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Review Article

Siwalik Giraffidae (Mammalia, Artiodactyla): A review

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Abstract

The article is based on the published literature regarding the family Giraffidae, particularly about the extinct Siwalik species. The provided information is collected from the previous published articles, aiming to produce the basic information of the Siwalik giraffids. The distribution of the Siwalik giraffid species is also briefly discussed.

Key words: Mammalia, Vertebrate, Giraffidae, Miocene, Siwaliks.

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INTRODUCTION

Pecora (horned ruminants) and Tragulina-Pecora are well-adapted ruminants. Fossils are recorded in Eurasia, North America and Africa during Neogene but the remains are rare during Eocene. Cervoids and giraffoids could have had predominantly vicariant origins within the pecora, giraffoids within Africa, Arabia and/or India and cervoids further north in Eurasia. Undoubted cervids then appeared from among cervoids in the early Miocene of Europe and East (Khan *et al*., 2006).

During the later portions of Tertiary times northern India was a great center for the adaptive radiation of 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 put great information on the problem of the evolution and the classification of Giraffidae (Colbert, 1935).

Some of the important classification schemes for Giraffidae are made by Murie (1871), Lydekker (1882), Von Zittel (1925), Pilgrim (1911), Bohlin (1927) and Matthew (1929). In 1871,James Murie published a paper in the Geological Magazine entitled, “On the Systematic Position of *Sivatherium giganteum* of Falconer and Cautley, in which he discussed the relationship of *Sivatherium* to *Bramatherium* and to other artiodactyls. Murie was led to believe that *Sivatherium* and *Bramatherium* are closely related to the Antilocapridae and to the Saiga antelope based on the development of the horn cores. 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 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 Antilocapridae and Cervidae between *Sivatherium* and *Giraffa* (Colbert, 1935).

Rutimeyer, in his ‘Nattirliche 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 Cervina, as closely related to elk. *Helladotherium* from Pikermi was considered as being related to 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 (Colbert, 1935). 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 and they directly related to the modern *Giraffa* and to such fossil forms as *Helladotherium* from Pikermi. Lydekker's realization that these several fossil forms are true giraffes, and that

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they should be combined with the modern giraffes 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 (Colbert, 1935).

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. In 1911, Dr. Pilgrim published a memoir entitled 'The Fossil Giraffidae of India.' Although this work was based on with the Siwalik giraffes, it contained a supplementary consideration of the evolution of the Giraffidae. There is a phylogenetic diagram of the Giraffidae which classifies the family in the following manner (Colbert, 1935). The Giraffidae shows in phylogenetic relationship that it has the following members of the family Palaeotraginae*, Palaeotragus, Samotherium, Alcicephalus, Okapia, Indratherium,* and *Libytherium* in a sequential way (Colbert, 1935).

The Giraffidae's classification is marked by the multiplication of subfamilies, of which one, Progiraffinae, is founded on rather scanty material, and another, Helladotheriinae, consists of genera that might very well be placed within two different but well-established groups, Palaeotraginae and Sivatheriinae. The family Helladotheriinae is classified at that time that includes the following genera *Helladotherium, Vishnutheriu,* and *Giraffokeryx.* Progiraffinae includes only the genus *Progiraffa.* Giraffinae includes the genus *Giraffa* and *Orasius*. Sivatheriinae includes the genera *Sivatherium, Hydaspitherium, Bramatherium* and *Urmiatherium*.

Abel's classification of Giraffidae, published in 1919 in his 'Stiimme der Wirbeltiere,' is essentially the same as that of von Zittel. He divides the family into two subfamilies, Giraffinae and Sivatheriinae. 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 (Colbert, 1935). The family Giraffidae includes Palaeotraginae, Sivatheriinae, Giraffinae*,* and Progirafflnae.

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 (Colbert, 1935). Matthew (1929) in his 'Critical Observations upon Siwalik Mammals,' pointed out the desirability of including *Okapia* among Palaeotraginae, thereby making three subfamilies of Giraffidae instead of four (exclusive of "Progiraffinae"). Matthew's classification is given below: The subfamily Palaeotraginae includes *Palaeotragus, Samotherium*, *Giraffokeryx* and *Okapia*. The subfamily Giraffinae includes the genera *Giraffa, Orasius* and *Honanotherium.* The subfamily Sivatheriinae includes the genera *Sivatherium, Indratherium, Helladotherium, Bramatherium* and *Hydaspitherium.*

A careful consideration of the problem of a classification of Giraffidae will demonstrate the validity of Matthew's views as to the inclusion of *Okapia* in 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 (Colbert, 1935). Bohlin has separated the okapi from the Palaeotraginae in having: the frontals are narrow in the modern form as compared to the fossil species, the horns are placed in a slightly different position in *Okapia* from the positions of the horns in *Palaeotragus* or *Samotherium*, the frontals in the okapi tend to develop pneumatic sinuses within them whereas the sinuses are not pronounced in *Palaeotragus* and related genera, there are minor differences in the dentition, no outer cingulum on DM2 in the okapi, whereas in *Palaeotragus* and *Samotherium* the cingulum is present, and 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 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 *Palaeotragus* they are much larger. Thus we may regard the okapi as more primitive in its horn development than is *Palaeotragus*. 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 *Palaeotragus*, but in *Samotherium* the horn cores have shifted somewhat to the rear, due to the elongation of the skull. In O*kapia* the dentition is very brachyodont 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 (Colbert, 1935).

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 Palaeotraginae, but in this persistent genus very few of the advanced habitus characters that characterize the fossil genera have been developed (Colbert, 1935).

The genus *Giraffokeryx* was created by Pilgrim in 1910, on the basis of upper and lower cheek teeth. Pilgrim (1911) in his monograph of the Siwalik Giraffidae, placed *Giraffokeryx* along with *Helladotherium* and *Vishnutherium* in a separate subfamily, Helladotheriinae. Bohlin (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 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. (Colbert, 1935).

Consequently Pilgrim's subfamily Helladotheriinae would seem to be unnecessary. The subfamily Progiraffinae, created by Pilgrim (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 to Palaeotraginae (Colbert, 1935).

Palaeotraginae includes primitive, medium sized giraffids, having as a rule one pair of supraorbital 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 (Colbert, 1935).

The giraffid species reported from the above mentioned literature (many have become synonym) includes *Palaeotragus rouenii* Gaudry, *Palaeotragus parvus* (Weithofer) synonym of *P. rouenii, Palaeotragus vetustus* (Wagner) synonym of *P. rouenii, Palaeotragus microdon* (Koken), *Palaeotragus coelophrys* (Rodler and Weithofer), *Palaeotragus decipiens* Bohlin. *Palaeotragus quadricornis* Bohlin, *Palaeotragus expectans* (Borissiak), *Achtiariaex pectans* (Borissiak), *Giraffokeryx punjabiensis*, *Okapia johnstoni* (Sclater), *Samotherium boisseri*, *Samotherium neumeyeri* (Rodler and Weithofer), *Samotherium sinense* (Schlosser), *Samotherium tafeli* (Killgus), *Samotherium eminens* (Alexejew), *Alcicephalus neumeyeri* Rodler and Weithofer, *Chersonoterium* Alexejew synonym of *Samotherium*, *Chersonotherium eminens* Alexejew, *Shianshithenrum* Killgus, synonym of *Samotherium, Shanshitherium tafeli* Killgus, *Propalaeomeryx sivalensis* Lydekker, *Progiraffa exigua* Pilgrim, *Giraffa camelopardalis* (Linnaeus), *Giraffa sivalensis*, *Giraffa affinis* (Falconer and Cautley) synonym of *G. sivalensis, Giraffa punjabiensis* Pilgrim, *Giraffa priscilla* Matthew, *Giraffa nebrascensis* Matthew and Barbour, *Orasius atticus* (Gaudry and Lartet), *Orasius eximius* Wagner, *Orasius speciosus* (Wagner), *Honanotherium schlosseri* (Pilgrim), *Sivatherium giganteum* Falconer and Cautley, *Indratherium majori*, *Bramatherium perimense* Falconer, *Hydaspitherium megacephalum* Lydekker, *Hydaspitherium grande*, *Hydaspitherium magnum* Pilgrim, *Hydaspitherium birmanicum*, *Vishnutherium iravaticum* Lydekker, *Helladotherium duvernoyi* Gaudry, *Helladotherium gaudryi* De Mecquenem. *Griquatherium cingulaum* Haughton, *Libytherium maurusicum* Pomel.

Protoceratidae of North America have been linked to Giraffidae by some authors, on the basis of certain resemblances between the members of the two groups. Schlosser, especially, would derive Giraffidae directly from Protoceratidae. Both Bohlin and Matthew have shown, however, that the resemblances between Protoceratidae and Giraffidae are due to convergence, and that these two families are really separated from each other by differences of basic importance (Colbert, 1935).

There are certain resemblances in the teeth between 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 Protoceratidae and 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 Protoceratidae, and of frontal origin in Giraffidae (Colbert, 1935).

Matthew (1929) made the following remarks with regard to the origin of Giraffidae and the relation of this family to the North American Protoceratidae that "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 derives 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) (Colbert, 1935).

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 in adaptive 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 (Colbert, 1935).

Siwalik Giraffids

The Siwalik giraffid species are provided in Table 1. The Kamlial Formation represents *Progiraffa exigua.* The Chinji Formation indicates *Giraffokeryx punjabiensis* Pilgrim, 1910; *Giraffa priscilla* Pilgrim, 1911 (Matthew, 1929; Colbert, 1933, 1935; Pilgrim, 1937, 1939; Raza, 1983; Akhtar 1992; Barry *et al.*, 2002; Badgley *et al.*, 2008; Khan *et al.*, 2008, 2009). The family Giraffidae represents only two living species, Okapi (*Okapiajohnstoni*) and Giraffe (*Girffacameloparadalis*). Both species today are present in Africa (Ethiopian region). However, the Giraffidae have a rich fossil history consisting of approximately thirty species throughout the Neogene of the Old World.

Table I: The Siwalik species of the family Giraffidae. The Siwalik species can be distinguished on the basis of their dentition and skull patterns.

Species	Appearance in the Siwalik Hills of Pakistan
Giraffa sivalensis Falconer and Cautley, 1843	Upper Siwaliks
Bramatherium geraadsi Falconer, 1845	Upper Siwaliks
Sivatherium giganteum Falconer and Cautley, 1836	Upper Siwaliks
Bramatherium perimense Falconer, 1845	Middle Siwliks
Giraffa punjabiensis Pilgrim, 1910	Middle Siwaliks
Helladotherium grande Gaudry, 1860	Middle Siwliks
Hydaspitherium birmanicum Pilgrim, 1910	Middle Siwaliks
Hydaspitherium grande Lydekker, 1878	Middle Siwaliks
Hydaspitherium megacephalum Lydekker, 1876	Middle Siwaliks
Hydaspitherium magnum Pilgrim, 1910	Middle Siwaliks
Vishnutherium iravaticum Lydekker, 1876	Middle Siwaliks
Giraffokeryx punjabiensis Pilgrim, 1910	Lower Siwaliks
Giraffa priscilla Matthew, 1929	Lower Siwaliks
Progiraffa sivalensis Pilgrim, 1911	Lower Siwaliks

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