INTRODUCTION

During the later portions of Tertiary times northern India was a great center for the adaptive radiation of the Giraffidae. In the Siwalik deposits of Upper Miocene, Pliocene, and Pleistocene age there is a considerable assemblage of fossil giraffes of varied form, and a study of these Siwalik giraffes throws a great deal of light on the problem of the evolution and the classification of the Giraffidae. A recent review of the fossil giraffes in the Siwalik collection of The American Museum of Natural History has suggested to the present author certain considerations regarding the classification and the phylogeny of the Giraffidae. Some of the questions having to do with the evolution and the classification of this family of artiodactyls will be discussed below.

PREVIOUS CLASSIFICATIONS OF THE GIRAFFIDAE

Some of the more important classification schemes for the Giraffidae are those of Murie (1871), Rütimeyer (1881), Lydekker (1882), von Zittel (revised edition, 1925), Pilgrim (1911), Abel (1919), Bohlin (1927), and Matthew (1929).

MURIE, 1871

In 1871 Dr. James Murie published a paper in the Geological Magazine entitled, 'On the Systematic Position of the Sivatherium giganteum of Falconer and Cautley,' in which he discussed the relationships of Sivatherium to Bramatherium and to other artiodactyls. Basing his conclusions on the development of the horn cores, Murie was led to believe that Sivatherium and Bramatherium are closely related to the Antilocapridae and to the saiga antelope. He stipulated that the connections between Sivatherium and the modern giraffe are of minor importance. Although Murie did not outline a classification for the fossil Giraffidae, he did present a sort of phylogenetic diagram in which he showed Sivatherium as being directly related to Bramatherium, to the saiga and to the
pronghorn antelope. He interposed the Antilocapridae and the Cervidae between *Sivatherium* and *Giraffa*.

**Rütimeyer, 1881**

Rütimeyer, in his ‘Natürliche Geschichte der Hirsche,’ published in 1881, failed to realize the relationships existing between the large Siwalik giraffes and the modern giraffe. He placed *Giraffa* among the Cervidae, as closely related to the elk. *Helladootherium* from Pikermi was considered as being related to the giraffe, and consequently it was placed with the giraffe among the deer. *Sivatherium*, *Bramatherium*, and *Vishnutherium* from the Siwaliks were assigned to a position among the antelopes, contiguous to the *Damilis* group of South Africa.

**Lydekker, 1882**

It remained for Lydekker to show, in his large monograph on the Siwalik Camelopardalidae published in 1882, that the Siwalik genera, *Sivatherium*, *Hydaspitherium*, *Bramatherium*, etc., are true giraffes, directly related to the modern *Giraffa* and to such fossil forms as *Helladootherium* from Pikermi. Lydekker's realization that these several fossil forms are true giraffes, and that they should be combined with the modern giraffe in one family, is a distinct advance over the views of previous authors.

Lydekker did not divide the Camelopardalidae, as he called it, into lesser groups or subfamilies, but he did arrange the seven genera which he considered as constituting the family in a certain "order of their relationship to one another, indicating a gradual diminution in the length of the limbs and of the neck from the giraffe to the sivathere." Lydekker's arrangement was as follows.

\[
\begin{align*}
\text{Camelopardalis} &= \text{Giraffa} \\
\text{Orasius} \\
\text{Vishnutherium} \\
\text{Helladootherium} \\
\text{Hydaspitherium} \\
\text{Bramatherium} \\
\text{Sivatherium}
\end{align*}
\]

This arrangement is valid in that it indicates the relationships of *Orasius* to *Giraffa* and it groups the large giraffids together. Lydekker considered the Camelopardalidae as most closely related to the Cervidae.

**Von Zittel (revised edition, 1925)**

The English translation of von Zittel's 'Textbook of Palaeontology,' published in 1925, includes the Giraffinae and the Sivatheriinae as two
separate subfamilies among the family Cervicornia. The arrangement is as follows.

Family Cervicornia
   Subfamily 1.—Moschinae
   2.—Cervulinae
   3.—Cervinae
   4.—Protoceratinae
   5.—Giraffinae
   6.—Sivatheriinae

According to this classification the genera constituting the two subfamilies are as follows.

Giraffinae
   Helladotherium
   Palaeotragus
   Samotherium
   Camelopardalis

Sivatheriinae
   Sivatherium
   Bramatherium
   Hydaspitherium

PILGRIM, 1911

In 1911, Dr. Pilgrim published a memoir entitled ‘The Fossil Giraffidae of India.’ Although this work was directly concerned only with the Siwalik giraffes, it contained a supplementary consideration of the evolution of the Giraffidae. On page 29 of the publication under consideration there is a phylogenetic diagram of the Giraffidae which classifies the family in the following manner.

Giraffidae

<table>
<thead>
<tr>
<th>Palaeotraginae</th>
<th>Progiraffinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palaeotragus</td>
<td>Progiráffa</td>
</tr>
<tr>
<td>Samotherium</td>
<td>Giraffinae</td>
</tr>
<tr>
<td>Alcicepalus</td>
<td>Giraffa</td>
</tr>
<tr>
<td>Okapia</td>
<td>Orasius</td>
</tr>
<tr>
<td>Indratherium</td>
<td>Sivatherinae</td>
</tr>
<tr>
<td>Libytherium</td>
<td>Hydaspitherium</td>
</tr>
<tr>
<td>Helladotheriinae</td>
<td>Helladotherium</td>
</tr>
<tr>
<td>Vishnutherium</td>
<td>Bramatherium</td>
</tr>
<tr>
<td>Giraffokeryx</td>
<td>Urmiatherium (placed here rather than in the Bovidae)</td>
</tr>
</tbody>
</table>
This classification is marked by the multiplication of subfamilies, of which one, the Progiraffinae, is founded on rather scanty material; and another, the Helladotheriinae, consists of genera that might very well be placed within two different but well-established groups, the Palaeotraginae and the Sivatheriinae. This will be discussed more fully below.

ABEL, 1919

Abel’s classification of the Giraffidae, published in 1919 in his ‘Stämme der Wirbeltiere,’ is essentially the same as that of von Zittel. He divides the family into two subfamilies, the Giraffinae and the Sivatheriinae.

BOHLIN, 1927

In 1927 Birger Bohlin published an elaborate monograph, ‘Die Familie Giraffidae,’ a very thorough study of the giraffes, with the fossil material collected by the Swedish expeditions in North China serving as its basis. His classification of the family is given below.

**Giraffidae**

**Palaeotraginae**
- Palaeotragus
- Giraffokeryx
- Achtiaria
- Samotherium
- Alcicephalus
- Chersonotherium
- Shanshitherium

**Giraffinae**
- Giraffa
- Honanotherium
- Orasius

**Okapiinae**
- Okapia

**Sivatheriinae**
- Sivatherium
- Indratherium
- Bramatherium
- Hydaspitherium
- Helladotherium
- Griquatherium
- Vishnutherium
- Libytherium

[Progiraffinae]
[Progiraffa]

Bohlin’s classification is the most comprehensive and perhaps the best of all the proposed schemes of giraffid taxonomy. His creation of a separate subfamily for the okapi may be disputed; a discussion of this question will be offered below.

MATTHEW, 1929

Dr. Matthew, in his ‘Critical Observations upon Siwalik Mammals,’ pointed out the desirability of including *Okapia* among the Palaeotraginae, thereby making three subfamilies of the Giraffidae instead of four
(exclusive of the "Progiraffinae"). Matthew's classification is given below.

**Giraffidae**

<table>
<thead>
<tr>
<th>Palaeotraginae</th>
<th>Giraffinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palaeotragus</td>
<td>Giraffa</td>
</tr>
<tr>
<td>Samotherium</td>
<td>Orasius</td>
</tr>
<tr>
<td>Giraffokeryx</td>
<td>Honanotherium</td>
</tr>
<tr>
<td>Okapia</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sivatheriinae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sivatherium + Indratherium</td>
</tr>
<tr>
<td>Helladotherium + Bramatherium</td>
</tr>
<tr>
<td>Hydaspitherium</td>
</tr>
</tbody>
</table>

**The Relationships of Okapia**

A careful consideration of the problem of a classification of the Giraffidae will demonstrate the validity of Dr. Matthew's views as to the inclusion of Okapia in the Palaeotraginae. Bohlin's separation of the okapi into a distinct subfamily is seemingly a flaw in his otherwise admirable classification of this group of artiodactyls. It would seem as if he has placed too much emphasis on minute, and for the most part unimportant characters, and in doing this he has disregarded the great preponderance of characters that typify Okapia as a truly primitive palaeotragine. Okapia is, in all of its essential characters, a structurally primitive Miocene giraffe (more primitive than Palaeotragus or Samotherium) that has persisted on to the present day in a region conducive to the continuation of such an early form.

Bohlin has separated the okapi from the Palaeotraginae because:

1. —The frontals are narrow in the modern form, as compared to the fossil species.
2. —The horns are placed in a slightly different position in Okapia from the positions of the horns in Palaeotragus or Samotherium.
3. —The frontals in the okapi tend to develop pneumatic sinuses within them, whereas the sinuses are not pronounced in Palaeotragus and related genera.
4. —There are minor differences in the dentition; there is no outer cingulum on DM² in the okapi, whereas in Palaeotragus and Samotherium this cingulum is present.
5. —The skeleton of the okapi differs in small details, especially those of proportions, from the skeleton of Palaeotragus.
These are differences of minor importance. Now let us look at Okapia and the fossil Palaeotraginae for the purpose of making comparisons between major anatomical characters.

The skull of Okapia is in most respects more primitive than the skull of the fossil Palaeotraginae. The canine-premolar diastema of the mandible is much shorter in the okapi than it is in the fossil forms, showing that the modern species has retained a short muzzle, a primitive and a diagnostic heritage character. In the okapi the frontals are narrow, which is to be expected in a relatively primitive artiodactyl. In Palaeotragus the frontals are wide, and this may be considered as an habitus character, subsequent to the narrow frontal region. An examination of various groups of ungulates will show that the skull tends to elongate first, after which it widens, if the tendency to widen exists at all. That is, elongation precedes lateral expansion. Consequently we may expect a primitive giraffid, such as the okapi, to have a narrower frontal region than a more advanced form in which the cranium has broadened out.

Of course, as Bohlin has shown, the frontals of the okapi contain rather large sinus cavities, which are lacking in Palaeotragus and Samotherium. It may be quite probable that the development of the frontal sinuses in the okapi are of a secondary nature, and that they have been acquired more or less independently in the long period of time that has elapsed between the Miocene and the present day. But this is no reason for excluding the okapi from a place as a relatively primitive palaeotragine. It is a primitive genus that has developed certain specialized characters during the passage of geologic time.

In Okapia the horn cores are rather small, whereas in Palaeotrabus they are much larger. Thus we may regard the okapi as more primitive in its horn development than is Palaeotrabus. Of course, one might argue that the small horns in the okapi are degenerate structures, secondarily reduced from larger horns, but in answer to this argument it might be said that the horn cores in the okapi have retained a primitive position over the orbit, and this would favor their being truly primitive structures. This primitive position of the horn cores is retained in Palaeotrabus, but in Samotherium the horn cores have shifted somewhat to the rear, due to the elongation of the skull.

In Okapia the dentition is very brachydont—a primitive character. In Palaeotragus and Samotherium the teeth are considerably higher than is the case in the modern genus, showing that the fossil forms are relatively advanced in the stage of their phylogenetic development.
The skeleton of the okapi is certainly primitive. It shows little of the elongation of the limbs, or of transverse growth of the skull and skeletal elements that appear in the more advanced Giraffidae.

Therefore, considering Okapia with regard to its major anatomical characters, without special emphasis on small, single features, we see that it is a very primitive giraffid, more primitive even than Palaeotragus, and that it is a satisfactory structural ancestor for the Palaeotraginae. It has the diagnostic heritage characters of the Palaeotraginae, but in this persistent genus very few of the advanced habitus characters that characterize the fossil genera have been developed.

The Relationships of Giraffokeryx; Other Problems

The genus Giraffokeryx was created by Pilgrim in 1910, on the basis of upper and lower cheek teeth. In 1911, this author, in his monograph of the Siwalik Giraffidae, placed Giraffokeryx along with Helladotherium and Vishnutherium in a separate subfamily, the Helladotheriinae. Bohlin, in 1927, went to the other extreme and reduced the genus Giraffokeryx to synonymy with Palaeotragus, including it, naturally, in the subfamily Palaeotraginae. Both of these authors were founding their conclusions on the evidence of teeth alone.

An almost complete skull of Giraffokeryx in the American Museum gives much evidence that helps to solve the question of the taxonomic position of the genus. This skull has recently been described by Colbert (1933), and it is shown to be essentially a Palaeotragus-type with an extra pair of horn cores on the frontals. Therefore the genus Giraffokeryx properly belongs in the subfamily Palaeotraginae, where it was placed by Bohlin and later by Matthew. It is, however, a separate genus, quite distinct from Palaeotragus, but closely related to it.

Bohlin and Matthew have both given conclusive evidence to show that the genera Hellodotherium and Vishnutherium should be included in one subfamily with Sivatherium, Hydaspitherium, Bramatherium, etc. Consequently Pilgrim's subfamily Helladotheriinae would seem to be unnecessary.

The subfamily Progiraffinae, created by Pilgrim in 1911, is based on rather insufficient material. The genus Progiraffa (Propalaeomeryx) may be perfectly valid, and it may deserve separation from the other Giraffidae as a distinct subfamily, but at the present time the material is not plentiful enough to prove this. Until further material is discovered it would seem best to include this genus tentatively among the Palaeotraginae.
The reader is referred to Matthew’s ‘Critical Observations upon Siwalik Mammals,’ published in 1929, for illuminating notes and discussions concerning the Siwalik Giraffidae.

With the foregoing discussion in mind we may now attempt a new classification scheme for the Giraffidae.

Classification of the Giraffidae

Giraffidae

Large, ruminating artiodactyls, with heavy, rugose cheek teeth. The skull may or may not have horn cores, but if they are present they show a great variety of development. Bones of cranial roof pneumatic. Lateral metapodials and digits atrophied.

Palaeotraginae

Primitive, medium sized giraffids, having as a rule one pair of supra-orbital frontal horn cores. There may be a second pair of horn cores at the anterior extremities of the frontals. Horn cores in the form of simple tines, well developed in the males, feebly developed or absent in the females. Skull usually elongated.

Cheek teeth brachyodont, with moderately coarse sculpture of the enamel. Limbs and neck slightly elongated.

Palaeotragus Gaudry, 1861

*Palaeotragus rouenii* Gaudry—Generic type. Pontian, Lower Pliocene; Pikermi, Samos.

*Palaeotragus parvus* (Weithofer). Synonym of *P. rouenii*.

*Palaeotragus vetustus* (Wagner). Synonym of *P. rouenii*.

*Palaeotragus microdon* (Koken). Pontian, Lower Pliocene; China.

*Palaeotragus coelophrys* (Rodler and Weithofer). Pontian, Lower Pliocene; Maragha, China.

*Palaeotragus decipiens* Bohlin. Pontian, Lower Pliocene; China.

*Palaeotragus quadricornis* Bohlin. Pontian, Lower Pliocene; Samos, Maragha, China.

*Palaeotragus expectans* (Borissiak). Sarmatian, Upper Miocene; Sebastopol.

Achtiaria Borissiak, 1914

Synonym of *Palaeotragus*

*Achtiaria expectans* (Borissiak)—Generic type.

Giraffokeryx Pilgrim, 1910

*Giraffokeryx punjabiensis* Pilgrim—Generic type. Lower and Middle Siwaliks, Lower Pliocene; India.
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**Okapia** Lankester, 1901

*Okapia johnstoni* (Sclater)—Generic type. Recent; Africa.

**Samotherium** Forsyth Major, 1888

*Samotherium boisseri* Forsyth Major—Generic type. Pontian, Lower Pliocene; Samos.

*Samotherium neumeyeri* (Rodler and Weithofer). Pontian, Lower Pliocene; Maragha, China.

*Samotherium sinense* (Schlosser). Pontian, Lower Pliocene; China.

*Samotherium tafeli* (Killgus). Lower Pliocene; China.

*Samotherium eminens* (Alexejew). Lower Pliocene; Odessa.

**Alcicephalus** Rodler and Weithofer, 1890

Synonym of *Samotherium*

*Alcicephalus neumeyeri* Rodler and Weithofer—Generic type.

**Chersonotherium** Alexejew, 1916

Synonym of *Samotherium*

*Chersonotherium eminens* Alexejew—Generic type.

**Shanshitherium** Killgus, 1922

Synonym of *Samotherium*

*Shanshitherium tafeli* Killgus.—Generic type.

Provisionally Placed in the Palaeotraginae

**Propalaeomeryx** Lydekker, 1883

*Propalaeomeryx sivalensis* Lydekker—Generic type. Lower Siwaliks (?), Lower Pliocene; India.

**Progiraffa** Pilgrim, 1908

*Progiraffa exigua* Pilgrim—Generic type. Bugti beds, Lower Miocene; Sind.

**Giraffinae**

Large giraffids with a moderately brachycephalic skull. Horns variously developed, being located on the parietals and the frontals. In *Giraffa* a single median horn is also present, located on the nasals. Horn cores rounded or flattened on the ends, and covered with hair. Skull roof with highly developed sinus cavities.

Cheek teeth brachydont, with heavily rugose enamel. Limbs and neck greatly elongated.

**Giraffa** Brisson, 1756

*Giraffa camelopardalis* (Linnaeus)—Generic type. Recent; Africa.

*Giraffa sivalensis* (Falconer and Cautley). Upper Siwaliks, Pleistocene; India.

*Giraffa affinis* (Falconer and Cautley). Synonym of *G. sivalensis*. 
Giraffa punjabiensis Pilgrim. Middle Siwaliks, Pliocene; India.
Giraffa priscilla Matthew. Lower Siwaliks, Lower Pliocene; India.
Giraffa nebrascensis Matthew and Barbour. Pleistocene; Nebraska. (This genus?)

**Orasius** Oken, 1816

Orasius atticus (Gaudry and Lartet). Pontian, Lower Pliocene; Pikermi.
Orasius eximius Wagner. Synonym of O. atticus.
Orasius speciosus (Wagner). Synonym of O. atticus.

(The reader should refer to Matthew, 1929, p. 546, for a discussion of this genus. The name "Orasius" is used here only in a provisional way.)

**Honanotherium** Bohlin, 1927

Honanotherium schlosseri (Pilgrim)—Generic type. Pliocene; China.

**Sivatheriinae**

Gigantic giraffids, with large, heavy brachycephalic skulls. Horn cores variously developed, being of frontal and parietal origin. Skull roof with large sinus cavities.
Cheek teeth moderately hypsodont, with heavily rugose enamel. Limbs not elongated but very heavy. Body heavy.

**Sivatherium** Falconer and Cautley, 1835

Sivatherium giganteum Falconer and Cautley—Generic type. Upper Siwaliks, Pleistocene; India.

**Indratherium** Pilgrim, 1910

Synonym of Sivatherium

Indratherium majori Pilgrim—Generic type. Upper Siwaliks, Pleistocene; India.

**Bramatherium** Falconer, 1845

Bramatherium perimense Falconer— Generic type. Middle Siwaliks, Pliocene; Perim Island.

**Hydaspitherium** Lydekker, 1878

Hydaspitherium megacephalum Lydekker—Generic type. Middle Siwaliks, Pliocene; India.

Hydaspitherium grande Lydekker. Middle Siwaliks, Pliocene; India.

Hydaspitherium magnum Pilgrim. Middle Siwaliks, Pliocene; India.

Hydaspitherium birmanicum Pilgrim. Irrawaddy beds, Pliocene; Burma.

**Vishnutherium** Lydekker, 1876

Vishnutherium iravaticum Lydekker—Generic type. Irrawaddy beds, Pliocene; Burma.
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HELLADOTHERIUM Gaudry, 1860

*Helladotherium duvernoyi* Gaudry—Generic type. Pontian, Lower Pliocene; Pikermi, Samos.

*Helladotherium gaudryi* de Mecquenem. Pontian, Lower Pliocene; Maragha.

GRIQUATHERIUM Haughton, 1922

*Griquatherium cingulatum* Haughton—Generic type. Pleistocene; South Africa.

Of Uncertain Position

LIBYHERIUM Pomel, 1893


RELATIONSHIPS OF THE GIRAFFIDAE TO THE PROTOCERATIDAE

The Protocerotidae of North America have been linked to the Giraffidae by some authors, on the basis of certain resemblances between the members of the two groups. Schlosser, especially, would derive the Giraffidae directly from the Protoceratidae. Both Bohlin and Matthew have shown, however, that the resemblances between the Protoceratidae and the Giraffidae are due to convergence, and that these two families are really separated from each other by differences of basic importance.

There are certain resemblances in the teeth between the Protoceratidae and the more primitive Giraffidae, resemblances that may be attributed to primitive heritage characters carried over from a common Eocene ancestor. The skull resemblances, especially in the development of numerous pairs of horn cores in several genera of these two families, are due entirely to a convergence in evolutionary trends. Both the Protoceratidae and the Giraffidae produced horn cores anterior to and posterior to the orbits. But these horn cores are derived from different skull elements in the two groups. This is well illustrated by the anterior horn cores, which are of premaxillary origin in the Protoceratidae, and of frontal origin in the Giraffidae.

Dr. Matthew\(^1\) made the following remarks with regard to the origin of the Giraffidae and the relation of this family to the North American Protoceratidae.

"The family appears to be a group of specialized survivals of the Middle Miocene Palaeomerycinae, of which *Dromomeryx*, the American genus, is the only one known from complete skulls and associated skeletons. The horns of *Dromomeryx* are of giraffoid type, long, straight, probably skin-covered, nondeciduous, supra-orbital, and with a basal

---

wing that suggests the later complications in the sivatheriines. Teeth quite close to *Palaeotragus* and *Giraffokeryx*.

"Schlosser would derive giraffes from Protoceratinae, but this does not seem to be a tenable phylogeny. The protoceratines are an early specialized group of Traguloidea, with no approach to the Pecora in foot characters. The Giraffidae are true Pecora, fully developed as such in the feet, and nearly related through Palaeomerycinae to the primitive Cervidae (cf. *Eumeryx* of the Stampian Oligocene of Mongolia)."

**Phylogeny of the Giraffidae**

In the accompanying chart (Fig. 1), an attempt has been made to represent the phylogeny of the Giraffidae in a graphic form. On this chart the geologic distribution of the family is represented along the vertical axis, whereas the geographical extent is shown along the horizontal axis. The three subfamilies of the Giraffidae are shown by parallel shading; the Palaeotraginae being represented by vertical lines, the Giraffinae by oblique lines and the Sivatheriinae by horizontal lines. The primitive Palaeomerycidae, from which the Giraffidae might have been derived, are shown also. Certain genera, such as *Propalaeomeryx*, *Griquatherium*, etc. are omitted from this chart.

It will be seen that the Giraffidae is a family of Miocene derivation, having its origin in the Holarctic region. It is characterized by the rapidity of evolution of its subfamilies and genera; all of the great variety of giraffid form and structure having been established since late Miocene times.

The evolutionary development of the group took place in Europe and Asia. The okapi and the giraffe, the one a persistent primitive genus and the other a genus that specialized early in the evolutionary history of the group, migrated to Africa from the Holarctic center of origin. The survival of these two forms in Africa, far from the center of origin of the family, is what might be expected. Matthew has shown, in his 'Climate and Evolution,' that persistent primitive species migrate away from the center of origin and their place is taken by more specialized forms. Or, to put it in a different way, the primitive and inadaptive species are pushed out by the specialized, adaptive species, so they must needs find refuge in peripheral regions, far distant from their place of origin.

With regard to the rapidity of evolution among the Giraffidae and the center of ultimate origin for the group, I take the liberty once more of quoting from Dr. Matthew.¹

Fig. 1. The Phylogeny of the Giraffidae. The stratigraphic occurrences of the genera are represented by their vertical arrangement, and their geographic distribution is shown by their horizontal arrangement. Lines of shading represent taxonomic divisions, as follows.

**Giraffidae**
- Palaeotraginae
- Sivatheriinae
- Giraffinae

**Palaeomerycidae**
- vertical lines
- horizontal lines
- oblique lines
"I do not in fact think that the Giraffidae are an old family, or that any of them are very wide apart in spite of the diversity of skull structure. The lack of diversity in tooth structure is, to my mind, not due so much to the lack of change in the teeth as to the rapidity of change in the skull, and the whole family derives from late Miocene palaeomerycines, an antiquity decidedly less than most mammalian families."

"All in all, I cannot see anything more primitive in the Chinji Giraffidae than Pikermi can show, and I see no reason for hunting a separate evolution center for the giraffes in Africa when the Holarctic Miocene palaeomerycines afford a perfectly good ancestral group."

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