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A NEW SPADEFOOT TOAD FROM THE OLIGOCENE OF MONGOLIA WITH A SUMMARY OF THE EVOLUTION OF THE PELOBATIDÆ[1]

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The Third Asiatic Expedition of the American Museum discovered in the Hsanda Gol formation in the Tsagan Nor basin of outer Mongolia a beautifully preserved pelobatid. This single specimen is of unusual interest as representing the group from which the modern spadefoot toads arose, to spread on one side across Europe and on the other into North America. It is the oldest known fossil which belongs unquestionably to the Pelobatidæ.

The Hsanda Gol formation has been assigned to the Oligocene.[2] The specimen described below was found associated with a varied mammalian fauna, mostly rodents. Eleven species and nine genera of the latter have already been described by Matthew and Granger.[3] The formation consists mostly of sandy clays. The terrain during Oligocene times was therefore similar to that to which modern spadefoot toads are restricted, except that it may have contained more clay and less sand. The climate was apparently semiarid.

PELOBATIDÆ

Macropelobates osborni,[4] new genus and species

TYPE.—No. 6252; an incomplete skeleton, crushed anteriorly, but well preserved.

HORIZON AND LOCALITY.—Hsanda Gol formation, Tsagan Nor basin, Mongolia.

DIAGNOSIS.—Undoubtedly a pelobatid in that it exhibits the following characters: Anomocœlous[5], with the coccyx not ankylosed to sacrum; coccyx with a single condyle; teeth present on upper jaw; coracoids suggesting an arciferal condition; an enormous prehallux (spade); epiphyses absent (cartilaginous); a bony encrustation on the frontoparietal, nasal and squamosal.

Agrees with *Pelobates* in: Maxillary teeth guarded mesially by a ridge, but this more pronounced than in *Pelobates;* neural processes of anterior vertebræ long and

[1] Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 27.

[2] Matthew, W. D., and Granger, Walter. 1923. Amer. Mus. Novitates, No. 101, p. 1.

[3] *Op. cit.*

[4] Named for Professor Henry Fairfield Osborn, who has been so largely the inspiration of the Third Asiatic Expedition.

[5] For this term see Noble, 1922.

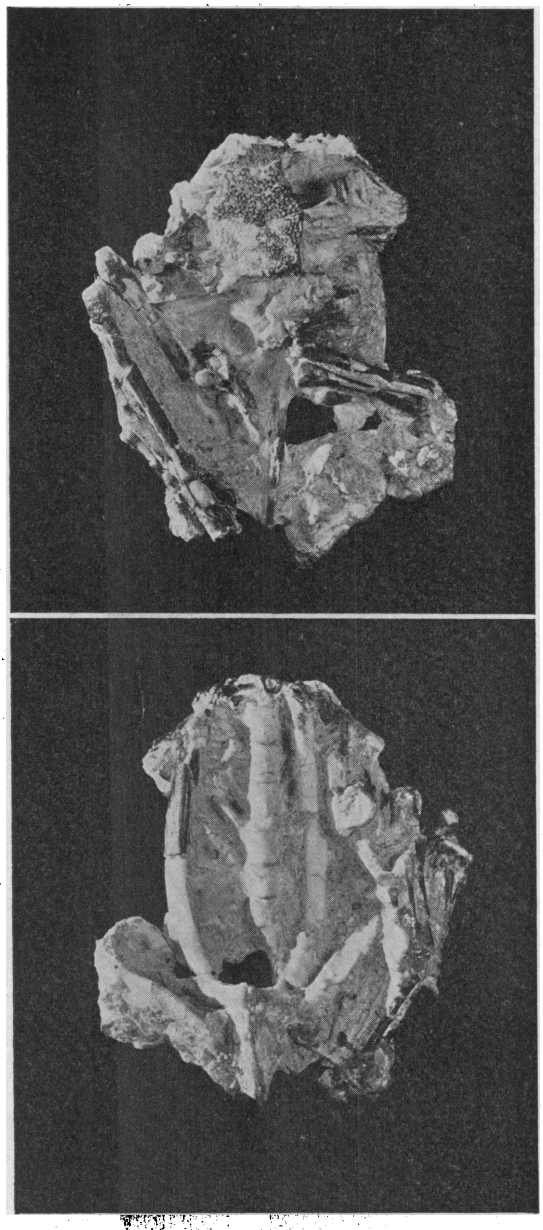
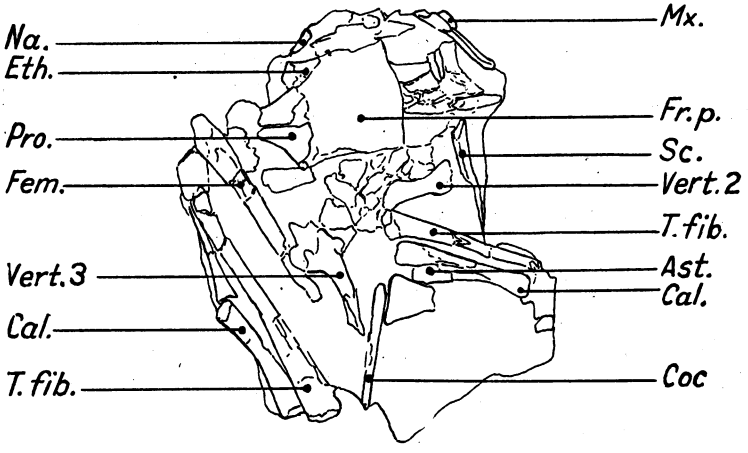
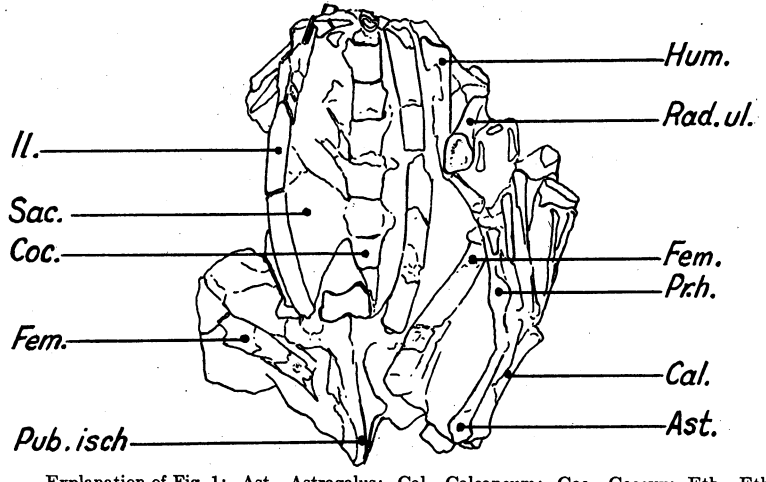


Fig. 1. *Macropelobates osborni* Noble, type specimen. A, dorsal, and B, ventral aspect.



A



B

Explanation of Fig. 1: Ast., Astragalus; Cal., Calcaneum; Coc., Coccyx; Eth., Ethmoid; Fem., Femur; Fr. p., Frontoparietal; Hum., Humerus; Il., Ilium; Mx., Maxilla (fragment); Na., Nasal (fragment); Pr. h., Prehallux; ▲Pro., Proötic; Pub. isch., Puboischium; Rad. ul., Radioulna; Sac. Sacral diapophysis; Sc., Scapula (part); T. fib., Tibiofibula; Vert. 2., Vertebra (apparently the 2d); Vert. 3., Vertebra (apparently the 3d).

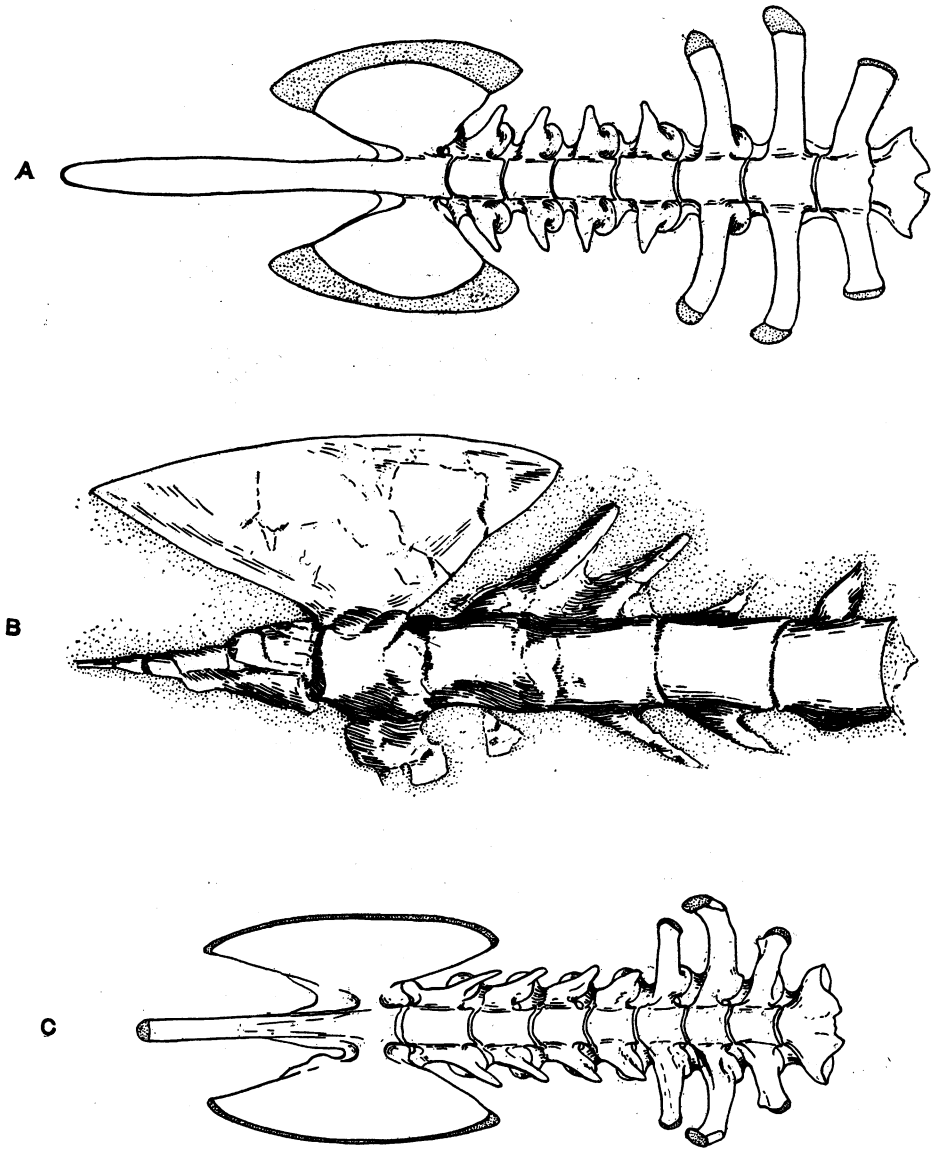


Fig. 2. Vertebral columns ventral aspect. A, *Scaphiopus couchii* Baird; B, *Macropelobates osborni* Noble; C, *Pelobates fuscus* (Laurenti).

pointed (possibly exaggerated through crushing); coracoid with an expanded mesial end; squamosal with a large sheath of bony encrustations upon its lateral surface; presacral vertebræ with transverse processes directed very obliquely forward (but not quite as much as in *P. fuscus*).

Agees with *Scaphiopus* in: Puboischial plate as long as at least three presacral vertebræ; ilium longer than the femur; coccyx longer than the sacral wings; only one segment in the prehallux (as in *S. couchii* and *S. hammondii*, but not *Scaphiopus holbrookii* and *S. dugesii*).

Distinguished from the other fossorial pelobatids by: Size very large; coccyx and sacrum not fused (this condition appears as a variation in *Pelobates*); transverse processes of vertebræ immediately anterior to the sacrum, narrow; sacral diapophyses as wide as the ventral surfaces of three and one-half presacral vertebræ (three in *Scaphiopus*, five in *Pelobates*); transverse diameter of sacral wings contained in the longitudinal diameter a trifle over two times; coccyx slender; radioulna rather wide and slightly curved (Fig. 3E); astragalus and calcaneum very slender (Fig. 3G); puboischial plate solid, the pubis apparently ossified and forming part of this plate.

Description of Type Specimen.—Skull strongly ossified and sheathed as in *Pelobates* with a secondary deposit of bone, the frontoparietal completely covered with this pitted sheathing (except anteriorly where it has obviously been broken away); a fragment of a nasal present and covered with this ossification; the squamosal destroyed anteriorly, but the remaining part sheathed laterally as in *Pelobates*, this sheathing more than twice as long and twice as wide as the anteroposterior diameter of the unsheathed dorsal surface of the squamosal. Ethmoid entirely ossified, lateral wings fairly well preserved and similar to the ethmoid of *Scaphiopus* except that they appear more massive; left nasal represented by two fragments which would indicate that the nasals had originally the same form as in *Scaphiopus* and *Pelobates*, at least they were in broad contact in the mid-line; frontoparietal single, its bony sheathing fractured along the sides posteriorly and hence no lateral processes as in *Scaphiopus* or *Pelobates;* both proötic and dorsal part of the squamosal exposed and without bony encrustations; squamosal and pterygoid represented only by fragments which may be matched with parts of the homologous bones in *Scaphiopus;* a fragment of the right maxilla present; the teeth walled in mesially by a pronounced ridge (Fig. 4A).

Vertebral column typically anomocœlous, the coccyx articulating by a single condyle with the sacrum; the dorsal surfaces of only three of the vertebræ exposed and these surfaces very much broken. Apparently the anterior vertebræ were provided with long transverse processes and the neural spines were long and slender; the longest neural spine retained is slightly longer than the ventral surfaces of any of the presacral vertebræ, and about equal to the greatest anteroposterior diameter of the exposed dorsal surface of the proötic. The transverse processes of the two vertebræ immediately anterior to the sacrum well preserved, these proportionately more slender than in *Pelobates* and directed not so obliquely forward as in that genus. The longest of these transverse processes is a little longer than the greatest length of any of the vertebræ, possibly just equal to these vertebræ if they were disarticulated. Sacral vertebræ with strongly dilated diapophyses, the transverse diameter of these wings slightly shorter than half the longitudinal diameter; longitudinal diameter of these diapophyses equals the longitudinal diameter of three and one-half presacral verte-

bræ; coccyx broken but longer than the longitudinal diameter of the sacral wings, nearly equal in length to five of the vertebræ together; coccyx in no way contributing to the sacrum.

Coracoids both broken but very similar to *Pelobates;* the mesial end expanded, this expansion over twice as wide as the narrow middle portion of the coracoid; glenoid part of the coracoid expanded about once and a half or more the width of the narrow portion of the coracoid. Both humeri broken but the fragments in no way different from those of *Pelobates;* radioulna broken but apparently wider than in *Pelobates* and with a shallower distal articulation (Fig. 3E); part of the right scapula present, massive; two fragments, which I take to be the right and left suprascapulæ, differ from similar structures in *Pelobates* and *Scaphiopus* in having the posterior process narrower, more massive (Fig. 4B).

Pelvis apparently more complete than in *Pelobates* and *Scaphiopus;* pubis may have been ossified, at least there is no space for a pubic cartilage. Longitudinal diameter of the acetabulum equals the distance between the posterior margin of the acetabulum and the posterior margin of the ischium; longitudinal diameter of the puboischial plate equal to the length of three and one-third vertebræ; ilium, as measured from the apparent suture between the ilium and ischium, distinctly longer than the femur; femur very slightly longer than the tibiofibula; femur and tibiofibula without epiphyses (these cartilaginous in life). Calcaneum and astragalus much slenderer than in either *Pelobates* or *Scaphiopus* (Fig. 3F and G); calcaneum slightly longer than astragalus; these elements free from each other and less in contact than in *Scaphiopus;* calcaneum slightly less than half the length of the tibiofibula. Prehallux enormous and formed of a single bone, which apparently is in contact with the astragalus as in *S. couchii* and *S. hammondii* and not separated by a bone (which has been variously named) as in *S. holbrookii* and *P. fuscus;* apparently a single bone lateral to the prehallux and also a space for a cartilage as in *S. couchii.* Prehallux less than half as long as the third metatarsal; the metatarsals more or less complete; the third metatarsal a trifle shorter than the astragalus.

MEASUREMENTS

Length of frontoparietal	20	mm.
Distance from middle of occiput to edge of squamosal	21	"
Longitudinal diameter of the exposed dorsal surface of proötic	6	"
Transverse diameter of the squamosal encrustation	6.5	"
Distance from the posterior edge of the base of the sacral diapophysis to the anterior margin of the fourth vertebra anterior to the sacrum	26.5	"
Longitudinal diameter of the sacral diapophysis	22	"
Transverse diameter of the sacral diapophysis	9.5	"
Coccyx	24.5	"
Radioulna	19.5	"
Ilium from ilioischial suture	44	"
Femur	41	"
Tibiofibula	40	"
Calcaneum	19.5	"
Longitudinal diameter of prehallux	6.8	"
Height of prehallux	5	"

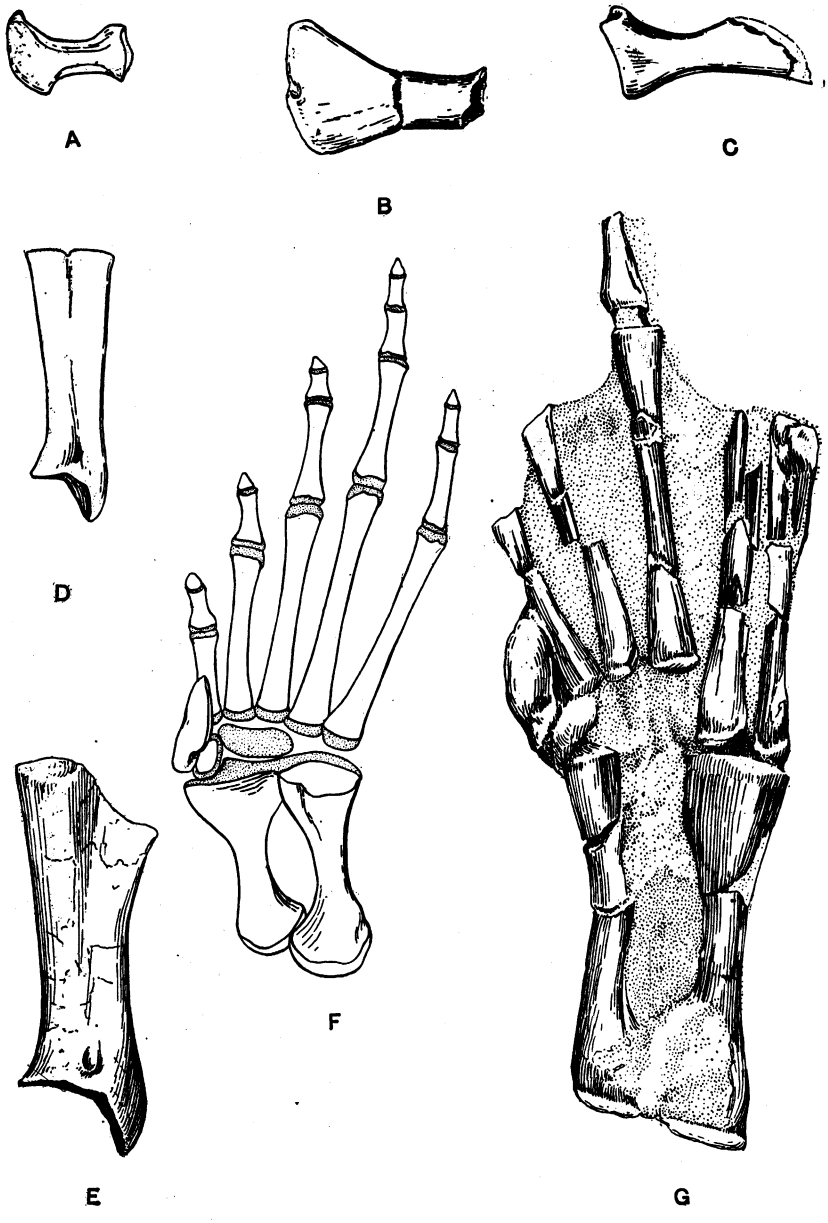


Fig. 3. A comparison of various skeletal elements of *Pelobates*, *Scaphiopus* and *Macropelobates*. A, left coracoid of *Pelobates fuscus* (Laurenti); B, left coracoid of *Macropelobates osborni* Noble; C, right coracoid of *Macropelobates osborni* Noble; D, left radioulna of *Scaphiopus couchii* Baird, median aspect; E, left radioulna of *Macropelobates osborni* Noble, median aspect; F, left foot of *Scaphiopus couchii* Baird, ventral view; G, left foot of *Macropelobates osborni* Noble, ventral view.

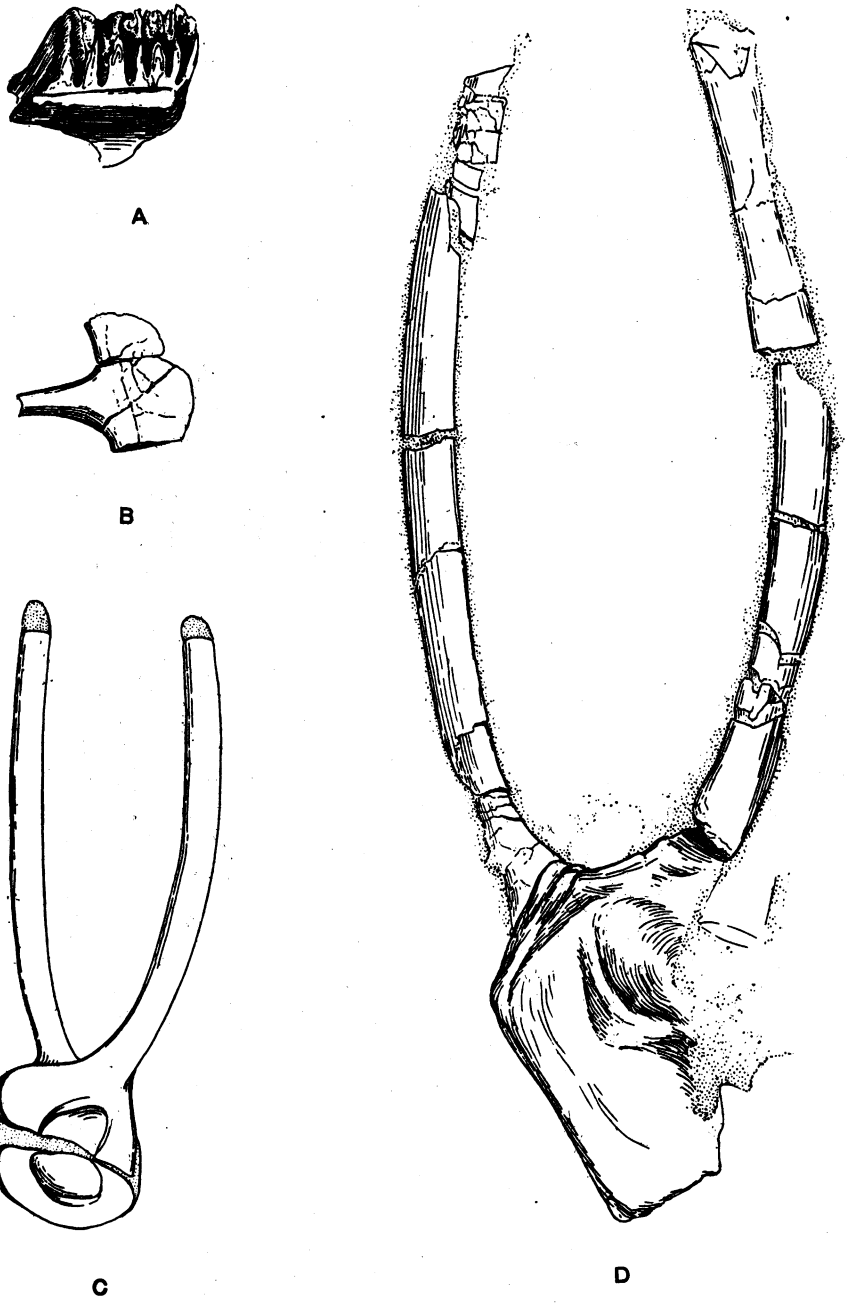


Fig. 4. A, fractured piece of maxilla of *Macropelobates osborni* Noble; B, a portion of the suprascapula of *Macròpelobates osborni* Noble; C, pelvic girdle of *Scaphiopus couchii* Baird; D, pelvic girdle of *Macropelobates osborni* Noble.

THE ORIGIN AND DISPERSAL OF THE PELOBATIDÆ

The species described above exhibits the characteristic features of the fossorial pelobatids. These diggers are not the most primitive pelobatids. They form a rather uniform group, and some, such as Fejérváry (1921, 1923), who delight in naming every series of related genera, would distinguish this group as a subfamily. I have recently had occasion to sketch the broad lines of evolution within the Salientia (Noble, 1922). Since then it has been my privilege to study more intensively the primitive discoglossids. This work has served to strengthen the theses expressed and has lent no support to the recently devised "systems" of Bolkay (1919, 1922) and Fejérváry (1917, 1921, 1923). As a matter of fact, the first of these systems is based upon a misconception as clearly shown by Fejérváry (1921), while the second has little in its support, if enough forms are considered. The double sacrum which Fejérváry discusses in such detail cannot be considered primitive or very distinctive. *Atelopus*, for example, may or may not exhibit such a condition.

The pelobatids arose from the more primitive discoglossids of which *Liopelma* and *Ascaphus* are the only surviving representatives. This group was characterized by such fundamental features as amphicœlous vertebræ, a coccyx with a single condyle, and ten vertebræ, exclusive of coccyx which is itself of a primitive type. The pectoral girdle is exceedingly primitive in lacking an acromion and in having the scapula extending down into the "procoracoid region" as a single element. These features will be discussed in more detail elsewhere, but in the present connection, I desire to emphasize the primitive nature of these two genera, and hence will distinguish them as a family distinct from their discoglossid relatives. For this family the name **LIOPELMIDÆ**[1] seems appropriate.

The more generalized pelobatids as represented by *Megalophrys* have advanced beyond the Liopelmidæ in: (1) the ossification of the intervertebral cartilages (centra) which usually adhere to the more anterior vertebræ forming a procœlous vertebral column; (2) reduction of the number of presacral vertebræ to eight; (3) loss of ribs apparently by fusion with the vertebræ; (4) restriction of the ossification in the ventral part of scapulocoracoid and the development of an acromion; (5) reduction of pubis and expansion of sacral diapophyses. There were other less obvious changes in the hyoid and appendages. The musculature, however, was not greatly modified, except that certain elements such as the caudalipuboischiotibialis were lost. The pelobatids appar-

[1] I follow present-day custom in using the oldest generic name in forming the family name.

ently early developed excessive bony or calcareous deposits in their derm, for we find such encrustations not only in the integument of the head but also along the back of several species of *Megalophrys*.

The second stage in the progressive modification of the pelobatids is represented by *Macropelobates*. The prehallux has become enlarged, the bony encrustations ankylosed to the skull and the sacral diapophyses greatly expanded. The two former modifications are apparently adaptive and correlated with a fossorial life. The modern spadefoot toads differ only slightly from *Macropelobates*. The coccyx has become ankylosed to the sacrum (remaining free as a variation in some specimens of *Pelobates*).[1] No modern spadefoot toad attains the size of *Macropelobates*. There are also differences between these genera in proportion which seem to make the recent forms better diggers.

The final modification in the evolution of the pelobatids was one which has occurred many times in the specialization of the Salientia. The maxillary teeth were lost. This change accompanied a dwarfing in size and a modification in structure. The tympanum was lost and the eustachian tubes became vestigial. The two genera *Ophryophryne* and *Scutiger* which exhibit this change may have evolved directly from *Megalophrys*, for their osteology is very similar in spite of their different outward appearance. They exhibit, however, the enormously expanded sacral diapophyses of *Pelobates* and similarly curved procoracoids (Boulenger, 1919; Procter, 1921). A determination of the exact relationships of these genera will have to await a more detailed study of their osteology and myology.

It may be asked, when did the changes outlined above actually occur? The Liopelmidæ are found to-day only in the northwestern United States and in New Zealand. It is probable, therefore, that they existed in southeastern Asia during late Mesozoic or early Tertiary times. By the Oligocene the spadefoots had evolved and were living in Mongolia. Since then they have succeeded in migrating westward across favorable sandy areas of Asia to western Europe and eastward across the Bering Strait connection, southward to southern Mexico. The toothless forms are found to-day only at high altitudes in certain mountains of Sikkim, Kashmir, Tonkin, Tibet and the Chinese province of Szechuan. They apparently arose from stocks existing in this region. The distribution of the other genera cannot be so easily accounted for. *Pelodytes* has been considered by Boulenger (1899) as close to *Pelobates*,

[1] It is fused in 10 specimens of *Scaphiopus holbrookii*, 2 of *S. couchii*, 1 of *S. dugesi*, 2 of *S. hammondii*, and 2 of *Pelobates fuscus* in the American Museum.

but it exhibits many unique features and it does not seem likely that this genus arose directly from *Pelobates*. *Megalophrys*, although primitive in many respects, has extended its range only from southern China and the Philippines to India. Although found in the Malay Archipelago and in Borneo, it apparently never succeeded in pushing south and eastward into those East Indies which are not typically oriental in their faunal relations. No pelobatid occurs in New Guinea, as usually stated in textbooks (Nieden, 1923). *Asterophrys* is a brevicipitid as pointed out by Van Kampen (1923). I suggested (1922, p. 73) that *Lechriodus* (= *Batrachopsis*) was probably a toothed bufonid. Thanks to the kindness of Dr. P. N. Van Kampen, I have recently examined a specimen of *L. melanopyga* and may now confirm that opinion.

In Figs. 5 to 7, I have shown the pectoral musculature and thigh musculature of this specimen. The following features stamp *Lechriodus* as a bufonid in spite of its expanded sacral diapophyses:

(1) Sartorius distinct from the semitendinosus.
(2) Semitendinosus deep, not visible ventrally.
(3) Tendon of semitendinosus piercing gracilis major and minor (as in various Australian bufonids).
(4) Episternocleidohumeralis longus[1] distinct from supracoracoideus.
(5) Supracoracoideus profundus distinct from supracoracoideus superficialis.

None of these features is found in any pelobatid (*Scaphiopus*, *Pelobates*, *Pelodytes* and *Megalophrys*).

Lechriodus also has a double condyle on the coccyx which is found among pelobatids only in the specialized *Pelodytes*. I have discussed (Noble, 1922, p. 11) the several exceptions to the form of the sacrum as being diagnostic of family relations. *Lechriodus* may now be definitely relegated to the Bufonidæ.

If no pelobatids are found in the Papuan or Australian region, has the family arisen since the Indo-Australian connection was broken? This seems to be the best interpretation. If, therefore, we place the origin of the Pelobatidæ at the beginning of the Tertiary, we have still to account for the somewhat restricted range of the apparently primitive *Megalophrys*. Many factors, such as desert barriers or temperature, may have prevented their spread, but of these we have no definite knowledge. All evidence points toward an origin of the pelobatids in southern Asia during early Tertiary times, and to their differentiation, during the Oligocene or earlier, into spadefoots which have succeeded in spreading

[1] I have followed the nomenclature of Anthony and Vallois, 1914, Bibliog. Anat., XXIV, p. 271.

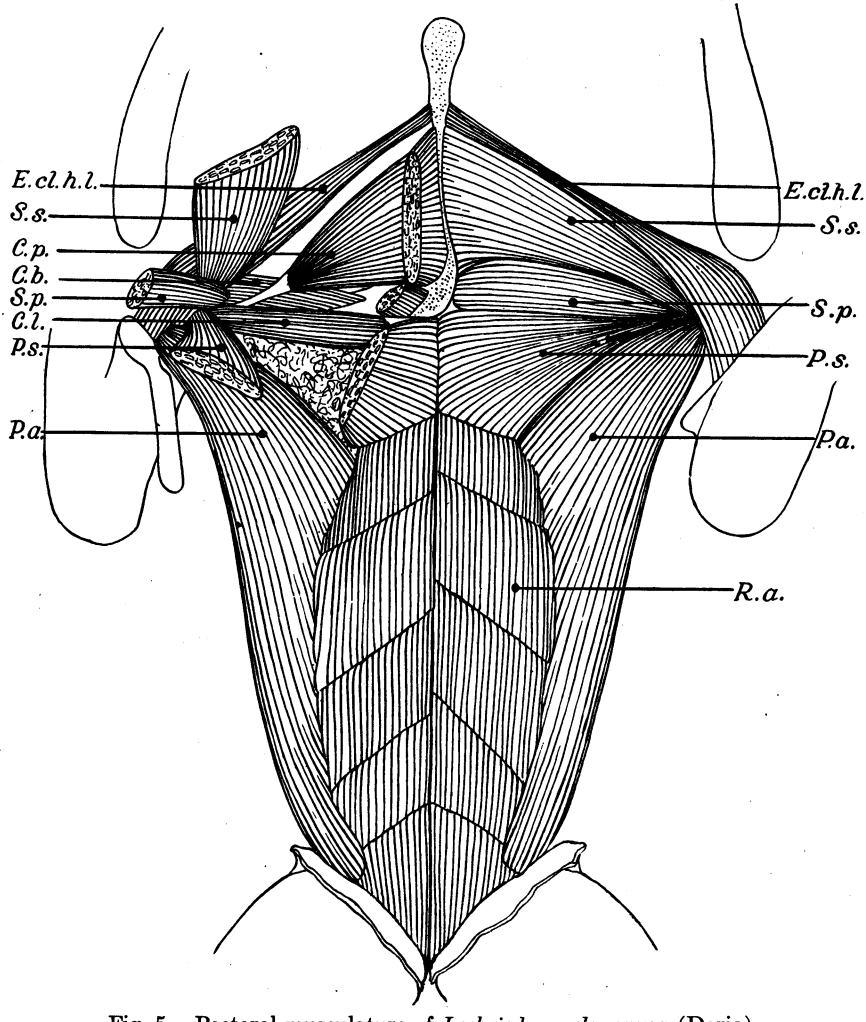


Fig. 5. Pectoral musculature of *Lechriodus melanopyga* (Doria).

A. cl. h, Acromio cleidohumeralis; C. b., Coracobrachialis brevis; C. l., Coracobrachialis longus; C. p., Coracoradialis proprius; E. cl. h. l., Episternocleidohumeralis longus; P. a., Pectoralis abdominalis; P. s., Pectoralis sternalis; R. a., Rectus abdominis; S. p., Supracoracoideus profundus; S. s., Supracoracoideus superficialis.

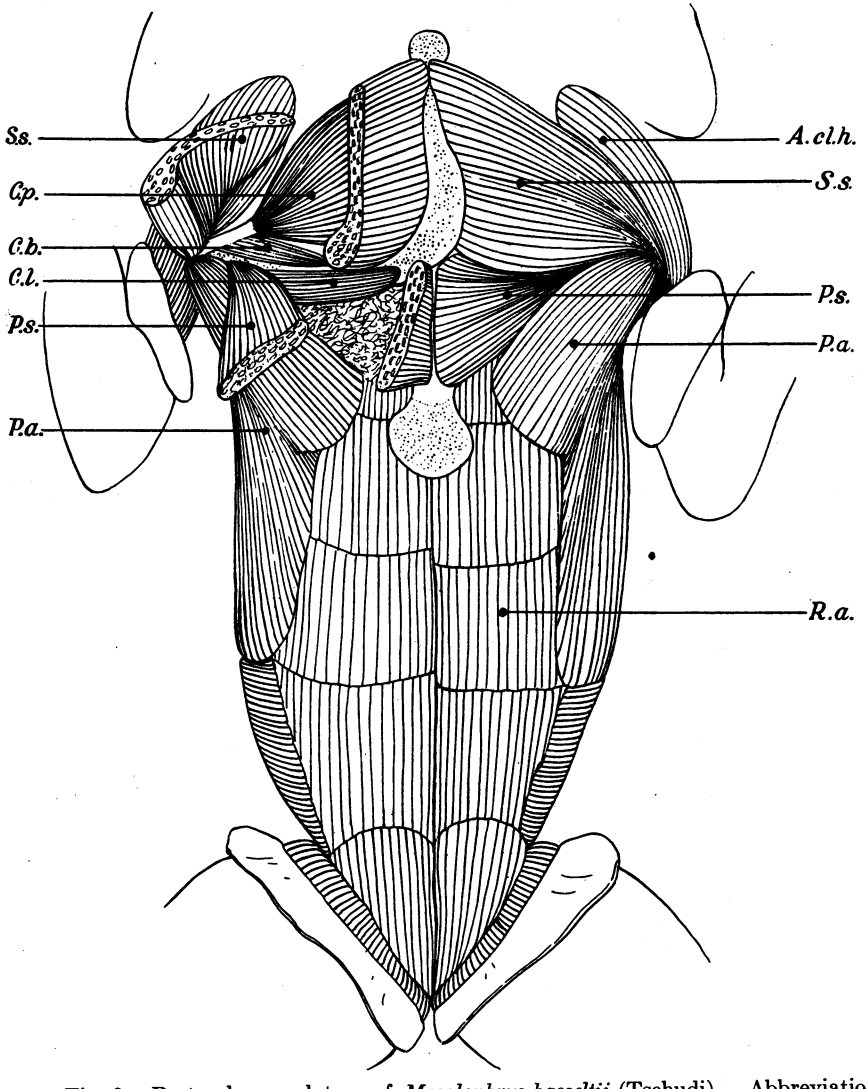


Fig. 6. Pectoral musculature of *Megalophrys hasseltii* (Tschudi). Abbreviations same as in Fig. 5.

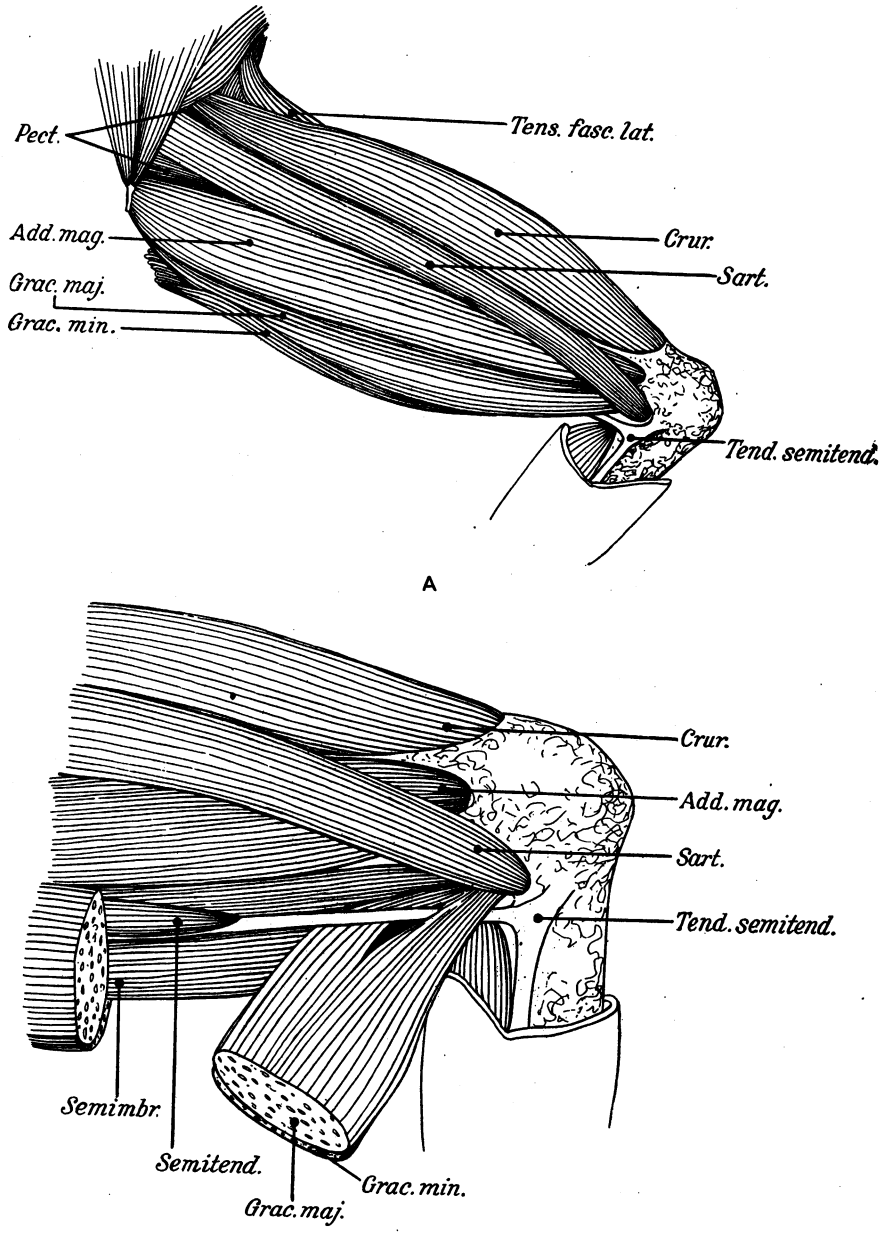


Fig. 7. Thigh muscles of *Lechriodus melanopyga* (Doria), ventral aspect. A, the superficial muscles; B, the distal muscle complex.

Add. mag., Adductor magnus; Crur., Cruralis; Grac. maj., Gracilis major; Grac. min., Gracilis minor; Pect.=Pectineus Sart., Sartorius; Semimbr., Semimembranosus; Semitend., Semitendinosus; Tens. fasc. lat., Tensor fasciæ latæ; Tend. semitend., Tendon of semitendinosus.

westward into Europe and eastward to Mexico and eastern United States. Finally, part of the primitive stock residing in the mountains of southern Asia was modified by a loss of their dentition.

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