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PARAPITHECUS GRANGERI (PARAPITHECIDAE, OLD WORLD HIGHER PRIMATES) NEW SPECIES FROM THE OLIGOCENE OF EGYPT AND THE INITIAL DIFFERENTIATION OF CERCOPITHECOIDEA

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ABSTRACT

Among many primate fossils from the badlands of Oligocene age in the Fayum Province, Egypt, are specimens of a new species of the genus *Parapithecus*. The new materials for the first time provide evidence of the upper dentition and mandibular materials show that all the early determinations as to the dental formula of the type species of *Parapithecus*, *P. fraasi*, were incorrect. The new species, *P. grangeri*, is here described. It is suggested that the family Parapithecidae is best ranked in Cerecopithecoidea and that, in fact, *Parapithecus* and *Apidium* are the earliest known cercopithecoids.

Introduction

Several score fossil primates have been recovered in the course of seven expeditions to the Fayum badlands of Egypt, UAR, between 1961 and 1968. These specimens include some four dozen finds (mostly isolated teeth) of a new species of *Parapithecus*, larger than the type species and presumed to be somewhat younger than it. All known specimens of the new species of *Parapithecus* (described below) were recovered from Yale Quarry I which is located in the Upper Fossil Wood Zone of the Jebel el Qatrani Formation about 250 feet below the top of that formation. The level of Quarry I is the highest Fayum horizon that is richly fossiliferous. The Jebel el Qatrani Formation is capped by a basalt that has been dated by the potassium/argon method at 24.7 ± 2 million years B.P. by Evernden and Curtis at Berkeley and at 27.0 ± 3 by Armstrong at Yale (see Simons and Wood, 1968). Geological evidence suggests that the basalt was implaced on the underlying Jebel el Qatrani Formation a considerable time after deposition of those beds. In places the entire Formation (110-270 meters thick) had been eroded away before the basalt flow occurred. Thus, a tentative age of 28 to 30 million years seems probable for the Upper Fossil Wood Zone from which the fossils described here were recovered. Such a dating supports the evidence derived from faunal correlation that all the Fayum mammalian fossils from the Jebel el Qatrani are of Oligocene age and that they are all older by around ten million years than are any other African deposits that yield fossil cercopithecoids.

The new species of *Parapithecus* is of special interest as its dental anatomy appears to provide plausible evidence of relationship to the ancestry of the Old World Monkeys, Ceropithecoidea. The new material also provides adequate evidence to make a definite settlement of the taxonomic position of not only *Parapithecus* but *Apidium* as well. The latter is represented in our new collection by an even greater number of specimens. These two genera are by far the most common African Oligocene primates. They are known not only from jaws, teeth and cranial fragments but also probably are represented in the nearly 100 isolated postcranial bones from Yale Quarry I which are definitely primate. On grounds of their proper size, anatomy, and frequency of correlation with finds of jaws and teeth most of these can be provisionally referred to the Parapithecidae, to which both *Parapithecus* and *Apidium* belong.

Abbreviations

Abbreviations used in this paper are as follows:

C	canine (C^1 = upper canine, C_1 = lower canine)
dP	deciduous premolar (dP^3 = third upper deciduous premolar)
M	molar (M^1 = first upper molar, M_2 = second lower molar)
P	premolar (P^3 = third upper premolar, P_4 = fourth lower premolar)

CGM Cairo Geological Museum, Cairo, Egypt
SNM Naturhistorisches Museum, Stuttgart, Germany
YPM Peabody Museum of Natural History, Yale University, New Haven, Connecticut

SYSTEMATICS
ORDER PRIMATES
SUPERFAMILY CERCOPITHECOIDEA
FAMILY PARAPITHECIDAE
SUBFAMILY PARAPITHECINAE
GENUS *Parapithecus* Schlosser 1910, 1911
TYPE *Parapithecus fraasi*

(Fig. 2)

GENERIC DESCRIPTION. Dental formula $\frac{2.1.3.3.}{2.1.3.3.}$, as in only *Apidium* and probably *Amphipithecus* among catarrhines. Differs from the contemporary parapithecine genus *Apidium* in showing comparatively larger $\frac{C}{C}$ and markedly smaller M_3, centroconid typical of *Apidium* absent and hypoconulids of M_{1-3} relatively reduced, principal upper cusps at corners of a square, not with hypocone much more lingually situated as in *Apidium*. *Parapithecus* lacks the large pericone cusp developed from the anterior part of the lingual cingulum of the protocone in *Apidium*. Differs from later Cercopithecidae and from all Old World Higher Primates, but agrees with *Apidium* in uniformly showing small central cusp in upper P^{2-4} between main inner and outer cusps and apparently homologous with the paraconule of M^{1-3}. Differs from *Apidium* in showing no trace of the wrinkling and polycuspidation of teeth characteristic of the latter.

Parapithecus grangeri, new species[1]

(Fig. 1)

TYPE. CGM 26912, left mandibular ramus with P_3-M_3, collected from the eastern edge of Yale Quarry I, by E. L. Simons in February, 1966.

[1]This species is named in honor of the late Walter Granger of the American Museum of Natural History, whose untiring collecting efforts in the Fayum in 1906 led indirectly to the discovery of earliest Higher Primates there. In an earlier paper (Simons, 1969) I used the name *Parapithecus grangeri* and presented drawings and photographs of its dentition and that of the type of *P. fraasi*. However, this was not intended to be the publication establishing the name of the new species, and a careful review of that paper shows that the technical phrasing of Article 13 (a) of the *International Code of Zoological Nomenclature* (Stoll, 1964) is not satisfied: ". . . a name published after 1930 must be . . . accompanied by a statement that purports to give characters differentiating the taxon." Therefore the 1969 paper can be ignored for purposes of nomenclature. In my book on primate evolution

HYPODIGM. Type and CGM 26918, right jaw fragment with P_3-M_3; YPM 21017, right mandibular fragment with M_{1-3}; 21019a, right mandibular fragment with dP_{3-4}, M_{1-2}, M_3 in crypt; 23954, right jaw fragment with P_3-M_3 and part of ascending ramus; 23973, left jaw fragment with M_{1-2} and about 40 isolated upper and lower teeth at Yale. (This is a tentative count. Positive identification is not possible for every one of the 40 teeth.)

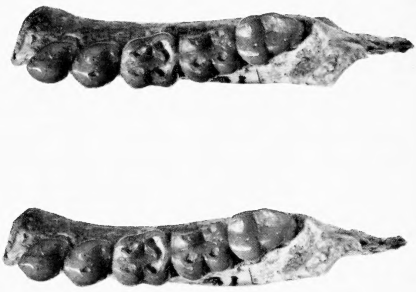

FIG. 1. Stereo pair of the occlusal view of the teeth, type specimen of *Parapithecus grangeri*, CGM 26912. Scale × 2.

HORIZON AND LOCALITY. All known specimens from Yale Expedition Quarry I, Upper Fossil Wood Zone, Jebel el Qatrani Formation, Oligocene Epoch, Fayum Province, Egypt.

SPECIFIC CHARACTERS. Comparable measurements on teeth and mandible ranging from about 10 to 25% larger than in type species, *P. fraasi*, which is presumably older and from lower in the section (see Table 1). *P. grangeri* showing a tendency toward more marked reduction of M_3 relative to M_2 and with much larger and more robust mandible relative to absolute size of teeth in full adults (with M_3 erupted) than in type species. Mandib-

(Simons, 1972: p. 191) the species *P. grangeri* was mentioned a second time as a species then in press, although again it was not my intention to make that brief reference to the work that established the name. Even though no type specimens were designated, the passage did make a partially comparative statement: "Most of the new *Parapithecus* finds are 15 to 20 percent larger than the type of *Parapithecus fraasi*, which was evidently found at a lower level than Quarry I, where the new species occurs. This new parapithecine has been named *Parapithecus grangeri* (Simons, 1972)." The present contribution is the actual paper that was then in press at a date prior to publication of my book, but because of a difference about its editing, that paper was not published in the journal to which it had been submitted, and it is here published for the first time as the initial description of this species.

TABLE 1. Comparative dental and mandibular measurements in *Parapithecus*.

Measurements of teeth in mm	*Parapithecus fraasi**		*Parapithecus grangeri*			*Parapithecus grangeri* Yale specimens			
	Type SNM 12639a Left	Right	Type CGM 26912	CGM 26918	YPM 21017	YPM 23796	YPM 23796	YPM 23954	YPM 23973
P_3 length	3.3	3.0	4.3	—	—	3.8	—	4.2	—
breadth	2.5	2.5	3.3	—	—	2.7	—	3.2	—
P_4 length	3.3	3.3	4.2	4.1	—	4.0	—	4.3	—
breadth	2.7	2.5	3.8	3.6	—	3.0	—	3.5	—
M_1 length	4.2	4.2	4.7	4.7	—	4.6	4.5	4.5	5.0
breadth	3.2	3.3	4.4	4.4	—	4.1	4.0	4.2	4.6
M_2 length	4.3	4.2	5.0	4.7	5.5	4.2	4.9	4.9	4.8
breadth	3.4	3.5	4.5e**	—	4.5	3.8	4.3	4.8	4.5
M_3 length	4.2	4.4	4.6	4.3	5.0	3.9	—	4.6	—
breadth	3.3	3.3	3.9	—	4.0	3.2	—	3.8	—
Overall size measurements									
anteroposterior length P_3 to M_3	18.5		22.0	20.0e	—	20.0	—	21.8	—
anteroposterior length of molars	12.5		14.5	14.0	15.0e	13.3	—	14.5	—
anteroposterior length from C to M_3	23.5		—	—	—	—	—	29.5	—
front of M_3 to back of articular process	13.0		—	—	—	—	—	19.6	—
mandibular depth under P_3	7.5		9.0	8.5	—	8.2	9.0	10.0	—
mandibular depth under M_3	7.5		10.7	9.5	10.0	9.2	9.0	11.0	—

*Measurements from Kälin (1961) correcting those of Schlosser (1911).
**c = estimated measurement.

ular depth, anteroposterior breadth of ascending ramus and length of tooth row from 20 to 30% larger than in type species. Horizontal ramus deepens posteriorly in *P. grangeri* from P_3 to M_3 (see Table 1), while that in type of *P. fraasi* does not.

General Discussion

The type and only specimen of *Parapithecus fraasi* has long figured in textbooks of anthropology and paleontology as an important basal form with various postulated relationships to later primates. The history of study of this animal, or rather history of misinterpretation of it, is instructive since it clearly demonstrates the problems that arise when there is only one individual fossil specimen (representing a group) and when few of those who wrote of it had bothered to see the actual specimen itself.

Confusion began with the initial description, for at the start Schlosser (1911) drew three wrong conclusions about it. These were: (1) that the type specimen was a juvenile; (2) that the symphysis was unfused; and (3) that the dental formula for it is $\frac{1.1.3.3.}{1.1.3.3.}$ (the same as in modern *Tarsius*). Although Schlosser recognized that the morphology of the molars and premolars of *Parapithecus* justified placement of the group it represented among the Higher Primates, he concluded that the Parapithecidae must have been an extinct side branch in primate evolution. This was because he was unable to reconcile the apparent reduction of the lower incisors to one pair with an ancestral relationship to descendant forms that possess two incisor pairs. As I have discussed at length (Simons, 1972) the numerous new jaws of *Parapithecus* and of the closely related genus *Apidium* show that the symphysis was fused in members of both genera at a subadult stage of growth; therefore the asymmetrical crack in the symphyseal region of the type of *Parapithecus fraasi* is an artifact. It is not indicative that the animal possessed an unfused symphsis as Schlosser (1911) initially and Kälin (1961) later believed. Both were misled because of damage there to the type and only specimen. The alveolae and surrounding bone of the central incisor pair, as well as that of the larger lateral incisors, were entirely broken away before Schlosser studied the find, and the two mandibular bodies and the central incisors were then simply glued together. This missing bone also led to an unnatural distortion of the relationships of the horizontal rami of the mandible, for when glued together with this wedge missing they diverge at a much higher angle than would have been the actual case in life. All known Oligocene and Miocene monkeys and apes do have posteriorly divergent horizontal rami, but in this case the divergence is exaggerated. It thus (incorrectly) resembles the high angle of posterior divergence seen in *Tarsius*. It was this mistaken resemblance in mandibular construction to that of *Tarsius*, together with the incorrect determination of dental formula that impeded understanding of the phyletic relationship of *Parapithecus*.

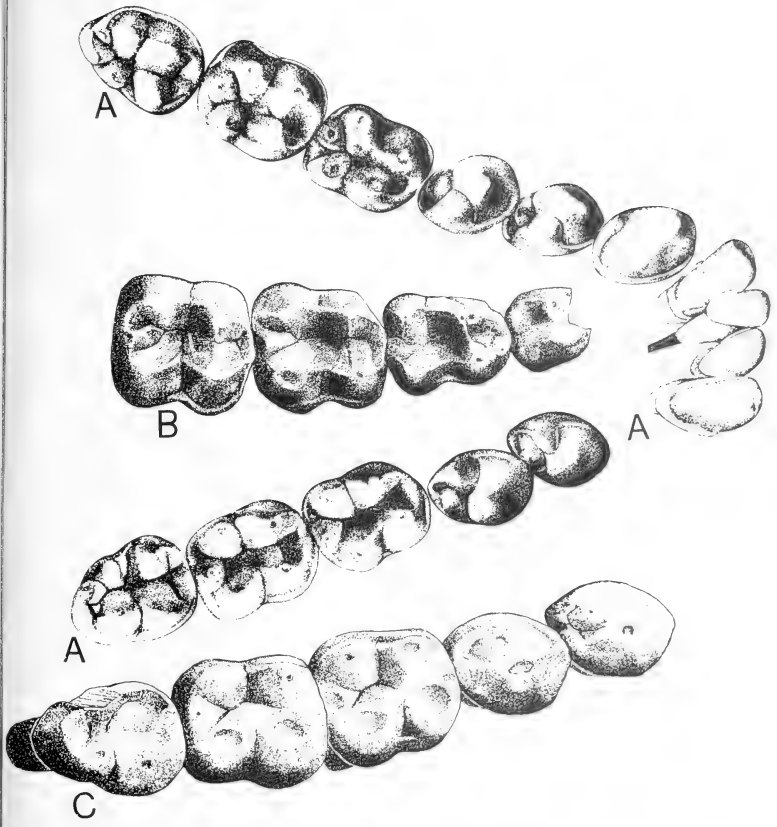

FIG. 2. Comparison of *Parapithecus fraasi*, type (*A*) with adult *Parapithecus grangeri* (*C*) and a juvenile specimen of the latter (*B*). Scale approximately × 4.9 for both. (*A*) SMN 12639a, type of *P. fraasi*, lower dentition lacking lateral incisors and right P_2. Scale approximately × 4.9. *A* is taken from Kälin, 1961. (*B*) YPM 23796, juvenile *P. grangeri* right lower dP_{3-4}, and M_{1-2}. Scale approximately × 4.9. (*C*) YPM 23954, *P. grangeri* right lower P_3-M_3. Scale approximately × 4.9.

The animal, for these two mistaken reasons, seemed to have affinities with the tarsioids.

After description of *Parapithecus* in 1911, stereophotographs of the occlusal views of teeth in the type and only specimen of *P. fraasi* were distributed. From these crown views it was apparently not possible to see the great disparity in height between the tall tooth Schlosser took to be the canine and that immediately following it. In 1915 Schwalbe incorrectly concluded, after examining only a cast, that the dental formula was 2.1.2.3. below, as in Old World monkeys and apes. Later Gregory (1922) who was also working from photographs and casts announced in no uncertain terms that Schwalbe's interpretation of the dental formula *had to be* correct. But Gregory was wrong, and he even went further to state the incorrect conclusion that *Parapithecus* ". . . . may well be regarded as standing in or quite near to the line of ascent leading to the anthropoid apes and eventually to man." He also considered *Parapithecus* more tarsier-like than *Propliopithecus*, and concluded that the latter stood "in or near the base of the gibbon line." Although Gregory thus implied strongly that *Parapithecus* should be considered a stage typifying the earliest Hominoidea, he noted the overall similarity in the premolars and molars that exists between *Parapithecus* and *Apidium*. He further discussed the similarity between *Apidium* and *Oreopithecus* which was subsequently dealt with in detail by Simons (1960), and concluded that *Apidium* conformed well with what should be expected for an early Oligocene stage in the evolution of the cercopithecoid monkeys. This was apparently the only early recognition of *Apidium* as related to cercopithecoid monkeys. Remane (1921), writing about the same time as Gregory, suggested that because of the nearly complete reduction of the paraconid crest in *Parapithecus* that it might be a primitive representative of the Hylobatidae, but reasoned that because the paraconid crest (still present in the dryopithecines) had already been eliminated, *Parapithecus* should be excluded from the ancestry of Pongidae. Much more recently Kälin (1961) published a full study of *Parapithecus fraasi* which appeared only a scant two years before the flow of new material from the Fayum represented by the many Yale expedition primate finds. Kälin also objected to Schlosser's early interpretation of the dental formula, which had been correct, save for the incisor count. Moreover, he too concluded that the crack in the symphyseal region of the type specimen constituted evidence that the animal possessed an open symphysis. Therefore Kälin was just as puzzled about the relationships of *Parapithecus* as most authors who had written of it previously had been. He reasoned that one could not derive *Propliopithecus* from a *Parapithecus* stage as Gregory had implied. In any case such a derivation would be highly suspect because species of the two genera are contemporaries. Kälin decided that *Parapithecus* was a primate transitional between Higher and Lower Primates: in this, he echoed Schlosser who had based his conclusion on a mistake. In addition Kälin concluded that the form represented such a distinctive group that it should be made the basis of a new superfamily Parapithecoidea.

With the discovery of dozens of new specimens of both *Parapithecus* and *Apidium* in the Fayum it became clear that the correct dental formula for both genera is $\frac{2.1.3.3.}{2.1.3.3.}$, that both these parapithecids had fused symphyses and comparatively small canines, but, unlike the similar-sized marmosets, had the articular condyle of the mandible situated relatively higher above the level of the tooth row. In a series of papers (Simons, 1967, 1969, 1971) I have pointed out the extraordinary likeness to be found between the molar morphology of the modern African swamp monkey, *Miopithecus talapoin*, and that of *Parapithecus*. In *Parapithecus* the lower molar cusps are already arranged in a quadrate pattern as in Old World Monkeys. Moreover, in *Parapithecus* the paraconid is missing and the hypoconulid is too reduced to be significant functionally. The much-reduced hypoconulid of *Parapithecus* is situated in exactly the position where the talapoin possesses a flattened area or shelf, presumably representative of the formerly present hypoconulid. Like monkeys, the unworn molars of *Parapithecus* are more high-crowned than is the case for the contemporary Fayum dryopithecines, and the upper molars are much more quadrate in arrangement of the principal cusps than is the case in *Apidium* or the Fayum apes. It would not be difficult to convert the upper molar of *Parapithecus* into that seen in the modern cercopithecoids. In this connection I should point out my disagreement with the argument of Von Koenigswald (1969) that the crown morphology of the teeth of *Apidium* is not relevant to consideration of the origin of the cercopithecoid dentition.

The modern cercopithecoid monkeys are very frequently cited as having (among Primates) remarkably uniform tooth structure, and they possess a standard dental formula as well: $\frac{2.1.2.3.}{2.1.2.3.}$. Any student of mammalian paleontology will be aware that many families of Mammalia include much greater diversity of dental shapes and dental formulae than do the modern Old World monkeys, particularly when a group is known with "time-depth" as is the case here. This point was well-discussed long ago by Gregory (1920). Moreover, most mammalian families that have an adequate fossil record can be traced back to Eocene times when they include species much more primitive than are any extant members of such families. Therefore, neither the generalized features of some of the parapithecine postcranial bones, nor the possession of $P\frac{2}{2}$ seem adequate to me to justify retention any longer of Kälin's superfamily, Parapithecoidea, for these African Oligocene primates. Most important is the recent study of Conroy (1974) on parapithecid postcranial bones. This shows through morphological and multivariate analysis that such postcranials as can be confidently assigned to the Parapithecidae are all (in their morphometrics) close to those of various monkeys. In the same fashion Conroy, Schwartz and Simons (1974) have shown that the dental eruption sequence in *Apidium*, which appears to be the same in *Parapithecus*, is like monkeys and apes, not like prosimians. For all these reasons there can no longer be any doubt that

Parapithecidae are monkeys, not prosimians: zoogeographic considerations ally them with cercopithecoids—not ceboids.

What one looks for in determining the relatedness of ancestors and descendants among fossil mammals is the first emergence of the distinctive or "specialized" features that later become more exaggerated, or sometimes, uniformly typical of the descendant group. Paleontologists will be familiar with a whole series of papers in which the earliest emergent characters of a higher category (superfamily, suborder or order) are discerned, for instance, Schaeffer (1947) and Radinsky (1969). In making such a placement of *Parapithecus* close to Old World Monkeys as is advocated here it should not be forgotten that, even if it should prove to be near the ancestry of modern African monkeys, species of this genus, *Parapithecus*, are dated at around 28 to 30 million years old. Having existed so long ago, *Parapithecus* could reasonably be expected to have possessed primitive features that are no longer found in Old World Monkeys. These should not disqualify it from superfamilial association with them, any more than do such features in the basal members of any other group of mammals that evolved during the last two-thirds of the Tertiary. Thus parapithecids can correctly be termed: primitive *monkeys*.

In sum, the loss of the paraconid crest in lower molars of *Parapithecus* can be taken as a resemblance to monkeys rather than gibbons, and reinforces the other evidence of marked similarity in molar morphology between *Parapithecus*, *Cercopithecus*, and *Miopithecus*. Research that I have reported elsewhere (Simons, 1967) shows that *Apidium* is generically distinct from *Parapithecus* but both have almost identical morphology of the anterior teeth and should therefore be placed in the same subfamily. The recent Yale expeditions to the Fayum badlands of Egypt under the direction of the author and of G. E. Meyer have provided more information as to the craniology of *Apidium* than is the case for *Parapithecus*, but it seems highly probable that the two resemble each other in major structural details. Both had fused mandibular symphyses, and in *Apidium* the metopic suture is fused in early life and postorbital plates develop. Therefore, there seems to be no doubt that these animals had reached at least the grade of organization of the New World Monkeys if not higher. Both had much more foreshortened faces than did their dryopithecine contemporary *Aegyptopithecus*, and probably both differed from it slightly in the shape and position of the tympanic. Both should be placed in the same family, Parapithecidae. Their ranking among the Cercopithecoidea need in no way imply that the parapithecids would or could have been directly ancestral to any surviving Old World Monkey group but does leave open the possibility that *Parapithecus* may well prove to have been such an ancestor. This arrangement, rather than classifying these genera in a separate superfamily, makes the best sense in the state of present evidence.

Working on the assumption that *Parapithecus* is close to the ancestry of the cercopithecoids, two heretofore little recognized facts emerge. These

are firstly, that loss of the second premolars among the ancestors of the cercopithecoid monkeys occurred independently from and later than the similar reduction already found in the earliest apes (*Oligopithecus*, *Propliopithecus*, *Aegyptopithecus*, and *Aeolopithecus*). Secondly, the small heels of M_3 in *Parapithecus* resembling as they do those of *Miopithecus* and *Cercopithecus*, strongly indicate the probability that, among Cercopithecoidea, enlarged M_3 heels are a later, or more specialized, development. The cases of independent development of large M_3 heels among various separate lines of herbivorous mammals are too numerous to require detailed tabulation, but they certainly show that various cercopithecoid lineages could have separately developed such talonid enlargement at some time subsequent to the Oligocene.

Summary

A new species of *Parapithecus*, *P. grangeri*, is described. The parapithecines are the most common mammals of the Fayum Oligocene. They probably did not become extinct thereafter. Their cheek tooth morphology and indeed the morphology of the whole mandible is extraordinarily like that of the smallest African monkey, the swamp monkey. Not many known or strikingly different features separate parapithecids and cercopithecids.

To some, *Parapithecus*, as described here, may still seem so clearly set off from modern monkeys as to require placement outside Cercopithecoidea. The degree of separateness, however, is exaggerated by a lack of intermediate forms resulting from the very poor paleontological knowledge that we have of Miocene, Pliocene, and early Pleistocene monkeys in Eurasia and Africa. Were intermediate forms better known it would be possible to be much more definite than anyone can now be as to the times and nature of the development of the narrowly limited dental and locomotor systems of the Old World Monkeys. [See Schultz (1970)].

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STYLE Authors of biological papers should follow the CBE *Style Manual* Third Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey*, Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

NOMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

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REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

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