Comparative Anatomical Study on the Relationships between the Vestigial Pelvic Bones and the Surrounding Structures of Finless Porpoises (*Neophocaena phocaenoides*)

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**ABSTRACT.** Morphology of the modern cetaceans represents the result of adaptation of the ancestral terrestrial mammals to aquatic life through their evolutional processes. Some of the primitive fossil cetaceans are known to have both fore and hind limbs, whereas the pelvic bones of modern cetaceans are, in general, a pair of slender rod-like structures within the abdominal wall muscles just anterior to the anus with no articulations to the axial skeleton in both sexes. It is interesting and important to consider the causes and processes of how the hind limbs were lost and how the pelvis was reduced during the process of adaptation. In the present study, we tried to evaluate the topography and function of rudimentary pelvic bones of the finless porpoise (*Neophocaena phocaenoides*), one of the members of the odontocete cetaceans, with special references to the structures around the pelvic bones. Some soft tissues such as M. ischiocavernosus relating to the pelvic bone are transformed following the drastic reduction of the pelvis. This transformation tells us that the cetaceans adapted to the aquatic life during evolutional processes chose the tail flukes driven by the powerful trunk muscles for locomotion, instead of modifying the hind limbs into hind flippers as seen in pinnipeds. On the other hand, it is evident that a function of the pelvic bones of the male finless porpoise was supporting the penis as those of terrestrial mammals. It is noteworthy that the morphological features of the ancestral terrestrial mammals can be traced when they are carefully compared with those of the finless porpoise.

**KEY WORDS:** comparative anatomy, finless porpoise, pelvic bone.

It is evident that the cetacean and the terrestrial artiodactyls are sister taxa based on the recent studies, e.g. [19]. Characteristic morphologies such as the modified forelimbs and the streamlined body shape of the modern cetaceans represent the results of adaptation of the ancestral terrestrial mammals to the aquatic way of life through evolutionary processes. Above all, it is interesting and important to consider the causes and processes of how the hind limbs were lost and how the pelvis was reduced during the process of adaptation. On the other hand, existence and function of the hind limb are discussed in some of the primitive fossil cetaceans, e.g. [25]. However, *Dordon atrox* (formerly *Prozeuglodon atrox*) [26] found from more recent lower Eocene beds in Egypt, had vestigial hind limbs with no bony connection with the vertebral column and were used possibly for very limited purpose such as mating [11]. What are the differences in anatomical features we can find on the soft tissues around the pelvic bones in modern cetaceans during the processes of losing the hind limbs and reducing the pelvis through the evolutional processes mentioned above?

In terrestrial mammals, e.g. the domestic mammals, the innominate bone representing the pelvic girdle consists of three bony elements, the ilium, the pubis and the ischium. These three bones meet at the acetabulum where they articulate with the femur. Both the innominate bones unite at the mid-ventral line as the pubic symphysis and the dorsal region they articulate with the sacrum darsally, which is an element of the vertebral column, at the auricular surface on the ilium [6]. In most of the modern odontocete cetaceans, their vestigial pelvic bones are, in general, a pair of slender rod-like structures within the abdominal wall muscles just anterior to the anus on both sides. In most of the mysticete cetaceans, however, the pelvic bones are crescent-shaped and consisted of three parts [5]. The pelvic bones do not have bony articulations with the vertebral column in any of the cetacean species and they lack the appendicular skeleton except in some great whales such as *Balaenidae*, *Balaenopteridae* and *Physeteridae* that occasionally or usually have rudimentary femur or even tibia [3, 15, 16, 23]. There are several works on the structures relating to the rudimentary pelvic bones in narwhal (*Monodon monoceros*) [13], pygmy sperm whale (*Kogia breviceps*) [21], and harbour porpoise (*Phocoena phocoena*) [22], but they gave no discussion on their evolutionary or functional significances.

Comparative investigations on a specific region of the cetaceans and the terrestrial mammals are necessary to understand the morphological changes took place during the evolutionary processes. In the present study, we tried to analyze the topography of the rudimentary pelvic bones of cetaceans and evaluated their functions with special references to the structures around the pelvic bones.
MATERIALS AND METHODS

Animals: We dissected three finless porpoises (*Neophocaena phocaenoides*) in the present study (Table 1 and Fig. 1).

Methods: Specimens NSMT32590 and 33556 were fixed with 10% formalin (Kashima Kagaku Yakuhin, Saitama, Japan) and kept in 50% ethanol (99% ethanol, SHINWA, Tokyo, Japan). NSMT32685 was dissected in fresh condition. Specimens were dissected carefully using splint tweezers (Watanabe, Tokyo, Japan), and occasionally with micro-surgery forceps (Straight, tip 0.10 × 0.06 mm, Dumont, Switzerland) under an operating microscope (OPMI 111, Carl Zeiss, Germany) for the detailed investigation. Gross findings were recorded by drawings and photographs were taken by a 4 × 5 inches view camera (TOYO 45G, TOYO, Tokyo, Japan) using negative/positive Polaroid films (Type 55 P/N, Polaroid Land, U.S.A.), a 35 mm SLR camera (Nikon F90 and Micro Nikkon 55 mm f=1:3.5, Nikon, Japan), and a digital camera (DCR-PC120, Sony, Tokyo, Japan). The photographs taken by the 4 × 5 cm view camera were enlarged on special paper for microfiche (Fuji Projection Paper Type C, Fuji photo film, Tokyo, Japan) by an enlarger (Model 45MXT, BESELER, Linden, U.S.A.) as templates for detailed drawing by pencil. Line drawings were completed after the template photo was erased by the sodium-thio-sulfite (Super Fujifix, Fuji film, Tokyo, Japan) after saturation with Weigert’s variation of Lugol’s solution [2]. The 35 mm photos were digitized by a film-scanner (Nikon LS1000, Nikon, Tokyo, Japan). Digital pictures were processed by a personal computer (PowerBook G4, Apple Computer, Cupertino, U.S.A.) using Adobe Photoshop 6.0/7.0J and Adobe Illustrator 9.0.2/10.0J and made into the schemas when they are necessary.

RESULTS

Vestigial pelvic bones: The pelvic bones of finless porpoises were composed of a pair of slender rod-like bones. In both NSMT32590 and 32685, pelvic bones were completely ossified, whereas in NSMT33556, both extremities of pelvic bones were not ossified. They were located within the abdominal wall muscles just anterior to the anus on both sides (Fig. 2). No bony articulations between the pelvic bones and the vertebral column could be confirmed. The pelvic bones in male specimens were more elongated, robust and larger than those of a female. The relationships between the vestigial pelvic bones and the surrounding soft tissues are described as follows: First, the M. ischiocaudalis originated from the caudal portion of the pelvic bone and extended caudally to attach the chevrons (Figs. 2 and 4). Second, the M. ischiocavernosus had the origin at the caudal portion of latero-dorsal surface of the pelvic bone and covered M. bulbospongiosus, which had the origin more anteriorly than the former (Fig. 3). These two muscles in males tended to be larger than those in female. In the case of males, a pair of Crura penis, arising from the medio-ventral surface at almost middle of the pelvic bones with very strong attachments, united to form the Corpus cavernosus penis and extended cranially to the genital aperture spiraling 180 degree clockwise. The Corpus spongiosus urethrae join the Corpus cavernosus penis from above completing the inner structure of the penis, Corpus penis. The penis has an elongated conical shape with distal end tapering off as are the case with ruminant artiodactyls. The M. retractor penis, which originated from the cranial surface of the rectum, attached to the winding portion of the penis and pulled it caudally.

Abdominal wall muscles: Muscles of the abdominal wall in the finless porpoise were similar to those of domestic animals in constituent elements, but the proportional size of each muscle was specifically different. The muscles were M. obliquus externus abdominis, M. obliquus internus abdominis, M. transversus abdominis and M. rectus abdominis. Findings that closely related to the vestigial pelvic structures in the finless porpoise are summarized as follows: First, majority of the caudal end of M. rectus abdominis constituted a strong dorso-caudad aponeurosis (Fig. 2, B) and it spread over the Fascia thoracolumbalis. From the major part of M.rectus abdominis a small muscular slip extending to the cranial end of the pelvic bone (Fig. 2, A) and an aponeurotic sheet spreading over the superficial surface of the M. ischiocaudalis (Fig. 2, C) were confirmed to diverge. Second, in the most caudal portion of the M. transversus abdominis, the strong inner fascia of the muscle originated from the lumber Proc. transversus and suspended the vesti-
Vestigial pelvic bones: The term ‘pelvic bone’ has been widely used in cetacean description for the rudimentary innominate bone. The vestigial pelvic bones of the finless porpoise were confirmed to have the basic form and configuration as found in the smaller odontocete cetaceans in general. There were few comparative anatomical works on the pelvic bones and the surrounding soft tissues of finless porpoise. Howell [12] could be the only reference on pelvic structures of the Chinese finless porpoise (*Neomorphos phocaenoides*). Our findings were similar to those of Howell in that we found no bony connection of the pelvic bones with...
the vertebral column and no rudimentary appendicular skeletal elements were confirmed in the animal. In both NSMT32590 and 32685 pelvic bones were completely ossified, whereas in NSMT33556, the smallest individual, both extremities of pelvic bones were not ossified yet. Extent of ossification of the pelvic bones could increase with age. The relationship between the male genital organs and vestigial pelvic bones in the finless porpoise was consistent with the description by Eschiricht and Reinhardt [9], in which the penis attached to the pelvic bones in male bowhead whale (*Balaena mysticetus*). It is evident that the pelvic bones of the finless porpoise male act to support the penis in similar way as those of terrestrial mammals. The penis is usually invisible externally in its resting condition because it is hidden in the abdominal wall. The pelvic bones of male tend to be more massive, longer, and larger than those of female. These findings agree with the descriptions on the killer whale (*Orcinus orca*) [8] and the harbour porpoises (*Phocoena phocoena*) [27] respectively. Although Howell described some structures around the vestigial pelvic bones of the Chinese finless porpoise (*Neomeris phocaenoides*) including the M. ischiocaudalis and the M. ischiocavernosus, he made no discussion on the functional significance of the structures [12]. Generally, ‘M. ischiocaudalis’ is a term defined and widely used for cetaceans but not recognized in terrestrial mammals, and hence not included in Nomina Anatomica Veterinaria [14]. In case of cetaceans, there are various descriptions on this muscle. For examples, M. ischiocaudalis of *Phocoena phocoena* was considered as equivalent to M. levator ani of humans [22] based on Eisler’s descriptions on human musculature [7]. Although there are some exceptions terminology used for the same muscle, such as M. ischiococygeus [4] in *Phocoena phocoena*, the term ‘M. ischiocaudalis’ has been widely accepted; in *Monodon monoceros* [13], in *Balaenoptera borealis* [20], in *Kogia breviceps* [21], in *Balaenoptera physalus* [17] and in *Balaena mysticetus* [24]. In the present study, we identified the muscle, which originated from posterior surface of the pelvic bone and inserted on several chevrons, as ‘M. ischiocaudalis’. Based on the relationship of the pelvic bones to the surrounding soft tissues including Corpus cavernosus penis, the bone could be a fused remnant of the Os pubis and the Os ischii, instead of Os ilium and Os ischii which was proposed by Abel [1] based on a result of observations on the shape of the pelvic bone in *Phocoena communis* (*Phocoena phocoena*).

**Abdominal wall muscles:** We would like to lay stress on the important functional contribution of the dorso-caudal shift of the insertion of M. rectus abdominis, which is closely related to the ventral flexion of the caudal body trunk (tail) together with the M. hypaxialis (equivalent to the M. psoas major of terrestrial mammals) during the dorso-ventral undulation of the tail causing main propulsive force for swimming. This movement may antagonistic to that of the enormous M. hyperaxialis. Howell [13], Schulte and Smith [21] and Slijper [22] also described that the insertion of M. rectus abdominis transferred dorso-caudally and merged with the Fascia thoracolumbalis in the narwhal (*Monodon monoceros*), the pygmy sperm whale (*Kogia breviceps*), and the harbour porpoise (*Phocoena phocoena*), however, they gave no discussion on the functional relationship and significance of the structures. In domestic animals having the pelvis, the caudal end of the M. rectus abdominis usually insert to the anterior edges of the both pubic bones at the Pecten ossis pubis. In the present study on the finless porpoise, among the three portions of the M. rectus abdominis insertions, we did confirm the presence of a muscular slip insert on the cranial tip of the pelvic bone, whereas the

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**Fig. 4.** Semi-schematic illustration of a ventral view of the caudal trunk in a male finless porpoise (NSMT33556). The dorsal lateral caudal vein [14] cooling the intra-abdominal gonads emerged at the caudal border of M. obliquus internus abdominis (OIA) and the inserting strong aponeuroses of M. rectus abdominis (RA), right above the pelvic bone. The caudal borders of RA and OIA are homologous to the Lig. inguinale (*1*)
rest of the muscle insertions changed their direction, ran dorso-caudally along the free caudal border of M. obliquus internus abdominis and inserted on the Fascia thoracolumbalis. This indicates that the structural relationship found in terrestrial quadraped is still maintained in the finless porpoise. In other words, at the process of muscular transition from the abdomen to the tail, the muscles consisting of the abdominal wall were replaced by the M. hypaxialis which lay deep in the cranial part, and became exposed because the abdominal wall disappeared as it shifted dorsally and merged into the Fascia thoracolumbaris. Thus the surface contour is maintained continuously smooth although the deeper structures differ remarkably. What are the above-mentioned findings suggest? As the pelvic bones reduced in size and changed the position, they may help the function of M. hypaxialis that flex the peduncle ventrally. That is to say, main propulsive force produced by the dorso-ventral M. hypaxialis that flex the peduncle ventrally. Moreover, as the peduncle becomes slender, it could make the markedly smooth streamlined shape from the abdominal to caudal portions, reducing the drag to minimum during swimming.

In terrestrial mammals, some sacral vertebrae fused to make a sacral bone. The Pars lateralis of sacrum is understandable being made up of the costal elements of the sacral vertebrae and articulate with the ilium to compose the pelvis. We confirmed that mesodermal connection of the pelvic bone of the finless porpoise to the axial skeleton (lumbar transverse processes) is via strong inner fascia of M. transversus abdominis (Table 2).

At the same time, as the distal portion of abdominal wall muscles traverse the M. hypaxialis superficially from cranio-ventral to dorso-caudal direction at the caudal end of abdominal cavity (similar to the split inserting tendons of the M. flexor digitorum superficialis holds down the distal part of the M. flexor digitorum profundus tendon in human hand), the contracting abdominal wall muscles may achieve the structure that protect the M. hypaxialis from slacking when flexing the trunk. Moreover, as the peduncle becomes slender, it could make the markedly smooth streamlined shape from the abdominal to caudal portions, reducing the drag to minimum during swimming.

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Table 2. List of elements equivalent to ribs in the typical thoracic region of terrestrial mammals

<table>
<thead>
<tr>
<th>Region</th>
<th>Costal elements</th>
<th>Articulated with</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finless porpoise</td>
<td>Proc. transversus (Proc. costarius )+ Deeper fascia of TA*</td>
<td>Pelvic bone</td>
</tr>
<tr>
<td>Terrestrial mammal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervical region</td>
<td>Tuberculum ventrale (fused with vertebra)</td>
<td>–</td>
</tr>
<tr>
<td>Thoracic region</td>
<td>Costa (articulated with vertebra)</td>
<td>–</td>
</tr>
<tr>
<td>Lumbar region</td>
<td>Proc. costarius fused with vertebra “Proc. transversus”</td>
<td>–</td>
</tr>
<tr>
<td>Sacral region</td>
<td>Pars lateralis (incorporated to Sacrum)</td>
<td>Ilium</td>
</tr>
</tbody>
</table>

* TA: M. transversus abdominis.
in the case of the cetaceans that re-adapted to the aquatic habitat, they maintained this dorso-ventral swinging of the trunk for locomotion. The pinnipeds took to the limbs, which are the locomotive contrivance on land, as the main motive force in swimming, while the cetaceans choose the caudal trunk and produced the tail flukes similarly as in the sirenians. The principle is basically the same as that in fishes, where fishes undulate their caudal trunk and tail laterally, whereas the cetaceans flex and extend their caudal part dorso-ventrally for producing the propulsive force. This is probably because the musculature and related structure for locomotion were already adapted to dorso-ventral undulation in terrestrial mammals before they started going back to the sea. It is supported that phylogenetically distant sirenians have also chosen the same way in the process of adaptation.

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