Epiphyseal Union, Tooth Eruption, and Sexual Maturation in the Common Tree Shrew, with Reference to Its Systematic Problem

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ABSTRACT. The epiphyseal union, eruptive sequence of the permanent teeth, and sexual maturity are examined in 150 common tree shrews (*Tupaia glis*), and are compared with those in other mammals including primates. The sequence of epiphyseal union is: elbow–hip–ankle–wrist–knee–shoulder. The sequence of epiphyseal union in mammals is not so fixed as has been previously considered. The eruptive sequence of the permanent teeth in the common tree shrew is more similar to that of insectivores than primates. The gonads are examined histologically to determine the sexual maturation. The order of completion of these three developmental aspects is also investigated and is compared with those in other mammals. Although the tree shrews have many similarities with platyrrhines in the development of the eco-sensitive organs such as the epiphyses of the extremities, their inclusion in the order Primates is still doubtful.

INTRODUCTION

The tree shrews were first classified as a member of the family Soricidae (Insectivora) by DIARD in 1820, and RAFFLES (1821) proposed the new genus *Tupaia* for these animals. Whereas they have been generally considered to be insectivores since then, some authors have drawn attention to their morphological resemblance to the primates (DORAN, 1878; PARKER, 1885; etc.).

Many arguments have been put forward in this century on the systematic position of the tree shrews (KAUDERN, 1910; GREGORY, 1910; etc.). CARLSSON (1922) reviewed the previous literatures on tree shrews and first referred them to the suborder Prosimiae, order Primates. This classification has received support from a number of papers published by LE GROS CLARK since 1924. SIMPSON (1945) established a superfamily, the Tupaioidea (Infraorder Lemuriformes, Suborder Prosimii, Order Primates) for the tree shrews together with the fossil primates, *Anagalidae*.

Formerly, the phylogenetic affinity of the tree shrews to the primates was discussed mainly in terms of their resemblance to Malagasy lemurs. Through a re-evaluation of the evidences—for the classification of the tree shrews into the order Primates—formerly studied by other authors, in dental, orbital, and basicranial morphology, VAN VALEN (1965, 1967) placed the tree shrews in the order Insectivora. MCKENNA (1966) also excluded tree shrews from primates, mainly based on the morphology of the auditory bulla. Subsequently, many researchers have agreed that the similarities between living tree shrews and primates may be attributable to convergences or retention of primitive characters (MARTIN, 1968a; SZALAY, 1972; etc.).

On the other hand, STRAUS (1949) and MARTIN (1966) proposed a separate order for the tree shrews, and named it the Tupaioidea. STEUERWALD (1969) also stated that many features of tree shrews indicate an essentially primitive mammalian status, with a considerable degree of resemblance to marsupials.

The exclusion of the tree shrews from primates, however, is not yet fully accepted, because this problem is closely related to the definition of the order Primates. Recently, some authors, in attempts to define this order, pointed out the significance of specific anatomical features, such as the branching pattern of the carotid system, the formative bones of the auditory bulla, and the reproductive system, to distinguish primates from the other mammalian orders (McDOWELL, 1958; McKENNA, 1966; MARTIN, 1968a; CARTMILL, 1972, 1974). Since these features undergo much modification with advancing age in prenatal and postnatal periods, ontogenetic studies of the features are indispensable to assess their significances. However, there have been no such studies on these structures of the tree shrews, except the embryological investigations of the auditory bulla by SPATZ (1966) and MACPHEE (1977). Little is known also about physical growth and development of the tree shrews which would allow the comparison of the features mentioned above.

The developmental stages of mammals have been generally examined based on the degree of epiphyseal union, tooth eruption, and sexual maturation, and maturity in higher primates has been judged by the completion of these three aspects. STEVENSON (1924), STRONG (1925), etc. have been claimed that the sequence of epiphyseal union had a basic uniformity throughout mammals. Although recently, however, the variations of the sequence of epiphyseal union among mammals were pointed out by many authors (WASHBURN, 1943; CURGY, 1965), the epiphyseal sequence is considered to be fixed among the species in a given order of mammals (SCHULTZ, 1956, 1969). In addition, it has been said that the eruptive sequence of the permanent teeth is invariable within a family (SCHULTZ, 1935; SLAUGHTER, PINE, & PINE, 1974; SCHWARTZ, 1974). Accordingly, it seems that the sequence of epiphyseal union and the tooth eruption are possibly used as criteria of systematics in mammals.

The present work aims to elucidate the characteristic mode of development and to discuss the systematic status of the tree shrews in comparison with primates and other mammals, especially the insectivores. For this purpose, (1) epiphyseal union of the extremities and (2) eruption of the permanent teeth were investigated, as well as (3) maturation of the gonads.

The studies of the tree shrews have hitherto been conducted on the general growth (MORRIS, NEGUS, & SPERTZEL, 1967; SORENSON, 1970; SHIMADA, 1973; SCHWAIER, 1975), and on the prenatal development of the dentition (KINDAHL, 1957) and of the cranium (SPATZ, 1964; STARCK, 1967). It seems that no data have been published on the sequence of epiphyseal union of the extremities and on the histological growth and development of the gonads. There are a few papers on the eruptive sequence of the permanent teeth (LYON, 1913; BENNEJEANT, 1936; SHIGEHARA, 1975); SLAUGHTER, PINE, and PINE (1974) discussed the eruptive sequence of the postcanine teeth.

MATERIALS AND METHODS

The subfamily Tupaiinae comprises five genera: *Tupaia*, *Anathana*, *Urogale*, *Tana*, and *Dendrogale*, and 12 species are known as members of the genus *Tupaia*. Among them, the common tree shrew (*Tupaia glis* DIARD) is the largest in size, body weight sometimes exceeding 200 g (NAPIER & NAPIER, 1967), and semi-arboreal in habit.

The materials used in this study were 150 (75 males and 75 females) common tree shrews of unknown ages. These were maintained in the Department of Zoology (12 males and 18 females) and the Primate Research Institute (1 male) of Kyoto University, and the Department of Oral Anatomy of Tohoku University (62 males and 57 females), and later sacrificed and fixed in 10% formalin. Six young were born during the breeding, though they died within a few days after birth. Since breeding conditions were not the same, data on gonadal development are based on the Tohoku University specimens alone.

The sequence of epiphyseal union of the extremities was examined by radiographs taken of dead specimens in a prone position. Following WASHBURN (1943), six joints were investigated: shoulder (proximal part of humerus), elbow (distal part of humerus, proximal parts of radius and ulna), wrist (distal parts of radius and ulna), hip (femoral head), knee (distal part of femur, proximal parts of tibia and fibula), and ankle (distal parts of tibia and fibula). The degree of epiphyseal union were classified into the following four stages with assigned scores:

Epiphysis (ossification center) not yet appeared......0,
Epiphysis appeared but union not yet started......1,
Partial union.......2,
Complete union (including the persistence of the epiphyseal line)......3.

The skeletal score is defined here as the sum of the scores at 12 epiphyses in one specimen and is used to indicate the relative age of the individuals. The total scores for each epiphysis is the sum of the scores in the column of Table 1 for the given epiphysis, and the mean score for each joint is calculated from the total scores for epiphyses involved. Total score for each epiphysis does not reflect the exact degree of epiphyseal union, because if the stage of partial union (score 2) in some epiphysis lasts for long, total score for the epiphysis becomes larger than that of a epiphysis with relatively short duration of partial union, even when these two epiphyses reach the stage 3 at the same time. Accordingly, it is not adequate to decide the order of completion of epiphyseal union based only on the scores. In this study, the sequence of epiphyseal union was determined based on the attainment of stage 3 in each joint.

The eruptive condition of the permanent teeth was observed also by radiographs. The criterion of eruption in this study was based on alveolar eruption, and the following four stages were employed to evaluate the eruptive condition:

a: tooth germ not yet calcified,
b: tooth germ calcifying but not yet erupted,
c: tooth erupting,
d: complete eruption.

The formation of the dental root was also evaluated using:

−: root not yet calcified,
+: root calcifying,
++: root complete.

Since no difference in the order of development of the bone and the teeth were found between sexes, both sexes were dealt with together.

The developmental change of the gonads, i.e., testes and epididymides in males, and ovaries in females, was observed histologically. The materials were taken out from specimens, fixed in 10% formalin, embedded in paraplast, sectioned at 8 μ, and stained with Mayer's haematoxylin and eosin. The mean diameter of the seminiferous tubule for each specimen was calculated from diameters of ten round-shaped tubules, which were measured by ocular micrometer.

Since no comparable data from insectivores has been available, the same examination as on the common tree shrew is conducted on 334 (156 males and 178 females) Ryukyu house shrews (*Suncus murinus riukiuanus* KURODA).

RESULTS AND DISCUSSION

EPIPHYSEAL UNION OF THE EXTREMITIES

The order of the initial appearance of the epiphyses among six joints examined cannot be determined in this study, because young materials were not sufficient. All the epiphyses of these joints have already appeared even in the youngest material except newborns (Table 1). The epiphyseal union starts nearly at the same time in the shoulder, wrist, and knee regions. The three epiphyses in the elbow complete their union first among six joints in both males and females. The union in the ankle region is completed simultaneously with that of the hip in males, but slightly later than the hip in females. The two epiphyses in the wrist fuse with their diaphyses, and are followed by those at the knee. Finally, the complete union in the shoulder region occurs. The sequence of epiphyseal union of the extremities in the common tree shrew is in both sexes: elbow–hip–ankle–wrist–knee–shoulder (Tables 1 & 2).

In the Ryukyu house shrew, on the other hand, some differences exist between males and females in the time of completion of epiphyseal union, and union is completed generally earlier in the female than in the male. The epiphyseal union in the shoulder and knee regions is retarded and these two joints show the so-called lapsed union, in which the epiphyseal cartilage partially persists until an extremely old age. However, there is no difference be-

Table 1. Stage of epiphyseal union of the extremities in the common tree shrew.

	Humerus		Radius		Ulna		Femur		Tibia		Fibula		Skeletal	No. of
	p.	d.	p.	d.	p.	d.	h.	d.	p.	d.	p.	d.	score	individuals
Males	0	0	0	0	0	0	0	0	0	0	0	0	0	4
	1	1	1	1	1	1	1	1	1	1	1	1	12	3
	1	3	3	1	3	1	1	1	1	2	1	1	19	1
	2	2	3	2	2	2	1	1	1	2	1	1	20	1
	2	2	3	2	3	2	3	2	2	3	1	1	26	1
	2	3	3	2	3	2	3	2	2	3	2	3	30	5
	2	3	3	3	3	3	3	2	2	3	2	3	32	3
	2	3	3	3	3	3	3	2	2	3	3	3	33	1
	2	3	3	3	3	3	3	2	3	3	3	3	34	1
	2	3	3	3	3	3	3	3	3	3	3	3	35	4
	3	3	3	3	3	3	3	3	3	3	3	3	36	31
Total score for every epiphysis	19	26	28	23	27	23	24	19	20	26	20	22		Total 55
Females	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	1	1	1	1	1	1	1	1	1	1	1	1	12	2
	1	2	2	1	1	1	1	1	1	1	1	1	14	1
	2	2	2	1	2	1	1	2	1	2	1	2	19	1
	2	3	2	1	2	1	2	2	2	2	1	2	22	1
	2	3	3	1	3	1	3	2	2	2	2	2	26	1
	2	3	3	2	3	2	2	2	2	2	2	2	27	2
	2	3	3	2	2	3	3	2	2	3	2	3	30	3
	2	3	3	3	3	3	3	2	2	3	2	3	32	1
	2	3	3	3	3	3	3	2	3	3	3	3	34	1
	2	3	3	3	3	3	3	3	3	3	3	3	35	2
	3	3	3	3	3	3	3	3	3	3	3	3	36	39
Total score for every epiphysis	21	29	28	21	26	22	25	22	22	25	21	25		Total 56

p: proximal epiphysis; d: distal epiphysis; h: head; 0: not yet appeared; 1: appeared, but not yet united; 2: partial union; 3: complete union.

Table 2. Sequence of epiphyseal union at six joints in the common tree shrew.

		Elbow			Hip	Ankle		Wrist		Knee			Shoulder
Score		Hu.d.	Ra.p.	Ul.p.	Fe.h.	Ti.d.	Fi.d.	Ra.d.	Ul.d.	Fi.p.	Ti.p.	Fe.d.	Hu.p.
Males	Total score for each epiphysis	26	28	27	24	26	22	23	23	20	20	19	19
	Mean score of each joint		27		24	24		23			19.7		19
Females	Total score for each epiphysis	29	28	26	25	25	25	21	22	21	22	22	21
	Mean score of each joint		27.7		25	25			21.5		21.7		21

Hu: humerus; Ra: radius; Ul: ulna; Fe: femur; Fi: fibula; Ti: tibia; p: proximal epiphysis; d: distal epiphysis; h: head.

Table 3. Sequence of epiphyseal union at six joints in the Ryukyu house shrew.

		Elbow			Ankle	Wrist		Hip	Shoulder	Knee		
	Score	Hu.d.	Ra.p.	Ul.p.	Ti-Fi. d.	Ra.d.	Ul.d.	Fe.h.	Hu. p.	Fe.d.	Ti.p.	Fi.p.
Males	Total score for each epiphysis	81	77	72	67	60	60	54	39	39	36	36
	Mean score of each joint		76.7		67	60		54	39		37	
Females	Total score for each epiphysis	88	85	84	74	74	74	63	46	41	39	39
	Mean score of each joint		85.7		74	74		63	46		39.7	

Hu: humerus; Ra: radius; Ul: ulna; Ti-Fi: Tibio-fibula; Fe: femur; Ti: tibial part of tibio-fibula; Fi:fibular part of tibio-fibula; P: proximal epiphysis; d: distal epiphysis.

tween males and females in the overall order: elbow-ankle–wrist–hip–shoulder–knee (Table 3).

Thus the sequence of epiphyseal union in the common tree shrew is different from that in the Ryukyu house shrew, and is also different from the general pattern in primates: elbow–hip–ankle–knee–wrist–shoulder (SCHULTZ, 1969). Although most of the cercopithecoids and man follow the general pattern in primates, the orang-utan (*Pongo*) and gorilla (*Gorilla*) (SCHULTZ, 1956) differ from the tree shrews, cercopithecoids, and man by a special tendency towards early union of the proximal epiphysis of the humerus. STRAUS (1949) explained this tendency in great apes as a specialization related to brachiation. On the other hand, a sequence similar to the common tree shrew is observed in some platyrrhines: night monkey (*Aotus*) (THORINGTON & VOREK, 1976); tamarin (*Saguinus*), capuchin monkey (*Cebus*), and squirrel monkey (*Saimiri*) (TAPPEN & SEVERSON, 1971); and marmoset (*Callithrix*) (SCHULTZ, 1956).

In the common tree shrew, the epiphyseal union in the shoulder and knee are completed later than those in the other joints under consideration. These two joints correspond to the regions where lapsed union are found in some small mammals such as rat (DAWSON, 1925), mouse (STRONG, 1925; DAWSON, 1935), guinea pig (ZUCK, 1938), and the Ryukyu house shrew (present study). The lapsed union has been observed also in the hip joint of the opossum (WASHBURN, 1946). The epiphyses of the knee in the common tree shrew show no lapsed union, and it seems that its epiphyseal plates disappear at an early stage of development (ca. 2.5–3 months; MARTIN, 1968b). It would seem likely that the lapsed union in some small mammals is a primitive reptilian features, rather than a secondarily acquired one. The delayed epiphyseal union in the shoulder and knee of the common tree shrew and of some platyrrhines may be interpreted as reflection of their ancestral condition, although this issue requires further study.

The earliest epiphyseal union in the elbow is common to the primates and mammals hitherto reported (Tables 4 & 5). It is followed by the hip and then ankle in the tree shrew and primates, except tamarins, whereas a reverse order, ankle–hip, is found in most of other terrestrial mammals including the Ryukyu house shrew. However, there is no sufficient evidence now to determine the exact meaning of the discrepancy of the order between the tree shrew-primates and the terrestrial mammals. The clear regularity found in the se-

Table 4. Sequence of epiphyseal union at six joints in the common tree shrew and primates.

Species, genus, or group	Sequence	Upper extremity	Lower extremity
Tupaia glis (present work)	E–H–A–W–K–S	E–W–S	H–A–K
*Lemur** (TODD, 1930)	E–H–A–K–W–S	E–W–S	H–A–K
*Aotus** (THORINGTON & VOREK, 1976)	E–H–A–W–K–S	E–W–S	H–A–K
*Saguinus** (TAPPEN & SEVERSON, 1971)	E–A–H–W–K–S	E–W–S	A–H–K
*Cebus** (TAPPEN & SEVERSON, 1971)	E–H–A–W–K–S	E–W–S	H–A–K
*Saimiri** (TAPPEN & SEVERSON, 1971)	E–H–A–W–K–S	E–W–S	H–A–K
Marmoset (SCHULTZ, 1956)	E–H–A–W–K–S	E–W–S	H–A–K
*Nasalis** (SCHULTZ, 1942)	E–H–A–K–W–S	E–W–S	H–A–K
Gibbon* (TODD, 1930; SCHULTZ, 1944)	E–H–A–K–W–S	E–W–S	H–A–K
*Pongo** (TODD, 1930; SCHULTZ, 1941)	E–H–A–K–S–W	E–S–W	H–A–K
*Pan** (TODD, 1930)	E–H–A–K–W–S	E–W–S	H–A–K
Pan (SCHULTZ, 1940, 1944)	E–H–A–K–W–S	E–W–S	H–A–K
*Gorilla** (TODD, 1930)	E–H–A–K–S–W	E–S–W	H–A–K
*Gorilla** (RANDALL, 1944)	E–H–S–A–K–W	E–S–W	H–A–K
*Homo** (STEVENSON, 1924)	E–H–A–K–W–S	E–W–S	H–A–K
New World monkeys* (TODD, 1930)	E–H–A–K–W–S	E–W–S	H–A–K
New World monkeys (SCHULTZ, 1956)	E–H–A–K–S–W	E–S–W	H–A–K
Macaques (WASHBURN, 1943)	E–H–A–K–W–S	E–W–S	H–A–K
Old World apes* (TODD, 1930)	E–H–A–K–W–S	E–W–S	H–A–K

* The data have been rearranged by the author into the regional sequence on the basis of original data on the time of epiphyseal union; E: elbow; S: shoulder; W: wrist; H: hip; K: knee; A: ankle.

quence of the other three joints (wrist, knee, and shoulder) has not been observed in primates and terrestrial mammals. In each group of these animals, the sequence of epiphyseal union is more fixed among the three joints of the lower extremity than among the three joints of the upper extremity. As for the sequence of epiphyseal union among the three joints of the lower extremity, hip–ankle–knee is reported for primates, except tamarins, and ankle–hip–knee for the terrestrial mammals with a few exceptions. The hip–ankle–knee sequence in the lower extremity, however, cannot be considered as a synapomorphic character of primates, because this sequence is found also in the opossum and hedgehog as reported by

Table 5. Sequence of epiphyseal union at six joints in mammals other than primates.

Order, genus, or group	Sequence	Upper extremity	Lower extremity
Marsupialia			
Opossum (WASHBURN, 1946)	E–S–W–H–A–K	E–S–W	H–A–K
Insectivora			
Suncus (present work)	E–A–W–H–S–K	E–W–S	A–H–K
Hedgehog (WASHBURN, 1946)	E–H–A–W–K–S	E–W–S	H–A–K
Rodentia			
Rat* (DAWSON, 1925)	E–A–H–K–W–S	E–W–S	A–H–K
Carnivora			
Dog* (SMITH & ALLOCOCK, 1960)	E–A–W–H–S–K	E–W–S	A–H–K
Dog* (SISSON, 1953)	E–A–S–W–H–K	E–S–W	A–H–K
Perissodactyla			
Horse* (SISSON, 1953)	E–A–H–K–W–S	E–W–S	A–H–K
*Tapir** (TODD & TODD, 1938)	E–A–(H, K, W, S)	E–(W, S)	A–(H, K)
Rhinocerotidae* (TODD & TODD, 1938)	(E, A, K, W, S)–H	(E, W, S)	(A, K)–H
Artiodactyla			
*Ox** (SISSON, 1953)	E–A–H–K–W–S	E–W–S	A–H–K
*Bos** (KOCH, 1935)	E–A–H–K–W–S	E–W–S	A–H–K
*Odocoileus** (TODD & TODD, 1938)	E–A–H–W–K–S	E–W–S	A–H–K
*Cervidae** (TODD & TODD, 1938)	E–A–H–W–K–S	E–W–S	A–H–K
*Bovidae** (TODD & TODD, 1938)	E–A–H–W–K–S	E–W–S	A–H–K
*Ovis** (TODD & TODD, 1938)	E–A–H–W–K–S	E–W–S	A–H–K
pig* (SISSON, 1953)	E–A–H–W–K–S	E–W–S	A–H–K
Hyracoidea			
*Hyrax** (TODD & TODD, 1938)	E–A–H–(K, W)–S	E–W–S	A–H–K
Proboscidea* (TODD & TODD, 1938)	E–(A, K, S)–W–H	E–S–W	(A, K)–H

For abbreviations, see Table 4.

WASHBURN (1946). This similarity of hip–ankle–knee sequence pattern is not a significant evidence for judging the tree shrew as a member of the order Primates, and this pattern in the common tree shrew, primates, and opossum may be suggesting some possibility of its relation to their arboreal life.

The early union at the shoulder joint in great apes suggests that the sequence of epiphyseal union may be affected by factors such as the loading system on each epiphysis during locomotion. SIMON (1978) reported in his experimental study that the change of the locomotion resulted in the acceleration or retardation of the time of completion of epiphyseal union. The sequence of epiphyseal union is not so fixed in a given taxonomic group as has been previously considered.

ERUPTION OF THE PERMANENT TEETH

The dental formula for the common tree shrew is: $I\,\frac{1\text{–}2}{1\text{–}3}\ C\,\frac{1}{1}\ P\,\frac{2\text{–}4}{2\text{–}4}\ M\,\frac{1\text{–}3}{1\text{–}3} = 38.$

Upper jaw: The molars, which have been embryologically regarded as the deciduous teeth in mammals, begin to erupt before other permanent tooth germs begin to calcify (Table 6). The premolars precede the anterior teeth both in calcification and eruption (Figs. 1a, b, c). Among the three premolars, P^4 erupts first and P^2 last. I^2 erupts earlier than the other anterior teeth. In summary, the eruptive sequence of the upper permanent teeth is: the start of eruption, M^1–M^2–M^3–(P^4, P^3)–P^2–(I^2, I^1, C^1); the completion of eruption (Table 7), M^1–M^2–M^3–P^4–P^3–P^2–I^2–(I^1, C^1).

Lower jaw: The lower teeth, with a few exceptions, erupt generally before the corresponding upper teeth. The molars erupt after the eruption of the deciduous teeth, as in the upper jaw (Table 6; Fig. 2a). Judging from the state of calcification of the dental roots, the sequence of molars is: M_1–M_2–M_3. The calcification in premolar tooth germs begins almost

Table 6. Stage of tooth eruption in the upper and lower jaws.

Upper teeth									No. of individuals	Lower teeth										No. of individuals
I^1	I^2	C^1	P^2	P^3	P^4	M^1	M^2	M^3		I_1	I_2	I_3	C_1	P_2	P_3	P_4	M_1	M_2	M_3	
d	d	d	d	d	d	d	d	d	30	d	d	d	d	d	d	d	d	d	d	31
d	d	d	d	c	d	d	d	d	1	d	d	d	d	d	c	d	d	d	d	1
c	d	c	d	d	d	d	d	d	1	d	c	d	d	d	c	d	d	d	d	1
c	d	c	d	c	d	d	d	d	1	d	c	d	c	d	d	d	d	d	d	2
c	c	c	d	d	d	d	d	d	1	d	c	d	c	d	c	d	d	d	d	2
c	c	c	c	d	d	d	d	d	1	c	c	d	c	d	c	d	d	d	d	1
c	c	c	c	c	d	d	d	d	4	c	b	d	c	d	c	d	d	d	d	2
c	c	c	c	c	c	d	d	d	1	c	b	d	c	d	b	c	d	d	d	1
b	b	b	c	c	c	d	d	d	1	b	b	c	b	c	b	c	d	d	d	2
b	b	b	c	c	c	d	d	c	1	b	b	c	b	c	b	c	d	d	c	1
b	b	b	b	c	c	d	d	c	1	b	b	c	b	c	b	b	d	d	c	1
b	b	b	b	c	c	d	c	c	2	b	b	c	b	c	b	b	d	d	/	1
b	b	b	b	b	b	d	d	c	2	b	b	c	b	c	b	b	d	c	c	1
b	b	b	a	b	b	d	c	c	1	b	b	b	b	c	b	b	d	c	c	1
b	b	a	b	b	b	c	c	/	1	b	a	b	b	b	b	b	c	c	c	1
a	a	a	b	b	b	c	c	c	1	b	a	b	a	b	b	b	c	c	c	1
a	a	a	b	b	b	c	c	/	2	b	b	b	a	b	a	b	c	c	b	1
a	a	a	a	a	a	c	c	b	1	a	a	b	b	b	b	b	c	c	c	1
										a	a	a	a	b	b	b	c	c	c	1
										a	a	a	a	a	a	a	c	c	b	1

a: not yet calcified; b: calcifying, but not yet erupted; c: erupting; d: erupted.

Table 7. Stage of root formation in the upper and lower jaws.

Upper teeth I^1	I^2	C^1	P^2	P^3	P^4	M^1	M^2	M^3	No. of individuals
++	++	++	++	++	++	++	++	++	30
+	++	++	++	+	++	++	++	++	1
+	++	+	++	++	++	++	++	++	1
+	+	+	++	++	++	++	++	++	1
+	+	+	++	+	++	++	++	++	1
+	+	+	+	+	+	++	++	++	1
+	+	+	+	+	+	++	++	+	5
+	+	−	+	+	+	+	+	+	1
−	−	−	+	+	+	+	+	+	1
−	−	−	−	+	+	+	+	+	1
−	−	−	−	−	−	+	+	+	4
−	−	−	−	−	−	+	+	/	3
−	−	−	−	−	−	+	+	−	2

Lower teeth I_1	I_2	I_3	C_1	P_2	P_3	P_4	M_1	M_2	M_3	No. of individuals
++	++	++	++	++	++	++	++	++	++	30
++	+	++	+	++	++	++	++	++	++	3
++	+	++	+	++	+	++	++	++	++	2
+	+	++	+	++	+	+	++	++	++	5
+	+	+	+	+	+	+	++	++	+	1
+	−	+	+	+	+	+	++	++	+	1
+	+	+	+	+	−	+	++	+	+	1
+	+	+	+	+	+	+	++	+	/	1
+	−	+	−	+	+	+	++	++	+	1
+	−	+	−	+	−	+	++	+	+	1
−	−	+	−	+	−	−	++	+	+	1
−	−	−	−	+	−	+	+	+	+	1
−	−	−	−	−	−	−	+	+	+	2
−	−	−	−	−	−	−	+	+	−	3
−	−	−	−	−	−	−	+	−	−	1

−: not calcified; +: calcifying, but incomplete; ++: complete.

at the same time as the start of M_3 eruption. I_3 and P_2 are smaller in size than the other permanent teeth, and accordingly earlier in both the start and the completion of eruption (Fig. 2b). The eruption of P_4 follows them, followed by C_1 and I_1, then by P_3, and finally by I_2 (Fig. 2c). Therefore, the sequence of the lower permanent teeth is: the start of eruption, M_1–M_2–M_3–P_2–I_3–P_4–(I_1, C_1)–P_3–I_2; the completion of eruption (Table 7), M_1–M_2–M_3–(P_2, I_3)–P_4–I_1–P_3–C_1–I_2.

Although the eruptive sequence in the upper jaw is not exactly the same as that in the lower jaw, the tendency for the premolars to be replaced earlier than the anterior teeth is recognized both in the upper and lower jaws. It is noteworthy that all the anterior teeth are replaced almost at the same time in the upper jaw, in other words, all the anterior deciduous teeth are shed at about the same time and there are no functional teeth in the anterior part of the upper jaw until the corresponding permanent teeth are emerged.

Tooth replacement in the Ryukyu house shrew does not occur after birth. KINDAHL (1959) reported that deciduous tooth germs in *Suncus* (*Crocidura*) *orangiae* were absorbed during the foetal period. It may be considered, therefore, that all the teeth that erupt after birth in the Ryukyu house shrew are of the permanent teeth.

The criteria employed for the common tree shrew is not appropriate to make clear the eruptive sequence of permanent teeth in the Ryukyu house shrew. The oral epithelium covers all the calcified teeth until the food intake begins, and breaks immediately after, at two or three weeks of age. By this time, the alveolar bone formation and tooth eruption have been completely finished. Although all the dental crowns are roentgenographically in an erupted condition during the alveolar bone formation, it is difficult to determine the eruptive sequence, because the development of the jaw bones is retarded in comparison with the tooth formation. It is concluded that the permanent teeth is completed at about the weaning, that is, three weeks after birth.

BENNEJEANT (1936, cited by REMANE, 1960) gave the eruptive sequence of the permanent teeth of the "Tupai" as M_1–M_2–M_3–I_1–I_2–C–P_2–P_3–P_4, but the sequence obtained in the present study is different from his result. The sequence in which the premolars are replaced earlier than the anterior teeth has also been reported in several species of insectivores. For

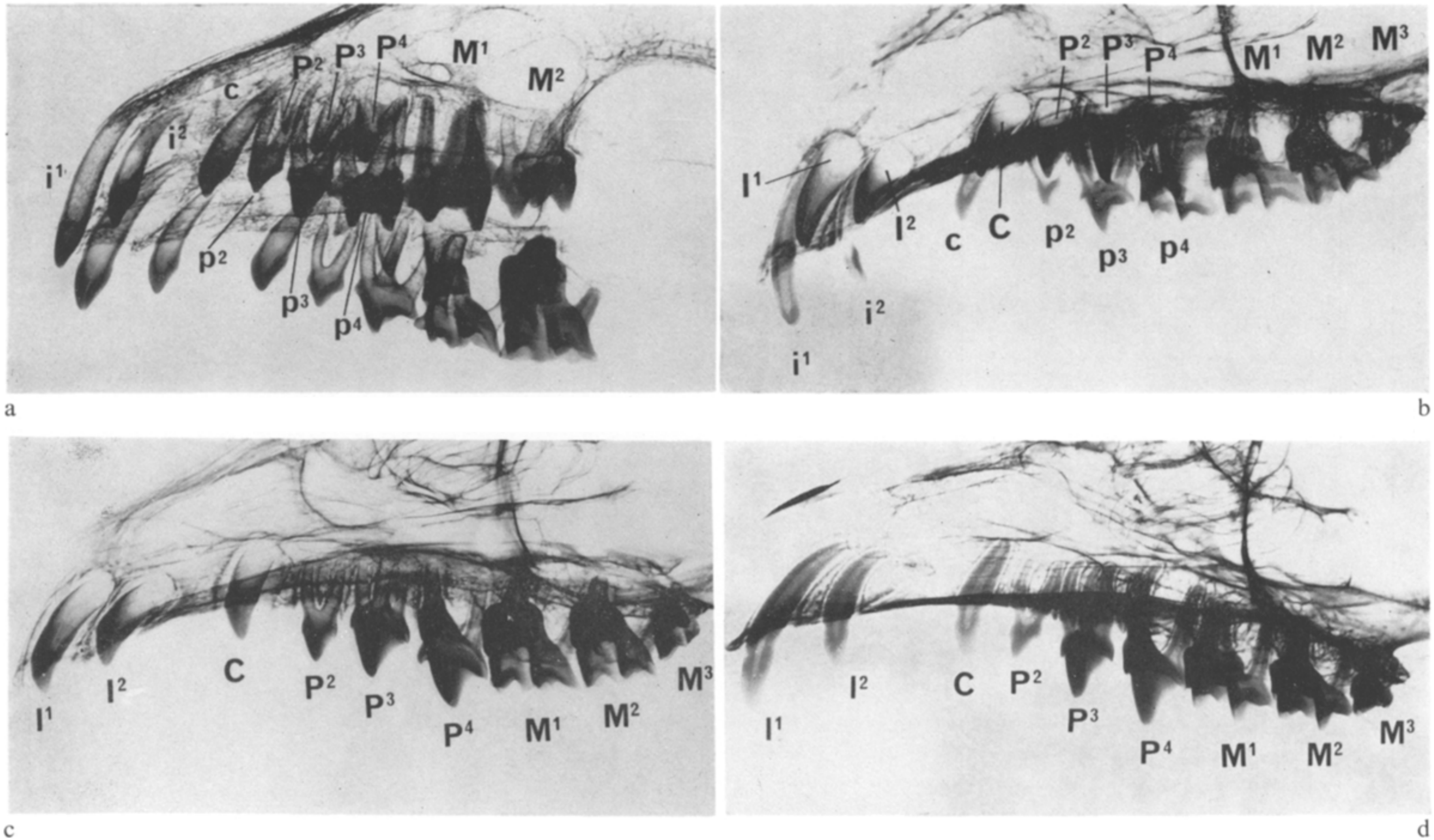

Fig. 1. Radiographs of the four eruptive stages in the upper permanent teeth. a: Molars are erupting; b: All the antemolar tooth germs begin to calcify; c: I^1, I^2, and C^1 begin to erupt; d; All the permanent teeth are fully in place.

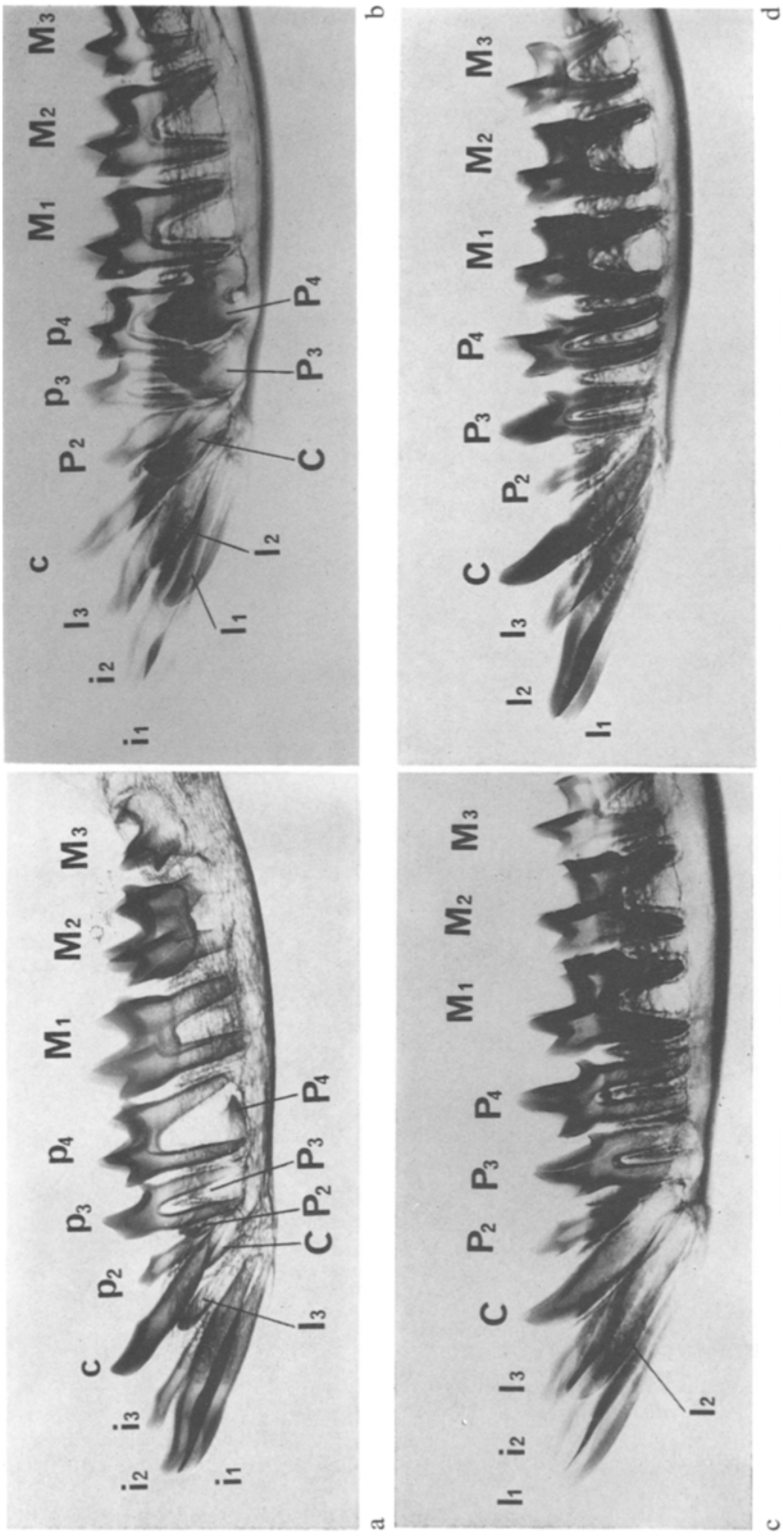

Fig. 2. Radiographs of the four eruptive stages in the lower permanent teeth. a: Molars are erupting. All the erupted antemolars are deciduous teeth; b: All the molars have completely erupted. Among the other permanent teeth, only I_3 and P_2 are erupting; c: All the anterior teeth are nearly in place; d: All the permanent teeth have already erupted.

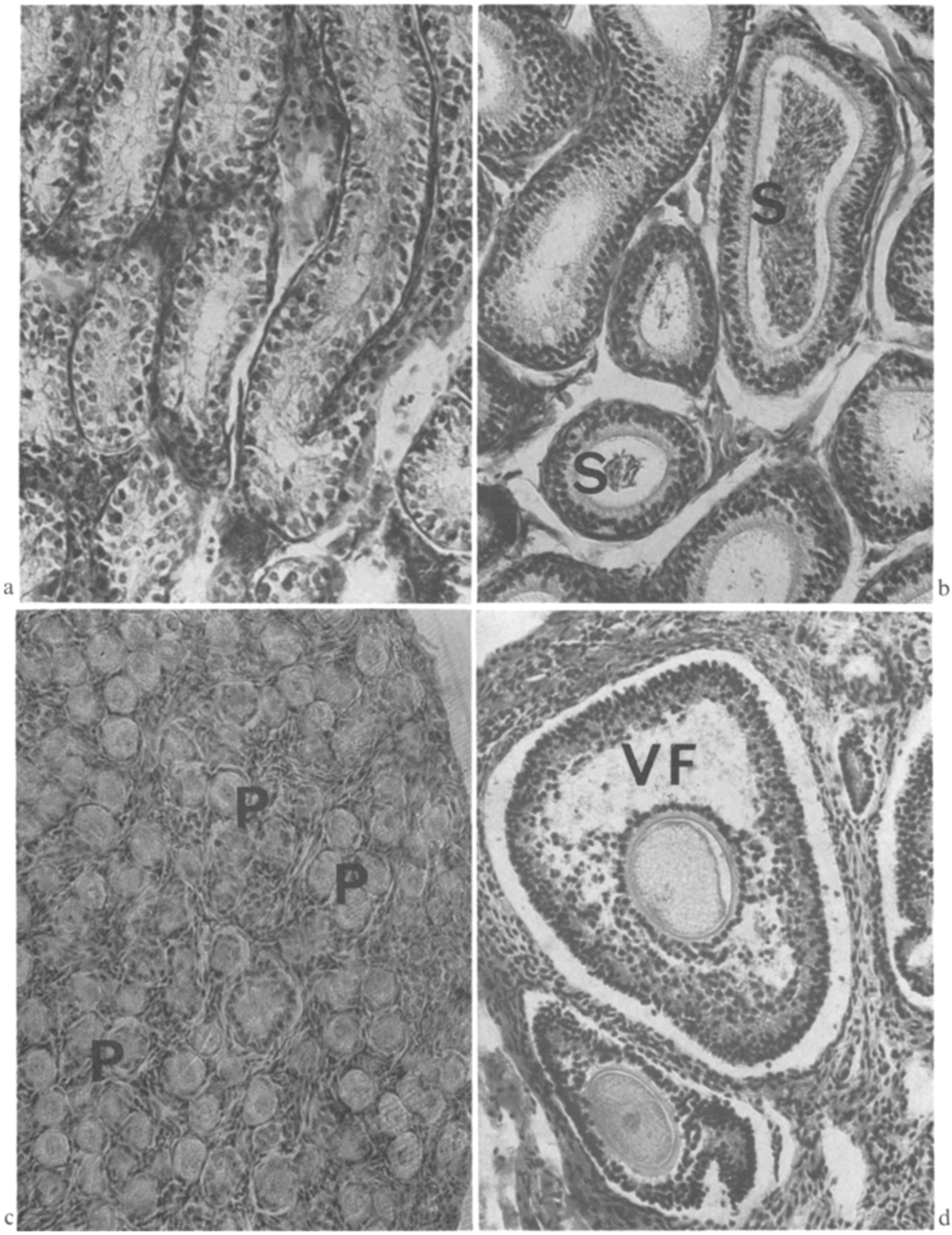

Fig. 3. Microscopic pictures of the gonads. a: Testis in young male. H–E, × 80; b: Epididymis in adult male. H–E, × 80; c: Ovary in young female. H–E, × 80; d: Ovary in adult female. H–E, × 80; S: spermatozoa; P: primordial follicle; VF: vesicular follicle.

instance, the Japanese shrew mole (*Urotrichus talpoides*), (USUKI, 1967) has the sequences P^2–P^3–P^4–I^1–(I^2, p^1)–C^1 in the upper jaw, and P_2–P_3–P_4–I_1–C_1 in the lower jaw; the furry snouted shrew mole (*Dymecodon pilirostris*), (HANAMURA, 1969) has the sequences (P^2, P^4)–P^3–I^1–C^1–p^1 in the upper jaw, and (P_2, P_3, P_4)–I_1–C_1–p_1 in the lower jaw. The Japanese shrew mole, in which tooth replacement taken place in rapid succession, also shows the simultaneous replacement of the upper anterior teeth observed in the common tree shrew.

In extant prosimian as well as other members of primates, M^2_2 and especially M^3_3 show delayed eruption and M^1_1 or M^2_2 is followed by incisors, but not by premolars (SCHULTZ, 1959; SCHWARTZ, 1974). It may reasonable to consider that the delayed eruption of M^2_2 and M^3_3 of primates have some relation to their elongated period of growth. The hypothetical sequence molar–incisor–premolar, which was assumed by SCHULTZ (1935) and REMANE (1960) for the ancestral primates, is observed in night monkey (*Aotus*) (SCHULTZ, 1935; THORINGTON & VOREK, 1976), one of the New World monkeys, and not in the extant prosimians, whose sequence is similar to that in higher primates.

As for the temporal relation between the eruption of the permanent teeth and the epiphyseal union in the common tree shrew, the epiphyseal union of five joints other than shoulder has been completed by the time of complete eruption of all the permanent teeth. At this time, however, a narrow fissure is still present between the proximal epiphysis and the diaphysis of humerus.

SEXUAL MATURATION

It has generally been accepted that under laboratory conditions tree shrews can become pregnant throughout the year (SPRANKEL, 1961; MARTIN, 1968b; SCHWAIER, 1975), though it is still uncertain whether or not wild tree shrews have a definite breeding season (LYON, 1913; WADE, 1958; MARTIN, 1968b). In this study, seasonal changes of adult gonads are not observed histologically.

In newborn males, no lumen is observed in seminiferous tubules and epithelial cells of these tubules do not show any regular arrangement. By the time when the tubule diameter reaches about 75 μ or more, the epithelial cells of the seminiferous tubules have become arranged in a regular fashion (Table 8; Fig. 3a). Epiphyseal union in the extremities has not yet begun by this time, though all the epiphyses have already appeared. After the complete union of all the epiphyses, and the maximum diameter of the seminiferous tubules exceed 100 μ, the spermatozoa both in testes and epididymides can be seen. Adult males with thick tubules (160–190 μ in their maximum diameter) have abundant spermatozoa both in testes and epididymides all year round (Fig. 3b).

The spermatozoa cannot be seen until the eruption of the permanent dentition has been completed.

In newborn females, most oocytes are surrounded by pregranulosa cells that form primordial follicles (Fig. 3c). Some of these primordial follicles become to the secondary follicles through the primary follicles before all the epiphyses appear. Before the completion of the epiphyseal union in the elbow and hip regions, some number of vesicular follicles appear in the ovaries. Follicular enlargement, which produce mature follicle, is seen almost at the same time as epiphyseal union in the shoulder. These vesicular follicles develop into mature follicles without involution after the complete union of all the epiphyses in the extremities (Fig. 3d). These matured vesicular follicles are seen only after the eruption of the permanent teeth has been completed.

Table 8. Developmental condition of male gonads at seven stages of skeletal growth.

Skeletal score	Mean diameter of tubules (μ)	Lumen of tubules	Spermatozoa Testes	Spermatozoa Epididymides	No. of individuals
12	45.3	−	−	−	3
26	58.3	−	−	−	1
30	73.0	−	−	−	5
32	75.5	−	−	−	1
32	88.4	+	−	−	2
36	111.5	+	+	−	6
36	176.4	+	+	+	3

−: not observed; +: observed.

In the Ryukyu house shrew, matured follicles are seen shortly after the weaning in females. In males, on the other hand, spermatozoa are not observed until four weeks of age, and only spermatids are present in the testes at the time of weaning.

Sexual maturation is reached in both sexes of the common tree shrew later than the completion of epiphyseal union of the extremities, although the interval between the times of these occurrences may be very short, especially in females. KAUFMANN (1965) reported that female receptivity in the common tree shrew was reached at three and half months of age, and a similar result (16th week after birth) was obtained by MORRIS, NEGUS, and SPERTZEL (1967). Whereas the age of sexual maturation cannot be determined in the present study because of lack of information on the exact age of the specimens, it may be reasonably estimated from data reported by MARTIN (1968b) and SORENSON (1970) that sexual maturation in captive tree shrews is attained at an age between 3 months and 4 months in both sexes.

Sexual maturation in the Ryukyu house shrew is reached at 5 weeks in males and 3 weeks in females and is considerably more rapid than other insectivores; for example, the American shrew (*Blarina brevicauda*) matures at 8 weeks of age (PEARSON, 1944). On the other hand, the earliest maturation in primates so far reported is that of the mouse lemur (*Microcebus*), which is attained at the age of 7 to 10 months (NAPIER & NAPIER, 1967). It may be considered that the age of sexual maturation in the tree shrew lies between that of insectivores and that of primates.

ORDER OF THE COMPLETION OF DEVELOPMENT

In the common tree shrew, the completion of dental eruption (D) occurs first, followed by the epiphyseal union (E), and finally the sexual maturation (S) is attained. This temporal order of completion in this species is here expressed as D-E-S type; that is to say, sexual maturation is attained after the bone and dentition have been completed. On the other hand, D-S-E type is observed in the Ryukyu house shrew. This difference of the latter from the former is primarily due to the lapsed union at the knee and shoulder joints of the Ryukyu house shrew.

No ready-made comparable data on the type of completion in other mammals are available, but the types for some mammals can be deduced from the works by many other authors who dealt with the development of these three aspects (Table 9). As far as known data indicate, it becomes clear that there are three major types in the order of completion in mammals. D-E-S type in small or medium-sized species including the common tree shrew; S-D-E type in large or domesticated species; D-S-E type in some small species which show lapsed epiphyseal union.

The common tree shrew shares D-E-S type with the only reported two species of platyr-

Table 9. Types of the order of completion of epiphyseal union (E), eruption of the permanent teeth (D), and sexual maturation (S) in various mammals as arranged and adapted from original data.

Order and genus	Type of development	Sources
Primates		
Homo	S–(D, E)	STEVENSON, 1924; FLECKER, 1942
Gorilla	S–D–E	SCHULTZ, 1942; RANDALL, 1944
Pan	S–(D, E)	SCHULTZ, 1940; NISSEN & RIESEN, 1949, 1964
Pongo	S–D–E	SCHULTZ, 1941
Macaca fuscata	S–D–E	INOUE & HAYAMA, 1962; HAYAMA, 1965
Macaca mulatta	S–D–E	HURME & WAGENEN, 1961
Saimiri	D–E–S	LONG & COOPER, 1968; TAPPEN & SEVERSON, 1971
Saguinus	D–E–S	CHASE & COOPER, 1969; TAPPEN & SEVERSON, 1971; HERSHKOVITZ, 1977
Tupaia glis	D–E–S	Present work
Insectivora		
Suncus	D–S–E	Present work
Rodentia		
Rattus	D–S–E	DAWSON, 1925; Biol. Data Book
Mus	D–S–E	STRONG, 1925; Biol. Data Book
Cavia	D–S–E	ZUCK, 1938; Biol. Data Book
Carnivora		
Canis fam.	S–D–E	SISSON, 1953; SMITH & ALLOCOCK, 1960
Canis lupus	D–E–S	RAUSH, 1967; MECH, 1974
Canis mesomelas	D–E–S	LOMBAARD, 1971
Felis dom.	S–D–E	SISSON, 1953
Artiodactyla		
Bos	S–D–E	KOCH, 1934; SISSON, 1953
Sus	S–D–E	SISSON, 1953; CURGY, 1965
Perissodactyla		
Equus	S–E–D	SISSON, 1953
Marsupialia		
Didelphis	S–D–E	WASHBURN, 1946; NESSLINGER, 1956

rhines, squirrel monkeys and tamarins, and two species of wolves, that differ from catarrhines with S-D-E type and from the Ryukyu house shrew and some rodents with D-S-E type. Although epiphyseal union has not been fully known for wild mammals, it can be generally said that S-D-E type is found in comparatively larger mammals and D-E-S type in smaller ones. On the other hand, however, the domestic dog (*Canis familiaris*), having close affinities with wolves (*C. lupus*), shows S-D-E type which observed in larger mammals. Accordingly, it would seem possible that the type of completion is liable to modification by acceleration of sexual maturity resulting from the shift of environment by domestication. Correspondence of the type of completion between the common tree shrew and platyrrhine, therefore, cannot be regarded as clear evidence for their close phylogenetic affinity, and D-E-S type in the common tree shrew may be rather taken as the general type of small and medium-sized mammals.

SUMMARY AND CONCLUSION

The epiphyseal union, eruption of the permanent teeth, and sexual maturation were examined in 150 common tree shrews in a cross-sectional study, and were compared with those in the Ryukyu house shrew and other mammals including primates. The order of completion of these aspects was also investigated.

The sequence of epiphyseal union is: elbow–hip–ankle–wrist–knee–shoulder. The sequence of epiphyseal union in mammals is not so fixed as has been previously considered, and may be affected by such as the loading system on the epiphysis of long bones.

The eruptive sequence of the permanent teeth in the common tree shrew is more similar to that of insectivores than primates.

The gonads are observed histologically to determine sexual maturation, and the sexual maturation in both sexes seems to be completed between the third and fourth month of age.

The order of the completion of development among the bones, the dentition, and the gonads in the common tree shrew is the same as those in platyrrhines and other small mammals but different from catarrhines and other large mammals.

Although the common tree shrew has many similarities with platyrrhines in the development of the eco-sensitive organs such as the epiphyses of the extremities, it bears more resemblance to insectivores in the development of the teeth, which is phylogenetically considered as one of the conservative physical features. In conclusion, the inclusion of the tree shrews in the order Primates is still doubtful.

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