CLASSIFICATION AND PHYLOGENY OF THE SUPERFAMILY PLATANISTOIDEA, WITH NOTES ON EVIDENCE OF THE MONOPHYLY OF THE CETACEA

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ABSTRACT

Important basis provided by the morphological studies on the skeleton, digestive and respiratory organs of the Platanistoidea have further proved that this group can be divided into four families. Considering the characteristics of the skeleton and other morphological features, the phylogenetic relationships among the four families are discussed. The systematic sequence of the families should be Iniidae, Lipotidae, Pontoporiidae and Platanistidae. Some characters noticed in the investigations are evidence in favour of the monophyly of the cetacea.

INTRODUCTION

The superfamily Platanistoidea possesses a number of primitive characters similar to the Oligocene-Miocene Squalodontoidea, some characters similar to the primitive forms of the higher cetacean families and some specialized structures. Two different opinions advocating divide or combination concerning the classification of the Platanistoidea have been held over a long period of time.

In the middle of the 19th century, Gray (1863, 1866) first divided the Platanistoid dolphins into groups. In his catalogue, *Platanista* constitutes the fourth family of Cetacea—Platanistidae; *Inia* constitutes the fifth family—Iniidae; *Pontoporia* was placed into the sixth family—Delphinidae. Flower (1869) gave another opinion before long, put together the above mentioned three genera into the Platanistidae. He made *Platanista* and *Inia* belong to the subfamily Platanistinae and Iniinae respectively and placed *Pontoporia* into the subfamily Iniinae provisionally.

At the beginning of the 20th century, Miller (1918) named *Lipotes*, the fourth genus of the modern Platanistoids, and referred it to the Iniidae. In another paper published in 1923, he followed Gray in recognizing Platanistidae and Iniidae and still considering *Pontoporia* a member of the Delphinidae. Nevertheless, he has placed *Pontoporia* into the subfamily Stenodelphininae to differ from other groups of the Delphinidae. Kellogg (1928) held the same opinion as Miller did, whereas Winge (1918) maintained to put *Platanista*, *Inia*, *Pontoporia* and the newly discovered *Lipotes* together into the Platanistidae. In this period, argument concerning divide or combination of the Platanistoids was continued and different opinion was set in whether *Pontoporia* belongs to Platanistoids.

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In 1936 Slijper adopted the concept in favour of combination and placed all the living genera of Platanistoids into the family Platanistidae. Following Slijper's opinion, Simpson (1945) recognized Platanistidae but retained three subfamilies and, moreover, established superfamily Platanistoidea in the higher category. This taxonomical system has been accepted by most cetologists ever since. Slijper's system has been adopted by Norman and Fraser (1948), Slijper (1962), Nishiwaki (1965, 1972), Tomilin (1974), Matthews (1978), Lockley (1979), and others. Simpson's system has been followed by Fraser and Purves (1960), Carvalho (1961), Marcuzzi and Pilleri (1971), Brownell and Herald (1972), Mead (1975), Rice (1977), and others. The single family system was also adopted by Hershkovitz (1966), but a new name Susuidae which he proposed has not been accepted by other cetologists. Authors studying fossil Platanistoids such as Kellogg (1944, 1955), Rensberger (1969) have continued to recognize the iniid as a distinct family. Gaskin (1976) who is studying modern cetaceans has followed their opinion.

The investigations of Platanistoid dolphins have gained great attention again since 1960s. Kasuya (1973) recognized the Platanistidae, Iniidae and Pontoporiidae of the Platanistoidea on the basis of the study of the tympano-periotic bone. In a paper on the study of *Lipotes*, van Bree and Purves (1975) put it in the Iniidae. Pilleri et al. (1976) proposed to separate *Inia*, *Lipotes* and *Pontoporia* from the Platanistidae and put them in the Iniidae. The coexistence of the one family system (Slijper, 1936; Simpson, 1945) with the two and three family systems (Pilleri *et al.*, 1976; Kasuya, 1973) occured. In 1978, Zhou *et al.* proved that *Lipotes* is not closely related to *Inia* and the differences between the two genera exceed those between the Delphinidae and Phocoenidae, and placed *Lipotes* into a separate family—Lipotidae. After this, Pilleri and Gihr (1980) have turned to use a four family system, but no argument has been given.

The present paper summarizes the important basis provided by the morphological studies of the skeleton, digestive and respiratory organs of *Inia* (Flower, 1869; Mead, 1975; Lönnberg, 1928; Pilleri and Gihr, 1976c, 1977; Yamasaki and Kamiya, 1981; Zhou, Li and Pilleri, 1982), *Lipotes* (Miller, 1918; Chen and Chen, 1975; Zhou *et al.*, 1978, 1979a, b; Chen *et al.*, 1980; Liu and Lin, 1980; Zhou and Li, 1981), *Pontoporia* (Burmeister, 1867; Flower, 1869; Carvalho, 1961; Schenkkan, 1972; Yamasaki *et al.*, 1974, 1975, 1977; Mead, 1975; Pilleri and Gihr, 1976b; Yamasaki and Satomi, 1976) and *Platanista* (Eschricht, 1852; Anderson, 1879; Arvy and Pilleri, 1970; Yamasaki and Takahashi, 1971; Takahashi and Yamasaki, 1972; Yamasaki *et al.*, 1972; Purves and Pilleri, 1973; Pilleri and Gihr, 1976a; Yamasaki, Komatsu and Kamiya, 1977) and further proves that the Platanistoids can be divided into four families. The phylogenetic relationships among the four families and the evidence in favour of the monophyly of the cetacea are also discussed.

BASIS OF THE CLASSIFICATION OF THE SUPERFAMILY

An uniform understanding of the genera of Platanistoids has been acquired early

TABLE 1. COMPARISON OF THE COMPARTMENTS OF THE STOMACH OF CETACEA

	Fore-stomach	Main stomach	Connecting channel	Pyloric stomach
Iniidae	1	1	1	1
Lipotidae	0	3	0	1
Pontoporiidae	0	1	1	1
Platanistidae	1	2	1	1
Ziphiidae	0	1	0	many compartments
Physeteridae	1	1	0	1
Monodontidae	1	1	1	1
Delphinidae	1	1	1	1
Phocoenidae	1	1	1	1
Balaenopteridae	1	1	0	1

in the third decade of the twentieth century. However, no identical result on the classification in family rank has been obtained so far. The materials studied which were mostly confined to skulls have something to do with the matter. When studying the affinity between *Lipotes* and *Inia*, Zhou *et al.* (1978, 1979a) compared attentively the vertebrae, sternums, flipper skeletons and other available materials of external and internal structures in addition to the careful comparison of the structure of the skulls. As a result of these studies, the close relationship between *Lipotes* and *Inia* was refuted. In recent decade, the studies of the skeleton and digestive tract of Platanistoids by Yamasaki *et al.*, Pilleri *et al.* and Zhou *et al.* have provided important basis for the classification of the modern Platanistoids.

Table 1 indicates that the stomachs of other modern cetaceans consist of fore-stomach, main stomach and pyloric stomach except those of the Ziphiidae in which the fore-stomach is absent. They differ from each other only in the present (Delphinidae, Monodontidae, Phocoenidae) or absent (Physeteridae, Balaenopteridae) of the connecting channel. The stomachs of different groups of Platanistoids differ from each other not only in the above mentioned characters, but also in the subdividing of the main stomach or not (Fig. 1). Both *Inia* and *Platanista* possess fore-stomach, but the main stomach is single chambered in the former and divides into two compartments in the latter. In *Lipotes* and *Pontoporia* the fore-stomach is lacking. The main stomach divides into three compartments and the connecting channel is absent in the former, while the latter possesses single chambered main stomach and the connecting channel. The differences between the stomach of any two groups of Platanistoids go beyond the mutual differences between the stomach of most of the odontocetes. Refer to the Artiodactyla, the number of compartments of the stomach goes so far as to be the main character in distinguishing Infraorder Tragulina (3 compartments) and Infraorder Pecora (4 compartments). Thus the structure of the stomach is one of the key characters in weighing the degree of separation among different groups of Platanistoids.

The structure of the skeleton is still important basis in classifying the Platanistoids. Attention should be paid first of all to four note-worthy differences between *Inia* and three other groups of Platanistoids. 1. The palatal portion of the two

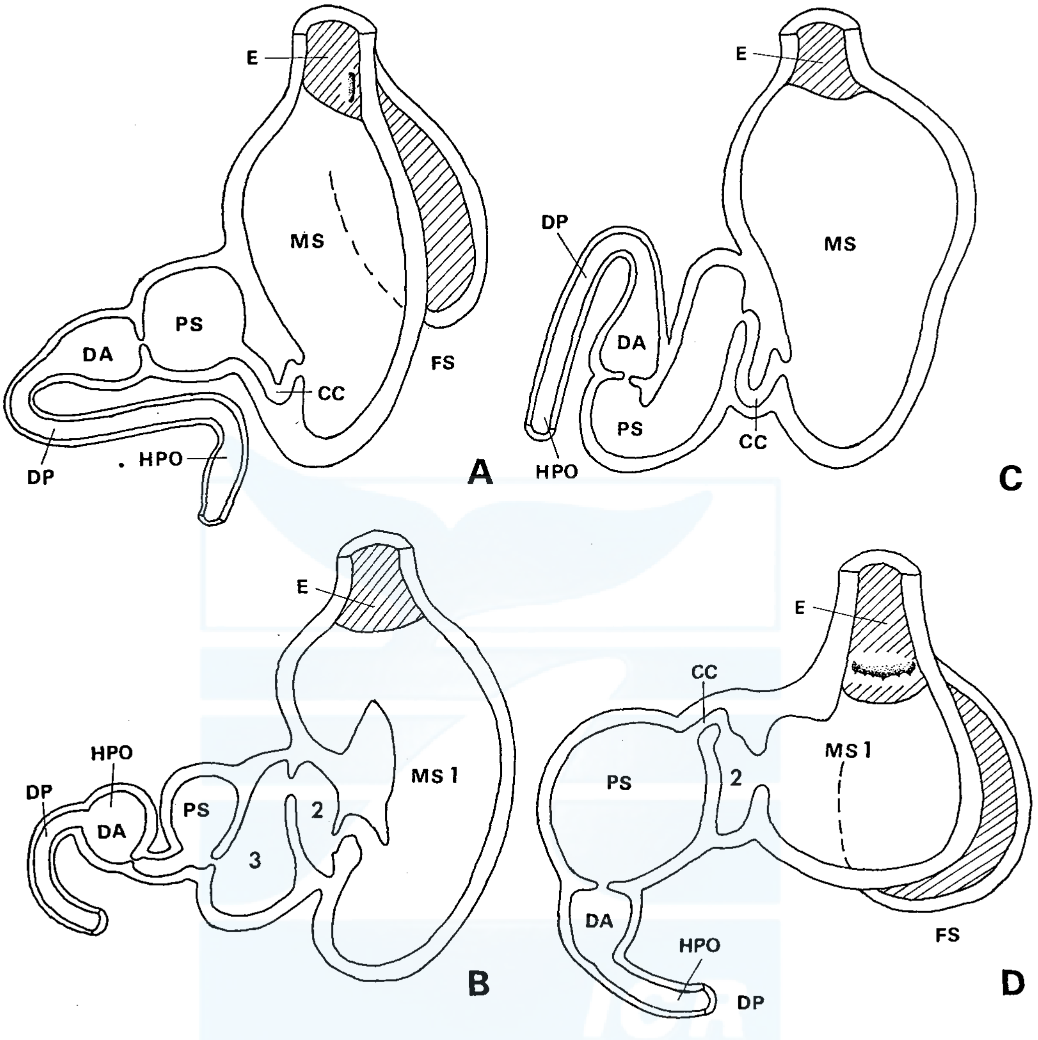
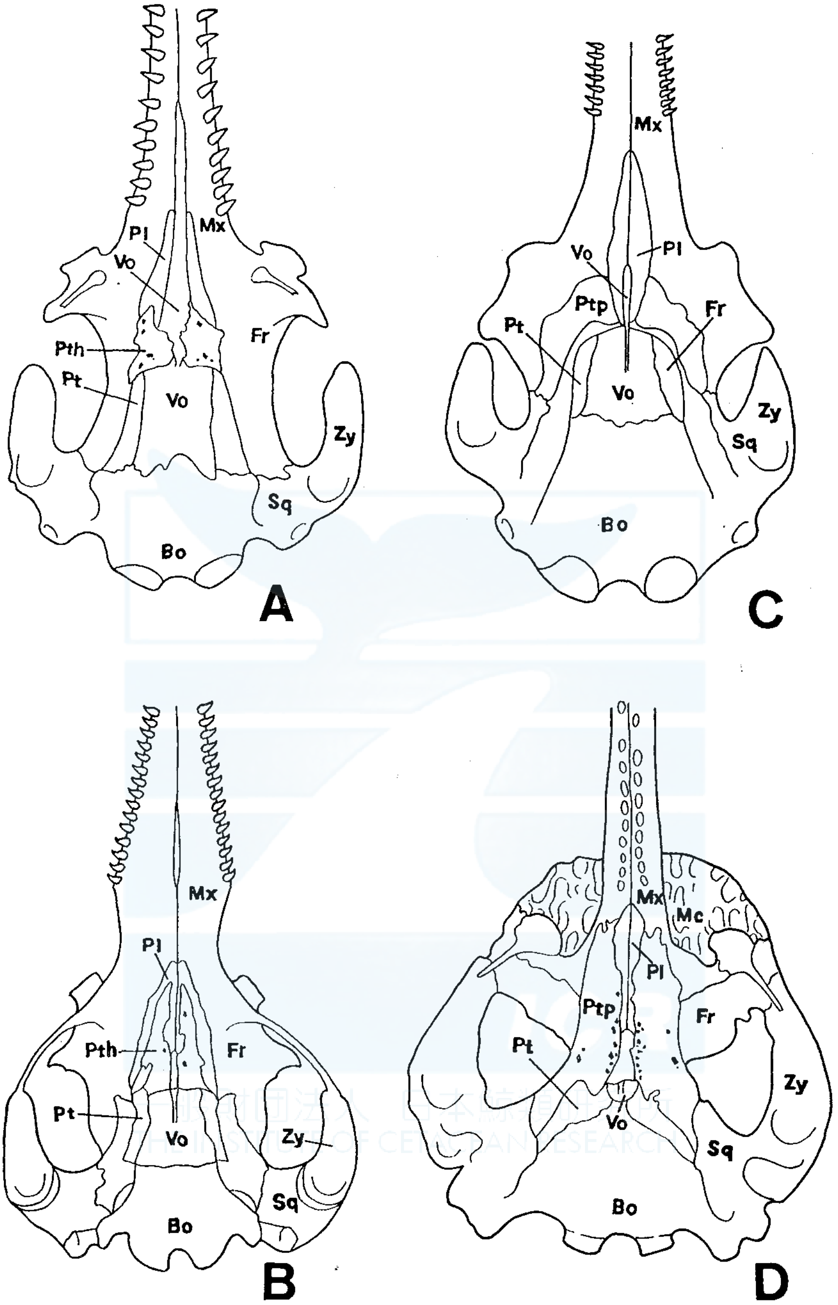


Fig. 1. Diagram of the stomach of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*.
CC. connecting channel; DA. duodenal ampulla; DP. duodenum proper; E. esophagus; FS. fore-stomach; MS. main stomach; MS1. first compartment of main stomach; 2. second compartment of main stomach; 3. third compartment of main stomach; PS. pyloric stomach; HPO. opening of hepato-pancreatic duct.

→Fig. 2. Ventral aspect of skull of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*.
Bo. basioccipital; Fr. frontal; Mc. maxillary crest; Mx. maxilla; Pl. palatine; Pt. pterygoid; Pth. pterygoid hamulus; Ptp. lateral plate of pterygoid; Sq. squamosal; Vo. vomer; Zy. zygomatic process of squamosal.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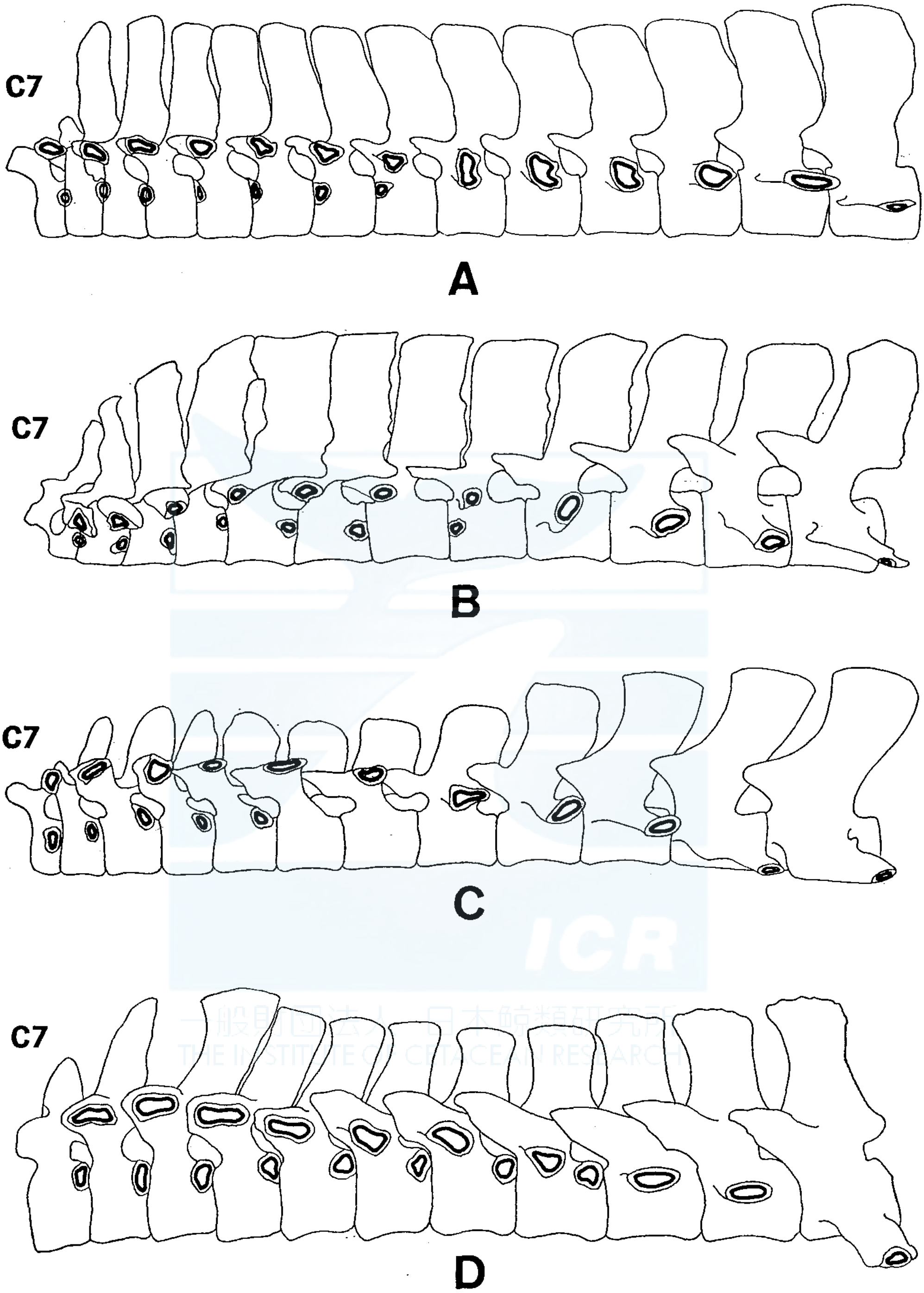

Fig. 3. Thoracic vertebrae of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica* showing costal facets (bold line).

maxillas and palatines of *Inia* is separated by the vomer. In three other groups of Platanistoid, the palatal portion of maxilla contacts that of the opposite side (Fig. 2). 2. Only irregular tubercles are found on the ventral aspect of the pterygoid hamuli of *Inia*, whereas the pterygoid hamuli of *Lipotes* possess a thin plate which recurves dorsally. This portion enlarges to form the lateral plate of pterygoid in *Pontoporia* and *Platanista*. 3. In *Inia*, the costal facets are located at the

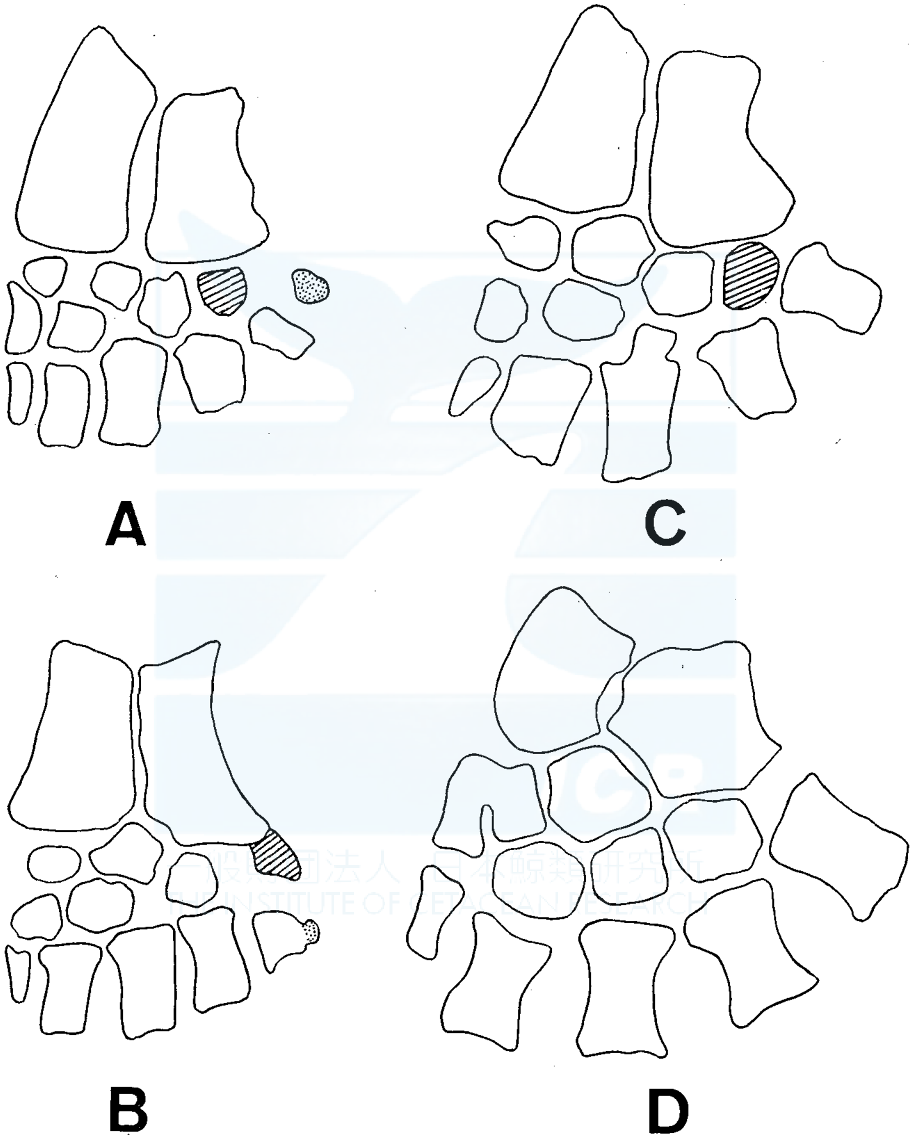

Fig. 4. Flipper skeleton (not including phalanges) of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*. Ulnare hatched; pisiform stippled.

anterior and posterior edges on each centrum of the first two thoracic vertebrae and occured at the anterior edge only in the hinder thoracic vertebrae. In *Lipotes*, they are located both at the anterior and posterior edges of the centrum of the first vertebra and occured at the posterior edge only on the centrum of the 2nd—5th thoracic vertebrae. In the 7th thoracic vertebra, the facet occurs on the anterior edge only. The costal facets are located at the hind edge on the centrum of the thoracic vertebrae in most individuals of *Pontoporia*. In few individuals, those of 5th or 4th—5th thoracic vertebrae are situated at the front edge of the centrum. All costal facets of the thoracic vertebrae of *Platanista* are situated at the hind edge of the centrum (Fig. 3). 4. According to the radiograph published by Pilleri and Gihr (1976a, b, c), the ulnare and pisiform are free in *Inia*; the ulnare is free but the pisiform is missing in *Pontoporia*; both bones are missing in *Platanista*. According to our specimens, although the ulnare and pisiform of *Lipotes* are fused to the ulna and 5th metacarpal respectively, they are still distinguishable (Fig. 4).

The tympano-periotic of the cetacea has moved ventrally and lost the direct

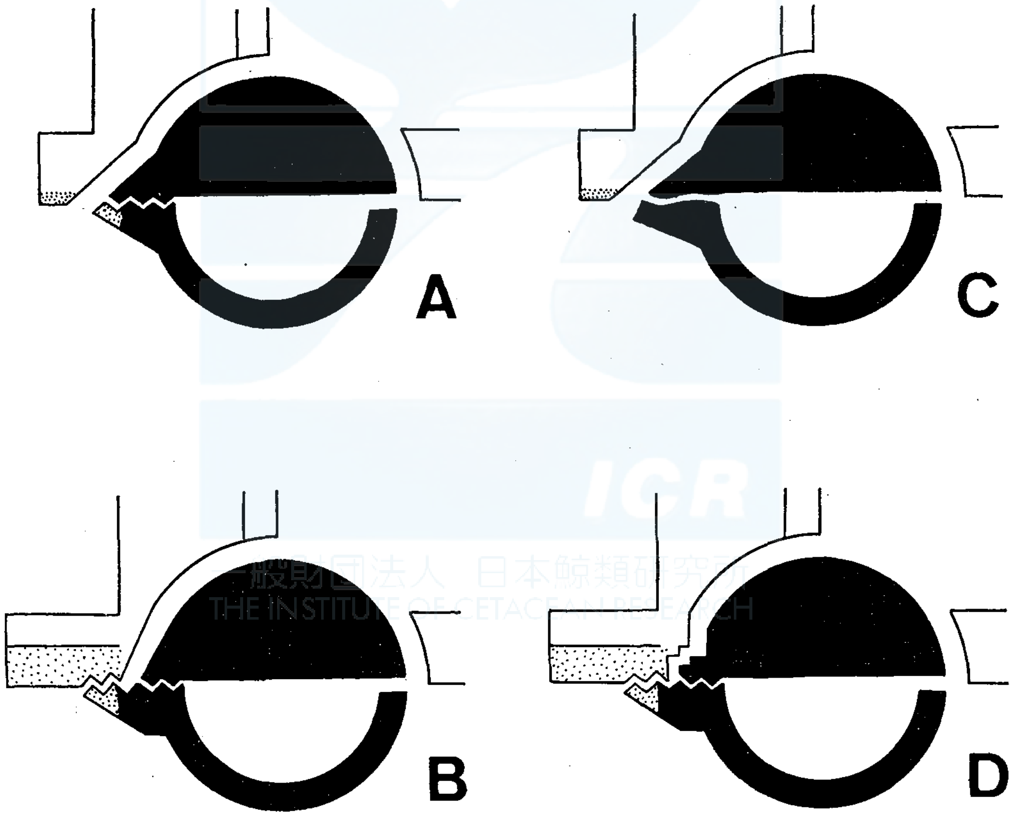

Fig. 5. Connection between tympano-periotic and skull in (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*, Waved edge indicates suture of bones and dotted are the laminated structure. (A) and (C): fixed with ligament; (B) and (D): direct joining. (Modified from Kasuya, 1973,)

TABLE 2. COMPARISON OF THE MAIN CHARACTERS OF THE FAMILIES OF THE SUPERFAMILY PLATANISTOIDEA

Characters	Iniidae	Lipotidae	Pontoporiidae	Platanistidae
Hairs	sparsely on snout	absent	absent	absent
Blow hole	transverse, crescentic	longitudinal, elliptic	transverse, crescentic	longitudinal, slitlike
Apical bronchus	arising from trachea slightly higher than bifurcation of right and left bronchi	arising from trachea markedly higher than bifurcation of right and left bronchi	arising from trachea just above bifurcation of right and left bronchi	arising from trachea markedly higher than bifurcation of right and left bronchi
Stomach	fore-stomach, single main stomach, connecting channel and pyloric stomach present	fore-stomach absent, three compartments of main stomach and pyloric stomach present	fore-stomach absent, single main stomach, connecting channel and pyloric stomach present	fore-stomach, two compartments of main stomach, connecting channel and pyloric stomach present
Opening of hepato-pancreatic duct	located at duodenum proper	located at duodenal ampulla	located at duodenum proper	located at duodenum proper
Caecum	absent	absent	absent	present
Ratio of intestinal length to body length	19—20	12.5—14.9	24.0—37.3	3.6—4.9
Maxillary crest	absent	absent	absent	very well developed
Zygomatic process of squamosal	not reaching supraorbital process of frontal	not reaching supraorbital process of frontal	reaching supraorbital process of frontal	reaching orbital plate of frontal from which a supra-orbital process is usually developed
Palatal portion of two maxillas	separated by vomer	in contact	in contact	in contact
Bony plate of pterygoid hamulus	small tubercles on ventral aspect of pterygoid hamulus	thin bony plate recurves dorsally	enlarges to form lateral plate of pterygoid	enlarges to form lateral plate of pterygoid
Connection between tympano-periotic and skull	fixed with ligament	posterior process of tympanic bulla loosely sutured to squamosal	fixed with ligament	posterior process of tympanic bulla loosely sutured to squamosal
Teeth	crown with nodular enamel rugosity	crown with reticulate enamel rugosity	crown simple	crown simple, upper tooth rows merged together and almost in contact
Costal facet of thoracic vertebrae	located mostly at anterior edge of centrum	located mostly at posterior edge of centrum	located at posterior edge of centrum in most individuals	located at posterior edge of centrum
Carpals	7, ulnare and pisiform present	4—5, ulnare fused to ulna and pisiform fused mostly to 5th metacarpal	6, ulnare present, pisiform missing	5—6, ulnare and pisiform missing

joining to the skull in various degrees in the course of the adaptations to the aquatic life. In *Lipotes* and *Platanista* the posterior process of tympanic bulla is still loosely sutured to the skull (Kasuya, 1973; Zhou *et al.*, 1979a). The tympano-periotic of *Inia* and *Pontoporia* is fixed with ligament to the skull (Fig. 5). Besides, *Inia* and *Lipotes* differ from *Pontoporia* and *Platanista* in having the zygomatic process of squamosal not reaching the supraorbital process of frontal. The distinction between the teeth of different Platanistoids is as follows: The crown of the teeth of *Inia* and *Lipotes* is covered with nodular and reticulate enamel rugosity respectively and that of *Pontoporia* and *Platanista* is simple. The upper tooth rows of *Platanista* merge together and are almost in contact with each other. *Platanista* also differs from three other Platanistoids and all other living odontocetes in having the curious maxillary crest.

The morphological distinctions between different Platanistoids showing in Table 2 are far more than those between different families of most mammals. This fact proves that each of the four Platanistoid dolphins represents a separate lineage derived from the primitive ancestor at an early stage of the evolutionary process. Their taxonomic categories should be referred to family rank.

PHYLOGENY

The traditional view concerning the relationship of different Platanistoid dolphins is that *Lipotes* is closely related to *Inia* and that *Pontoporia* is close to them. The systematic sequence of these groups has been arranged as A and B by most authors (Simpson, 1945; Carvalho, 1961; Marcuzzi and Pilleri, 1971; Kasuya, 1973; Tomilin, 1974; Mead, 1975; Matthews, 1978 other). It has been arranged as C by Slijper (1936, 1962) and some authors (Norman and Fraser, 1948; Nishiwaki, 1965, 1972) according to the sequence of naming. There are still few other sequences (Fraser and Purves, 1960; Hershkovitz, 1966; Rice, 1977). According to the informations now understood, these arrangements can not express the natural relationships of Platanistoids.

A

subfamily Platanistinae
  (or family Platanistidae)
  genus *Platanista*
subfamily Iniinae
  (or family Iniidae)
  genus *Inia*
  genus *Lipotes*
subfamily Pontoporiinae
  (or family Pontoporiidae)
  genus Pontoporia

B

family Platanistidae
  genus *Platanista*
  genus *Inia*
  genus *Lipotes*
  genus *Pontoporia*

C

family Platanistidae
  genus *Platanista*
  genus *Inia*
  genus *Pontoporia*
  genus *Lipotes*

By inference from the analysis of the characters, the phylogenetic relationships among the families of Platanistoids may be expressed as Fig. 6. The Iniidae is a side branch diverged from primitive Platanistoids. This family is characterized

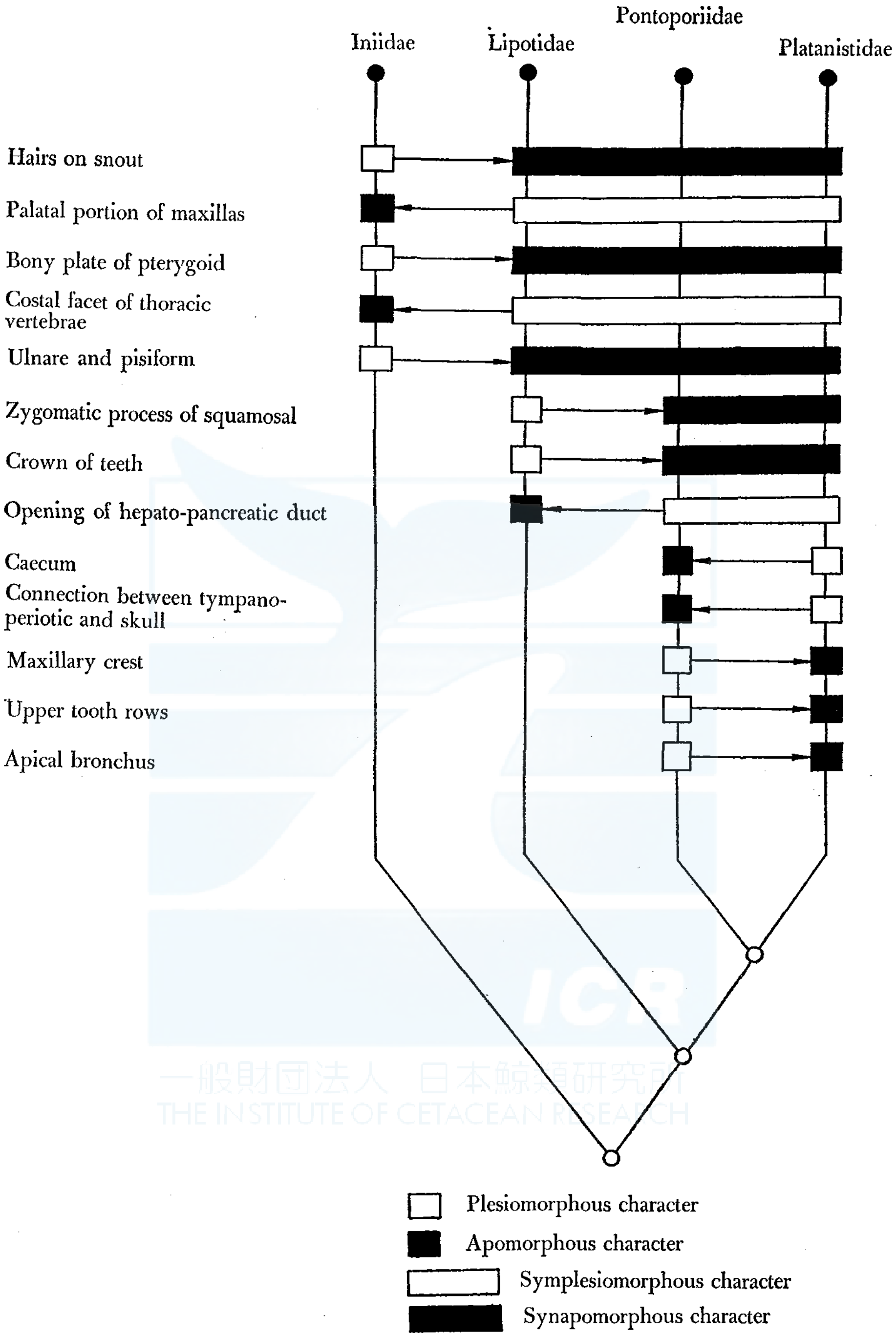

Fig. 6. Diagram of the phylogeny of the superfamily Platanistoidea.

by apomorphous characters, i.e. the separation of the palatines by the vomer and the location of most of the costal facets at the anterior edge of the centrum of the thoracic vertebrae, which differentiate Iniidae from other Platanistoids. The position of the head of the ribs articulating to the centrum of the thoracic vertebrae indicated by the costal facets is features differentiated during the early stage of adaptation to the aquatic life. In view of the fact that the costal facets of the thoracic vertebrae of Delphinoidea and Physeteroidea locates on the posterior edge of the centrum, the position of that of Iniidae probably situates opposite that of all other living odontocetes. The synapomorphous characters of Lipotidae, Pontoporiidae and Platanistidae are the development of the bony plate of pterygoid hamuli and the reduction of the carpals. Through the development of the recurved thin plate from the irregular small tubercles of pterygoid hamulus and the formation of the former to the well-developed lateral plate of pterygoid, the evolutionary sequences of this feature can be seen. The evolutionary trend of the carpals is the fusion of the ulnare and pisiform to adjacent bones or missing of both bones.

The Lipotidae is the second branch descended from the primitive Platanistoids. A series of features of the Lipotidae such as the bony plate of pterygoid hamuli, costal facet of thoracic vertebrae, carpals, zygomatic process of squamosal and crown of teeth is relatively more primitive than those of Pontoporiidae and Platanistidae. The Lipotidae also differs from these two families by the apomorphous character in having the hepato-pancreatic duct opens into the duodenal ampulla.

The Pontoporiidae and Platanistidae have diverged from the primitive Platanistoids slightly later than the Lipotidae. The maxillary crest, upper tooth rows, carpals and apical bronchus of Platanistidae are characters more specialized than those of the Pontoporiidae, whereas the caecum and the direct joining of the tympano-periotic to the skull in the same family are primitive characters as compared with those of the Pontoporiidae. The mosaic distribution of the Plesiomorphous characters and apomorphous characters between Pontoporiidae and Platanistidae also has been formed.

The structure of the digestive tract of Iniidae remains relatively close to the ancestor. In Lipotidae and Pontoporiidae the fore-stomach is absent, the stomach of the former is most specialized in the losing of the fore-stomach and the dividing of the main stomach into three compartments. The digestive tract of Platanistidae is characterized by the differentiation of the main stomach and notable shortening of the intestine on the one hand, and is unique among odontocetes in retaining the caecum on the other hand. The transverse crescent shaped blow hole of Iniidae and Pontoporiidae is similar to that of most of the recent odontocetes, whereas the shape of the blow hole of Lipotidae and Platanistidae has been changed separately. The process of moving of the apical bronchus from the right bronchus to trachea hasoccured in the course of phylogenetical development. The degree of forward shift of the apical bronchus varies in different group of Platanistoids. The reduction of the visual apparatus has taken place in relation to the increase of the turbidity of the water and the weakening of the light. The eyes of the

Pontoporiidae are comparatively well-developed and those of the fresh water Platanistoid species exhibit a marked regression. The eyes of the Platanistidae are almost completely blind. The degree of reduction of the eyes is in order of Pontoporiidae, Lipotidae, Iniidae, then Platanistidae (Zhou, Pilleri and Li, 1980). The orbit of Platanistoids is reduced in correspondence with the regression of the eye. In the case of Iniidae and Lipotidae, the zygomatic process of the squamosal is not lengthened in correspondence with the reduction of the orbit and is not in contact with the supra orbital process of the frontal. The unique maxillary crest of the Platanistidae functions together with the air sinuses in the reflection of the sound signals. It was probably developed parallel with regression of the eye to compensate for the loss of vision (Pilleri, 1979). The development of the brain of the Platanistoid families is comparatively low as compared with that of other living odontocetes. In totality, the Iniidae is the family keeping relatively more primitive characters and the Platanistidae is the most specialized one. The systematic sequence of the families in accordance with their evolution should be Iniidae, Lipotidae, Pontoporiidae and Platanistidae.

According to the fossils of the primitive Platanistoids discovered, these four families probably diverged during the Miocene from the marine ancestor originated from the Squalodontoidea. Three of the recent families of Platanistoids have entered fresh-water rivers secondarily, whereas Pontoporiidae has remained in coastal waters. Although the structures of Platanistoids have been differentiated during the long period of evolution, their development level is still lower than that of other recent odontocetes. Further studies on fossil groups of the Platanistoids are needed.

EVIDENCE OF THE MONOPHYLY OF THE CETACEA

Whether the cetacea originated from a common ancestor or two or several ancestors is a disputed problem. Slijper (1962) and some Soviet investigators have reached a conclusion in favour of polyphyly that the three suborders of the cetacea probably originated separatly from respective terrestrial ancestors. On the contray, Gaskin (1976) and van Valen consider that the cetacea as a whole are probably monophyletic. The basis of their argument is a series of morphological characters which are common to mysticetes and odontocetes such as the loss of the pelage, the lacking of the true vocal cord, the similarity in the structure of the tympanic bulla and the shape of the lung, the oblique position of the diaphragm and the moving of the blow hole to the dorsal aspect of the head, etc. The cytogenetic studies of Arnason (1969, 1972, 1974) and Kulu (1972) are also quoted by them to indicate the close agreement of mysticetes and odontocetes in the number and shape of the chromosomes as well as the distribution of C-heterochromatin in the chromosomes. No reasonable explanation would be obtained if the cetaceans were not of common ancestry.

A character common to mysticetes and odontocetes, which has not been brought to great attention yet, has been noticed during the studies on the phylogeny of the Platanistoids. That is, the stomach of most cetaceans is composed of three compartments, the fore-stomach, main stomach and pyloric stomach. The fore-stomach covered with esophageal epithelium is not subdivided further and the glandular stomach is divided into two or more compartments. The cetacean stomach composed of single chambered fore-stomach and subdivided glandular stomach is different from that of any other mammals. This fact makes me to come over to the side of the monophyly.

The mysticetes are grazers and the odontocetes are predators. Since they differ not only in feeding methods but also in food, the similarity of the stomach could not be explained by parallel adaptations. If the cetaceans were not of common origin, it would be impossible for majority of them to possess the fore-stomach formed by the esophagus and the subdivided glandular stomach. It is reasonable to infer that such basic structure was developed before the differentiation of the mysticetes and odontocetes. It is the symplesiomorphous character of the two groups and another evidence of the monophyly of the cetacea.

Certain characters which were thought to be found in mysticetes only still remain in some Platanistoids, such as the hair on the snout of Iniidae and the caecum of Platanistidae. These features add evidence to support the monophyly of the cetacea. It should be stated that the unique musculus palpebrales of the cetaceans (Hosokawa, 1951) is also a proof which has not been cited by previous authors.

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