B can be distinguished.

a) Kita-Nakagusku (Kita)

Only 7 metacarpals of this site are available. The length varies from 57,1 till 110,6 (Appendix 1). The percentage of maximum to minimum metacarpal size exceeds 193 and is far much more than in the subspecies *Cervus nippon centralis* that has a percentage of 117,6 (N=25; MATSUMOTO & OTSUKA, 2000). According to MATSUMOTO &

OTSUKA (2000) there is only one size group in morph B. However, Fig. 5 shows that there are, in optimistic way three sizes. All metacarpals have a massivity above 0.20; the robustness is large again (Appendix 2). Also here, if the metacarpals became larger in size, the massivity declines.

b) U-site

Only 5 complete metacarpals (Appendix 1) are available. Their length is running from 59,1 mm till 112 mm. The percentage of maximum to minimum metacarpal size exceeds 189 and is far much more than in the subspecies *Cervus nippon centralis* that has a percentage of 117,6 (N=25; MATSUMOTO & OTSUKA, 2000). Also here we can distinguish in an optimistic way three size-groups (Fig. 6; Table, 2). All the metacarpals have a massivity above the 0.20 (Appendix 2).

c) Chinen

From this site 10 metacarpals are available. The length of the metacarpals ranges from 58 mm till 97,6 mm. The percentage of maximum to minimum metacarpal size exceeds 168 and is far much more than in the subspecies *Cervus nippon centralis* that has a percentage of 117,6 (N=25; MATSUMOTO & OTSUKA, 2000). Here we can recognize 4 size-groups (Fig. 7); size 1 and 2 in morph A, size 3 and 4 in morph B. All the metacarpals have a massivity above the 0.20 (Appendix 2).

All three sites together

If we combine the material from the three sites of Okinawa, we get the following diagram (Fig. 8). This diagram shows one cluster, in which it is impossible to distinguish different size-groups.

III. Iejima Island, Gohezu cave

From the work of HASEGAWA *et al.*, (1978) we learn that 18 metacarpals are available. Thirteen are complete enough for this research.

HASEGAWA *et al.* (1978) do not indicate if there are different morphotypes. However, based on the antlers they figure (HASEGAWA *et al.*, 1978, Plate 4 and 5), there must be a *Muntiacus* type and a *Cervus* type. In the *Cervus* type there is a large variation of morphologies.

The range of the length of the metacarpals runs from 45 mm till 112,5 mm. The percentage of maximum to minimum metacarpal size exceeds 400 and is far much more than in the subspecies *Cervus nippon centralis* that has a percentage of 117,6 (N=25; MATSUMOTO & OTSUKA, 2000). The massivity from all metacarpals is above 0.20 (appendix 1).

If we make a scatter diagram from the massivity (length/Dt. Dist.) from metacarpals we observe one cluster (Fig. 9) in which it is not possible to give clear-cut size groups.

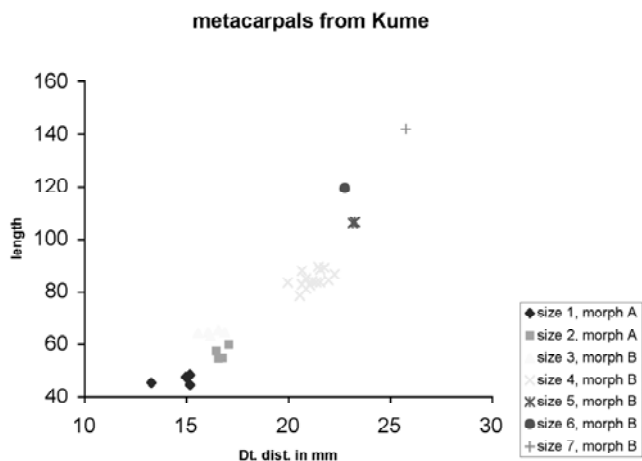


Fig. 4. Diagram of Kume metacarpals. Morph = morphotype.

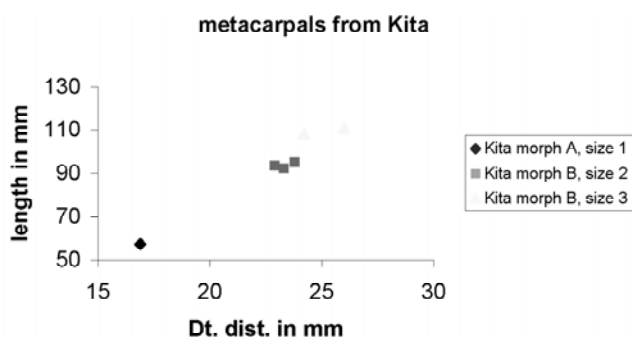


Fig. 5. Diagram of Kita metacarpals.

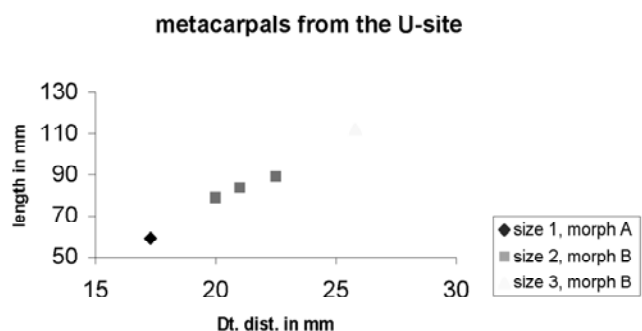


Fig. 6. Diagram of U-site metacarpals.

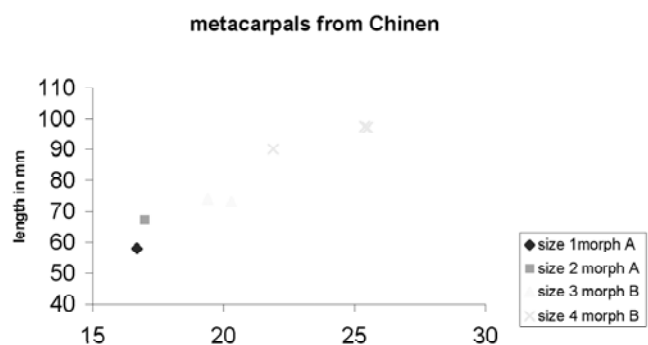


Fig. 7. Diagram of Chinen metacarpals.

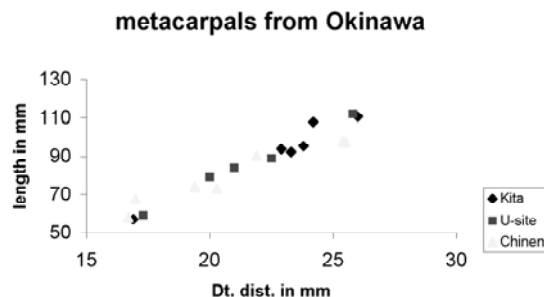


Fig. 8. Diagram of all Okinawa metacarpals.

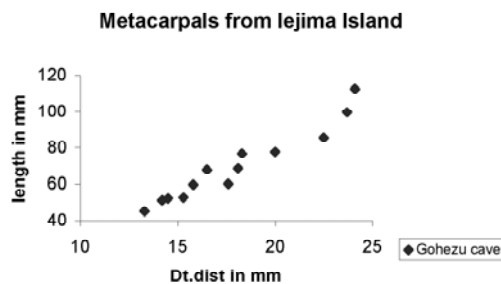


Fig. 9. Diagram of Iejima metacarpals.

Remarkable is that the distal end of some of the antlers is chewed (HASEGAWA *et al.*, 1978: Plate 2), the same as we find in the material of Crete. Further we can observe in Plate 10 of HASEGAWA *et al.* (1978) that 9 of the 20 cubonaviculars are fused with the metatarsals. This is 45%. In Crete we find this in 5,9% (DE VOS, 1979: table 15). In *Myotragus balearicus* from Mallorca, of which the metapodials are very shortened the percentage is 75. As such fusion may have had a functional meaning the percentage of fusion might be an indication of the degree of adaptation (LEINDERS & SONDAAR, 1973).

Masbate, Philippines

H.S. Solheim II and O.H. Beyer excavated the Masbate deposits in the early fifties. According to a letter (dated Sept. 10, 1952) of H.S. Solheim II to Hooijer of the Rijksmuseum van Natuurlijke Historie (nowadays called National Museum of Natural History, Naturalis), the material was coming from three different sites on a tall limestone shaft. The mountain sticks up out of the surrounding valley with almost vertical sides. It is about a mile around at the base, about 400 feet high and about a city block on top. There are quite a few caves in it, both large and small, most of them showing human presence. One of the sites was a small cave about halfway up the side. The other two sites were on the top, one in a large cave and the other a small refuse pile with potsherds and shells, right at the edge of the top. The material was found on or near the surface and some of it is thinly covered with a limestone

accretion. Solheim II thought that the bones are probably older than 2000 years ago. The material was sent to D.A. Hooijer for determination. In a letter of Hooijer (dated January 16, 1953) to Beyer, Hooijer wrote that the mammalian specimens from Masbate come from three different sites, Ma 45, Ma 46 and Ma 47 respectively, and every single specimen was marked accordingly. Hooijer wrote further in that letter that all the mammalian specimens belong to pig and deer. He determined the pig as *Sus spec.* and the deer as *Cervus spec. div.* Hooijer in his letter wrote that the cervid material is more heterogeneous; there are at least three size classes. He paid special attention to the stocky metacarpal (Ma 45).

Two fossil metacarpals (Ma 45, Ma 621) are available from the cave of Masbate. They have the following measurements.

Specimen no	length	Dap prox	Dt prox
Dap dist	Dt dist	massivity	
Ma 45	126,6	19,0	28,3
15,5	27,8	0,21	
Ma 621	109,5	15,5	22,2
8,9	27,3	0,24	

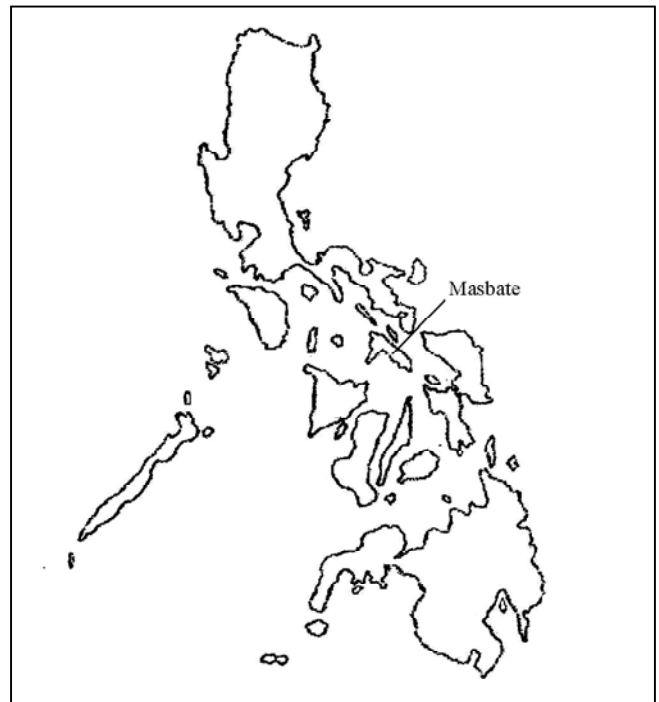


Fig. 10. Map of Philippines with the position of Masbate.

<i>Rusa marianna</i>	130,1	19,8	26,1	16,8	25,8	0,19
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The two metacarpals have a massivity larger than 0.20. These metacarpals fall concerning size and massivity in the group of metacarpals size 2 and 3 of Crete (Appendix 2). If we are dealing here with one or two size groups is not clear, as the material is too scanty. However, the

metacarpals are much more massive than the recent *Rusa marianna* or *Cervus philippinensis*, which has normal continental proportions. Probably we are dealing with a new species.

The presence of pig and cervids is remarkable because also MATSUMOTO & OTSUKA (2000) reported that the Late Pleistocene fissure and cave deposits in the Ryukyu islands mainly yield *Cervus astylodon* dated to about 20.000 to 35.000 B.P., and wild boar fossils dated to about 18.000 B.P. (TAKAI & HASEGAWA, 1971). The authors continue by stating: "Occurrence patterns of these two earlier and later species vary with locality. Some localities alternatively yield either the latter fossil or the earlier fossil or both".

DISCUSSION

Taxonomy and nomenclature

As well in the Greek islands Crete, Karpathos, Kassos, as in the Ryukyu Islands, and Masbate we find a large variation in sizes and morphotypes in the cervids, which go beyond the size variation in a continental population. The smaller forms are shortened or more robust the largest forms are slender.

The question is how to interpret the taxonomy of the

large variation in size. One of the options is to consider all the material from one island or islands as one species. In the early 20th century SIMONELLI (1907, 1908) did this for the Cretan material and indicated all the material as *Cervus cretensis*. Later on this was followed by KUSS (1965, 1967, 1970, 1973), although KUSS (1965, 1967, 1970, 1973) already reported that a large variability in size and morphology existed within the species *cretensis* and that there were a few specimens with sizes going beyond the variation of the species *cretensis*. In 1975 (b) KUSS, on basis of size, considered the material from Crete to belong to two species, a small one (*cretensis*) and a large one, for which he erected a new species name, *rethymnensis*. In first instance KUSS considered the material from Karpathos (KUSS, 1967) and Kassos (KUSS, 1969) as similar to the Cretan cervid *Candiacervus cretensis*. In 1975 (b) KUSS considered the material from Karpathos as two species (*Candiacervus cerigensis* and *Candiacervus pigadiensis*), which are different from the Cretan species. In the same year he attributed the material from Kassos to the species *Candiacervus cerigensis* from Karpathos.

KOTSAKIS *et al.* (1976) still considered the deer remains originating from the locality Bate Cave (Crete) to belong to one species, *cretensis*, with the exception of a few very large bones, which they indicated as "Cervo taglia media"

and “Cervo taglia grande”. Although, KOTSAKIS *et al.* (1979) acknowledged the difference in length between the bones, they still thought that this quantitative aspect was not sufficient to establish a new species.

In a biometrical approach of post-cranial material from several sites of Crete DE VOS (1979) distinguished six size groups in the fossil cervid remains. Within the cranial material of the Cretan cervids, DE VOS (1984) distinguished four morphotypes of skull, three size groups in the teeth, three morphotypes of the upper P², two types of wear patterns, teeth with and without a cingulum, further five types of antlers. DE VOS (1984) concluded, based on postcranial and cranial material, that there were at least leading to eight taxonomic units: *Candiacervus ropalophorus*, *Candiacervus* sp. IIa, IIb, IIc, *Candiacervus cretensis*, *Candiacervus rethymnensis*, *Candiacervus* sp. V, *Candiacervus* sp. VI.

As there is an overlap within the measurements of the smaller size groups, and the large material is scanty, it is not possible to make clear-cut species. DE VOS (1979, 1984) didn't like to split up the Cretan material into species, but liked to call them taxonomic units or morphotypes, although some sizes had already become a species name given by SIMONELLI (*cretensis*) and KUSS (*rethymnensis*).

In her unpublished thesis CAPASSO BARBATO (1989) attributed without arguments the material of *Candiacervus* species IIa, b and c of DE VOS, 1984, to the species *Candiacervus ropalophorus*, although DE VOS (1979) clearly proved statistically that the populations of the site Gerani 4 (with *Candiacervus ropalophorus*) and Liko (with *Candiacervus* species II) are significant different in size. Further CAPASSO BARBATO (1989) ignored the distinction in antler morphology in the species IIa, b, c, without discussing it. She put the sizes 1,2a,b,c, and 3 in in the subgenus *Candiacervus*, within the genus *Megaceros*.

The large species *Candiacervus rethymnensis*, *Candia - cervus* species V of DE VOS 1984 (= *Cervus dorothenis* CAPASSO BARBATO, 1989) and *Candiacervus* species VI of DE VOS 1984 (= *Cervus major* CAPASSO BARBATO & PETRONIO, 1986) were put by CAPASSO BARBATO (1989) in a new subgenus (*Leptocervus*) within the genus *Cervus*. CALOI & PALOMBO (1996) put *rethymnensis* in the genus *Pseudodama* with a question mark. Even so with *?Pseudodama (Leptocervus) dorothenis* and *?Pseudodama (Leptocervus) major*.

So, there are different opinions concerning the number of species in Crete: according to DE VOS (1979, 1984) there is one genus with eight taxonomic units, or morphotypes. According to CAPASSO BARBATO (1989) and CALOI & PALOMBO (1996) there are two genera with five species.

In the Ruykyu islands of Japan cervid material is reported from Okinawa (MATSUMOTO, 1926), Ishigaki (OTSUKA & HASEGAWA, 1973), Ie-jima (HASEGAWA *et al.*, 1978), Kume and Tokunoshima (OTSUKA *et al.*, 1980b). Also in this material there is an overlap in measurements. The material is scanty and it is difficult to make clear-cut

species. The Japanese colleagues MATSUMOTO & OTSUKA (2000) attributed the material of the Ryukyu Islands to one species (*Cervus astylodon*) and distinguished several morphotypes. Every island has its own morphotype.

Concluding we can say that there is a large variation in sizes within the metacarpals. It is possible to make size classes, but as scatter diagrams based on the measurements show an overlap in the different size classes, it is difficult to make clear-cut units. In my opinion the best option for the moment is to indicate the different size classes as taxonomic units or morphotypes.

The large variation in size

The next question is how to explain the large variation in size.

One of the opinions was to explain it as sexual dimorphism. MALATESTA (1980) suggested, that the difference between the thicker and thinner metapodials in the Cretan material was due to sexual dimorphism. This explanation is not very likely, because the size variation is too large (the smallest metacarpal 88,4 mm, while the largest is 284 mm). Also MATSUMOTO & OTSUKA (2000: 159) deny the existence of sexual dimorphism in the Ryukyu material, by stating: “the variation seen in limb bones does not indicate sexual dimorphism”

In addition, MALATESTA (1980) gave another explanation. For the presence of large elements, MALATESTA (1980: 91) stated: “probably they represent exceptional cases of reappearance of ancestral genetic configuration”. But as many of such large elements are found at different localities (DE VOS, 1979), the largest metatarsal being of about four times the length of the smallest (DE VOS, 1979: table 12), it is more realistic to suppose that we are dealing with different taxonomic units.

KUSS (1975b) explained the large size range in the material from different localities of the small species (*cretensis*), as well as the large species (*rethymnensis*) as a consequence of diminution in size of the two species in the course of time. However the small and large material is found disarticulated and is coming from the same cave from the same level.

The explanation of diminution in size during time we also find back by MATSUMOTO & OTSUKA (2000) for the Kume material. Large huge deer specimens assigned to *Cervus astylodon* from early Pleistocene sediments in Okinawa demonstrates according to MATSUMOTO & OTSUKA (2000) that the Late Pleistocene *astylodon* is a miniaturized form of the early Pleistocene *astylodon*. Further they stated that the wide variation in size of the limb bones of the smaller morphotypes suggests that they represent different populations sampled at different times. But also here MATSUMOTO & OTSUKA (2000) stated that the bones of the four morphotypes they distinguish in Kume are found disarticulated and are coming from 1 meter thickness. Further the authors stated that:” In some localities (Nanbu-

mine, Minatogawa, and Kitanakagusuku-hinigusuku) only one size group, whether large or small, was found, and in other sites (Jibu-do Cave, and Kamikurukubaru) all sizes of specimens were unearthed". This is more or less the same in the Cretan taxonomic units.

In both cases, Crete and Ryukyu Island, it is more realistic to suppose that they are contemporaneous.

Another explanation is that there is an adaptive radiation. This idea is strongly promoted by DE VOS (1979, 1996, 1998, 2000). In this model an ancestor comes on the island and an adaptive radiation took place by sympatric evolution leading to cervids in different niches. This is supported by the differences in size and chewing mechanism of the cervids, which are found in the same level. CALOI & PALOMBO (1996) also acknowledge that the cervids of Crete occupy different niches.

First DE VOS (1979, 1984) and DE VOS & DERMITZAKIS (1985, 1986) and DERMITZAKIS & DE VOS (1985-1986, 1987) suggested two invasions: This idea was followed by CAPASSO BARBATO (1992b) and CALOI & PALOMBO (1996). However, DE VOS (1996), based on literature study and his own observations in the field, concluded that there was only one invasion.

This is also what we find in the Kume material. Apart from differences in size among the four morphotypes, also proportions of jaws and limb bones are different (MATSUMOTO & OTSUKA, 2000).

Who the ancestor is, is not known. For the Cretan deer are no known relatives on the mainland, although various candidates have been suggested as ancestor. Two continental genera and two species have been given special attention: *Cervus peloponnesiacus* and *Megaceros verticornis*. However, not one of these candidate species is clearly more closely related to them than are other cervids of the continent (DE VOS, 1996).

Also for the Ryukyu deer there is no ancestor. MATSUMOTO & OTSUKA (2000) stated that the direct ancestor of *Cervus astylodon* is unknown.

Although we cannot exclude allopatric speciation, it is more realistic to suppose that the speciation took place in the islands itself. So what is left are parapatric speciation and sympatric speciation. As there are no great differences in habitat, parapatric speciation seems not very likely, but cannot be excluded either. Sympatric speciation makes the best chance.

From Masbate (Philippines) we have only two metacarpals, but they show clearly that they are shortened. They show resemblance with the smaller size groups of Crete. In any case they are different from the small *Cervus philippinensis*, which has continental massivity.

CONCLUSIONS

— There is a wide range in size and massivity of the postcranial material from cervids, especially within the

metacarpals;

- Some are shortened others are taller than the continental forms;
- About the taxonomy there is a discussion;
- The explanation for the wide range is a sympatric evolution;
- In the islands of Greece, the Ryukyu Islands and Masbate we find a parallel evolution.

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APPENDIX 1

Measurements of the metacarpals from Ryu-Kyu Islands

KUME ISLAND

Metacarpal no	length	Dap. Prox	Dt. prox.	Dap. Dist.	Dt. Dist.	massivity
Kume 2	45,2	7,9	12,7	7,5	13,3	0,29
Kume 3	44,4	9	14,6	8,1	15,2	0,34
Kume 5	48,2	9,4	15,5	8,4	15,2	0,31
Kume 6	47,3	9,4	14,4	8,2	15	0,31
Kume 7	54,7	10,4	16	8,5	16,8	0,31
Kume 8	54,6	10,2	15,7	8,9	16,6	0,3
Kume 9	57,2	10,5	16,9	8,7	16,5	0,29
Kume 15	59,8	11,9	18,1	9	17,1	0,29
Kume 11	64,3	9,8	16,3	8,2	16,1	0,25
Kume 14	64,3	10,6	16,9	8,5	16,9	0,26
Kume 12	64,1	9,6	16	8,4	15,6	0,24
Kume 10	62,6	10,6	15,8	8,1	16,2	0,26
Kume 13	65,2	9,7	16,2	8,7	16,6	0,25
Kume 74	83,3	12,7	20,9	10,8	20	0,24
Kume 20	84,2	13,2	20,5	11,7	22	0,26
Kume 23	86,4	13,8	21,2	11,5	22,3	0,26
Kume 77	84,8	12,7	20,1	11,5	20,9	0,25
Kume 24	88,9	14	20,6	11,6	21,8	0,25
Kume 25	88,2	12,9	19,8	12,2	21,6	0,24
Kume 49	86,1	13,3	19,9	11,1		
Kume 80	83,9	13,1	21,1	11,3	21,2	0,26
Kume 21	82,4	13,3	21	11,4	21,1	0,26
Kume 85	87,8	13	19,2	10,7	20,7	0,24
Kume 26	89,3	13,8		11,6	21,5	0,24
Kume 18	83,4	13,6	20,5	11,1	21,6	0,26
Kume 104	81	13,4	20,6	11,8	20,9	0,26
Kume 16	78,4	13,1	20,9	11,7	20,6	0,26
Kume 17	82,6	12,8	20	11,5	20,7	0,25
Kume 22	83,5	13,5	21,2	11,3	21,4	0,26
Kume 27	106,3			12,3	23,3	0,22
Kume 84	105,9	14,4	23,1	12,4	23,2	0,22
Kume 28	119,2	13,5	20,8	11,4	22,8	0,21
Kume 30	141,6	16,3	24,7	12,8	25,8	0,18

KITA-NAKAGUSKU, OKINAWA

Kita 87	57,1	10,7	15,7	8,9	16,9	0,3
Kita ?	95,2	15,1	24,7	12,6	23,8	0,25
Kita 78	93,7	15,3	23,5	11,8	22,9	0,24
Kita 79	92,2	15,8	24	11,7	23,3	0,25
Kita 83	107,8	16,7	24,1	12,9	24,2	0,22
Kita 76	110,6	16,2		12,8	26	0,24
Kita 77	109,4	17	24	13		

U-SITE OKINAWA

U215	59,1	10,6	15,4	9,4	17,3	0,29
U299	78,9	13,2	19,8	10,6	20	0,25
U257	83,7	13,5	21,4	11,3	21	0,25
U200	89	14,7	20,9	11,8	22,5	0,25
U256	112	17,3	25,6	13	25,8	0,23

APPENDIX 1 continued
Measurements of the metacarpals from Ryu-Kyu Islands

Metacarpal no	length	Dap. Prox	Dt. prox.	Dap. Dist.	Dt. Dist.	massivity
CHINEN, OKINAWA						
Chinen 02	58	10,5	15,8	9,2	16,7	0,28
Chinen 01	67,3	10,6	16,6	9	17	0,25
Chinen 05	73,9	11,8		10,5	19,4	0,26
Chinen 06	73,3	12,2	19			
Chinen ?	74,9					
Chinen 04	79	13,4	20,4	11		
Chinen 02	72,9	12,5	20,3	10,1	20,3	0,27
Chinen 06	90	15,4	22,8	12,5	21,9	0,24
Chinen 08	97,2	17,3	26,4	13,7	25,5	0,26
Chinen 07	97,6	16,5	24,7	13,2	25,4	0,26
IEJIMA ISLAND, GOHEZU CAVE						
Gohezu 1	112,5	15,4	23,5	13,9	24,1	0,21
Gohezu 2	99,5	15,8	23,8	13,4	23,7	0,23
Gohezu 4	85,4	14,9	21,8	11,9	22,5	0,26
Gohezu 6	77,4	12,3	19,4	10,8	20	0,25
Gohezu 7	76,5	12,4	17,9	9,7	18,3	0,23
Gohezu 8	68,3	12	18	9,9	18,1	0,26
Gohezu 9	67,5	10,4	16,5	9	16,5	0,24
Gohezu 12	60	12,3	19,6	10,1	17,6	0,29
Gohezu 13	59,6	10,1	16,2	8,6	15,8	0,26
Gohezu 14	52,6	9,2	13,9	8,1	15,3	0,29
Gohezu 15	51,1	9,7	14,4	8,1	14,2	0,27
Gohezu 16	52,2	9	13,6	8	14,5	0,27
Gohezu 17	45	8	12,1	7,3	13,3	0,29
<i>Axis porcinus</i>						
BM1858.12.16.2	120	22,9	13,8	20,1	13,7	0,11
<i>Axis axis</i>						
BM1959.9.23.3	155,7	16,4	18,3	16,5	24,3	0,15
BM1959.9.23.3	154,4	16,1	18	16,5	24,8	0,16
<i>Blastocerus campestris</i>						
686a61.11.15.2	151,5	16,4	23,5	16	22,5	0,14
686a61.11.15.2	151,5	16,1	23,3	16,1	23	0,15
686c54.8.16.1	154,8	18,4	23,7	16,3	24,1	0,15
686c54.8.16.1	156	18	24,3	16	24,1	0,15
<i>Blastocerus bezoartis</i>						
686k	137,2	14,4	21	13,2	20	0,14
686k	137,3	14,1	21,2	13,3	20,3	0,14
<i>Mazama zetta</i>						
1878.8.31.13	122	14,9	23	13,7	23	0,18
1878.8.31.13	122,3	15	23,5	13,5	23,2	0,18
<i>Mazama rufa</i>						
684a	101,9	11,4	16,3	11,1	15,8	0,15
684a	102	11,4	16,4	11	15,9	0,15

APPENDIX 1 continued

Measurements of the metacarpals from Ryu-Kyu Islands

Metacarpal no	length	Dap. Prox	Dt. prox.	Dap. Dist.	Dt. Dist.	massivity
<i>Capreolus capreolus</i>						
1910.11.29.4	159,6	16,5	21,5	14,2	21,6	0,13
1910.11.29,4	158,2	16,7	21,7	14,1	21,8	0,13
688j	161,5	17,2	23	14,5	23,7	0,14
688j	161	17,2	23,4	14,5	23,3	0,14
1938.5.21.1	159,5	15	19,6	13,7	20,5	0,13
1975.13.11	159,9	16,4	21,7	14,4	21,9	0,13
1975.13.11	160	16,5	22,1	14,3	22,7	0,14
1933.6.7.1	153	15	20,5	14,3	21,7	0,14
1933.6.7.1	153,5	15	20,5	14,5	21,8	0,14
1936.6.4.1	155,9	15	20,4	14,4	21,5	0,13
1936.6.4.1	156,1	14,8	20,5	14,4	21,6	0,13
1933.6.7.2	150,8	15	21,1	14,5	21,5	0,14
1933.6.7.2	151	15	21	14,5	21,5	0,14
<i>Rangifer tarandus</i>						
St. 400878	197,5	25,4	33,5	21,4	40,7	0,2
St. 338639	199,2	25	33,8	21,2	41	0,2
St. 152728	189,6	24,9	32	19,8	40,5	0,21
St. 448996	183,8	23,3	32,2	19,6	38,3	0,2
St. 29840	177,2	23,1	32,5	20,3	38,3	0,21
St. 145958	203,5	26,3	36,6	22,9	43,6	0,21
St. 139348	195,2	25	35,7	20,4	41,6	0,21
St. 338749	184,9	25,1	35,2	20,6	42,4	0,22
St. 153681	205,5	27,1	37,4	22,6	44,7	0,21
St. 369969	199,8	26,4	35,3	21,1	43	0,21
<i>Megaloceros giganteus</i>						
St. 338450	319,8	47,1	70	42,5	72,6	0,22
St. 338453	313,6	44,9	64	42	69,5	0,22
St. 172262	322,9	47,5	64,5	43,1	70,6	0,21
St. 172286	323,6	49,6	67,5	43,1	72,2	0,22
<i>Cervus elaphus</i>						
St. 27056	283,1	32,3	45,2	30,5	45,4	0,16
St. 30051	269,4	31,8	43	28,6	42,5	0,15
<i>Candiacervus cerigensis</i>						
Kuss 1975: 55	110	17,1	24,5	16,1	27,9	0,25
Kuss 1975: 55	103,7	16,4	24,5	15,4	28,5	0,27
Kuss 1975: 55	89,6	14,1	20,9	13,7	24,1	0,26

APPENDIX 2
Size ranges and massivity indices

size	length			massivity				
	N	min.	mean	max.	N	min.	mean	max.
Crete (Greece)								
<i>Candiacervus ropalophorus</i> (size 1)	66	88,4	98,5	114,1	12	0,21	0,23	0,24
<i>Candiacervus</i> sp. (size 2)	45	99,2	110,8	122,2	10	0,22	0,23	0,24
<i>Candiacervus cretensis</i> (size 3)	3	131	138,4	144,2	1		0,2	
<i>Candiacervus rethymnensis</i> (size4)	4	185	194,8	206	2	0,17	0,17	0,17
<i>Candiacervus</i> sp. taglia media (size 5)	3	262	271,6	284	3	0,14	0,15	0,15
Karpathos (Creece)								
<i>Candiacervus cerigensis</i>	3	89,6	101,1	110	3	0,25	0,26	0,27
Continental species								
<i>Capra</i> sp.					1		0,24	
<i>Rangifer tarandus</i>	10	177,2	193,6	205,5	10	0,2	0,2	0,22
<i>Megaloceros giganteus</i>	4	313,6	319,9	323,6	4	0,21	0,21	0,22
<i>Cervus elaphus</i>	2	269,4	276,2	283,1	2	0,15	0,15	0,16
<i>Dama dama</i>					3	0,14	0,14	0,15
<i>Axis axis</i>	2	154,4	155	155,7	2	0,15	0,15	0,16
<i>Axis porcinus</i>	1		120		1		0,11	
<i>Rusa</i> sp.					1		0,16	
<i>Rucervus duvauceli</i>					1		0,15	
<i>Capreolus capreolus</i>	13	150,8	156,9	161,5	13	0,13	0,13	0,14
<i>Moschus</i> sp.					1		0,13	
<i>Blastocercus campestris</i>	4	151,5	153,4	156	4	0,14	0,14	0,15
<i>Blastocercus bezoartis</i>	2	137,2	137,2	137,3	2	0,14	0,14	0,14
<i>Mazama zetta</i>	2	122	122,1	122,3	2	0,18	0,18	0,18
<i>Mazama rufa</i>	2	101,9	101,9	102	2	0,15	0,15	0,15
Kume island (Japan)								
Kume morph A size 1	4	44,4	46,3	48,2	4	0,29	0,31	0,34
Kume morph A size 2	4	54,6	56,6	59,8	4	0,29	0,3	0,31
Kume morph B size 3	5	62,6	64,1	65,2	5	0,24	0,26	0,26
Kume morph B size 4	16	78,4	84,6	89,3	16	0,24	0,26	0,26
Kume morph B size 5	2	105,9	106,1	106,3	2	0,22	0,22	0,22
Kume morph B size 6	1		119,2		1		0,21	
Kume morph B size 7	1		141,6		1		0,18	
kita-Nakagusu, Okinawa								
Kita morph A size 1	1		57,1		1		0,3	
Kita morph B size 2	3	92,2	93,7	95,2	3	0,24	0,25	0,25
Kita morph B size 3	3	107,8	109,2	110,6	2	0,22	0,23	0,24
U-site, Okinawa								
U-site morph A size 1	1		59,1		1		0,29	
U-site morph B size 2	3	78,9	83,8	89	1	0,25	0,25	0,25
U-site morph B size 3	1		112		1		0,23	
Chinien, Okinawa								
Chinen morph A size 1	1		58		1		0,28	
Chinen morph A size 2	1		67,3		1		0,25	
Chinen morph B size 3	5	72,9	74,8	79	2	0,26	0,27	0,27
Chinen morph B size 4	3	90	94,9	97,6	3	0,24	0,25	0,26