RESEARCH ARTICLE

The Maturation of Skulls in Postnatal Risso's Dolphins (*Grampus griseus*) from Taiwanese Waters

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ABSTRACT: The degree of fusion between bones is a useful indicator of skeletal and sexual maturity for cetacean specimens preserved in museum collections. The aim of this study was twofold: first, to examine the degree of fusion between bony elements in skulls of Risso's dolphins (*Grampus griseus* Cuvier, 1812) from Taiwanese waters; and second, to analyze the relationship between skull maturity, body length, sexual maturity, and estimated age, with the aim of determining a useful skull predictor for maturity in Risso's dolphins. The stage of fusion of 20 superficial sutures or joints between selected skull bones was examined on 33 clean, dry skulls, which were salvaged from stranded or bycaught dead Risso's dolphins in Taiwanese waters during the years of 1994 – 2001. The bones of the caudoventral braincase fused early in development (basioccipital-exoccipital synchondrosis, supraoccipital-exoccipital suture), whereas fusion along the nuchal crest (fronto-interparietal and fronto-parietal sutures) occurred later. Some sutures remained open in some adult specimens (lacrimal/maxilla-frontal, squamosal-parietal, squamosal-exoccipital sutures, and the intermandibular symphysis). Bilateral asymmetry of the fusion process was not detected. Advanced fusion occurred in the fronto-interparietal suture along the medial aspect of the nuchal crest, and in the rostral nasal-frontal and distal maxilla-incisive sutures at total body length > 250 cm, and may be useful skull indicators of sexual maturity.

KEY WORDS: *Grampus griseus*, maturity, Risso's dolphin, skull, skeletochronology, Taiwan.

INTRODUCTION

Skulls are routinely studied as part of many investigations of mammalian biology. Both qualitative and quantitative features are examined to discern the presence and degree of sexual dimorphism, ontogenetic and individual variation, as well as geographic or oceanographic variation within and amongst populations (Perrin, 1975). Such data contribute substantially towards the answers of taxonomic, ecological, and evolutionary questions. Since these characters typically change during growth, an adult skull with relatively fixed characteristics is preferred for non-developmental aspects of these examinations (Perrin and Heyning, 1993). Unfortunately, skulls of many cetaceans in museum collections lack accompanying vital data of body size, reproductive status, or other age-related information, and thus the degree of ontogenetic fusion of sutures on the skull may be substituted as a useful predictor of maturity for these specimens (Dailey and Perrin, 1973).

Skull maturity related to chronological age is comprehensively documented in a pioneering study of spotted and spinner dolphins (genus *Stenella*) from the eastern tropical Pacific and Hawaiian waters (Perrin, 1975). Each complex of bones, serving a common function (bony apparatus), develops in a particular chronological sequence postnatally based on its adaptive functional development. A simplified technique based on a single site – the degree of fusion of the distal maxilla-premaxillary suture (referred to hereafter as maxilla-incisive suture) – is shown to be a reliable indicator to differentiate skeletally immature specimens in spotted (*Stenella attenuata* Gray, 1846) and spinner dolphins (*Stenella longirostris* Gray, 1828) (Dailey and Perrin, 1973), bottlenose dolphins (*Tursiops truncatus* Montagu, 1821) (Mead and Potter, 1990) and striped dolphins (*Stenella coeruleoalba* Meyen, 1833) (Calzada et al., 1997). On the other hand, fusion at this site was an unreliable predictor of skeletal maturity in short-beaked common dolphins (*Delphinus delphis* Linnaeus, 1758) (Perrin and Heyning, 1993), dusky dolphins (*Lagenorhynchus obscurus* Gray, 1828) (Van Waerebeek, 1993), and in Pacific white-sided dolphins (*Lagenorhynchus obliquidens* Gill, 1865) (Walker et al., 1986), since fusion occurred inconstantly in both sexually mature and immature dolphins.

Advanced fusion of the frontal-supraoccipital suture is 95% accurate as a predictor of sexually maturity in dusky dolphins (Van Waerebeek, 1993). It is apparent therefore, that the developmental process of each suture in the skull has its own chronological variation amongst species, and hence empirical baseline data needs to be established for each species, and perhaps for each regional population.

Risso's dolphin (*Grampus griseus* Cuvier, 1812) is a moderately small odontocete, commonly sighted throughout the world's temperate and tropical waters (Baird, 2002). Their cosmopolitan status (Taylor et al., 2008), however, belies the status of their seldom-studied biology. Surprisingly, there were few studies on the skeletal characters of Risso's dolphins, probably due to low numbers of specimens because they uncommonly strand (Kruse et al., 1999). The skulls of two females (3.2 m adult, 1.85 m immature calf) founded an early detailed morphological account (Flower, 1874), while further comprehensive illustrations from two sub-adult / adult and two immature specimens depict many of the sutures and joints analyzed herein (Van Bénéden and Gervais, 1868-80). Subsequent reports provided additional skull features to help clarify the taxonomic status of this species (True, 1889; Mizue and Yoshida, 1962; Ross, 1984). Other than a brief notation that the palatine-maxillary and maxilla-incisive sutures are "fully fused in old specimens" (True, 1889), we are not aware of systematic studies on either the development or on the maturation of the skeleton, including its skull, in Risso's dolphins.

The aim of this present study was to investigate the maturation of the skull in Risso's dolphins from Taiwanese waters, and in particular to examine the degree of fusion between the bony elements as seen on their dried, cleaned skulls preserved as museum specimens. We then analyzed the relationship between skull maturity, body length, sexual maturity, and estimated age, with the aim of finding an appropriate skull indicator of overall maturity. Principally we found that bony fusion occurred first in the caudoventral braincase, and then in sutures along the nuchal crest medially, followed by other sites, although some sutures remained open into adulthood. Fusions of three sutures were identified as accurate predictors of sexual maturity in Risso's dolphins. Anatomical terminology follows Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 2005; see also Mead and Fordyce, 2009) unless otherwise noted.

MATERIALS AND METHODS

Specimens

Clean, dry skulls salvaged from 33 dead Risso's dolphins (13 female, 11 male, nine of undermined sex, 136 – 284 cm TBL, total body length) stranded or bycaught in Taiwanese waters (1994 – 2001), were prepared and preserved in the National Museum of Natural Science (Taichung, Taiwan). Salvage date, sex, and standard external morphological data (Norris, 1961) were recorded (Supplement A). Reproductive maturity was assessed in nine dolphins (four female, five male): females were classified sexually mature if either milk was found in a mammary gland or a corpus luteum or corpus albicans was present in an ovary (Perrin and Reilly, 1984); males were classified as sexually mature if either a testis weighed more than 300 g (Kasuya and Izumizawa, 1981; Amano and Miyazaki, 2004) or if it measured more than 40 cm in length (Ross, 1984; Chen et al., 2011a). Age was estimated in three dolphins (one female, two males) by determining the number of growth layer groups (GLG) in routine histological preparations of longitudinally sectioned teeth, calibrated on one GLG representing one calendar year (Kruse et al., 1999; Amano and Miyazaki, 2004). In the case of nine dolphins without known TBL and sex, we considered that they were sexually mature when condylobasal length (CBL) > 465 mm (n = 3) and immature when CBL < 465 mm (n = 6) (Mizue and Yoshida, 1962). Condylobasal length (CBL – as a straight line from the tip of rostrum, incisive bone, to the occipital condyle – Perrin, 1975) was measured on 30 additional intact skulls to provide reference data for this determination.

Maturity examination

The maturation of the skull was evaluated by examination of the fusion between bones forming 20 selected superficial sutures, synchondroses, symphysis, or joints of the skull (Fig. 1). These particular fusion sites were selected based on our preliminary study of Risso's skulls and recommendations from previous studies on cranial maturity in other delphinids (Mead and Potter, 1990; Van Waerebeek, 1993; Calzada et al., 1997). Our definitions in alphabetical order:

BO-EO: the basioccipital-exoccipital synchondroses on the ventral surface of the cranium (left and right);

FR-FR: the interfrontal suture, examined on the most rostral extent visible superficially (**FR-FRro**) and the caudal extent (**FR-FRcd)**, but not the middle section which was covered by the nasal bones;

FR-IP: the fronto-interparietal suture on the dorsal surface of the cranium, medially between left and right FR-PR;

FR-PR: the fronto-parietal sutures at the nuchal crest (left and right side);

LC: the lacrimal/maxilla-frontal sutures (left and right);

MX-INdi: the bony rostrum between the antorbital notch and the rostral tips of incisive bone; the distal-most, or

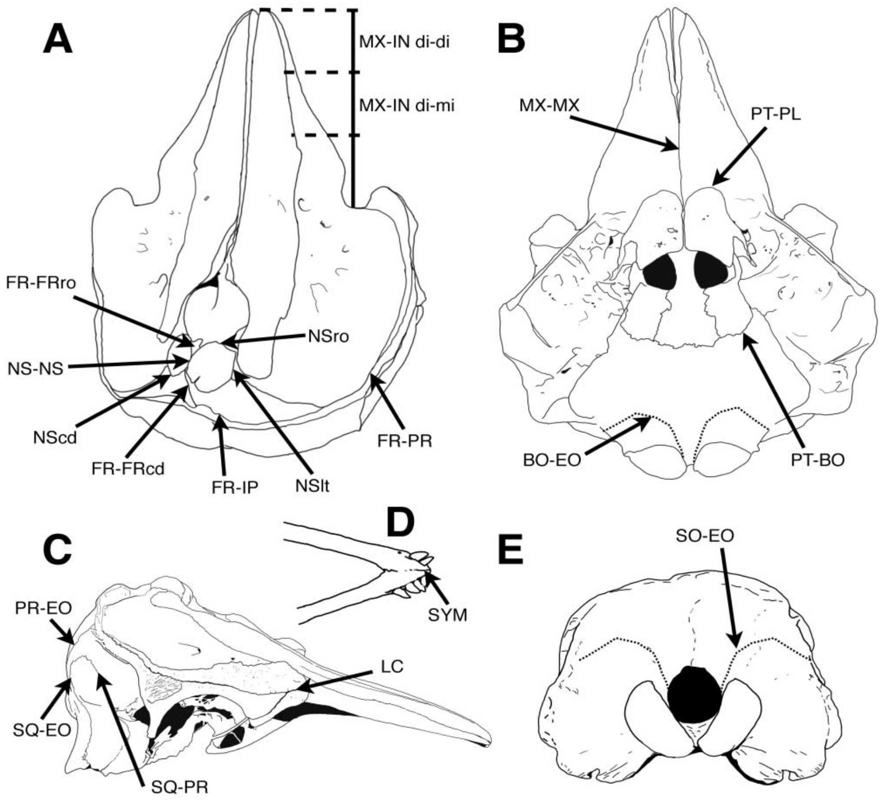

Fig. 1. Sketches of skulls of Risso's dolphin from Taiwanese waters showing the 20 superficial sutures, synchondroses, symphysis, or joints examined for fusion states: in dorsal view (A), ventral view (B), lateral view (C), ventral view of rostral ends of mandibles (D), and caudal view of skull (E). Abbreviations for fusion sites designated as per Materials and Methods.

most rostral one-third (**MX-INdi-di**) and the middle-third (**MX-INdi-mi**) of the maxilla-incisive sutures were evaluated along the dorsal surface of the rostrum (left and right);

MX-MX: the median intermaxillary suture on the caudal half of the ventral surface cranium;

NS: the nasal-frontal sutures, recorded as **NSro** (from rostally end of NS-NS to the rostral-lateral corner), **NSlt** (the rostral-lateral corner to the caudal-lateral corner) and **NScd** (from the caudal-lateral corner to the caudal end of NS-NS), both left and right were examined;

NS-NS: the internasal suture on the dorsal cranium;

PR-EO: the parietal-exoccipital sutures (left and right);

PT-BO: the pterygoid-basioccipital joints on the ventral surface of the basicranium (left and right) (the developmental history of the cetacean pterygoid is complex, possibly originating in membrane and cartilage, thus designation of joint type at this site is not clear);

PT-PL: the pterygoid-palatine sutures evaluated around its full periphery on the external surface (left and right);

SO-EO: the supraoccipital-exoccipital sutures on the external surface of the caudal cranium (left and right);

SQ-PR: the squamosal-parietal sutures (left and right);

SQ-EO: the squamosal-exoccipital sutures (left and right);

SYM: the full circumferential line of symphysis between the left and right mandibles.

The scoring method for skull maturation was based on the degree of movement and the degree of bony fusion between the adjacent bones (modified after Van Waerebeek, 1993). Fusions only refer to those which were visible to the unaided eye on the external surface of the skull.

Stage 0: the bones could be moved freely; there being no fusion;

Stage 1: the bones could not be moved, and the junction between the bony elements was clearly visible at all points;

Stage 2: partial obliteration of the suture line or joint, due to advancing fusion;

Stage 3: complete obliteration of the suture line or joint.

Data Analysis

To determine the efficiency of fusion stage of skull sutures or joints as indicators for sex maturity, a misclassification index (Mead and Potter, 1990) was

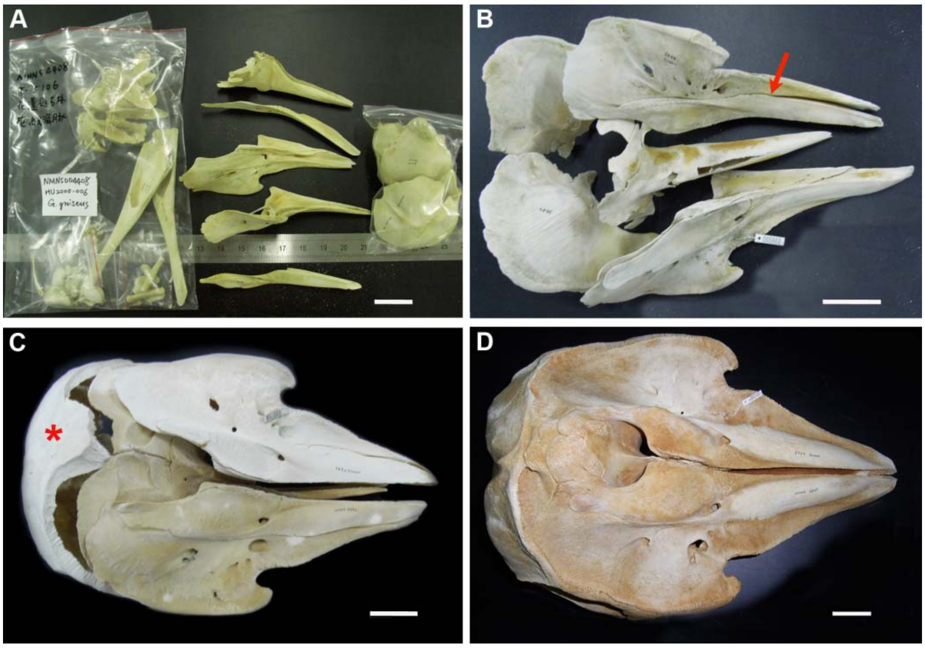

Fig. 2. Photographs of skulls of Risso's dolphins showing varying degrees of fusion, in dorsal view. Scale bar = 5 cm. A: All bones completely disarticulated, 136 cm, male, sexual maturity undetermined (stage 0). B: Some fusion (arrow) between incisive and maxilla of rostrum, 148 cm, sexually immature male. C: Intermediate fusion showing caudal skull (*) separation from rostral braincase and facial (sutures along the nuchal crest unfused), intermandibular symphysis unfused, 179 cm, sexually immature male. D: Advanced fusion, 254 cm, sexually mature male (many sutures at stage 2-3).

calculated. Wilcoxon signed-rank test was used to detect the bilateral asymmetry in the maturity stage between the sutures or joints on the left and right sides of the skull. Tests were carried out with packaged tools in the statistics software R (R Development Core Team, 2010), and were considered statistically significant at $P < 0.05$.

RESULTS

Skull Maturation Process

Generally, the fusion between bones was more advanced in dolphins with longer TBL (Fig. 2A-D). The least fusion was seen in the shortest male dolphin (136 cm TBL), of which the skull was completely disarticulated and the bony elements were all separate (Stage 0) (Fig. 2A). Intermediate levels of fusion were apparent in skulls of dolphins of longer TBL (Fig. 2B, C). In contrast, the most developmentally mature skulls came from one male (254 cm) and one female (272 cm). Both were sexually mature. Their sutures, joints, synchondroses and the symphysis were all fused (at least Stage 1) and many of them were at advanced stages of fusion (Stage 2 – 3) (Fig. 2D).

In the shorter dolphins (136 – 234 cm), eight sutures and joints (LC, NS, NS-NS, MX-MX, PT-BO, PT-PL, SQ-EO, SQ-PR), and the intermandibular symphysis (SYM) remained unfused (Stage 0), whereas in longer dolphins (254 – 284 cm) many of these (MX-MX, NS, NS-NS, PT-BO, PT-PL, and SYM) were fused in varying degrees (Stage 1 – 3) (Fig. 3). The degree of fusion in three other sutures (LC, SQ-EO, SQ-PR), however, showed an inconsistent relationship with increasing TBL in dolphins longer than 234 cm.

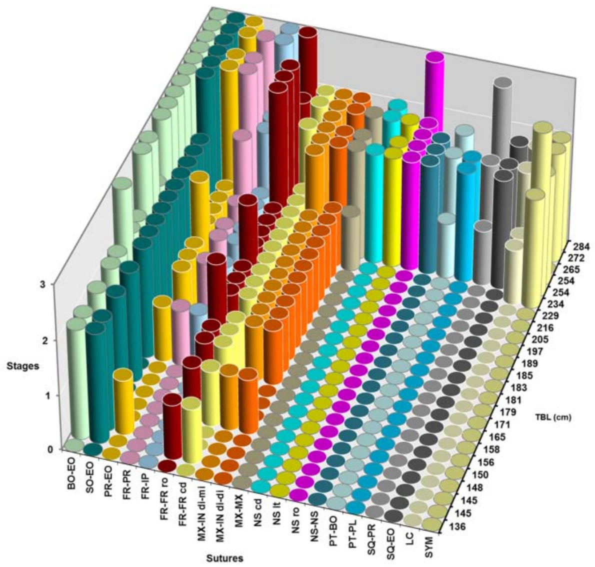

Fig. 3. Illustration showing relationship of fusion stage for 20 superficial sutures or joints in a developmental series of skulls from 24 Risso's dolphins (TBL) (abbreviations for fusion sites designated as per Materials and Methods).

Three other sutures, however, had a consistent pattern of fusion related to increasing TBL. For FR-FR, MX-INdi and PR-EO, the onset of Stage 0 occurred at TBL 145 – 181 cm and was consistently Stage 1 at TBL of 183 – 234 cm. They were generally at advanced stages of fusion (Stage 2 or 3) in dolphins at TBL > 254 cm. The suture and synchondrosis on the caudoventral braincase (BO-EO, SO-EO) remained open only in shorter dolphins (TBL 145 – 165 cm, stage 1), and both reached Stage 2 or 3 in longer ones (TBL > 171 cm).

Ages were estimated in three dolphins by counting growth layers in sectioned teeth. The degrees of fusions in a five-year-old female (TBL 229 cm) and a six-year-old male (TBL 234 cm) were almost the same, although more advanced fusions were seen at seven sites (FR-FRro, FR-PR, LC, MX-INdi-mi, MX-MX, SO-EO, and SYM) in the six-year-old one. In another female of 14 years old (TBL 272 cm), all examined sutures, the synchondroses, and the symphysis were fused and most had reached advanced fusion stages (Stages 2 or 3), except NS-NS and PT-PL (Stage 1).

Sexual maturity indicators

Sexual maturity was only examined in nine dolphins: six sexually immature (TBL 150 – 234 cm) and three sexually mature (TBL 254 – 284 cm). Advanced fusions (Stage 2 or 3) in FR-IP, MX-INdi-di, NSro, PR-EO, and SYM were found in all three sexually mature dolphins, and none in the immature (Stage 0). On the other hand, if the onset of sexual maturity occurs at TBL 250 cm (Amano and Miyazaki, 2004, Chen et al., 2011a), then the sutures FR-IP, MX-INdi-mi, NSro and PR-EO with misclassified rates of 0% would be more useful than those of FR-PR, PR-EO, and SYM with higher misclassified rates for indicating sexual maturity (Table 1).

Bilateral symmetry in maturation

No significant difference was detected in the fusion patterns of all 14 sutures or joints between the left and right sides of the skull (Wilcoxon signed-rank test, Table 2).

Table 1. Efficiency of fusion stage of skull sutures/ symphysis as indicator for sexual maturity, set at total body length (TBL) of 250 cm (after Mead and Potter, 1990).

Suture and Fusion Stage	TBL <250 cm	TBL >250 cm	Total Sample (*n*)	Percentage-misclassified
FR-IP *				
Stage 0, 1	25	0	25	0
Stage 2, 3	0	8	8	0
NSro (L)				
Stage 0, 1	25	1	26	3.9
Stage 2, 3	0	7	7	0
MX-INdi-di (L)				
Stage 0, 1	25	2	27	7.4
Stage 2, 3	0	6	6	0
PR-EO (L)				
Stage 0, 1	24	0	24	0
Stage 2, 3	1	8	9	11.1
FR-PR (L)				
Stage 0, 1	24	1	25	4
Stage 2, 3	1	7	8	12.5
SYM				
Stage 0, 1	24	2	26	7.7
Stage 2, 3	1	6	7	14.3

* Abbreviations of fusion sites were designated as per Materials and Methods.

Table 2. Wilcoxon Rank Test for bilateral asymmetry on the maturation stage of fusion of 12 superficial sutures, one joint, and one synchondrosis in Risso's dolphin skulls. No significant bilateral difference was detected ($P < 0.05$).

	n of pairs	W	*P*
BO-EO *	33	545	1.00
FR-PR	33	545	1.00
LC	33	545	1.00
MX-IN di-di	33	523	0.77
MX-IN di-mi	33	536	0.92
NS cd	33	539	0.93
NS lt	33	545	1.00
NS ro	33	555	0.86
PR-EO	33	554	0.90
PT-BO	32	494	0.74
PT-PL	33	564	0.75
SO-EO	33	545	1.00
SQ-EO	33	544	0.99
SQ-PR	33	545	1.00

* Abbreviations of fusion sites were designated as per Materials and Methods.

DISCUSSION

Process of skull maturation

In Risso's dolphins, various groups of skull bones had different fusion patterns. Bones of the caudoventral braincase were the earliest to fuse and were at advanced fusion before the onset of sexual maturity. Bones of craniodorsal skull (beneath the melon and narial tube-diverticular complex) commenced fusion approximately at a similar TBL to those in the caudoventral braincase, but took a longer time to complete the fusion process. They only reached an advanced fusion stage at the TBL of sexual maturity, i.e., relatively later. In contrast, sutures along the nuchal crest fused relatively later, and reached an advanced fusion stage when the dolphins attained a TBL close to the onset of sexual maturity. Sutures of the lateral braincase remained open at least in part in adulthood.

Overall, the sequence of postnatal development in Risso's dolphin skull was similar to that for spinner and spotted dolphins (Perrin, 1975) and harbor porpoises (*Phocoena phocoena* Linnaeus, 1758) (Gol'din, 2007) based on analyses of bony functional apparatuses. That is the bones of caudoventral braincase fused before those topographically associated with selected breathing/ sound producing structures of the skull (Perrin, 1975; Rommel et al., 2002). The intermandibular symphysis, functionally a part of the feeding apparatus, fused late in succession. Moreover, most skull elements in spotted and spinner dolphins mature to “adult configuration” (4 – 5 years of age) before onset of sexual maturity (9 – 11 years) (Perrin, 1975; Chivers and Myrick, 1993); whereas the complete process of skull maturation in Risso’s dolphins and harbor porpoises (see Gol'din, 2007) takes relatively longer. Even so, caution is suggested in this interspecies comparison since the examination methods were different amongst these studies (see above).

Suture fusion as predictor of sexual maturity

The fronto-interparietal suture at the medial aspect of the nuchal crest was an accurate predicator for sexual maturity in Risso’s dolphins (0% misclassified), based on onset of sexual maturity occurring at TBL 250 cm (Amano and Miyazaki, 2004, Chen et al., 2011a). This parallels a similar validation in dusky dolphins (their so-called frontal-supraoccipital suture) (Van Waerebeek, 1993). Furthermore, fusion along the distal rostrum (distal maxilla-incisive suture) was an equally valid predictor for sexual maturity. Advanced fusion of the distal portion of the maxilla-incisive suture as an indicator of sexual maturity has been confirmed in five small odontocetes: spotted dolphins (Dailey and Perrin, 1973; Douglas et al., 1984; Schnell et al., 1985; Yao et al., 2008), spinner dolphins (Dailey and Perrin, 1973; Douglas et al., 1986; Perrin et al., 1999), bottlenose dolphins (Mead and Potter, 1990; Van Waerebeek et al., 1990; Turner and Worthy, 2003), striped dolphins (Calzada et al., 1997), and Fraser's dolphins (*Lagenodelphis hosei* Fraser, 1956) (Perrin et al., 2003). We now add Risso’s dolphins to the list.

On the whole, we recommend three sutures, each as a good indicator of sexual maturity in Risso’s dolphins: the fronto-interparietal suture at the medial aspect of the nuchal crest, the distal maxilla-incisive suture along distal most one-third of the rostrum, and the rostral nasal-frontal suture at the rostral side of the nasal bone. All three were readily visible on the skull, and they were relatively consistent to identify in fusion stage with a low miscalculation rate (0%). Three other fusions also occurred at about sexual maturity: the parietal-exoccipital suture, the fronto-parietal suture, and the intermandibular symphysis. In these three, however, there was visual difficulty in clearly identifying the stage of fusion and they had high miscalculation rates, rendering them less useful for evaluations of skull maturation.

Bilateral symmetry in maturation

Bilateral asymmetry of the skull is a canonical character of odontocetes (Ness, 1967) and is considered fundamentally associated with the development of their echoimaging capability (Cranford et al., 1996). Even so, the development and the maturation of the bones in odontocete skulls seem to occur symmetrically – asymmetry in this process has not been reported. Likewise our study in Risso’s dolphins was unable to detect asymmetry in the maturation process of the skull, nor was it apparent in the maturation of their flipper bones (Chen et al., unpublished data).

Limitations of the study

This study is the first report of the maturation sequence in a developmental series of Risso’s dolphin skulls. We identified three sutures, of which advanced fusions were an accurate predictor of sexual maturity in our museum specimens. The strength of conclusions is restricted, however, by the small number of skulls with known TBL, sex, and chronological age. Risso’s dolphins vary morphologically throughout oceanographic regions (Kruse et al., 1999), and those from Taiwanese waters, underpinning this study, belong to the northwest Pacific population and have the shortest TBL worldwide (Chen et al., 2011a). The application of our skull maturation method to other populations of Risso’s dolphins is likely valid, but not tested. Further investigations on specimens from other regions are encouraged, especially those with greater numbers of longer and sexually mature dolphins, and those with teeth available for estimation of age. Such specimens and resultant information will greatly improve our knowledge of the biology of Risso’s dolphins around the world.

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Supplement A. Catalog number, sex, total body length (TBL), age, and sexual maturity for 33 Risso's dolphins, whose skulls preserved in National Museum of Natural Science (Taichung, Taiwan), formed the basis of this current study.

Catalog number	Sex [a]	TBL (cm)	Age	Sexual maturity [b]	Catalog number	Sex	TBL (cm)	Age	Sexual maturity
4408	M	136			8710	F	189		
5189	M	145			5202				
5255	M	145			2752				
6345	M	148		SI	6314	F	197		
6360	F	150		SI	5201	M	205		
4410	F	156[e]			2750	F	216		
5377	M	158			748a	F	229	5	
4407	F	165		SI	1331	M	234	6	SI
748b					5190	F	254[e]		SM
3737					6365	M	254		SM
3741					2373	F	265		
5266	F	171			6320				
5392	M	179		SI	1321	F	272	14	
1311	F	181			7206				
5203	M	183			6350				
5208	M	185		SI	5278	F	284		SM
5242									

a: F – female; M – male
b: SI – sexually immature; SM – sexually mature
e: TBL estimated from Rostrum-Anus Length (Chen et al., 2011b)

臺灣海域瑞氏海豚頭部骨骼成熟模式

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摘要：骨骼間的癒合程度可用以判定博物館收藏之鯨豚標本的性成熟和骨成熟程度。本研究之目標為透過研究臺灣海域瑞氏海豚（*Grampus griseus* Cuvier, 1812）頭骨各骨片之間癒合程度，分析頭骨成熟度、體長、性成熟及估計年齡間之關係，以尋找可有效估計瑞氏海豚成熟度之頭骨指標。本研究查驗了 1994-2001 年間於臺灣海域擱淺或誤捕之 33 隻瑞氏海豚的乾燥頭骨標本、表面可見的 20 個骨縫（sutures）或關節（joints）之癒合程度。背腹面頭蓋骨處之骨縫與關節最先開始癒合（基枕骨與外枕骨軟骨聯合 basioccipital-exoccipital synchondrosis，上枕骨與外枕骨縫 supraoccipital-exoccipital suture），頸脊部分（頂額縫 fronto-parietal suture，額骨與頂間骨縫 fronto-interparietal suture）為次。在成年個體中仍可見某些骨骼接縫或關節並未癒合（額淚-額頜縫 lacrimal/maxilla-frontal，鱗骨與頂骨 squamosal-parietal，鱗骨與外枕骨縫 squamosal-exoccipital sutures，前下頜韌帶聯合 intermandibular symphysis）。本研究並未發現癒合過程有左右不等的現象。頸脊中央部分的 額骨與頂間骨縫，鼻額縫吻端（rostral nasal-frontal suture）以及上頜骨與前頜骨縫（maxilla-incisive sutures）先端在海豚體長大於 250 公分後均達高度癒合程度，應可視為理想的性成熟骨骼指標。

關鍵詞：*Grampus griseus*、成熟度、瑞氏海豚、臺灣、頭骨、骨鑑齡分析。