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THE FOSSIL FROGS OF THE INTERTRAPPEAN BEDS OF BOMBAY, INDIA

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In a series of papers (1924, 1925, 1926, 1928) I have presented evidence that the present distribution of the frogs and toads could be explained without assuming that land bridges formerly existed in the southern hemisphere connecting South America with Australia or the latter with Africa. Metcalf (1923, 1923*a*), in discussing the distribution of the opalinid parasites of the Salientia, found it convenient to postulate extensive continental connections to account for his views of the dispersal of the latter. In a recent review (1929) of the same subject he has reiterated these views without giving consideration to the many objections which have been raised against them. Unfortunately the fossil record of the Salientia is very incomplete, but where it exists any theory of dispersal must be made to conform with it. Fossil frogs have been known from the Eocene beds of Bombay, India, for a long time. They were described by Owen (1847) as *Rana pusilla,* while Stoliczka (1869), after an examination of a series of specimens, referred them to *Oxyglossus.* The latter genus has a wide distribution to-day in southeastern Asia and adjacent islands. In view of the importance of fossil material in the present controversy, it seemed important to reexamine the available material of the species. The study was made possible by the kindness of Mr. Jayme Ribeiro who has loaned to the American Museum a collection of fifteen fossil-bearing slabs, and through the interest of Mr. W. E. Swinton of the British Museum, who has placed at my disposal the five specimens of the species in the British Museum.

A reexamination of this early described species of fossil frog also seemed advisable, because, if the facts set forth by Stoliczka (1869) were correct, the species would be the type of a well-defined new genus of frogs. Stoliczka (loc. cit., pp. 387–389) states:

"The nasals, frontals, parietals and occipitals are united to a single long and broad bone, without being distinguishable in any of the specimens examined. . . . The anterior prolongations of the frontals appear to be perfectly ossified, and united to the corresponding processes of the maxillaries. . . . Of the sternal bones nothing could be seen; they were probably not ossified."

I have not examined the type of *Rana pusilla*, but as some of the specimens in the British Museum collections were obtained by Mr. A. B. Wynne, the collector of Stoliczka's material, it seems probable that Stoliczka examined the British Museum specimens. Only one species of frog has been recorded from any of the Bombay Beds, and all of the recorded specimens come apparently from the same strata. We have, therefore, every reason to believe that the specimens available are referable to one species, the same which Owen and Stoliczka described. A detailed account of the beds from which the Ribeiro collection was obtained has been published by Ribeiro (1921). My thanks are due to Mr. S. H. Prater of the Bombay Natural History Society for calling my attention to this reference as well as for securing the loan of the Ribeiro collection.

Although there is great variability in the extent and character of the fossilization in the different specimens of both the Ribeiro and British Museum collections, there is no definite evidence that the series embraces more than one species of frog. The species cannot be referred to *Oxyglossus*, or *Oxydozyga*, as the genus is now called, because among the several conspicuous differences the sacral diapophyses are definitely dilated. This character was not noted by either Owen or Stoliczka, both of whom figured the pelvis. My material has been examined in oil of cedarwood or in xylol, with the help of a binocular microscope. Such treatment brings into view features not observable in the dry specimens. The many differences between the detailed description of Stoliczka (1869) and that given below seem due chiefly to the different methods of study. The material available to me is fragmentary but sufficient to show that the species must be removed not only from the genus *Oxyglossus* but also from the Ranidæ. It is interesting from the zoögeographic standpoint that I can find no characters to separate it from certain Australian bufonids.

Bufonidæ

Indobatrachus, new genus

TYPE.—*Indobatrachus pusillus* (Owen).

DIAGNOSIS.—Teeth on the maxillaries, premaxillaries and prevomers, none on dentaries; nasal and probably palatine bones present, the former free from adjacent elements; frontoparietals separated for the greater part of their length by a broad median fontanel, ethmoid broad and apparently unossified, squamosals small, each with an anteriorly directed process, parasphenoid T-shaped; vertebral column

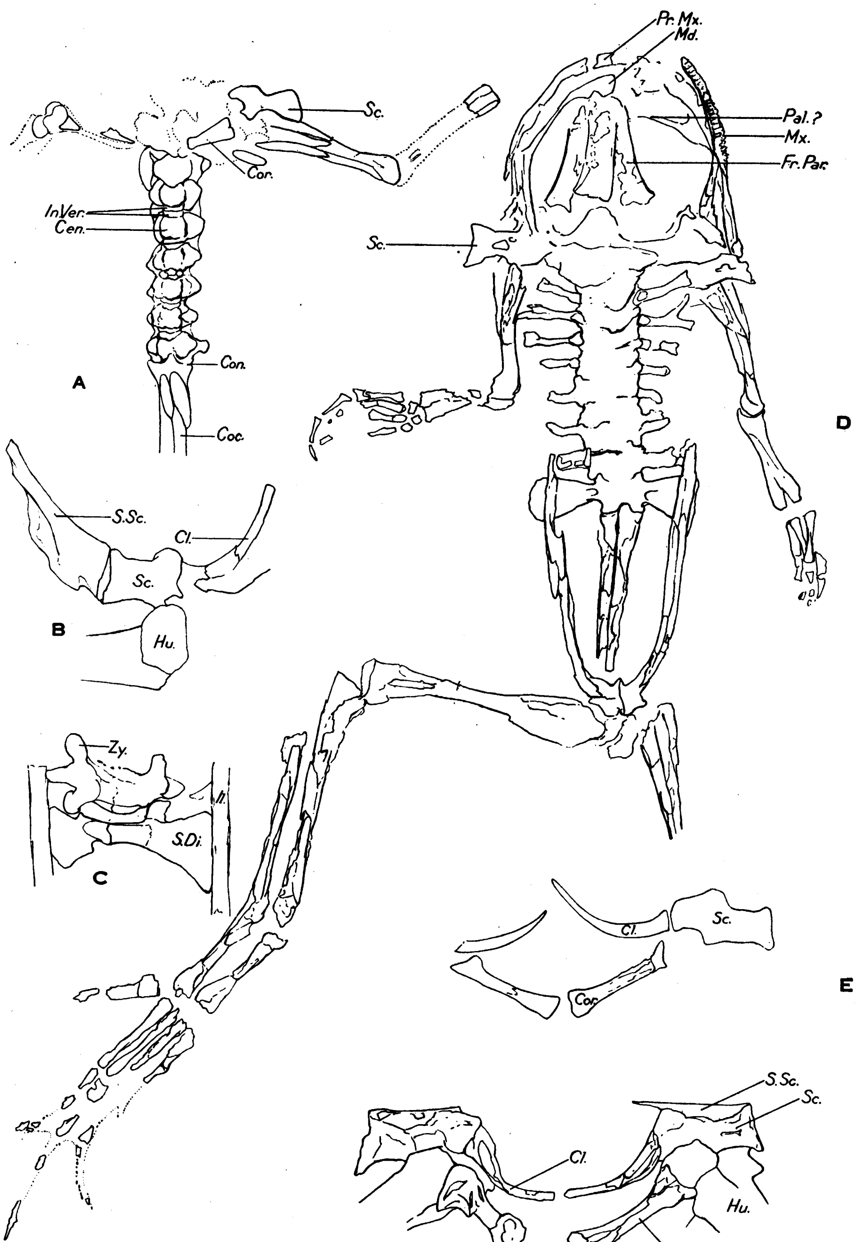

Fig. 1. *Indobatrachus pusillus* (Owen), parts of several specimens.

(a) Vertebral column, ventral surface. B. M. 3084 ×5.2.
(b) Part of right half of pectoral girdle. R. C. 10 ×7.8.
(c) Fragmentary sacrum. R. C. 3 ×7.8.
(d) Outline of B. M. 35107*a* × 5.2.
(e) Fragmentary pectoral girdle. R. C. 9 (reverse surface) ×7.8.
(f) Fragmentary pectoral girdle. B. M. 39485*b* ×7.8.
See List of abbreviations, page 13.

uniformly procœlous, but the intercentra more or less free from the body of the vertebræ in one specimen; nine vertebræ anterior to the coccyx; vertebræ with well marked zygapophyses; sacral diapophyses dilated; no ribs; coccyx without lateral processes; two condyles on the coccyx; pectoral girdle arciferal, or at least the clavicle which is arched diverges from the coracoid; coracoid narrow, the two ends of nearly the same width, no ossified omosternum or sternum; scapula about half as long as the humerus, suprascapula about twice as long as the scapula and well ossified; puboischium small, no prepubis; terminal phalanges long and tapering, with very small knobs on ends; no intercalary cartilages, radius and ulna fused, tibia and fibula fused, tibiale and fibulare free; on enlarged prehallux or prepollex; femur as long as tibia, about as long as vertebral column exclusive of the coccyx, head of femur a calcified ball.

COMPARISONS

When the entire series of specimens available for the above diagnosis are considered, certain characters reappear in different specimens, diminishing the chance of faulty interpretation of the material. In making comparisons between *Indobatrachus* and other genera, reference may be made to the specimens which show most clearly the characters in question. *Indobatrachus* is not a liopelmid, for it has only eight presacral vertebræ (B. M. 35107, Fig. I, D), no ribs (R. C. 7*a*, 10), and two condyles to the coccyx (R. C. 3, 4*a*, 6*a*, 7*a*, 10; B. M. 39485). It is not a discoglossid for no ribs are present and the vertebræ are definitely procœlous (R. C. 4*a*, 5, 8*a*, 9; B. M. 39485). The procœlous condition, also, excludes *Indobatrachus* from the Pipidæ. It is not a pelobatid, because two condyles are definitely present on the coccyx. It is not a ranid or a polypedatid, for it possesses broadly expanded sacral diapophyses. Leaving aside the Brachycephalidæ, which embrace a modern, neotropical group of genera, and the Palæobatrachidæ, because of their distinctive sacrum, there remain only the Bufonidæ, Hylidæ and Brevicipitidæ to consider. The Hylidæ may be definitely ruled out, for in several specimens (R. C. 3, 4, 10, B. M. 35107, 39485)the digits are well preserved, and no intercalary cartilages or space for the same are present. The question of whether *Indobatrachus* is a bufonid or brevicipitid rests chiefly on the character of the pectoral girdle. Several specimens of the series of fossils (R. C. 3, 4*a*, 5, 6*a*, 9, 10; B. M. 39485, 35107) show definitely that the clavicle was arched. A few firmisternal genera have arched clavicles (compare Noble and Parker 1926) but in the great majority of ranids the clavicle is straight as in *Rana*. On the other hand, the arched clavicle is characteristic of the arciferal pectoral girdle. In no specimen are the cartilages of the pectoral girdle indicated, but in several the coracoids are present, and in no case do their mesial ends meet in

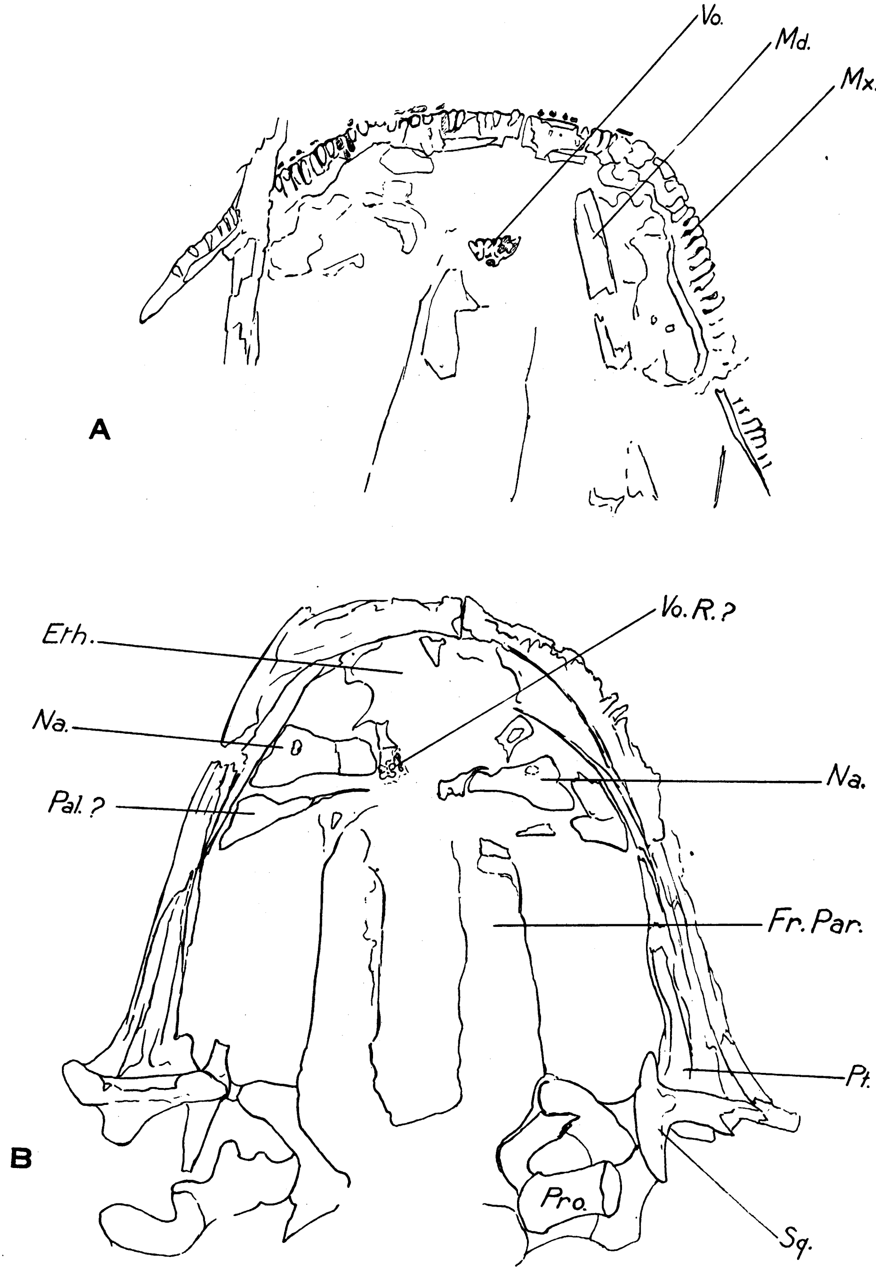

Fig. 2. Diagnostic characters of *Indobatrachus pusillus* (Owen), shown in two skulls.

(a) B. M. 39485*b* ×13.
(b) R. C. 3 ×13.
See list of abbreviations, page 13.

the manner typical of the firmisternal girdle. Two of the best preserved pectoral girdles are represented in figures 1, E; 1, F. In six other specimens (R. C. 3, 4*a*, 5, 6*a*, and two fossils of B. M. 35107) the coracoid and clavicle of at least one side are preserved, and these diverge in nearly

Fig. 3. Photograph of *Indobatrachus pusillus* (Owen), R. C. 3 ×3.1. The outline of one sacral diapophysis, and of one half the pectoral girdle, have been drawn in white.

the same degree as R. C. 9 shown in figure 1, E. There can be no doubt, therefore, but that the diverging coracoid and clavicle are characteristic of *Indobatrachus*. This is a character which distinguishes the arciferal girdle from most firmisternal girdles. Further evidence that *Indoba-*

trachus is a bufonid and not a brevicipitid is to be found in the vertebral column. In two specimens (R. C. 6*a*, 8) the sacral vertebra is definitely procœlous, while in several others there is some indication of this procœlous condition (Fig. 1, D). This would seem to exclude *Indobatrachus* at once from the Brevicipitidæ. There are, however, a few brevicipitid genera which retain the primitive procœlous condition of this vertebra instead of having it convex anteriorly as in most brevicipitids. In one specimen of *Indobatrachus* (B. M. 3084), which differs from the others in having an extensive replacement by calcite, the vertebral column has a distinctive appearance (Fig. 1, A). The intervertebral part of each vertebra, instead of being attached to the body of the vertebra as in most frogs, remains more or less free. This suggests that the intervertebral elements were more or less free in life. Among Salientia such a condition is known elsewhere only in some oriental pelobatids and in many Australian bufonids, where, however, the more usual condition is for the intervertebral disks not to be split but to form a single ball between the two centra. Another feature which stamps *Indobatrachus* as closely related to the Australian bufonids is the combination of maxillary teeth and dilated sacral diapophyses. Among the Bufonidæ only a few neotropical genera exhibit the two latter characters at the same time. In brief, although the fossil remains of *Indobatrachus* are not well preserved, the material available definitely excludes this genus from all families of Salientia other than the Bufonidæ and the Brevicipitidæ. The form of the clavicle, the divergence of clavicle and coracoid, the procœlous sacrum and the occasionally free intercentral disks point to *Indobatrachus* as a bufonid and not a brevicipitid. As *Indobatrachus* possesses teeth in the upper jaw, it would be referred to the "Cystignathidæ" or "Leptodactylidæ" of earlier classifications. No toothed bufonids have dilated sacral diapophyses, except the Australian genera and a few neotropical forms: *Paludicola*, *Eupemphix* and *Calyptocephalus*. If our interpretation of the shoulder girdle as arciferal is correct, *Indobatrachus* is a bufonid, closely related to the Australian genera.

DISCUSSION

The description given above differs radically from the account of Stoliczka of presumably some of the same material in many details, especially those of the skull, pectoral girdle, and sacrum. The evidence on which my statements are based may therefore be discussed in further detail.

The presence of vomerine teeth is deduced from two specimens, both of which are represented by drawings. In B. M. 39485 three sockets for teeth are clearly indicated on the left prevomer, and there is some indication of two other sockets. In R. C. 3, the dorsal aspect of the skull is exposed, but the whole skull has been crushed flat, and several ventral structures, such as what appear to be the palatines, lie in the same plane as the frontoparietals. I interpret two roughened bones lying in the vomerine region as the prevomers viewed from their dorsal aspect. In most specimens the maxillary teeth are for the most part lost, only the sockets remaining. Hence, the presence of sockets without teeth would be expected in the vomerine region of these same specimens. The skulls are for the most part poorly preserved in all the specimens. There can be scarcely any doubt, however, as to my identification of the nasals, ethmoid and prootic in this specimen (Fig. 2, B).

The sacrum was described as subcylindrical by Owen, and as club-shaped by Stoliczka. The sacral diapophyses are well preserved in a number of the specimens before me, and there can be no doubt that they are as much dilated as in many Australian bufonids, and more so than in any ranid. This fact alone demands the removal of the species from the Ranidæ. The form of the sacrum, clavicle and coracoid alone shows that the species could not be referred to *Oxyglossus*. In addition, the presence of vomerine teeth and the probable arciferal condition of the girdle exclude it from this genus. *Pusillus* is a small, large-headed frog, which, to judge from the formation in which it was found, apparently had aquatic habits. The various similarities in size and proportion between this species and the several forms of *Oxyglossus* cannot be taken as evidence of relationship. In many families of Salientia there are small aquatic frogs.

From the material available, it is impossible to state in exactly what characters *Indobatrachus* differs from the several Australian genera of toothed bufonids. It shows resemblance to *Crinia, Hyperolia, Adelotus, Philoria* and *Cryptotis*. These genera are distinguished from one another principally by the form of the pupil, the size of the sternum and other details not preserved in *Indobatrachus*. Frogs usually make poor fossils and even the best specimen in the Ribeiro collection (Fig. 3) is far from complete. Further, *Indobatrachus* was a small and very fragile form. The following measurements of R. C. 3 may be taken as an average size.

Tip of snout to posterior end of ischium	19 mm.
Tip of snout to posterior angle of jaw	6.5 mm.
Length of humerus	4.5 mm.
Length of femur	6.5 mm.
Tip of ilium to posterior edge of acetabulum	6.5 mm.

THE STATUS OF *Lithobatrachus*

The presence of a toothed bufonid in the Eocene of India lends support to the theory of a northern origin of the Australian frog fauna. Recently I described a fossil frog from the Miocene of Europe which gave additional support to this theory (Noble, 1928). As in the case of *pusillus*, the species was based upon material known for a long time but previously interpreted incorrectly. I referred the species to *Hyla*, a genus hitherto unknown as a fossil. More recently, Parker (1929), after an examination of the same material, has questioned my interpretation of the fossil, which, it should be emphasized, consists only of an impression with some bone fragments adhering. He considers the species the type of a new genus, *Lithobatrachus*, which he does not definitely assign to any family but assumes to be most closely related to the Pipidæ and Palæobatrachidæ. To include it in either of these families would mean a considerable revision of the definition of the group. Most of the characters which Parker employs in defining *Lithobratrachus* are shown in my photograph of the fossil (Noble, 1928, Fig. 5) and were considered at the time my description of the species was made. There are several reasons why Parker's interpretation cannot be accpted, and these may be considered, following the order of his description.

Many fossorial Salientia, such as *Kaloula* and various other brevicipitids, have a strongly ossified occiput with the occipital condyles lying entirely or for the greater part posterior to a line drawn between the posterior ends of the jaws (articulars). This is also true of narrow-headed aquatic types, such as *Xenopus tropicalis*, which swim swiftly through the water. On the other hand, broad-headed terrestrial forms, such as *Hyla* or *Rana*, and even aquatic species with a broad head, such as *Pipa pipa*, have the greater part of the condyles lying anterior to the same line. The fossil specimen under discussion is unquestionably a broad-headed form (Noble, 1928, Fig. 5), and hence we may feel sure that the occipital condyles lay on the same level of the anterior-posterior axis as the mesial ends of the clavicles in the fossil. This being true, there is no possibility that the slight elevation described by Parker as the first vertebra is really the impression of that structure, unless the vertebral column was disarticulated from the condyles and drawn posteriorly before fossilization. There is no evidence in the fossil that such a disarticulation occurred, and Parker interprets the first vertebra as making an articulation with the condyles. The slight impression which Parker compares to the first vertebra of *Xenopus* and *Pipa* lies on the same plane as the coracoid and resembles closely a piece which I considered a part of the procoracoid cast. This anterior piece has no connection with the skull and cannot have been made by a part of the exoccipitals as Parker suggests. The posterior imprint does not agree in detail with the first vertebra of either *Pipa pipa* or *Xenopus tropicalis.* Nor does it agree in detail with other possible structures such as the larynx or hyoid. The faint imprints which seem to be associated with the posterior impression are directed posteriorly like thyroid processes of the hyoid and not laterally like transverse processes of a vertebra. In brief, the imprints in question show no diagnostic characters, but the evidence is decidedly against these having been made by a first vertebra.

Parker figures the scapula of the fossil as terminating considerably short of the clavicle on both sides. There is no doubt that a depression occurs in the fossil at the point Parker assumes to be the proximal end of the scapula. The depression was apparently formed by a preglenoid process similar to that found in many Salientia. There is, however, a slight depression between this point and the clavicle. I assumed it to have been made by an ossified or calcified acromion such as occurs in the great majority of Salientia. On the left side of the fossil the anterior margin of the scapula can be traced until it meets the clavicle. There is no doubt that the left scapula at least was longer than Parker has figured it. This is of interest, for it definitely excludes the species from the Discoglossidæ, Pipidæ, and probably from the Palæobatrachidæ.

The Hylidæ are distinguished from the Bufonidæ primarily by the presence of an intercalary cartilage or bone between the last two phalanges of each digit. In describing the fossil, considerable attention was given to the digits. Unfortunately only one digit is clearly indicated and that only by an impression. It would not appear from Parker's figure of this imprint (Parker 1929, fig. 2*a*) that the terminal phalanx must have been actually curved and that its tip dug into the substratum. In ordinary museum skeletons of Hylidæ, the intercalary is difficult to see from the ventral surface because the proximal end of the terminal phalanx, being free to slide back over the intercalary, is drawn proximally on drying and covers the greater part of that element. I have examined hylids which have died and decomposed on a flat surface while being shipped to me from the tropics, and noted that in most of these cases the intercalaries were not covered but plainly visible from the ventral surface. The segment between the two last phalanges of the fossil specimen is too thick to be a syndesmosis. The impression is not a perfect one, but it agrees well in shape with the terminal phalanges of the several species of *Hyla* available to me in skeleton form.

Parker considers several other features in the fossil to support his view that its affinities are with the Pipidæ and Palæobatrachidæ. The impression of the skull is very poor, and there is no way of determining the limits of pterygoids, palatines, ascending processes of the maxillæ, or any other structures which might be present on a crushed palate. Hence, the comparison of this palate with that of *Xenopus* rests on a very unsound basis. Parker compares the clavicles with those of *Xenopus*. The coracoids and scapulas, which are better indicated, have no resemblance to those of *X. lævis* and *X. tropicalis*. Further, the element which Parker considers the dilated end of the clavicle differs in texture from the adjacent bone, and it may have been a replacement or cast of the procoracoid cartilage. Lastly, Parker believes there is evidence that the fossil possessed ossified pubes. The imprint on the right side of the ischial symphysis is in direct continuation with the femur and has the appearance of being an impression of a fractured piece of the calcified head of the femur. The imprint of the alleged left pubis was made by a fractured piece either of the ilium or of the pubo-ischium. Many Salientia in various families have calcified pubes, and these are firmly joined to the ischium. As shown in Parker's figure 1, the two imprints are of very unequal size, and the possibility of their having been formed by paired free pubes seems excluded.

In brief, the result of Parker's analysis is to bring out more clearly the difficulty of interpreting a fossil based for the greater part on an impression alone. The species shows no affinities to the Pipidæ. Its procœlous vertebræ, its free coccyx with two condyles, and its long scapula, exclude it from the family, and none of the similarities mentioned by Parker rests on a sound basis. Its supposed affinity to the Palæobatrachidæ is based chiefly on the assumption that the sacrum was double. There is no proof of this assumption. On the other hand, the greatly dilated sacral diapophyses and relatively short metacarpals exclude it from the genus *Palæobatrachus*, the only valid genus in the family. Since the fossil agrees with *Hyla* in all diagnostic characters, I have referred it to that genus. Until additional specimens of the species are discovered, *Lithobatrachus* should be referred to the synonymy of *Hyla*.

CONCLUSIONS

Oxyglossus pusillus (Owen) of the Eocene of India is a toothed bufonid (leptodactylid) closely related to *Crinia* and its allies of Australia. A new genus, *Indobatrachus*, is erected for the species. The discovery of a toothed bufonid in the Eocene of India lends support to the theory of a northern origin for the Australian frog fauna.

REFERENCES

METCALF, M. M. 1923. The Opalinid Ciliate Infusorians. Bull. U. S. Nat. Mus. No. 120.

1923*a*. The Origin and Distribution of the Anura. Amer. Nat., LVII, pp. 385–411.

1929. Parasites and the aid they give in problems of taxonomy, geographical distribution and paleogeography. Smithsonian Misc. Coll. 81, No. 8.

NOBLE, G. K. 1924. A new spadefoot toad from the Oligocene of Mongolia with a summary of the evolution of the Pelobatidæ. Amer. Mus. Novitates, No. 132, pp. 1–15. 7 figs.

1925. The evolution and dispersal of the frogs. Amer. Nat., LIX, pp. 265–271.

1926. An analysis of the remarkable cases of distribution among the Amphibia, with descriptions of new genera. Amer. Mus. Novitates, No. 212, pp. 1–24. 9 figs.

1928. Two new fossil Amphibia of zoögeographic importance from the Miocene of Europe. Amer. Mus. Novitates, No. 303, pp. 1–13. 6 figs.

NOBLE, G. K., AND PARKER, H. W. 1926. A synopsis of the brevicipitid toads of Madagascar. Amer. Mus. Novitates, No. 232, pp. 1–21. 14 figs.

OWEN, F. G. S. 1847. On the Batracholites, indicative of a small species of frog (*Rana pusilla*, Ow.). Quart. Journ. Geol. Soc. London, III, pp. 224–225. 2 figs.

PARKER, H. W. 1929. Two fossil frogs from the Lower Miocene of Europe. Ann. and Mag. Nat. Hist., Ser. 10, IV, pp. 270–281. 4 figs.

RIBEIRO, JAYME. 1921. The Geology of Worli Hill. Journ. Bombay Nat. Hist. Soc., XXVII, pp. 582–595.

STOLICZKA, F. 1869. Osteological notes on *Oxyglossus pusillus* (*Rana pusilla* Owen), from the tertiary frog-beds in the Island of Bombay. Mem. Geol. Survey of India, VI, pp. 387–394. Pl. IX.

List of Abbreviations

Cen. = Centrum.
Cl. = Clavicle.
Coc. = Coccyx
Con. = Condyles of coccyx
Cor. = Coracoid.
Eth. = Ethmoid.
Fr. Par. = Fronto-parietal.
Hu. = Humerus.
Il. = Ilium.
In. Ver. = Intervertebral elements (i.e., the split interdorsal and interventral).
Md. = Mandible.
Mx. = Maxilla.
Na. = Nasal.
Pal.? = Palatine?
Pr. = Prootic.
Pr. Mx. = Premaxilla.
Pt. = Pterygoid.
S. Di. = Sacral diapophysis.
S. Sc. = Suprascapula.
Sc. = Scapula.
Sq. = Squamosal.
Vo. = Vomerine teeth.
Vo. R.? = Dorsal aspect of vomerine tooth patch?
Zy. = Zygapophysis.