

## IDENTIFICATION OF *POMADASYS* SPECIES (PISCES, HAEMULIDAE) FROM AN ARCHAEOLOGICAL MIDDEN SITE IN NANKUANLI EAST (TAIWAN), BASED ON OTOLITH MORPHOLOGY

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**ABSTRACT.** — The morphology of the sagittae of the genus *Pomadasys* was used to identify otolith remains from an archaeological midden site in Nankuanli East (NKLE) in Tainan City in southwestern Taiwan. Of the 60 *Pomadasys* otoliths from the NKLE site, 50 were identified as belonging to four presently occurring species, namely *P. argenteus* (n = 37), *P. kaakan* (6), *P. maculatus* (1), and *P. quadrilineatus* (6). Ten otoliths, lacking distinguishable characteristics remained unidentified as to species. The sizes of the fishes that would have produced the predominant *P. argenteus* otoliths from the NKLE site were estimated using the relationships between fish length, fish weight, and the otolith length of modern fishes. The fish-size estimates from most otoliths were less than 152.15 mm in length and 59.68 g in weight, except for the extrapolated estimation of 598.03 mm in length from one extremely large-sized otolith that measured 26.43 mm in length. Species composition and distribution of *Pomadasys* fishes were compared between this archaeological site and the present-day status, and the implication of coastal adaptation on the estimated fish sizes of prehistoric NKLE inhabitants was discussed.

**KEY WORDS.** — otolith morphology, *Pomadasys*, taxonomy, salvage archaeology, species identification

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### INTRODUCTION

Otoliths are composed of calcium carbonate, inorganic impurities and a protein matrix, and are located in the labyrinth of the ear in Osteichthyes (Degens et al., 1969). There are three pairs of otoliths, the sagittae, the lapilli and the asterisci, which function as the mechanoreceptors for the acoustics and balance of the fish (Lowenstein, 1971). The sagittae are the largest among the three pairs of otoliths in most teleosts, whereas the asterisci are the largest in the ostariophysan fishes. The lapilli are the smallest among all of them (Popper & Lu, 2000).

The morphology of the sagittae is species specific, and thus the identification of fishes can be achieved with sufficient comparative materials. In addition, the relationship between otolith and fish size has been extensively investigated. Within species, there is a strong positive relationship with

high least-squares regression coefficients (Frost & Lowry, 1981; Harvey et al., 2000; Longenecker, 2008). This relationship is useful in estimating fish size by measuring the respective otolith size. These characteristics are commonly used to examine the diet content of piscivores (Fitch & Brownell, 1968), and to identify fossil otoliths from both sedimentary layers (Nolf, 1985, 1995; Stringer, 1992; Reichenbacher, 2004) and archaeological middens (Fitch, 1972; Huddleston & Barker, 1978; Gobalet, 1989; Dye & Longenecker, 2004). In archaeological studies, this information is further used to try to understand prehistoric animal exploitation, environmental changes, and coastal adaptations (Glassow & Wilcoxon, 1988; Colten, 1994; van Slyke, 1998; van Neer et al., 2002; Bolle et al., 2004).

A rescue archaeology project in a science-based industrial area called the “Tainan Science Park”, located in Tainan City in southwestern Taiwan has been in progress for almost

two decades (Tsang, 2005; Tsang et al., 2006). It contains 34 excavated archaeological sites, covering a time period from 5000 to 300 calendar years before present, primarily dated by ceramic artifacts. The archaeological remains include pottery, stone tools, shell and bone tools, as well as animal bones, plant remains, and human burials. Several archaeological sites revealed fish remains, including large amounts of bones, teeth, and otoliths. Fish remains at the site provide essential evidence when investigating why and how people settled in prehistoric Taiwan and their strategies for coastal adaptation.

A preliminary examination revealed that otoliths of the genus *Pomadasys* (Haemulidae) occurred at a relatively high frequency in the middens involved in this rescue project (Tsang et al., 2006). Fishes of the genus *Pomadasys*, commonly known as grunts have a circumtropical distribution with around 36 species in the coastal waters of both the Atlantic and the Pacific Oceans. Four species of *Pomadasys* occur in Taiwan: *P. argenteus* (Forsskål, 1775), *P. kaakan* (Cuvier, 1830), *P. maculatus* (Bloch, 1793), and *P. quadrilineatus* Shen & Lin, 1984. All are important as a marine food fish (Shao, 2009). In this study,

*Pomadasys* otoliths from archaeological middens were substantially identified by morphological comparison to otoliths of modern congeners. The sizes of the predominant grunt species identified from archaeological remains were estimated from the corresponding relationship between fish and otolith size. The species composition and distribution of the *Pomadasys* fishes from the archaeological sites were compared with present-day communities. The implication of coastal adaptation on the estimated fish sizes of the prehistoric inhabitants was then interpreted.

### MATERIAL AND METHODS

**Sampling design.** — The archaeological site of Nankuanli East (NKLE, 120°16'23"E and 23°07'07"N) is located in the Tainan Science Park in Shanhua, Tainan City (Fig. 1). Based on geological studies, the NKLE site is assumed to have been situated on the shoreline 5000 calendar years before present, but is now located more than 25 km inland due to dramatic changes in the topography (Tsang et al., 2006). When an area of about 2400 m<sup>2</sup> was excavated in the NKLE salvage archaeological site between Sep.2002

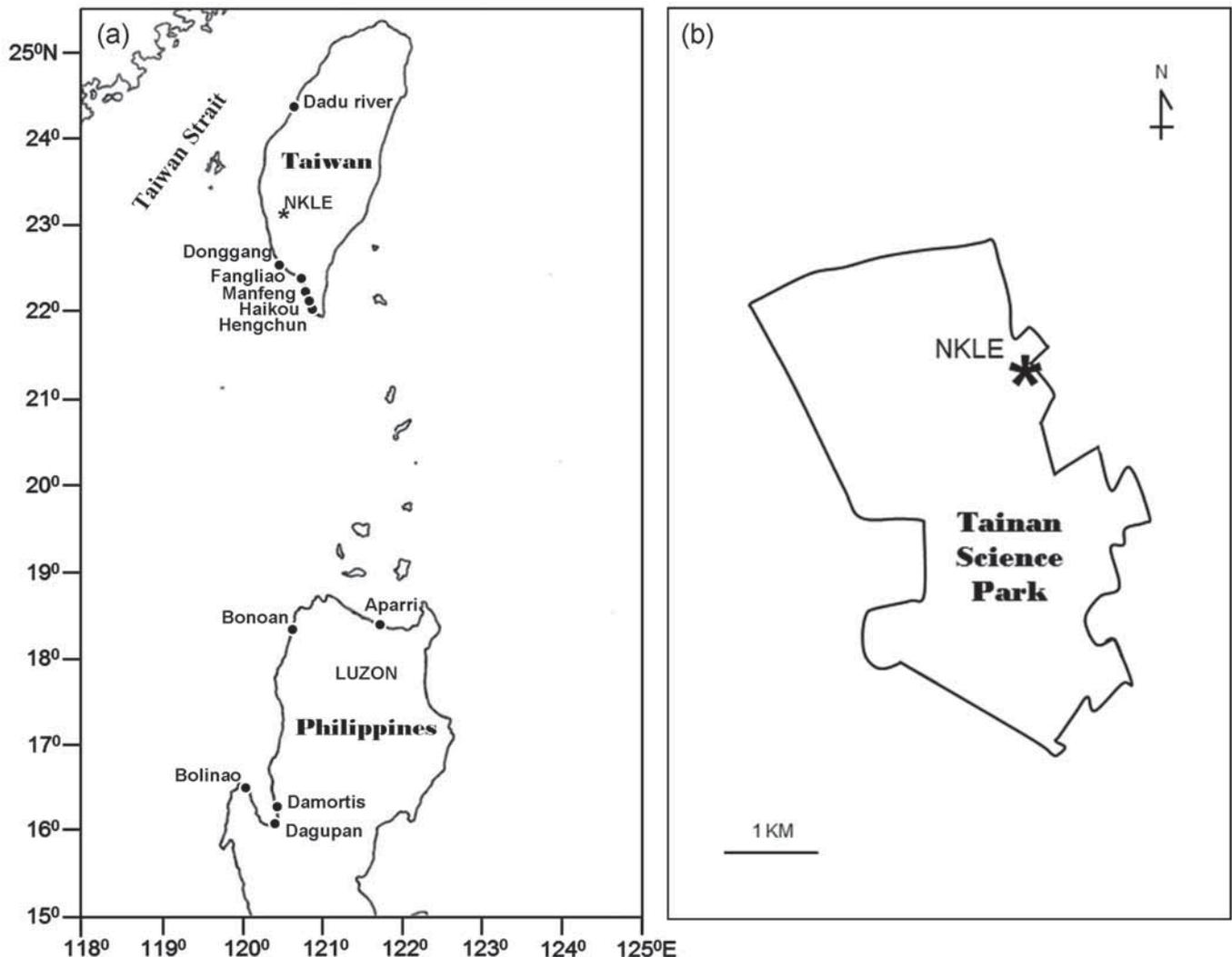


Fig. 1. Location of the sampling sites for the modern (a) and archaeological (b) *Pomadasys* otoliths. NKLE (Nankuanli East) archaeological site.

and Mar.2003, three major depositional layers of the Tapenkeng Culture were uncovered. The archaeological cultural component layers were located 7 m below the surface and contained an abundance of artifacts and faunal remains, dating back to a period between 4800 and 4200 calendar years before present based on radiocarbon-14 dating of ceramic artifacts. A total number of 826 fish otoliths, including 60 from *Pomadasys*, were sorted from the archaeological middens. All the archaeological otolith specimens were encoded by sagitta collection (SG) of the Institute of History and Philology, Academia Sinica (Tsang et al., 2006).

For the morphological comparison of otoliths, 71 fish representing the four modern *Pomadasys* species occurring

in the area were collected from fish markets in Taiwan and Luzon Island of the Philippines (Fig. 1a). From those, 34 were *P. argenteus* collected from Hengchun (n = 2), Fangliao (24), and Haikou (1) in southwestern Taiwan. Another seven individuals were collected from Bolinao (4) and Dagupan (3) in central-western Luzon Island, Philippines. For *P. kaakan*, the 13 individuals collected were from Donggang in southwestern Taiwan (3) and from the Dadu River in central-western Taiwan (10). Twenty-two *P. maculatus* were collected, four from Fangliao, and six from Donggang in southwestern Taiwan, nine from Aparri in northern Luzon Island, one from Damortis, and two from Bonoan in central-western Luzon Island, Philippines. For *P. quadrilineatus*, the two individuals collected were from Manfeng in southern Taiwan. After determining the total

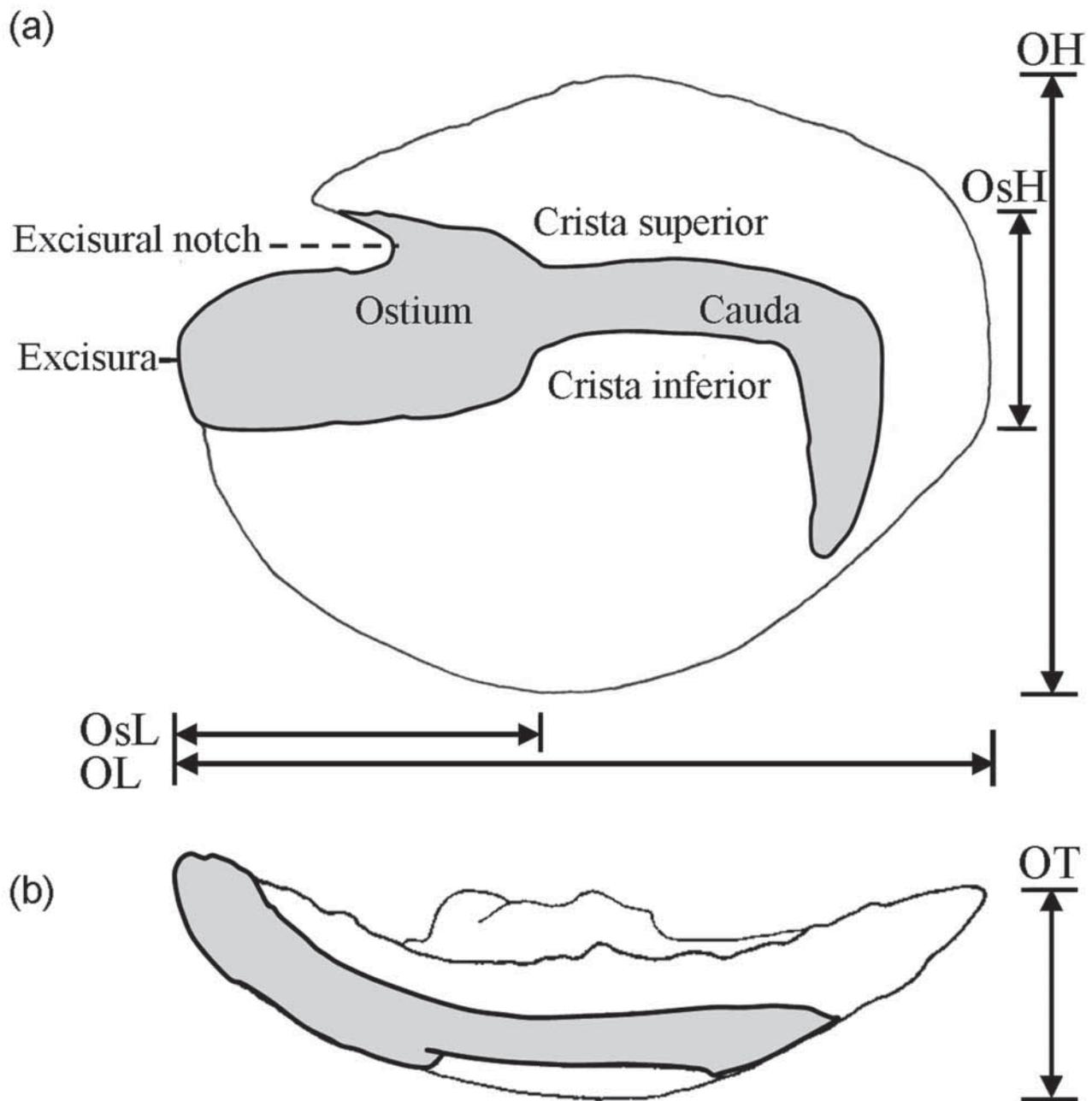


Fig. 2. Medial view (a) and dorsal view (b) of the otolith illustrating the features described and their measurements. The grey area is the sulcus. OH, otolith height; OL, otolith length; OT, otolith thickness; OsH, ostium height; OsL, ostium length.

length (LT, 0.01 mm) and weight (WT, 0.01 g) of the fishes collected, the sagittal otoliths were removed. The otoliths were then pretreated with a 3% solution of potassium hydroxide, rinsed with distilled water, and then air-dried. All modern otolith specimens were archived in the otolith collection of the National Museum of Marine Biology and Aquarium (NMMBOL).

**Otolith measurement and fish size estimation.** — Images of modern and archaeological otolith samples were digitised using a stereomicroscope (Discovery V20, ZEISS) with the aid of proper dimensioning and orientation. Otolith-shape characters were measured using imaging software (AxioVs40 V4.7.2.0, ZEISS). Otolith length (OL, 0.01 mm) was measured as the greatest distance from the anteriormost point to the posterior margin, approximately parallel to the sulcus. Otolith height (OH, 0.01 mm) was recorded as the greatest distance between the dorsal edge and the ventral edge, perpendicular to the otolith length. Otolith thickness (OT, 0.01 mm), usually in the central portion, was measured as the greatest distance between the medial and lateral surfaces. Ostium length (OsL, 0.01 mm) and ostium height (OsH, 0.01 mm) were the greatest lengths of ostium and the greatest distance between the crista superior and crista inferior of ostium, respectively (Fig. 2). Otolith descriptions

in this study followed the nomenclature presented in previous literature (Nolf, 1985; Smale et al., 1995; Iizuka & Katayama, 2008; Tuset et al., 2008; Lin & Chang, 2012). The relationships between otolith length (OL) and both the total length (LT) and body weight (WT) of the predominant species were established by linear ( $LT = aOL + b$ ) and curvilinear ( $WT = aOL^b$ ) regression analysis, respectively. Based on the fish-otolith size regression equations, we estimated the fish sizes from the species-identified otoliths found at the NKLE site.

### SYSTEMATIC DESCRIPTION OF RECENT *POMADASYS* OTOLITHS

#### Genus *Pomadasys* Lacepède, 1802

The general morphology of otoliths of the genus *Pomadasys* is oval in shape, moderately thick to thick, dorsal rim entire and ventral rim entire to lobed. The sulcus is ostial, with or without a notch, median in position, and heterosulcoid in shape. The ostium is rectangular in shape, with the cauda varying from strongly (60–65°) to markedly (80–90°) curved.

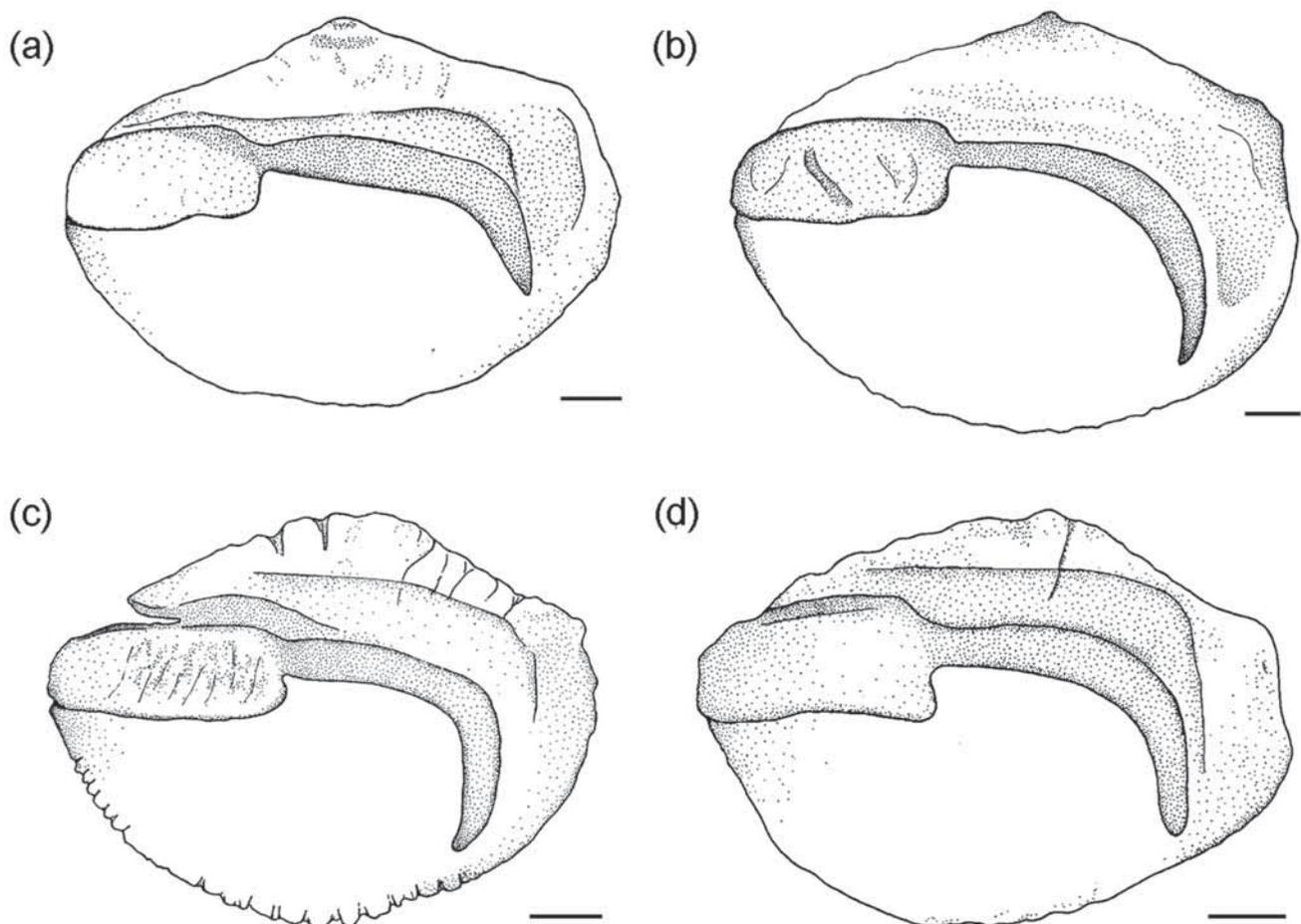


Fig. 3. Medial surfaces of the right sagittae of *Pomadasys argenteus*, NMMBOL00223 (a); *P. kaakan*, NMMBOL01952 (b); *P. maculatus*, NMMBOL00719 (c); *P. quadrilineatus*, NMMBOL00799 (d). Scale bar = 1 mm.

***Pomadasys argenteus* (Forsskål, 1775)**

(Fig. 3a; no. 1–2 in pl. 1)

**Material examined.** — 34 sagittae (NMMBOL 0223, 3160–3162, 3776–3777, 3780–3792, 3825–3831, 3978–3985).

**Description.** — Shape oval, with convex medial face and slightly concave lateral face. Central portion thick. Dorsal margin with conspicuous angles pointing upwards in the middle and posterodorsally, whereas the ventral margin rounded and entire. Crista superior moderately- to well-developed along ostium and posterior cauda, and ridge-like along anterior cauda. A dorsal trough located above the crista superior. Crista inferior moderately developed along ostium and well developed along cauda. Ostium elongate, with rounded posteroventral corner. Cauda flexes near tip, and the direction of the crista inferior changes notably in this area. Ostium usually well developed, creating moderately wide excisura. Excisural notch absent.

**Dimensions.** — OL, 6.04–19.44 mm; OH, 4.57–14.64 mm; OT, 1.36–5.68 mm; OsL, 2.60–10.01 mm; OsH, 1.25–4.04 mm.

**Diagnosis.** — The elongate ostium and the absence of a notch differentiate *P. argenteus* from *P. quadrilineatus* and *P. maculatus*, respectively. The disrupted curvature and position of the cauda of *P. argenteus* is slightly different from *P. kaakan*.

***Pomadasys kaakan* (Cuvier, 1830)**

(Fig. 3b; no. 3–4 in pl. 1)

**Material examined.** — 13 sagittae (NMMBOL 1952, 3796–3805, 3919–3920).

**Description.** — Shape oval, with convex medial face and slightly concave lateral face due to moderate thickness of central portion. Dorsal margin subangular and ventral margin round. Crista superior moderately developed along the ostium, ridge-like anterior and well-developed posterior to caudal flexion. Dorsal trough visible to crista superior. Crista inferior moderately developed along ostium, well developed along cauda. Ostium elongate with rounded posteroventral corner. Cauda flexion approximately halfway along its length, but curvature smooth (not angled). Excisura moderately wide, pointing anteriorly, without notch. Smaller samples of OL <8 mm (NMMBOL 3801, 3803, 3919, 3920) with shallow, very acute and pointing upwards excisural notch on dorsal margin near anterior ostium.

**Dimensions.** — OL, 5.91–10.42 mm; OH, 3.73–7.75 mm; OT, 1.30–3.14 mm; OsL, 2.47–4.59 mm; OsH, 1.17–2.10 mm.

**Diagnosis.** — The narrow ostium of this species is different from the deep ostium of *P. quadrilineatus*, and the position

of the caudal flexion (at its half) and its gentle curvature is distinct from *P. argenteus*. The otolith morphology of *P. kaakan* is very similar to that of *P. argenteus*, and a careful examination is necessary to differentiate the two. Most *P. kaakan* have an excisura without a notch, and even if they do, the excisural notch is very different from that of *P. maculatus*.

***Pomadasys maculatus* (Bloch, 1793)**

(Fig. 3c; no. 5–6 in pl. 1)

**Material examined.** — 22 sagittae (NMMBOL 0717–0720, 3816–3824, 3832–3834, 3923–3928).

**Description.** — Suboval in shape with moderately convex medial and moderately concave lateral faces. Thick centrally. Dorsal margin sinuate, ventral margin crenate. Crista superior and crista inferior moderately- to well-developed along sulcus. Dorsal trough visible to crista superior. Posteroventral corner of ostium round. Caudal flexion appears mid-length, turning downward nearly 90 degrees. Excisural notch deep and acute, pointing forward.

**Dimensions.** — OL, 5.28–8.57 mm; OH, 4.20–6.21 mm; OT, 1.12–2.27 mm; OsL, 2.60–4.51 mm; OsH, 1.26–2.09 mm.

**Diagnosis.** — The deep notch is diagnostic of *P. maculatus*. This species also shows a larger otolith height than *P. argenteus* and *P. kaakan* in a similar otolith length.

***Pomadasys quadrilineatus* Shen & Lin, 1984**

(Fig. 3d; no. 7–8 in pl. 1)

**Material examined.** — 2 sagittae (NMMBOL 0799, 1007).

**Description.** — Oval to oblong shape, slightly convex medial face and slightly concave lateral face. Dorsal margin slightly irregular and ventral margin rounded and minutely crenate in the middle. Crista superior well developed except for above the anterior cauda, where slightly ridge-like. Dorsal trough visible to crista superior. Crista inferior moderately developed. Cauda straight anteriorly, flexing sharply at two-thirds of the length. Ostium broad, the posteroventral corner wide, pointing posteriorly to form a lobe. Excisural notch absent.

**Dimensions.** — OL, 7.38–7.72 mm; OH, 5.02–5.52 mm; OT, 1.56–1.67 mm; OsL, 2.52–3.09 mm; OsH, 1.76–1.88 mm.

**Diagnosis.** — The broad ostium (caused in part by a deep trough near the dorsal margin of the ostium), with a well-developed posteroventral corner (creating a lobe) is diagnostic. The relative thinness and slender outline of the sagittae are also diagnostic.

**Keys to the identification of *Pomadasys* otoliths in Taiwan**

Otoliths of the *Pomadasys* species differ by the existence of an excisural notch, the curvature of the cauda, and the width of the ostium. The following is the dichotomous key to the four species in this study.

1. Excisura with deep notch, pointing forward .....  
.....*P. maculatus* (Fig. 3c)
- Excisural notch absent or excisura with shallow pointing upward notch.....2
2. Deep ostium (ostium height/ostium length above 0.61).....  
.....*P. quadrilineatus* (Fig. 3d)
- Ostium not so deep (ostium height/ostium length below 0.55).....3
3. Curvature begins in the posterior cauda, flexion with notable change in direction, usually with strongly angled cauda.....  
.....*P. argenteus* (Fig. 3a)
- Curvature begins in middle cauda, flexion is smooth, usually with gentle curved cauda ..... *P. kaakan* (Fig. 3b)

**Description of *Pomadasys* Otoliths from the NKLE Archaeological Site**

A total of 60 otolith specimens belonging to the genus *Pomadasys* were sorted in NKLE. Among them, 37 otoliths were identified as *P. argenteus*, accounting for 61.7% of the total. Six (10%) of the remaining otoliths were identified as *P. kaakan*, one (1.67%) as *P. maculatus*, and six (10%) as *P. quadrilineatus*. Ten specimens (16.67%) lacked distinguishable characteristics probably due to erosion and could not be identified.

***Pomadasys argenteus* (Forsskål, 1775)**  
(no. 9–10 in pl. 1)

**Material examined.** — 36 sagittae (SG 0251-2, 0254-2, 0262-1, 0263, 0264, 0266-2, 0267, 0268, 0270-2, 0271-1, 0271-3, 0272-3, 0273-2, 0274-2, 0274-10, 0274-13, 0274-14, 0275-10, 0275-7, 0277-1, 0277-3, 0277-4, 0277-5, 0278, 0280-1, 0280-2, 0280-3, 0280-4, 0280-5, 0282, 0285-4, 0285-5, 0288-6, 0291-1, 0291-2, 0168+0292).

**Dimensions.** — Only complete specimens measuring OL, 4.93–26.43 mm; OH, 3.63–16.32 mm; OT, 1.10–6.53 mm; OsL, 1.66–13.16 mm; and OsH, 0.91–6.06 were considered.

**Remarks.** — Thirty-seven specimens of this species were found in the NKLE archaeological site. However, based on the perfectly matching broken edges, one sagitta was found to represent two specimens that were found a substantial distance apart. The two pieces consisted of SG 0168 which was the anterior part and SG 0292 which was the posterior part (no. 10 in pl. 1). Thus the actual count was 36 sagittae. This particular sagitta measured 26.43 mm long, 16.32 mm in height and was 6.53 mm thick. It was extremely large compared to the rest of the samples, which measured 4.93–8.40 mm in length, 3.63–6.06 mm in height, and 1.10–1.96 mm in thickness.

***Pomadasys kaakan* (Cuvier, 1830)**  
(no. 11–13 in pl. 1)

**Material examined.** — 6 sagittae (SG 0253-3, 0270-1, 0270-3, 0272-1+0272-2, 0274-9, 0285-3).

**Dimensions.** — OL, 5.76–7.91 mm; OH, 4.03–5.72 mm; OT, 1.34–2.06 mm; OsL, 1.95–3.40 mm; OsH, 0.98–1.49 mm.

**Remarks.** — A comparison of the cauda shape revealed that these specimens were somewhat different from the rest. The cauda curved more gently unlike those from *P. argenteus*. Specimens SG 0272-1 and SG 0272-2 from a single archaeological spot were recognised as being from the same sagitta (no. 13 in pl. 1) that had broken in the middle. Specimens SG 0270-3, 0272-1+0272-2, 0274-9, 0285-3 have an excisural notch that point upwards, with acute angles and very shallow. Thus five sagittae out of the six specimens were recognised as belonging to *P. kaakan*.

***Pomadasys maculatus* (Bloch, 1793)**  
(no. 14 in pl. 1)

**Material examined.** — 1 sagitta (SG 0275-6).

**Dimensions.** — OL, 6.14 mm; OH, 5.11 mm; OT, 1.54 mm.

**Remarks.** — The ventral margin was slightly crenate and most of the features along the margin were probably lost through erosion. The most anterior portion of the otolith was lost. Regardless of the incompleteness, the deep otolith shape and sharp turning of the caudal flexion revealed the characters of *P. maculatus*.

***Pomadasys quadrilineatus* Shen & Lin, 1984**  
(no. 15–16 in pl. 1)

**Material examined.** — 6 sagittae (SG 0251-1, 0254-3, 0262-2, 0277-2, 0277-6, 0283).

**Dimensions.** — OL, 5.30–7.28 mm; OH, 3.79–5.01 mm; OT, 1.31–1.67 mm; OsL, 1.99–2.58 mm; OsH, 1.10–1.47 mm.

**Remarks.** — Six specimens are identified as *P. quadrilineatus* based on their broad ostiums and lobe-like ostium posteroventral corners.

**Estimation of the original fish size based on the otoliths of *P. argenteus* collected in the middens.** — Because *P. argenteus* was the most abundant species found in the NKLE archaeological site, their original sizes were estimated. Fig. 4 showed the relationships among fish total length (LT) and body weight (WT), and otolith length (OL) for the modern samples, which were  $LT = 2.87 \times 10^{-5} WT^{2.89}$  ( $R^2 = 0.99$ ,  $n = 28$ ),  $LT = 24.75OL - 55.66$  ( $R^2 = 0.98$ ,  $n = 33$ ) and  $WT$

$= 0.04OL^{3.48}$  ( $R^2 = 0.98$ ,  $n = 28$ ), respectively. Excluding the six otoliths with damaged posterior rims (SG 0274-2, 0277-5, 0280-1, 0280-2, 0280-3, 0280-5), the fish size of 30 complete otoliths from the NKLE site were estimated. Otolith lengths of the most archaeological otoliths ranged from 4.93–8.40 mm, which fell within the lower region of the regression equation used in the estimation and slightly beyond the 6.04 mm for the smallest length of modern otoliths. Accordingly, the fish sizes estimated from the otoliths in the NKLE site were less than 152.15 mm in total length and less than 59.68 g in weight, with a mean and standard deviation length of  $117.48 \pm 21.16$  mm and a weight of  $33.57 \pm 13.63$  g. One extremely large-sized otolith (SG 0168+0292) measured 26.43 mm in length, and was far beyond the 19.44 mm for the largest length of modern

otoliths. The extrapolated estimation of that particular fish was 598.03 mm in length, with an obviously variable extrapolation of 3225.54 g in weight (Figs. 4, 5).

DISCUSSION

Precise descriptions of the general otolith morphology of modern *Pomadasys* fishes made it possible to distinguish the congeneric otoliths from the fish remains. Consequently, species composition, distribution and size of the *Pomadasys* fishes in the archaeological site could be determined and compared with the modern species. In this study, the archaeological otoliths corresponded well with those of four modern *Pomadasys* species extant in Taiwan. Randall & Lim (2000) reported that these four species overlapped in their geographic distribution. Shao et al. (1993), Kuo & Shao (1998), Shao (2009), Chang et al. (2011) and our sampling indicated that these fishes seem to occupy slightly different areas along Taiwan’s coast. *P. argenteus* is often found along the southwestern to southeastern tip of Taiwan, *P. kaakan* and *P. maculatus* appear more frequently on the western coastline and the northern tip of Taiwan, whereas *P. quadrilineatus* is commonly found all around Taiwan. The predominant species of otoliths found in the NKLE archaeological site was *P. argenteus*, which coincides with its current distribution. According to the checklist in the FishBase, approximately 11 out of 36 modern *Pomadasys* fishes are distributed in the western Pacific (Froese & Pauly,

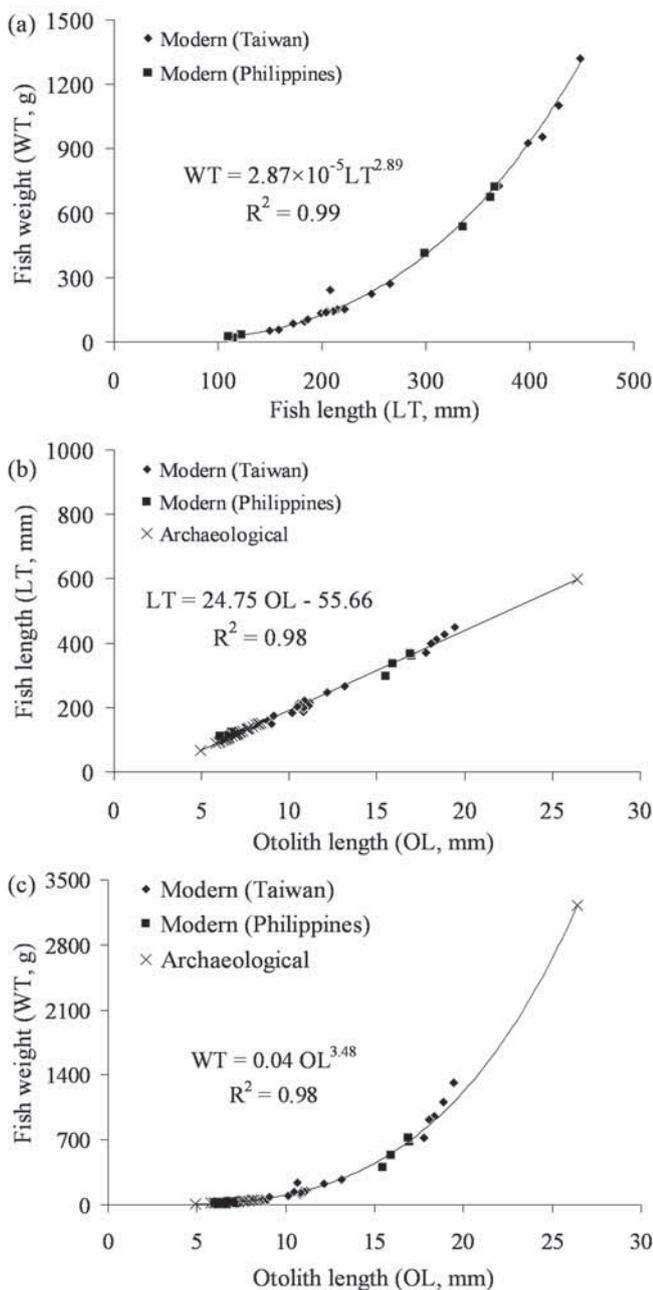


Fig. 4. Relationships between fish total length and fish weight (a), otolith length and fish total length (b), and otolith length and fish weight (c) of *Pomadasys argenteus*.

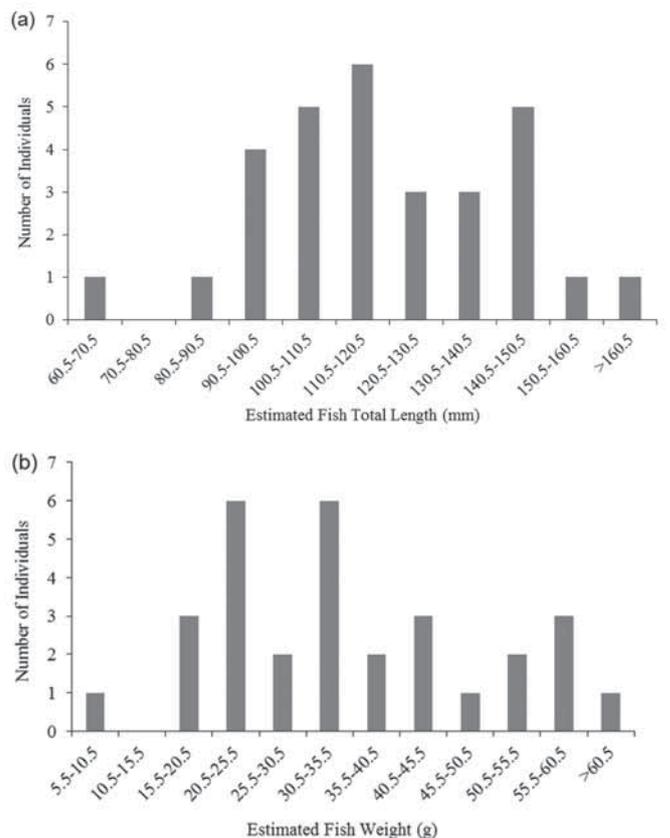


Fig. 5. Frequency distribution of estimated fish total length (a) and fish weight (b) for the otoliths of *Pomadasys argenteus* in the archaeological site of Nankuanli East, Tainan City, Taiwan.

2012). A further comparison of other archaeological otoliths with extant *Pomadasys* species has great potential to clarify and reconstruct the species composition and distribution of the fishes.

The estimation of original fish size for *P. argenteus*, the most abundant species in the NKLE archaeological site, provided a major implication of coastal adaptation for the prehistoric NKLE inhabitants. The SG 0168+0292 otolith specimen was a rare case having an extrapolated estimation of 598.03 mm in fish length, almost as large as the 660 mm of the maximum total length of *P. argenteus* recorded in Taiwanese waters (Shao, 2009). Most fish sizes estimated from *P. argenteus* otoliths in the NKLE site were less than 152.15 mm in total length and 59.68 g in weight (Fig. 4). The relatively smaller fish size of *P. argenteus* from the NKLE site could mean that prehistoric tribes might have had limited fishing practices. However, two alternative explanations are equally plausible. First, *Pomadasys* fishes might go through ontogenetic habitat shifts the same as other

Haemulidae fishes, with smaller individuals found nearshore (Appeldoorn et al., 2009). Small fish size could merely be indicative of the habitat fished. Second, many nearshore environments, such as estuaries, mangroves, and seagrass beds, are highly productive and support large numbers of small fishes. Thus, there should have been a certain connection between coastal habitat and the archaeological remains. The small fish sizes found at NKLE might be influenced by human behaviour (fishing practices), or were they influenced by environmental conditions (location and fish population characteristics). In addition, the majority of the total lengths of these fishes ranged between ca. 90 mm and 150 mm (Fig. 5a), indicating that this might be due to the mesh selection of their nets (van Slyke, 1998). The nettings they used were probably small mesh inshore seine nets based on the biology and ecology of this fish species, with an occasionally much larger fish. The above postulation was further supported by the wide discovery of stone sinkers at the archaeological site (Tsang et al., 2006). Thus, it seems that at the NKLE site, the inhabitants strongly favoured a

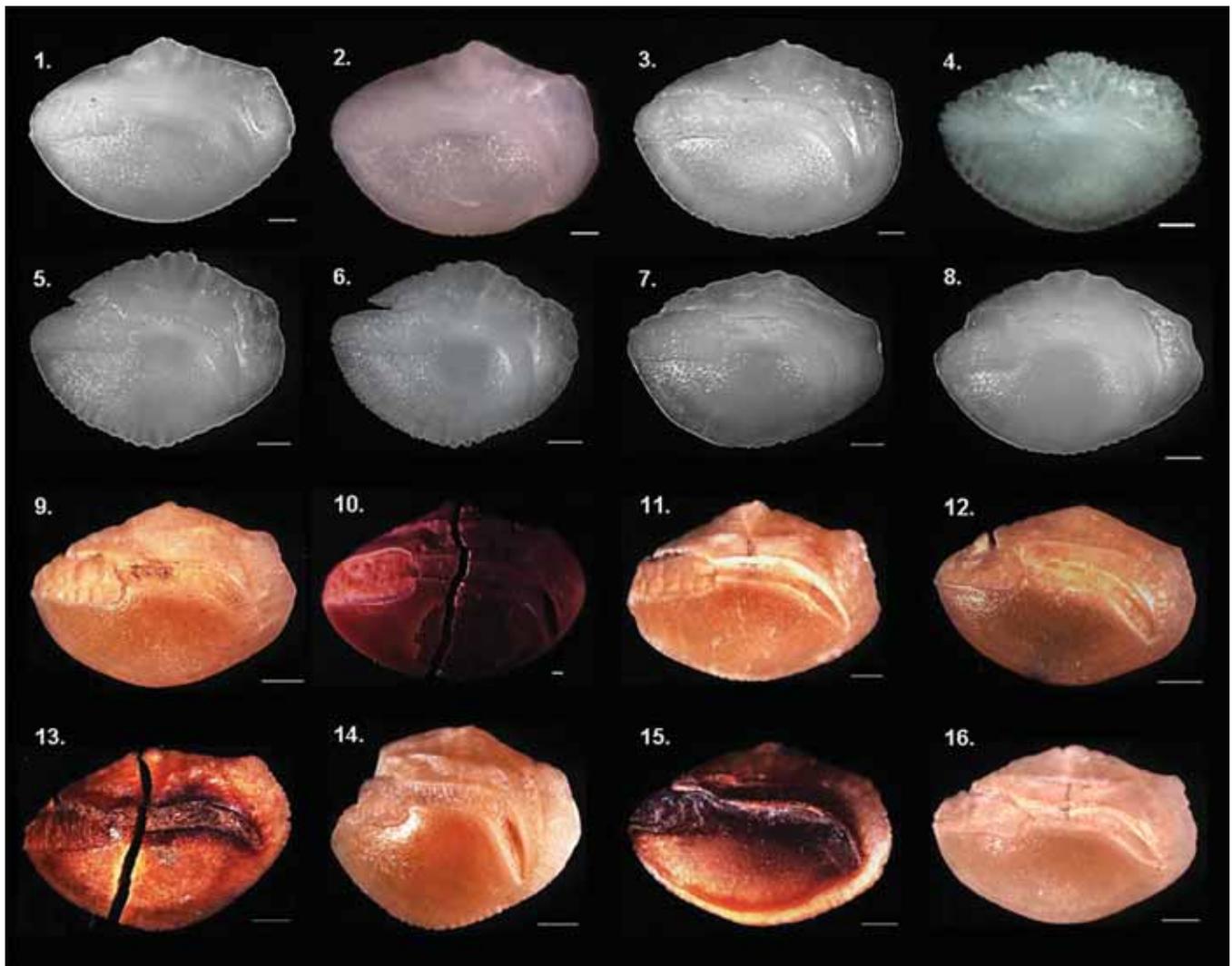


Plate 1. Modern (no. 1–8) and archaeological (no. 9–16) sagittae of the genus *Pomadasys*. *Pomadasys argenteus*: No. 1 (NMMBOL 0223), 2 (NMMBOL 3782), 9 (SG 0277-4), and 10 (SG 0168+0292); *P. kaakan*: No. 3 (NMMBOL 1952), 4 (NMMBOL 3798), 11 (SG 0270-1), 12 (SG 0274-9), and 13 (SG 0272-1+0272-2); *P. maculatus*: No. 5 (NMMBOL 0717), 6 (NMMBOL 0719), and 14 (SG 0275-6); *P. quadrilineatus*: No. 7 (NMMBOL 0799), 8 (NMMBOL 1007), 15 (SG 0251-1), and 16 (SG 0254-3). Scale bar = 1 mm.

coastal adaptation to marine fishery that went further than hook and line fishery (Huddleston & Barker, 1978; van Slyke, 1998).

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