

29. CLASSIFICATION OF THE PERISSODACTYLA

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The classification below includes all the valid genera of perissodactyls that we currently recognize. The classification attempts to be phylogenetic, as far as possible. We have created the minimum number of new taxa necessary to establish the phylogenetic relationships, but have changed the rank of many previously established suprageneric taxa to maintain their correct place in the hierarchy. The phylogenetic relationships in this classification are based on the phylogenies found in the summary chapter (Prothero and Schoch, this volume, Chapter 28). Original references to the names cited below can be found in Simpson (1945), the *Zoological Record* (published annually by the Zoological Society of London), and the series, *Bibliography of Fossil Vertebrates* (see Gregory *et al.*, 1988).

- Class Mammalia Linnaeus, 1758
- Subclass Theria Parker and Haswell, 1897
- Infraclass Eutheria Gill, 1872
- Superorder Ungulata Linnaeus, 1766
- Grandorder Altungulata Prothero and Schoch, 1989 (this volume, Chapter 28)
- Order Tethytheria McKenna, 1975 (new rank) [contents not subdivided here]
- Order Embrithopoda Andrews, 1906 [contents not subdivided here, except those relevant to perissodactyls]
 - Radinskya* McKenna, Chow, Ting, and Luo, 1989 (this volume, Chapter 3)
 - Heptaconodon* Zdansky, 1930
 - [?Lunania Chow, 1957]
- Order Perissodactyla Owen, 1848
- Suborder Hyracoidea Huxley, 1869
- Family Pliohyracidae Osborn, 1899
- Subfamily Geniohyinae Andrews, 1906
 - Seggeurius* Crochet, 1986
 - Geniohyus* Andrews, 1904
- Subfamily Sagatheriinae Andrews, 1906
 - Microhyrax* Sudre, 1979
 - Bunohyrax* Schlosser, 1910
 - Pachyhyrax* Schlosser, 1910
 - Megalohyrax* Andrews, 1903

- Sagatherium* Andrews and Beadnell, 1902
- Titanohyrax* Matsumoto, 1922
- Selenohyrax* Rasmussen and Simons, 1988
- Thyrohyrax* Meyer, 1973
- Merohyrax* Whitworth, 1954
- Subfamily Pliohyracinae Osborn, 1899
 - Prohyrax* Stromer, 1926
 - Paraplioherax* Lavocat, 1961
 - Plioherax* Osborn, 1899
 - Soqdoherax* Dubrovo, 1978
 - Kvabebihyrax* Gabunia and Vekua, 1966
 - Postschizotherium* von Koenigswald, 1932
- Family Procaviidae Thomas, 1892
 - Gigantohyrax* Kitching, 1965
 - Procavia* Storr, 1780
 - Heterohyrax* Gray, 1868
 - Dendrohyrax* Gray, 1868
- Suborder Mesaxonia Marsh, 1884
- Infraorder Hippomorpha Wood, 1937
- Superfamily Pachynolophoidea Pavlow, 1888
- Family Pachynolophidae Pavlow, 1888
 - Pachynolophus* Pomel, 1847
 - Anchilophus* Gervais, 1852
- Superfamily Equoidea Gray, 1821
 - Cymbalophus* Hooker, 1984 (= "*Hyracotherium*" *cuniculum*)
 - Systemodon* (= "*Hyracotherium*" *tapirinum*) Cope, 1881
 - Pliolophus* (= "*Hyracotherium*" *vulpiceps*) Owen, 1858
 - Hyracotherium sensu stricto* Owen, 1841 (not Owen, 1840, *contra* Simpson, 1945)
- Family Equidae Gray, 1821
 - Protorohippus* Wortman, 1896
 - Gobihippus* Dashzeveg, 1979
 - Orohippus* Marsh, 1872
 - Haplohippus* McGrew, 1953
 - Epihippus* Marsh, 1877 (= *Duchesnehippus*)
 - Mesohippus* Marsh, 1875
 - Miohippus* Marsh, 1874 (= *Pediohippus*)
- Subfamily Anchitheriinae Leidy, 1869
 - Anchitherium* Meyer, 1844
 - Hypohippus* Leidy, 1858
 - Megahippus* McGrew, 1938
 - Sinohippus* Zhai, 1962
- Subfamily Equinae Gray, 1821
 - Kalobatippus* Osborn, 1915
 - Archaeohippus* Gidley, 1906
 - Parahippus* Leidy, 1858
 - Merychippus sensu stricto* Leidy, 1857

- Tribe Hippotheriini Bonaparte, 1850 (new rank) [= Hipparionini Quinn, 1955]
Cormohipparion Skinner and MacFadden, 1977
Nannippus Matthew, 1926
Hipparion de Christol, 1832 (= *Proboscoidipparion*, *Notohipparion*)
Neohipparion Gidley, 1903
Pseudhipparion Ameghino, 1904 (= *Griphippus*)
Stylohipparion van Hoepen, 1932
Hippotherium Kaup, 1833
- Tribe Equini Gray, 1821
Protohippus Leidy, 1858
Calippus Matthew and Stirton, 1930
Pliohippus Marsh, 1874
Astrohippus Stirton, 1940
Hippidion Owen, 1869 (= *Parahipparion*, *Hyperhippidium*)
Onohippidium Moreno, 1891
Dinohippus Quinn, 1955
Equus Linnaeus, 1858 (= *Plesippus*, *Asinus*, *Hippotigris*, *Dolichohippus*,
Onager, *Hemionus*, *Kraterohippus*, *Kolpohippus*, *Sterrohippus*,
Neohippus)
- Family Palaeotheriidae Bonaparte, 1850
Propachynolophus Lemoine, 1891
Propalaeotherium Gervais, 1849
Lophiotherium Gervais, 1849
Palaeotherium Cuvier, 1804
Plagiolophus Pomel, 1847 (= *Paloplotherium*)
Pseudopalaeotherium Franzen, 1972
Paraplagiolophus Depéret, 1917
Leptolophus Remy, 1965
Cantabrotherium Casanova-Cladellas and Santafé-Llopis, 1987
- ?Hippomorpha incertae sedis
 Family Indolophidae Schoch, 1984
Indolophus Pilgrim, 1925
- Infraorder Moropomorpha Schoch, 1984 (new rank, =Tapiomorpha sensu Hooker, 1984)
- Subinfraorder Isectolophomorpha, new taxon
 Family Isectolophidae Peterson, 1919
Homogalax Hay, 1899
Isectolophus Scott and Osborn, 1887 (= *Parisectolophus*, *Schizolophodon*)
Sastrilophus Sahni and Khare, 1971
- Subinfraorder Rhinotapiomorpha, new taxon
Kalakotia Ranga Rao, 1972
Aulaxolophus Ranga Rao, 1972
- Parvorder Ancylopoda Cope, 1889 (new rank)
 Superfamily Lophiodontoidea Gill, 1872
 Family Lophiodontidae Gill, 1872
Lophiodon Cuvier, 1822 (= *Pernatherium*, ?*Hypsolophiodon*,
 ?*Leptolophiodon*)

- Paralophiodon* Dedieu, 1977 (= *Rhinocerocephiodon*)
Schizotherioides Hough, 1955
Toxotherium Wood, 1961
Paleomoropus Radinsky, 1964
Lophiaspis Depéret, 1910
Atalonodon Dal Piaz, 1929
Lophiodochoerus Lemoine, 1880
- Superfamily Chalicotherioidea Gill, 1872
 Family Chalicotheriidae Gill, 1872
Litolophus Radinsky, 1964
Olsenia Matthew and Granger, 1925
Eomoropus Osborn, 1913
Grangeria Zdansky, 1930
 [?Lunania Chow, 1957]
- Subfamily Schizotheriinae Holland and Peterson, 1913
Borissiakia Butler, 1965
Phylotillon Pilgrim, 1910
Macrotherium Lartet, 1837
Moropus Marsh, 1877
Tylocephalonyx Coombs, 1979
Ancylotherium Gaudry, 1863 (= *Metaschizotherium*, *Postschizotherium*,
Hoangkootherium, *Gansuodon*, *Chemositia*)
- Subfamily Chalicotheriinae Gill, 1872
Chalicotherium Kaup, 1833
Nestoritherium Kaup, 1859
- Parvorder Ceratomorpha Wood, 1937 (new rank)
Breviodon Radinsky, 1965
Parabreviodon Reshetov, 1975
- Magnafamily Deperetellidea Radinsky, 1965
 Family Deperetellidae Radinsky, 1965
Deperetella Matthew and Granger, 1925 (= *Cristindentinus*,
Diplocephodon)
Teleolophus Matthew and Granger, 1925
- Family Rhodopagidae Reshetov, 1975
Rhodopagus Radinsky, 1965
Pataecops Radinsky, 1966 (= *Pataecus*)
- Magnafamily Lophialetidea Matthew and Granger, 1925
 Family Eoletidae Schoch, 1989 (this volume, Chapter 2)
Eoletes Birjukov, 1975
- Family Lophialetidae Matthew and Granger, 1925
Schlosseria Matthew and Granger, 1926
Simplaletes Qi, 1980
Lophialetes Matthew and Granger, 1925
- Magnafamily Tapiroidea Burnett, 1830
Heptodon Cope, 1882
- Superfamily Tapiroidea Burnett, 1830
Helaletes Marsh, 1872 (= *Veragromovia*, *Chasmotheroides*)

- Desmatotherium* Scott, 1883
Selenaletes Radinsky, 1966
Dilophodon Scott, 1883 (= *Heteraletes*)
Haagella Heissig, 1978
Plesiocolopirus Schoch, 1989 (this volume, Chapter 15)
Colodon Marsh, 1890 (= *Paracolodon*, *Mesotapirus*)
 Family Tapiridae Burnett, 1830
Protapirus Filhol, 1877 (= *Tanyops*)
Eotapirus Cerdano and Ginsburg, 1988
Miotapirus Schlaikjer, 1937
Palaeotapirus Filhol, 1888
Paratapirus Depéret, 1902
Tapiriscus Kretzoi, 1951
Tapiravus Marsh, 1877
Megatapirus Matthew and Granger, 1923
Tapirus Brünnich, 1772 (= *Pinchacus*, *Cinchacus*, *Tapirella*,
Elasmognathus, *Acrocodia*, *Tapir*, *Syspotamus*, *Rhinochoerus*, *Tapyra*)

Superfamily Rhinocerotidea Owen, 1845

- Hyrachyus* Leidy, 1871 (= *Colonoceras*, *Metahyrachyus*, *Ephyrachyus*)
Chasmotherrum Rüttimeyer, 1862

Family Amarynodontidae Scott and Osborn, 1883

- Caenolophus* Matthew and Granger, 1925 (= *Teilhardina*, *Euryodon*)
Rostriamynodon Wall and Manning, 1986
Amarynodon Marsh, 1877 (= *Orthocynodon*)

Subfamily Cadurcodontinae Wall, 1982 (new rank)

- Sharamynodon* Kretzoi, 1942 (= *Lushiamynodon*)
Amarynodontopsis Stock, 1933
Sianodon Xu, 1965

Cadurcodon Kretzoi, 1942 (= *Paracadurcodon*)

Subfamily Metamynodontinae Kretzoi, 1942

- Megalamynodon* Wood, 1945
Paramynodon Matthew, 1929
Zaisanamynodon Beliaeva, 1971
Metamynodon Scott and Osborn, 1887 (= *Cadurcopsis*)
Cadurcotherium Gervais, 1873 (= *Cadurcamynodon*, *Hypsamynodon*)

Family Amarynodontidae incertae sedis:

- Gigantamynodon* Gromova, 1954
Huananodon You, 1977
Procadurcodon Gromova, 1960
Mesamynodon Peterson, 1931

Grandfamily Rhinocerotida Owen, 1845 (new rank)

Family Hyracodontidae Cope, 1879

- Subfamily Indricotheriinae Borissiak, 1923
Forstercooperia Wood, 1939 (= *Pappaceras*)
Juxia Chow and Chiu, 1963 (= *Imequincisoria*, *Guixia*)
Urtinotherium Chow and Chiu, 1963

- Paraceratherium* Forster Cooper, 1911 (= *Baluchitherium*,
Thaumastotherium, *Aralotherium*, *Dzungariotherium*)

Indricotherium Borissiak, 1915

Subfamily Indricotheriinae incertae sedis

- Benaratherium* Gabuniya, 1955

Subfamily Hyracodontinae Cope, 1879

- Triplopus* Cope, 1880 (= *Prothyracon*, *Eotrigonias*, *Ephyrachyus*)
Hyracodon Leidy, 1856
Epitriplopus Wood, 1927
Ardynia Matthew and Granger, 1923 (= *Ergilia*)
Triplopides Radinsky, 1965

Subfamily Allaceropinae Wood, 1932

- Prohyracodon* Koch, 1897 (= *Meninatherium*)
Ilianodon Chow and Xu, 1961
Eggysodon Roman, 1911 (= *Allacerops* Wood, 1932)

Family Rhinocerotidae Owen, 1845

- Teletaceras* Hanson, 1989 (this volume, Chapter 20)
Ronzotherium Aymard, 1886
Epiaceratherium Abel, 1910
Penetrigonias Tanner and Martin, 1976
Trigonias Lucas, 1900
Amphicaenopus Wood, 1927

Subfamily Diceratheriinae Dollo, 1885

- Subhyracodon* Brandt, 1878 (= *Caenopus*, *Leptaceratherium*)
Diceratherium Marsh, 1875

Subfamily Menocerotinae Prothero, Manning, and Hanson, 1986

- Menoceras* Troxell, 1921 (= *Moschoedestes*)
Pleuroceros Roger, 1898
Protaceratherium Abel, 1910

Subfamily Aceratheriinae Dollo, 1885

- Mesaceratherium* Heissig, 1969
Proaceratherium Ginsburg and Huguency, 1980
Floridaceras Wood, 1966
Aphelops Cope, 1873
Peraceras Cope, 1880

Aceratherium Kaup, 1832

- Hoploaceratherium* Ginsburg and Heissig, 1989 (this volume, Chapter 22)

Dromoaceratherium Crusafont and Villalta, 1955

Plesiaceratherium Young, 1937

Alicornops Ginsburg and Guérin, 1979

Subchilotherium Heissig, 1972

Chilotherium Ringström, 1924

Chilotheridium Hooijer, 1971

Acerorhinus Kretzoi, 1942

Sinorhinus Schlosser, 1903

Subfamily Rhinocerotinae Owen, 1845

Tribe Teleoceratini Hay, 1902

Diaceratherium Dietrich, 1931

Brachydiceratherium Lavocat, 1951

Prosantorhinus Heissig, 1973

Teleoceras Hatcher, 1894

Brachypotherium Roger, 1904

Aprotodon Forster Cooper, 1915

Brachypodella Heissig, 1973

Tribe Rhinocerotini Owen, 1845

Subtribe Dicerorhinina Ringström, 1924 (new rank)

Dicerorhinus Gloger, 1841 (= *Didermocerus*, *Ceratorhinus*)

Stephanorhinus Kretzoi, 1942

Lartetotherium Ginsburg, 1974

Coelodonta Bronn, 1831 (= *Tichorhinus*)

Subtribe Elasmotheriina Bonaparte, 1845 (new rank)

Hispanotherium Crusafont and Villalta, 1947 (= *Begertherium*,
Caementodon, *Beliajevina*, *Tesseledon*)

Iranotherium Ringström, 1924

Kenyatherium Aguirre and Guérin, 1974

Sinootherium Ringström, 1922 (= *Parelasmotherium*)

Elasmotherium Fischer, 1808

Subtribe Rhinocerotina Owen, 1845 (new rank)

Gaiotherium Colbert, 1934

Rhinoceros Linnaeus, 1758

Subtribe Dicerotina Ringström, 1924 (new rank)

Paradiceros Hooijer, 1968

Diceros Gray, 1821

Ceratotherium Gray, 1867

Rhinocerotidae *incertae sedis*:

Symphyssorrhachis Belyajeva, 1954

Meschotherium Gabunia, 1964

Ninxiatherium Chen, 1977

Punjabitherium Kahn, 1971

Infraorder Titanotheriomorpha Hooker, 1989 (new rank)

Superfamily Brontotherioidea Marsh, 1873

Family Lambdotheriidae Cope, 1889

Lambdotherium Cope, 1880

Xenicohippus Bown and Kihm, 1981

Family Brontotheriidae Marsh, 1873

Eotitanops Osborn, 1907

Pakititanops West, 1980

Palaeosyops Leidy, 1870 (= *Limnohyops*, *Limnohyus*, *Eometarhinus*)

Subfamily Dolichorhininae Riggs, 1912

Mesatirhinus Osborn, 1908

Rhadinorhinus Riggs, 1912

Dolichorhinus Hatcher, 1895

Subfamily Telmatheriinae Osborn, 1914

Telmatherium Marsh, 1872 (= *Leurocephalus*, *Manteoceras*)

Metatelmatherium Granger and Gregory, 1938

Sthenodectes Gregory, 1912

Protitanotherium Hatcher, 1895

Eotitanotherium Peterson, 1914

Notiotitanops Gazin and Sullivan, 1942

Duchesneodus Lucas and Schoch, 1982

Teleodus Marsh, 1890

Brontops Marsh, 1887 (= *Diplocionus*)

Menops Marsh, 1887 (= *Allops*)

Megacerops Leidy, 1870 (= *Brontotherium*, *Titanops*)

Asian brontotheres [synonymies and relationships not recently revised; many are invalid]

Sivatitanops Pilgrim, 1925

Desmatotitan Granger and Gregory, 1943

Hytitan Granger and Gregory, 1943

Epimanteoceras Granger and Gregory, 1943

Protitan Granger and Gregory, 1943

Microtitan Granger and Gregory, 1943

Dolichorhinoides Granger and Gregory, 1943

Gnathotitan Granger and Gregory, 1943

Rhinotitan Granger and Gregory, 1943

Pachytitan Granger and Gregory, 1943

Parabrontops Granger and Gregory, 1943

Metatitan Granger and Gregory, 1943

Titanodectes Granger and Gregory, 1943

Embolotherium Osborn, 1929

Protbolotherium Tang, You, Xu, Qiu, and Hu, 1974

Arctotitan Chow, 1978

Dianotitan Chow and Hu, 1959

Brontotheriidae *incertae sedis*:

Menodus Pomel, 1849 (*nomen dubium*)

Symborodon Cope, 1873

Sphenocoelus Osborn, 1895

Protitanops Stock, 1936

Diplacodon Marsh, 1875

Brachydiastematherium Böckh and Maty, 1876

Titanotherium Leidy, 1852

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