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A NEW INSECTIVORE FROM THE OLIGOCENE, ULAN GOCHU HORIZON, OF MONGOLIA[1]

BY GEORGE GAYLORD SIMPSON

Among the most noteworthy of the numerous new fossil mammals found by the American Museum Asiatic Expeditions in 1928 is an insectivore skull and skeleton assigned to me for study by Walter Granger, Palæontologist of the expedition, and described below.

The specimen is of unusual importance, not only because of its relatively fine preservation, but also because it represents a new family allied to the pro-lemuroid Tupaiidæ (being the first fossil of which this can surely be said) and thus casts light on the affinities of certain groups of Insectivora and also on the origin of the Primates, one of the most discussed of evolutionary problems.

The delicate material has been most skilfully prepared by Albert Thomson. The drawings of the skull and jaws are by John Germann; those of the skeletal parts by Louise W. Germann.

ANAGALIDÆ, new family

TYPE.—**ANAGALE**, new genus.

KNOWN DISTRIBUTION.—Basal Oligocene of Mongolia.

DIAGNOSIS.—Dentition complete (with possible exception of I^1). Incisors unspecialized, canines small. Molarization of upper premolars advanced, but only one main outer cusp on P^4. M^{1-2} subquadrate, paracone and metacone external, not crescentic. Projecting hypoconulid on M_3. Skull tupaioid in general structure. Orbit open, but with postorbital processes. Alisphenoid canal present, supraorbital and malar foramina absent. Large entotympanic bullæ with very large circular auditory openings. Radius and ulna and tibia and fibula separate. Strong tibial malleolus. Astragalus trochlea shallow, little oblique, with foramen, fibular crest higher. Astragalo-cuboid facets. Cuboid short, metatarsals not elongated. Unguals of pes flattened dorsoventrally and spatulate at tips.

It may be found that not all of these characters are common to possible other genera of the now monotypic family, but they are similar to the features used to distinguish other families of insectivores and clearly show that *Anagale* cannot be placed in any of the latter without extensive redefinition.

[1]Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 111.

Anagale[1] **gobiensis**, new genus and species

TYPE.—Amer. Mus. No. 26079. Nearly perfect skull and jaws with much of skeleton. Collected by the Chinese assistant "Buckshot," Central Asiatic Expedition, 1928.

HORIZON AND LOCALITY.—Lower Oligocene. Lower part of Ulan Gochu Formation, at Twin Oboes, in face of mesa east of Shara Murun Valley, Inner Mongolia.[2]

GENERIC AND SPECIFIC CHARACTERS.—Sole known genus and species of the family as defined above. Dental formula $\frac{?3}{3}.\frac{1}{1}.\frac{4}{4}.\frac{3}{3}$. Incisors subequal, canines single-rooted but nearly premolariform. $P\frac{1}{1}$ two-rooted, simple. P^2 three-rooted, with small inner cusp. P_3 without metaconid. Length P^1-M^3, 22.5 mm. P_1-M_3, 24.2 mm. Total length of skull, ca. 58 mm. Zygomatic breadth 35 mm.

DESCRIPTION

DENTITION

The tips of the premaxillaries are incomplete (the only imperfection of the skull) so that the presence of anterior incisors cannot be determined. There were at least two, and probably three, upper incisors, the complete formula being $\frac{?3}{3}.\frac{1}{1}.\frac{4}{4}.\frac{3}{3}$.

If present, I^1 was probably small and well separated from its mate of the opposite side. I^2 is small, styliform, single-rooted, the crown not expanded. It is almost erect, procumbent only in the slightest degree. I^3 is known only from alveoli, which show it to have been slightly larger than I^2 and probably of the same character. The upper canine is but little higher than I^2 and of about the height of P^2. It is stouter than the incisors. The posterior slope is very faintly heel-like but not cuspidate. The root is single, but with a slight median vertical groove.

The upper premolars, four in number and without diastemata, are chiefly remarkable for the extent of their molarization, which extends to P^2, and for its nature, which does not lead to duplication of the main outer cusp. P^1 is small, two-rooted, with very indistinct anterior and posterior basal cuspules. The crown is somewhat wider posteriorly. P^{2-4} are three-rooted. They are much worn, but the essential structure is clear. Each has a main outer cusp, preceded and followed by slight basal cuspules. There is an internal cuspule, progressively more prominent and slightly more anterior. P^4 is subquadrate, with evidence of a fourth cusp, an incipient hypocone or a prominent metaconule, although its apex is worn off.

The molars are also much worn, but the bases of the cusps reveal most of the structure except the possible development of conules. They are quadrate, transverse, with three main cusps. The paracone and metacone are subequal, external, noncrescentic. The external cingulum is represented only by a vague and slight basal swelling. There is no mesostyle, while parastyle and metastyle appear to have been present but very small. The protocone was large and was followed by a much smaller dependent hypocone or pseudhypocone. M^3 was similar but smaller, the external border strongly oblique, the contour triangular, the posterointernal cusp small or absent.

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[1] Ἀνα, above Γαλεη, literally "weasel" but very commonly used in zoological nomenclature as a combining form for insectivores (e.g., *Galerix*, *Microgale*, and many others). The name refers to the high position of this genus within the Insectivora and is also symphonious with its living allies among tupaiids *Anathana*, *Dendrogale*, and *Urogale*.

[2] For geographic and geologic occurrence, see Berkey, Granger, and Morris, 1929, and Osborn, 1929. The Ulan Gochu unconformably underlies the Baron Sog (Upper or Middle Oligocone) and is apparently conformable on the Shara Murun (Upper Eocene). *Anagale* is from an apparently basal Oligocene level. One specimen of *Embolotherium* was found in the same stratum at a slightly higher level and in the immediate neighborhood.

The lower incisors, three in number, are one-rooted, rather closely spaced, and styliform. I_3 is represented by the alveolus only. The lower incisors are more definitely procumbent than the upper. The lower canine is small, one-rooted, the crown resembling that of the incisors but higher and with a heel similar to that of the premolar but smaller.

The first three lower premolars increase progressively in size but are otherwise similar. Each has two roots, a high compressed main cusp, a low one-cusped heel, and a smaller but higher anterointernal cusp. There is no metaconid. P_4 is more definitely molariform. The lofty trigonid has subequal, opposite protoconid and metaconid and a low anteromedian paraconid. The heel is about equal in length to the trigonid or slightly less and is a little narrower. It is crested transversely at the posterior rim, but the cusp structure is obscured by wear.

M_{1-2} are of equal size and structure. The talonid is slightly larger than the trigonid. The latter is much compressed anteroposteriorly and was higher than the talonid. In the worn condition, the internal side is higher than the external, but this may differ from the original state. The character and position of the paraconid cannot be determined. M_3 has a similar but smaller trigonid. The talonid is elongate by reason of the posterior and slightly external projection of the hypoconulid, which is attached to the internal half of the talonid (as in the primitive lemuroid or tarsioid M_3).

Skull

In its general proportions and superficial appearance, the skull resembles that of *Erinaceus*, although numerous differences in structural details are apparent. The more striking superficial distinctions are the large and partially enclosed orbits, the broader interorbital region, more sloping superior contour of the face, large bullæ, and higher occiput.

The nasals, which are not fused, are long and slender, slightly expanded anteriorly where each is notched, and still more expanded posteriorly. The premaxillæ are small and abbreviated. Each sends a slender process upward and backward between the maxilla and nasal, but this stops far short of contact with the frontals. The palatine processes of the premaxillæ began anterior to the second incisors, but are broken off on the specimen. The facial exposure of the maxilla is very large and it has a stout but relatively short zygomatic process. The infraorbital foramen is single, of moderate size, and lies above the anterior root of P_3.

The lachrymal has a small but distinct crescentic facial expansion. The lachrymal tubercle is unusually prominent and there are two subequal foramina, one above and one below the tubercle. These are placed in notches near the rim, but rather more on its facial side.[1]

The frontals are broad and nearly flat. They likewise are unfused in this old individual. The sutural pattern differs from that of *Ptilocercus* or *Erinaceus* in the shorter posterior extension between the parietals and the shorter paired anterior processes between the nasals and maxillæ. Near the nasal suture but wholly within the frontals is a pair of vascular foramina, directed forward, each about 1.5 mm. from the median suture. Since these must open into the nasal chamber, they cannot be homologous with the supraorbital foramina of *Tupaia*, and the latter are absent.

[1]There are two foramina in the lachrymal of *Tupaia*, one below the tubercle and on the facial side of the rim, the other above and on the orbital side.

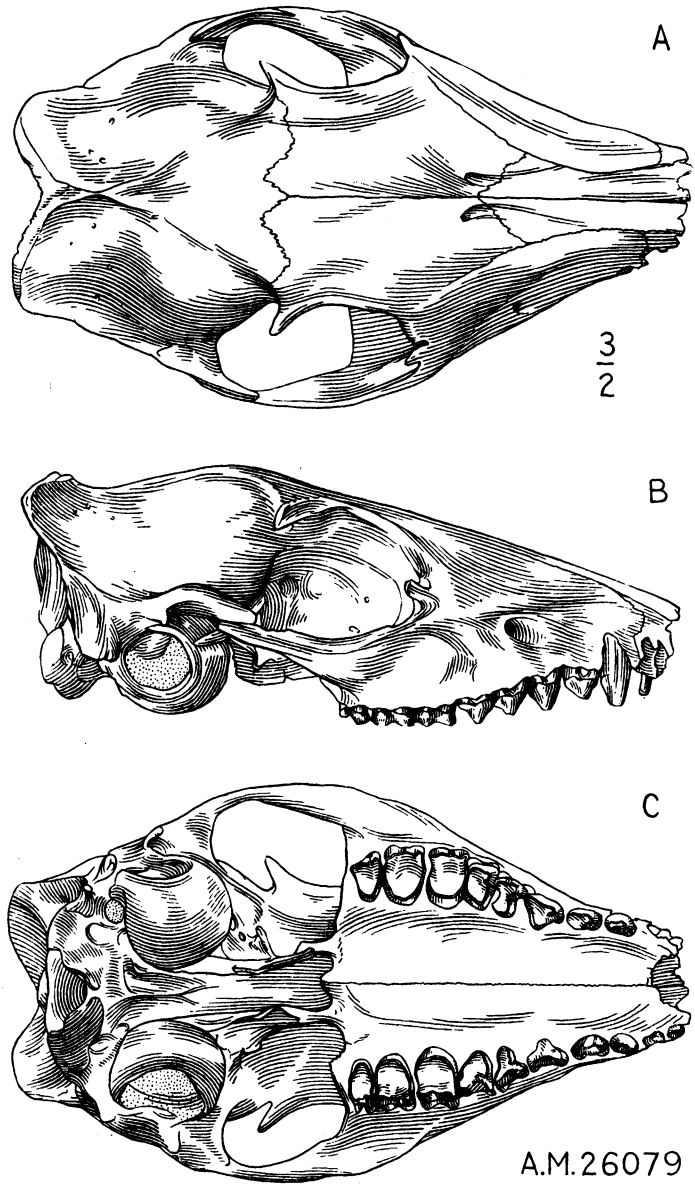

Fig. 1. *Anagale gobiensis.*
A, superior; B, Lateral; C, Palatal views of skull.
One and one-half times natural size.

The postero-external angle of each frontal is produced into a prominent, slender postorbital process, very like those of *Tupaia* save that they are slightly shorter and apparently did not meet processes from the jugal.

The parietals are fused and are much smaller over the cerebrum, the latter apparently being short but relatively large and well developed (better than in a living *Erinaceus* of comparable size). Faint crests arise from the bases of the postorbital processes and converge at a point immediately anterior to the occipital crest without becoming more prominent or forming a distinct sagittal crest. The occipital crest is very strong and much elevated, nearly as much as in *Gymnura* (which has, however, a strong sagittal crest as well). In the lateral concavities between this crest and the cerebral swellings, the parietals are pierced by irregular vascular foramina, five or six on each. No separate interparietal can be surely distinguished.

The squamous portion of the squamosal is small and extends forward much as in *Ptilocercus*. The glenoid fossa is triangular and nearly plane. The postglenoid process is a small nubbin between the glenoid and the auditory meatus. The zygomatic process of the squamosal is slender and extends forward to a point anterior to the postorbital process.

The jugal is slender but well developed and forms an essential part of the arch, maxilla and squamosal not being in contact. It appears to have no facial expansion but to send a slender process forward to the lachrymal along the upper side of the zygomatic process of the maxilla. It does not appear to have had a malar foramen or a postorbital process, the orbit being open behind. The posterior extension of the jugal is rod-like and reaches the glenoid fossa, as in marsupials (and *Tupaia*).

The occiput is high and quadrate, chiefly by reason of the great lambdoid crest. The bones are completely fused. Above the external ends of the condyles are pits, but apparently no foramina. The mastoid exposures are triangular and are lateral (as in tupaiids) rather than occipital (as in erinaceids).

The foramen magnum is subquadrate, transverse, with no superior notch but a well defined inferior notch. The articular surfaces of the condyles are nearly or quite continuous, anterior to this notch.

The basicranium is chiefly occupied by the large bullæ, which are noteworthy not only for their size but for their regularity of form, being almost perfect sections of spheres, and for their quite circular and remarkably large external auditory openings. The diameter of these openings is about 5.5 mm., that of the whole bulla (externally) about 10 mm.

Unlike the false bullæ of the lipotyphlous insectivores, these are sharply distinct from the basisphenoid. Within the left bulla (the shell of which was incomplete) was found a segment of a slender curved bone which I believe can only be the tympanic ring. If this is the case, the bulla is purely entotympanic, the true tympanic being annular and within the bulla—exactly the same condition as in *Tupaia* and its allies but in no other insectivores. Unlike *Ptilocercus*, the large bulla has cut off the petrosal from any exposure on the base of the skull. There is a distinct mastoid process in contact with the posterosuperior rim of the auditory opening, and a smaller, separate paroccipital process posterointernal to this.

The pterygoids and palatines form sharp continuous crests running nearly to the bullæ but not continuous with them. In the external angle between each of these and the bulla is a small sloping triangular alisphenoid shelf, at the anterior end of which the alisphenoid is produced into a sharp external pterygoid process, directed outward and

slightly downward. This arrangement is very like that of the tupaiids, save that in the present form the internal pterygoid plates seem to have continued at the palatal level (somewhat crushed in the specimen), as they very nearly, but not quite, do in some tupaiids.

The choanæ are considerably narrower than the palate. There is a small median posterior projection of the palatines. The palate is broad and was thinly ossified. It is somewhat crushed, but there appear to be definite paired vacuities. The maxillopalatine suture cannot be determined.

The orbitotemporal region, which so sharply distinguishes the menotyphlous and lipotyphlous insectivores, is unfortunately cracked somewhat so that sutures can hardly be determined positively. On the less crushed right side, however, there is an indubitable foramen opposite M^3 and at the angle between the median wall and floor of the orbit. The bone above and in front of this is visibly continuous without suture to the lachrymal. There seems little reason to doubt that this is the nasopalatine foramen and that the palatine is in contact with the lachrymal, excluding the maxilla from the frontal within the orbit, a diagnostic character of the Tupaiidæ and Macroscelididæ.

Cranial foramina

Infraorbital canal: small, about 85 mm. in length, infraorbital foramen over P_3.

Optic foramen: large, in orbitosphenoid, immediately above and anterior to the anterior lacerate foramen.

Anterior lacerate foramen: about equal to the foramen ovale in size.

Foramen rotundum: debouches with the anterior lacerate foramen, although they may be partially or completely separate more internally.

Alisphenoid canal: enters a small opening on the basal aspect to the alisphenoid, anterointernal to the foramen ovale, tunnels the base of the lateral pterygoid process, and passes out through a small opening in the external wall of the pit surrounding the anterior lacerate foramen and foramen rotundum.

Nasopalatine foramen: in the orbital plate of the palatine, opposite M^3.

Foramen ovale: subcircular, of moderate size, in the basal aspect of the alisphenoid, underhung by the anterior part of the bulla.

Post-glenoid foramen: large, internal to the post-glenoid process.

Stylomastoid foramen: wedged between the mastoid process and the bulla.

Eustachian foramen: at the anterointernal edge of the bulla immediately internal to the foramen ovale.

Posterior lacerate foramen: a slight gap around the posterointernal part of the bulla terminating postero-externally in a fairly large and almost circular foramen.

Carotid foramen: a small opening in the uppermost part of the exposed bulla at its posterior end immediately anterior to the large part of the posterior lacerate foramen.

Condylar foramen: very small and close to the articular surface of the condyle, between it and the posterior lacerate foramen.

Lachrymal foramen: there are two foramina in the lachrymal bone, both nearly marginal but rather on the facial side, one above and one below the lachrymal tubercle.

Various vascular foramina: a pair near the midline in the anterior part of the frontals, several in the parietals anterior to the lambdoid crest, and possibly others not positively identified.

The following foramina were doubtless present but cannot be distinguished on the specimen: anterior palatal foramen, posterior palatal foramen, ethmoidal foramen, sinus canal. Malar and supraorbital foramina are absent.

The other openings of the skull, nares, choanæ, auditory meatus, palatal vacuities, and foramen magnum have been described above.

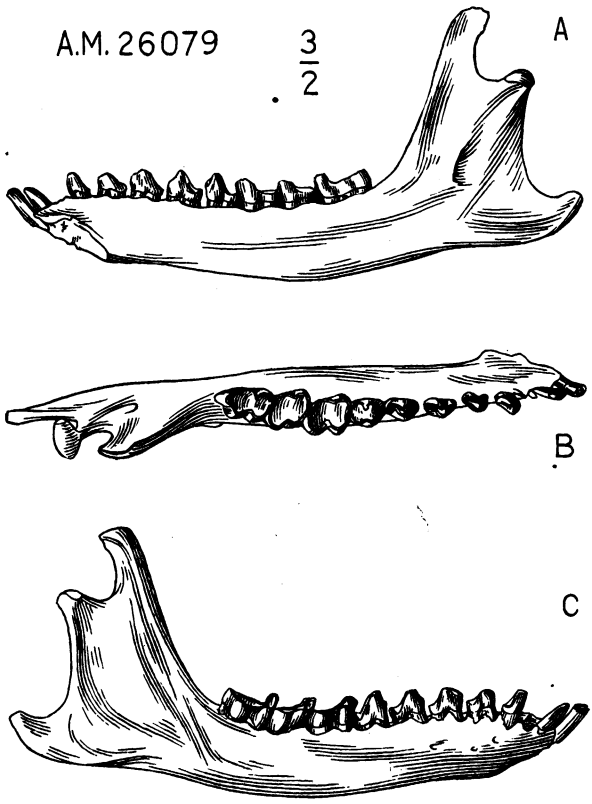

Fig. 2. *Anagale gobiensis.*
A, Internal; B, Superior; C, External views of right ramus of the lower jaw. One and one-half times natural size.

MANDIBLE

The right ramus of the lower jaw is perfectly preserved, the left less so. The moderately slender horizontal ramus has about the proportions seen in *Gymnura*. The largest mental foramen is beneath the anterior root of P_1. Two smaller ones are posterior to this, one between P_1 and P_2, and one beneath the anterior root of P_3. The angular process is pointed and hook-like, but is somewhat deeper than in *Tupaia*

and projects directly backward rather than backward and downward. The articular condyle is elevated far above the dental level, and its transverse articular surface is slightly convex anteroposteriorly, as in many insectivores. The posterior border falls straight downward from it, not downward and forward. The coronoid process is very slender and high, slightly recurved. The relief of the inner side is slight save for a horizontal ridge and underlying concavity on the angle. The dental foramen is a small vertical slit at the molar level, with a very faint, short, oblique mylohyoid groove beginning at its lower end.

VERTEBRÆ

The entire cervical series is preserved. The atlas has a fairly prominent median dorsal tubercle, but no distinct ventral tubercle. The transverse processes are short but rather heavy, the ventral excavation not being deep. The structure is rather generalized, but closer to that of *Ptilocercus*, for instance, than of *Gymnura*. The

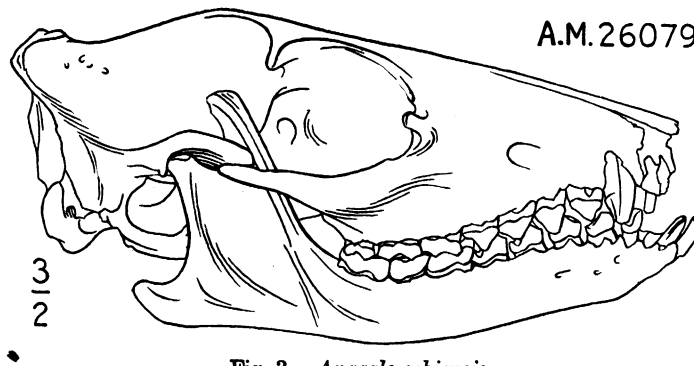

Fig. 3. *Anagale gobiensis.*
Outline of skull and jaw with teeth in occlusion.
One and one-half times natural size.

arrangement of the canals is of the usual primitive type, seen also in both tupaiids and erinaceids. The axis has a prominent peg-like odontoid process. The relief of the inferior surface is not pronounced, but there is a sharp single median crest and lateral concavities. The transverse processes project to about the same line as the posterior end of the centrum and are pierced by the vertebrarterial canals which issue in the distinct notches between these processes and the atlanteal facets. The neural spine is expanded into an anteroposterior plate, but its outline is damaged.

The succeeding cervicals are of the basic type typically developed (although with numerous variations in details) in the erinaceids, tupaiids, and related groups. The centra are somewhat flattened dorsoventrally and bear a slight ventral keel on the third and fourth vertebræ. The transverse processes of the third are simple and not unlike those of the axis. On the succeeding two vertebræ the transverse processes are expanded distally, and from their bases arise slender processes which project forward beneath the transverse processes of the next preceding vertebræ (cf. *Tupaia*, *Gymnura*, etc.). The sixth vertebra differs sharply from the others by the sharp division of the transverse process into dorsal and ventral lamellæ (transverse process proper or diapophysis and costal process or pleurapophysis). The dorsal part is like

that of preceding vertebræ, while the ventral is directed outward and downward, compressed transversely, and broadly expanded anteroposteriorly. The nature of these processes on the seventh vertebra cannot be determined.

All of the cervicals (except the atlas) have distinct neural spines. These decrease in height from the axis to the sixth, while that of the seventh is abruptly higher, over twice that of the sixth, in transition to the very elevated anterior dorsal spines.

Parts of about fifteen dorsolumbars are present, but the preservation is rather poor. Of the anterior dorsals (preserved in series with the cervicals) nothing can be said beyond the fact that they had lofty slender neural spines, directed backward and reaching their greatest height at about the fourth or fifth. These spines constitute a marked adaptive difference from the tupaiids, but resemble *Rhynchocyon*, for instance.

Parts of six lumbars are preserved. Of these, three, in sequence, give most of the characters of the mid-lumbar region. The neural spines are broad anteroposteriorly, bluntly truncated, of moderate height, and directed forward. The zygapophyses are elevated and strong, with the articulation sharply concavo-convex transversely. The transverse processes are broad and long blades directed sharply outward and downward and somewhat forward. Small anapophyses are present, with the nerve exits through deep grooves or notches below them. No part of the sacrum has been identified. Isolated caudals are of quite usual type and indicate a long and heavy tail.

Anterior Extremity

The scapula has the approximate contour of *Gymnura* or *Tupaia;* the posterior border nearly straight, anterior and superior borders continuous and strongly curved, sharp posterosuperior angle, lofty spine, prespinous fossa larger than postspinous. It is less like that of *Ptilocercus*, *Erinaceus*, or *Rhynchocyon*. The posterior margin is strongly everted. The acromion is large and bifid, much as in *Gymnura*. The glenoid cavity has the same pyriform shape as in all of the genera mentioned. The coracoid process is broken off on both scapulæ of the specimen.

Imperfect proximal and distal ends of both humeri are preserved, but the shafts are missing. The head is ovoid and widely overhangs the posterior face of the shaft. The tuberosities are normal. The distal end is somewhat expanded. Its chief peculiarities are the large entepicondylar foramen, strong supinator crest, large globular capitulum, and narrow trochlea.

The proximal end of the ulna is stout, the olecranon expanded vertically and bent somewhat inward. The semilunar notch presents no unusual feature. Beneath and anterior to the coronoid process is a small, deep pit. The proximal part of the shaft is triangular, with large internoinferior and externosuperior faces and a narrow internosuperior face, all separated by prominent angulations. A prominent interosseous crest is present at about the middle of the externosuperior face. The distal end of this bone and the whole of the radius are unknown. The carpus is also lacking.

The manus is represented by an articulated fragment with the distal ends of two metacarpals, two complete digits, median and distal phalanges of a third, and distal phalanx of a fourth. These are probably parts of the first four digits of a right manus, although this is not wholly certain. Three of the digits (the second to fourth in any event) are of about equal size, but decrease slightly in length from one side to the other (from fourth to second on this interpretation). The articulations are of the expected type: metacarpal articulations half keeled, median articulations nearly

cylindrical but slightly grooved, distal articulations a little more grooved. The proximal and median phalanges are stout and not elongate. The distal phalanges are considerably longer than the others and form large, curved, laterally compressed claw cores with proximopalmar tuberosities. They are strongly fissured. In addition to this material there are isolated proximal ends of the third and fourth metacarpals of the left side. The articular surface of the fourth is nearly quadrate, wider on the external side. It projects beyond the third and has a small facet for the unciform. The articular surface of the fourth metacarpal is unusually narrow transversely.

Posterior Extremity

A few fragments of the pelvis reveal none of its important characters. The femur is also poorly represented, only the heads of both and imperfect distal end of one being present. The head is spherical, with a strong foveal pit, and is borne on a constricted neck. On the distal end the condyles are of about equal development. A small patella is preserved.

The left tibia is well preserved except for the malleolus, and proximal and distal ends of the left fibula are present. The two bones are completely separate. The tibia is of primitive structure and agrees with that of *Tupaia* except in its stouter proportions and the better-developed cnemial crest, which is more prominent and extends about half way down the shaft. From its broken base and from its articular facet on the astragalus, it is clear that the malleolus was large and prominent, as in the Menotyphla.

The proximal end of the fibula shows a rather large, irregular, triangular expansion, the upper side of which articulates movably with the tibia. The shaft was rather slender but complete. The distal end has a blunt expansion, with an oval facet for the astragalus on its median face and a supero-median triangular facet for the tibia. The open peroneal groove passes posterior to an irregular but distinctive lateral projection.

Of the tarsus, there is an astragalus (lacking the head) and a cuboid, both of the left side.

The astragalus is of insectivore type and closely resembles that of *Tupaia* except for the presence of an astragalar foramen and for minor details of the inferior facets. The trochlea is broad and fairly shallow. The margins are sharp, subequal, but the fibular margin more prominent (tupaioid as opposed to erinaceoid). The malleolar facets are of equal size and are nearly parallel but converge slightly anterosuperiorly. A small astragalar foramen is present in the trochlea near the superior end of the fibular crest. The ectal and sustentacular facets are of equal size (the ectal is larger in *Tupaia*) and the latter apparently was not quite continuous with the fibular or navicular facets (unlike *Tupaia*) but it approaches both much more closely than in *Erinaceus* or *Gymnura*. The neck projects anterointernally and has the direction and relative development seen in *Tupaia*. The external side of the head has a small articulation for the cuboid. The navicular articulation is not preserved.

The chief point of interest about the cuboid is that it is shorter proximodistally than in any of the related modern insectivores examined. In both erinaceids and tupaiids (and even in the Paleocene *Prodiacodon*) it is moderately elongate, and in the Macroscelididæ it is extremely long, whereas in the present form it is unusually short. The superior surface has a small internal facet for the astragalus (absent in *Ptilocercus* but present in *Tupaia*), concave anteroposteriorly, and a large facet for the calcaneum,

convex anterposteriorly and gently concave transversely. The latter facet is more oblique than in related forms, sloping distally in the dorsal and external directions. The plantar surface is marked by a large and sharply defined tuberosity which is transverse. The median surface has a crescentic proximal facet for the navicular, contiguous to that for the astragalus, and, distal to this, two small, separate, elevated facets for the third cuneiform. The surface for the fourth and fifth metatarsals is undivided and gently concave.

The length of the first metatarsal is unknown, but that of the others decreases in the following sequence: III, II, IV, V, the approximate lengths being 27, ca. 25, 23.5, and 20 mm., respectively. They are moderately stout bones and not especially elongate. The first metatarsal (represented only by the distal end from the left pes) is of about the same stoutness as the fifth. It is not known whether it was divergent. The proximal articulations of the third and fourth metatarsals are about as in *Gymnura* or *Tupaia* except that that of the third is less wedge-shaped, not contracting so much toward the plantar side. The fifth differs from *Gymnura* and agrees with *Tupaia* in not extending farther than the fourth proximally. It differs from *Tupaia* chiefly in the shorter but stouter external process which does not extend proximally. The distal articulations are of the usual transversely cylindrical type with plantar keels. The phalanges likewise have the usual type of articulation as in related forms, and in general have no interesting peculiarities except for the unguals. These differ from those of the front feet and from those of related living forms in being somewhat wider than deep proximally and distinctly flattened and depressed distally, almost spatulate, rather closely approximating the distal phalanges of some primitive lemuroids.

AFFINITIES

Previous discoveries in Mongolia include nothing closely comparable with *Anagale*. Four genera from the Cretaceous are confidently referred to the Insectivora and placed in two distinctive families, Deltatheridiidæ and Zalambdalestidæ (Simpson, 1928, and papers there cited). These share certain primitive characters with *Anagale*, such as the nearly complete dental formula, uninterrupted zygomata, etc. Especially in the case of the Zalambdalestidæ, they also have a few more advanced or divergent characters seen in the present genus, such as some degree of molarization of the premolars, narrow snout, contour of the mandible, and some other features, but these are ancestral characters of the Order Insectivora rather than indications of any special affinity. As would be expected, the Cretaceous families are more primitive on the whole, and some of their features would surely figure in the structural ancestry of *Anagale*, but they have no special generic or family resemblance to the latter, and some of their specializations (in the teeth if nowhere else) already exclude them from the ancestry of the Oligocene genus.

Two Paleocene genera, *Praolestes* and *Pseudictops* (Matthew, Granger, and Simpson, 1929), have been provisionally referred to the

Insectivora. They are known only from the teeth, which do not especially resemble those of *Anagale* in either case, and their reference to the Insectivora is very doubtful and made only in default of other indications.

Among Mongolian insectivores, the closest to *Anagale*, both in point of time and in structure, are *Tupaiodon* and *Palæoscaptor*[1] from the

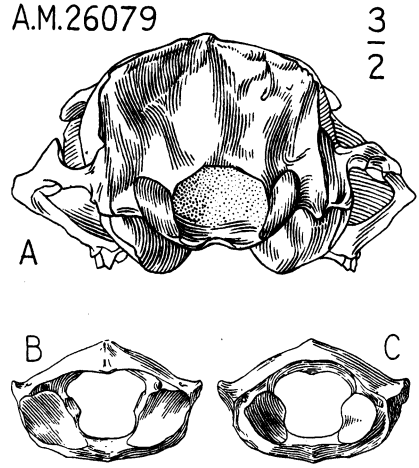

Fig. 4. *Anagale gobiensis*.
A. Posterior view of skull. B, Anterior view of atlas vertebra. C, Posterior view of atlas vertebra.
One and one-half times natural size.

Hsanda Gol, an Oligocene formation more recent than the Ulan Gochu. Matthew and Granger provisionally referred *Tupaiodon* to the Tupaiidæ and *Palæoscaptor* to the Soricidæ. Study of new material (including an upper jaw of *Palæoscaptor*) suggests, first, that these two genera are closely related and should not be referred to separate families, and, second, that they are less closely related to the Tupaiidæ or Soricidæ than to the Erinaceidæ. *Tupaiodon* differs in numerous dental characters from any known tupaiid but shows a rather close general agreement with primitive gymnurines, such as *Galerix*. None of its known characters excludes it from the Gymnurinæ. *Palæoscaptor* is essentially similar, particularly in the upper teeth, but is somewhat more specialized in the reduction of M_2, larger and more secant M_1, and enlargement of one pair of incisors. To a limited degree these characters are convergent toward the soricoids, but they are wholly consistent with

[1]1924. Matthew and Granger. There is also some important undescribed material which has been examined for its bearing on the present discussion.

erinaceoid relationships, being less extreme than in some members of the latter group, and the differences from true soricoids, as recognized by Matthew and Granger, are numerous and important. The tibia and fibula of *Palæoscaptor* are known, and they are totally unlike those of the Tupaiidæ (or of *Anagale*) but agree in every essential with the Erinaceidæ.

The question of relationships between *Tupaiodon* and *Palæoscaptor* on the one hand and *Anagale* on the other is largely resolved by this view as to the relationships of the former genera. It suffices to say that they are not closer to *Anagale* than are other presumed erinaceids, as discussed below.

More specific discussion of the wider relationships of *Anagale* may be prefaced by some further analysis of the dentition. The following are its most striking primitive dental characters:

Dental formula complete (with possible but improbable exception of I^1).
Incisors subequal, one-rooted, styliform.
Premolars all with divided roots.
Pattern relatively little changed from tuberculosectorial.

Although primitive, these characters are to some degree diagnostic when taken in conjunction with the geologic age. Unless there were strong contrary evidence in other parts (which is not the case), they would at once exclude the Centetoidea and the Soricoidea, since both groups had lost various of these primitive characters by the Oligocene or long before. The only primitive characters never seen in recent tupaiids are the retention of $P\frac{1}{1}$ (and probably of three upper incisors) and of the two-rooted P_2. The two-rooted P_1 does not appear in any known erinaceid, but the other primitive characters are present in various Gymnurinæ.

Small, more or less premolariform canines appear in various genera and species of all tupaioid and erinaceoid families but are not especially typical of any one.

P_2 and, more notably, P^2 are more advanced than in any other genus of insectivores known to me.[1] There does not appear to be any other tupaioid or erinaceoid with three roots on P^2. P^3 is of the general type usual in gymnurines. It is more complex than in *Ptilocercus* or *Tupaia*, but not more than in other tupaiines such as *Anathana* and of about the same pattern. P^4 about equally resembles the less complex

[1] P^2 is unknown in the probably insectivore family Plagiomenidæ, but from their extremely molariform P^{3-4} I suspect that it may have been as advanced as *Anagale* in this particular; but the dentition is otherwise so different as not to enter into this question.

of the gymnurine homologues and those usual in the tupaiids. P_{3-4} likewise show equal resemblance to tupaiids and erinaceids.

The upper molar structure is not wholly clear, but the following facts are ascertainable. The general contour is most nearly approached in those tupaiids with relatively large hypocones (cf. *Anathana*), being more transverse and apparently with relatively smaller hypocones than in the Macroscelididæ or Erinaceidæ. On the other hand the upper molars differ from the Tupaiidæ and resemble the latter two families in the external and non-crescentic paracone and metacone.

The lower molars are likewise of rather generalized erinaceoid-tupaioid type but differ from both groups in the short trigonids and in the perhaps more important character of a projecting hypoconulid or incipient third lobe on M_3.

In short, the dentition is peculiar but is not inconsistent with reference either to the Tupaioidea or to the Erinaceoidea. Taken by itself it would be inconclusive but would perhaps seem somewhat more suggestive of the latter group—a conclusion so opposed to the more conclusive osteological characters as to serve as an example of the often misleading character of the teeth alone as guides to family or higher relationships among these primitive groups.

Turning to the entire known structure of *Anagale*, its characters at once exclude near relationship with any but three established groups of mammals: the erinaceoids, the tupaioids, and the more primitive lemuroids. It is probably related to all three, but its closest relationships are clearly with the tupaioids. Some of the more important items of evidence for this view are as follows:

Dentition not inconsistent with tupaioid relationships.

Infraorbital canal relatively small and long.

Orbit large. Open posteriorly (unlike Recent Tupaiidæ) but with strong postorbital process (cf. *Rhynchocyon:* unlike Erinaceidæ and presumably like the ancestral tupaiid condition).

Lachrymal with moderate anterior, not superior, expansion, prominent spine, two foramina (cf. *Tupaia*).

Jugal large, with lachrymal contact and extending posteriorly to the glenoid fossa.

Mastoid exposure lateral rather than occipital.

Large bulla into which the basisphenoid does not enter, probably formed by an entotympanic with annular tympanic internal.

Cerebral hemispheres relatively large and globular.

Pterygoid crests and external pterygoid fossa almost exactly as in *Tupaia*.

Orbitotemporal region not wholly clear, but almost surely with palatolachrymal contact and nasopalatine foramen opposite M_3, as in Tupaiidæ but not in any Lipotyphla.

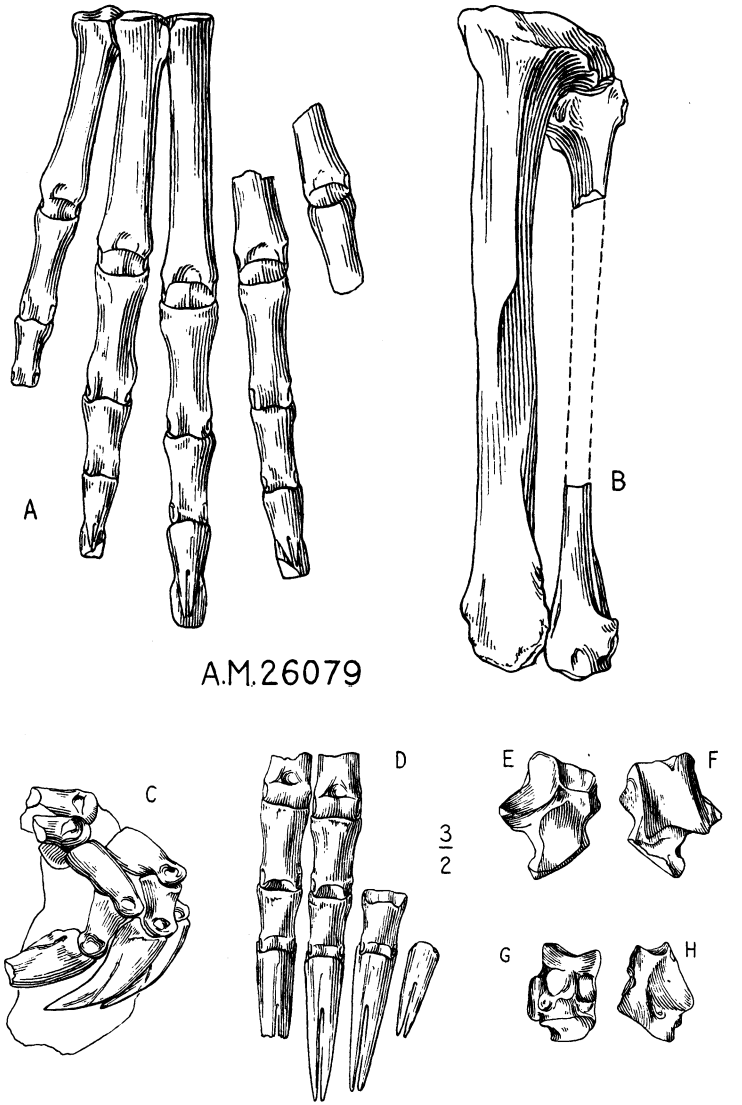

Fig. 5. *Anagale gobiensis.*

A, Dorsal view of right pes (partly restored from opposite foot). B, Anterior view of left tibia and fibula. C, Outer view (?) of phalanges of right (?) manus, *in situ*. D, Dorsal view of phalanges of right (?) manus. E, Posterior view of left astragalus. F, Anterior view of left astragalus. G, Inner view of left cuboid. H, Outer view of left cuboid. All one and one-half times natural size.

Cranial foramina (including alisphenoid canal and carotid foramen) like those of *Tupaia* in every essential.

Vertebræ tupaioid or erinaceoid in fundamental characters, but known parts not very distinctive between the two.

Known parts of fore limb also pointing to these two groups but not distinctive between them.

Tibia and fibula separate, prominent internal malleolus.[1]

Astragalus fundamentally tupaioid, although differing in some features, mostly primitive, as detailed above.

Tarsus and metatarsus not unduly elongate (cf. erinaceoids and Tupaiidæ but not Macroscelididæ).

The points of agreement with the Tupaiidæ are so numerous, so detailed, and so highly diagnostic that there can be no doubt that they indicate a rather close relationship.

On the other hand, this fundamental resemblance in basic character is accompanied by numerous differences of less importance. All of these are sufficiently emphasized in the diagnosis and descriptions above or in the further discussion of affinities below. To some extent these are merely primitive, as the open orbit or complete dental formula. To a very limited degree they are points of special resemblance to the erinaceoids on the one hand or to the lemuroids on the other, while certain of them, as the advanced structure of P^2, large unguals of the manus, or short cuboid, are aberrant specializations.

These resemblances to and differences from the Tupaiidæ seem best expressed by placing *Anagale* in a distinct family, Anagalidæ, of the superfamily Tupaioidea,[2] Order Insectivora. The relationship of the Anagalidæ and the Tupaiidæ seems to be nearly analogous to that of the Leptictidæ and the Erinaceidæ.

Certain other fossil insectivores have been considered as tupaioid or menotyphlan in relationship. The best known of these are the varied genera grouped under the Plesiadapidæ, referred to the Menotyphla by Matthew. This systematic position is supported chiefly by the fact that they, like the tupaiids, have a mixture of primate and of insectivore characters, yet with little or nothing specifically suggestive of the Tupaiidæ. While aberrant in many respects, the primitive primate characters appear to predominate, and I should prefer to follow Stehlin to the extent of referring them to the Primates.[3] This is further supported by the fact that in the known parts (including some skeletal and

[1]Their separation is, of course, primitive but is nevertheless a diagnostic character of great value, since the fused erinaceoid crus was already typically established in the Paleocene.

[2]Customarily referred to the Suborder Menotyphla, but this term was based on the Macroscelididæ, and there is now much doubt as to whether this family can be grouped with the Tupaiidæ.

[3]Although not to a section Cheiromyoidea.

other material not yet published in detail) they seem to share few or no characters with *Anagale* that are not also shared by undoubted primates.

Passing over some genera, especially *Galerix*, once referred to the Tupaioidea in error, there remain several early Tertiary genera sometimes placed here: *Entomolestes*, *Leipsanolestes*, *Adapisorex*. Teilhard (1927) has recently shown that *Adapisorex* is probably a leptictid, and, contrary to my original opinion, I have elsewhere (1929) reached the same conclusion regarding *Leipsanolestes*. The same may be true of *Entomolestes*. In any event, the teeth, an imperfect acquaintance with which constitutes our entire knowledge of these genera, are quite inadequate to prove true tupaiid relationships, and such reference is improbable. As very early probable erinaceoids they are doubtless not far removed from the tupaioid ancestry, but they cannot be referred to the latter group on present evidence. They have no special resemblance to *Anagale*.

Having established the fact that *Anagale* is related to the Tupaiidæ, it is necessary to examine its resemblances to other groups recognized as allies of the tupaiids in varying degrees: Macroscelididæ, Erinaceidæ, Leptictidæ, and lower lemuroids (Adapidæ, Notharctidæ, Lemuridæ).

Macroscelides, *Rhynchocyon*, and their allies form an aberrant group combining with many peculiar features of their own numerous characters otherwise found in the Tupaiidæ or Erinaceidæ but not in both. The general conclusion is fairly clear: that the Tupaiidæ and Erinaceidæ are derived from a common source, that they separated at some very early time (probably Paleocene or earlier), and that the Macroscelididæ are also derived from this common ancestry. The characters of the Macroscelididæ which resemble now one family and now the other are thus either (a) characters of the common tupaiid–erinaceid ancestry now lost in one group or the other, or (b) characters secondarily convergent toward one group or the other, or (c) characters developed either in the Erinaceidæ or in the Tupaiidæ after they had become separate. Upon the characters placed in category (c) depends whether the Macroscelididæ are to be considered as belonging to the Tupaioidea or to the Erinaceoidea, or neither. Most authorities place the tupaioid characters in this category, that is, they consider that the Macroscelididæ were derived from the tupaiid ancestry after the latter had diverged from the erinaceid ancestry. Careful study, however, led Albertina Carlsson to the opposite view of especial erinaceoid affinities. In the absence of fossil macroscelidids, the evidence is so evenly balanced that its interpretation depends on mere personal opinion as to the nature,

importance and antiquity of the various characters. Tabulation of numerous characters shows the following facts as to the bearing of *Anagale* on this problem:

1. *Anagale* already possessed all the characters shared by Tupaiidæ and Macroscelididæ.

2. It also possessed numerous definitely tupaiid characters (such as details of cranial foramina, bullæ, tibia and fibula, and astragalus) not found in the Macroscelididæ.

3. Characters shared by *Anagale* and the Macroscelididæ but not by the Tupaiidæ are few and are either primitive (as the open orbit and absence of molar foramen) or superficial and adaptive (as the long dorsal spines) and of no great phylogenetic significance.

As regards *Anagale* itself, it is seen that it is much closer to the Tupaiidæ than to the Macroscelididæ and that it is in no sense intermediate between the two. It produces no rapprochement of the two groups beyond showing the antiquity of the characters shared by them, but on the other hand does not tend to separate them more widely.[1]

The existence of a body of evidence tending to link the Tupaiidæ and the Erinaceidæ through a very remote common ancestry has long been generally recognized, as suggested above. *Anagale* bears on this point as follows:

1. It has most or all of the primitive characters retained in the Erinaceidæ but lost in the Tupaiidæ.

2. Except for a few, masked by its own divergent specialization (as by the shortened trigonids or the proximodistally compressed tarsus), it also has all the special characters shared by the Tupaiidæ and Erinaceidæ.

3. It also has a few special and non-tupaiid resemblances to the Erinaceidæ (such as those of the teeth or of the astragalus, detailed above).

The first fact tends to show the simple divergence in time of the Tupaiidæ. The second suggests that the tupaiid–erinaceid resemblance is one of true affinity and not of convergence. The third, although not very striking, tends in a limited degree to draw the two groups closer together.

More important evidence of the relationships between tupaiids and erinaceids may be furnished by the extinct (Cretaceous to Oligocene) American family Leptictidæ. This family is quite distinct from the Erinaceidæ, but is definitely erinaceoid in general structure. At the same time it has some points of definite resemblance to the Tupaiidæ not seen in the erinaceids. Full elucidation would require a monographic

[1]More detailed discussion would be out of place here, but the examination of dental and osteological characters incidental to the present study has led to the personal impression that the resemblances in these characters between the Macroscelididæ and the Tupaiidæ are rather more important, those between the former and the Erinaceidæ rather less important, than was concluded by Carlsson. In either event the Macroscelididæ are an extraordinarily aberrant group.

revision of the Leptictidæ, and the general problem has been briefly discussed by Gregory, so that it will be enough here to show that *Anagale* is not a member of this family but that these special resemblances do exist.

Anagale is excluded from the Leptictidæ, not only by the erinaceoid characters of the latter, such as the short and dorsal lachrymal expansion, occipital mastoid exposure, false bulla, fused tibia and fibula, and many others, but also by many of the peculiarly leptictid characters, such as the truly molariform P^4, intraorbital lachrymal foramen, squamosal foramina, club-shaped spine of the axis, etc.

There is a special resemblance in the teeth, although neither consistent nor detailed, in that M^{1-2} of the Leptictidæ are subquadrate and transverse, paracone and metacone external and non-crescentic, trigonids of lower molars short, M_3 talonid with projecting hypoconulid. The skull also has a few points of resemblance, such as the unpierced but large jugal and the rather similar alisphenoid canal. The leptictid tibia and fibula are fused, as in erinaceids, yet do not articulate with the calcaneum and have a well developed internal malleolus, as in *Anagale* and the tupaiids. The astragalus is in some respects intermediate between the tupaiid and erinaceid types, but not especially close to *Anagale*. It has the trochlea continuous to the posterior margin (although more deeply grooved than in tupaioids), strong internal malleolar facet, and sharp crests with the fibular somewhat higher—all points more or less suggestive of the tupaiids. Unlike *Anagale*, there is no astragalar foramen. Despite these and other resemblances, it is clear that the Leptictidæ and Anagalidæ, and hence likewise the Erinaceoidea and Tupaioidea, diverged long before the Oligocene.

As early as 1886, Parker made note of resemblances between the tupaioids and the lemuroids. Many subsequent studies have finally established the view that the tupaiids are the closest living relatives of the primates and that they cast considerable light on the origin of the latter. The recent detailed work of W. K. Gregory (esp. 1910, 1913), W. E. Le Gros Clark (1926) and Albertina Carlsson (1922) make unnecessary any general review of the evidence, but it is of importance to examine *Anagale*, the oldest definitely recognizable tupaioid, with this problem in mind.

Anagale has all the observable primate-like characters of *Tupaia*, with the following chief exceptions:

1. Open orbit.
2. No malar foramen.

3. Astragalar foramen.
4. Separate sustentacular and navicular facets on astragalus.
5. Relatively shorter phalanges.
6. Large claws on manus.
7. Shorter cuboid.

The first four characters are primitive, although it would have been supposed, *a priori*, that they would be lost in the common ancestry of the primates and the tupaioids. The last three are rather unimportant habitus characters of *Anagale*.

On the other hand, there is an equally or more important assemblage of characters in which *Anagale* approaches the primitive primates more closely than do the recent tupaiids:

1. Dentition distinctly more primate-like:
   a. $P\frac{4}{4}$.
   b. Premolars more affected by molarization.
   c. Upper molars subquadrate.
   d. Paracone and metacone less crescentic and more external.
   e. Trigonids short and narrower than talonids.
   f. Lemuroid projection of hypoconulid on M_3.
2. Shorter premaxilla.
3. Shorter facial expansion of lachrymal.
4. More prominent lambdoid crest.
5. Bullæ more spherical and with large auditory openings.
6. Fibula stouter and more curved.
7. Unguals of pes flattened and spatulate distally.

In view of its geologic age and general morphology, it is obvious that *Anagale* is not ancestral to any primate, and that it belongs definitely in the tupaioid line long after the separation of the primates. Some of these lemuroid characters are very probably convergent, yet the existence of such resemblances is just what one would expect in an early tupaioid offshoot, on the theory that these represent the protolemuroid stock. The existence in *Anagale* of all of the lemur-like characters of the tupaioids, with the rather trivial exceptions noted above, further strengthens this view and lessens the probability of these characters, in so far as common to all tupaioids, being to any significant degree convergent.

Carlsson has proposed that the tupaioids be removed from the Insectivora and made a suborder of Prosimiæ, while Gregory (1910) has made a separate Order Menotyphla. This really involves no great change from the accepted view of *Tupaia* and its allies as structurally intermediate between insectivores and primates, and the classification depends on personal emphasis of different aspects of the evidence. Yet the various resemblances of *Anagale* and of different groups of insec-

tivores as set forth here seem to me to support the classical retention of the Tupaioidea in the Insectivora as the more convenient arrangement.

RÉSUMÉ

1. *Anagale gobiensis*, new genus and species, is described on the basis of remarkably well preserved skull and jaws and much of the skeleton.

2. It is shown to be closely related to the Tupaiidæ but referable to an extinct and non-ancestral family Anagalidæ.

3. It is not closely related to any previously known fossil insectivores, none of which appears to be certainly referable to the Tupaioidea.

4. It is not intermediate between the Tupaiidæ and Erinaceidæ, being definitely allied with the former, but tends in some degree to strengthen the evidence of their remote common origin.

5. It tends more definitely to link the Tupaioidea and the Lemuroidea.

6. But it proves that the Tupaioidea have been distinct from all other groups of mammals from a time long antecedent to the basal Oligocene.

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