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## Family Tragulidae

**M**ODERN TRAGULIDS ARE A GROUP of small-sized artiodactyls including the smallest living hoofed mammal (Figs. 16.1, 16.2). They are nearly unknown to the public, although they are often captured, kept as pets or laboratory animals, and even bred in zoos. These enigmatic little creatures with enlarged upper canines in males are fascinating for study: on the one hand they are similar to all the other living ruminants (and therefore included in the suborder Ruminantia), but on the other hand they differ strikingly, which led us to grade them as primitive. Arising from their shy, nocturnal lifestyle in the dense undergrowth of tropical rainforests, they are hard to observe, and only fragmentary knowledge exists about their behavior. Their tiny, graceful appearance somewhat resembles a deer or antelope without antlers or horns, which results in the names mouse deer or chevrotains (French = juvenile goat) in common speech. Two genera live in two relict areas in Southeast Asia: Myanmar, Thailand, Vietnam, Malaysia, Sumatra, Indonesia, and the Philippines (*Tragulus*, the Lesser Malay mouse deer, and the Greater Malay mouse deer); and India and Sri Lanka (*Moschiola*, the Indian chevrotain). A third genus lives in the West and Central African rainforest from Sierra Leone to Uganda (*Hyemoschus*, the water chevrotain). With this small number of genera and species, tragulids are one of the least-diversified groups among existing ruminants with the exception of the Antilocapridae and Moschidae. All species are endangered in terms of loss of habitat by human destruction. *Hyemoschus* of Ghana is even included in the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) list of species because its survival is currently threatened.

The ancestors of these creatures were much more widely distributed in Eurasia and Africa: they were more diversely adapted, often with several sympatric species,



Fig. 16.1. A male lesser mouse deer, *Tragulus javanicus*, with the distinctive enlarged upper canines (photo by D. R. Prothero).

and were also more common. Because their present distribution is disjunct and their physique has remained primitive, they fulfill the criteria for being designated as “living fossils” (Janis, 1984; Thenius, 2000).

### BIOLOGY OF TRAGULIDS

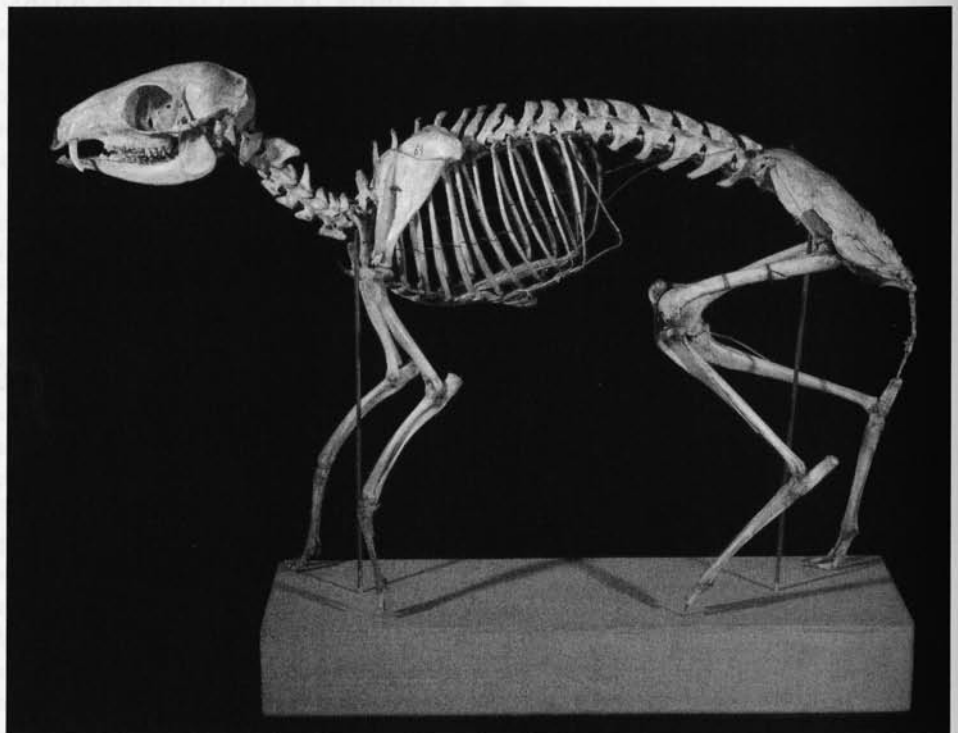
In general, studies on the biology of tragulids are rare. Although *Tragulus* has been examined in several physiological and ethological aspects, there are few studies on its behavior in the wild. *Hyemoschus* has been investigated both in the wild and in captivity, but its physiological processes have only been deduced. No physiological or behavioral studies on *Moschiola* exist at all.

Tragulids are nocturnal or crepuscular, as indicated by their comparatively large eyes. With their arched back and short limbs, they are well adapted to slip through the dense undergrowth in various forests. During the day, they rest in the vegetation, *Tragulus* sometimes in the branches of low trees. Their dark-colored coats, plain brown in *Tragulus* and with white stripes and spots in *Moschiola* and *Hyemoschus*, greatly affect camouflage. With their small body size, they are easy and important prey for snakes, crocodiles, birds of prey, and forest-dwelling cats.

*Hyemoschus* is always near water, and the animal takes to the water when pursued, hiding there under waterweeds or overhanging banks and roots of trees (Dubost, 1978). In this respect *Hyemoschus* occupies a particular ecological niche (forest-dwelling, fruit-eating, terrestrial, aquaphilous, small-sized, and nocturnal), unique in the African continent (Dubost, 1978). It is the ecological Old World equivalent of the Paca, a caviomorph in tropical forests of South America (Dubost, 1968; Eisenberg and McKay, 1974). Within *Tragulus* and *Moschiola*, some species prefer wetter and some drier areas in densely covered habitats (Pickford et al., 2004; Groves and Meijaard, 2005), but none is revealed to be as water-loving as *Hyemoschus*.

*Hyemoschus* is known to live alone (Dubost, 1978), and individuals of *Tragulus* also lead a largely solitary life (Eisenberg and McKay, 1974). They do not possess marking glands as do most other ruminants, but only preputial and anal ones. Urine and feces presumably serve to mark home ranges, particularly in males. *Tragulus* occasionally mark twigs with a chin gland. Ralls et al. (1975) recorded stamping as communication between widely separated individu-

Fig. 16.2. Skeleton of a male *Tragulus javanicus* stored at the Naturhistoriska Riksmuseet Stockholm. Phalanges are partly missing. Length 35 cm (photo by Mikael Axelsson).



als of *Tragulus* and found that various vocalizations during encounters form an important social interaction. The same is true for the barking alarm of *Hyemoschus* (Dubost, 1978). Territorial and ritualized fighting behavior is primitive. The males stand in an antiparallel and not in a head-to-head stance (Dubost, 1965; Ralls et al., 1975). With their sabre-like elongated upper canines, the opponents try to slash each other's neck, sides, and bellies, causing long gashes on head and body (Fig. 16.3). Often death is a consequence, as the decreasing ratio of males to females with increasing age in the wild leads us to assume (Dubost, 1978). A toughened skin forms an effective shield on the back to protect the animal from antagonistic strokes (Dubost and Terrade, 1970). It ensures protection of the viscera both during intraspecific attacks and as the animal slips through the dense undergrowth. The same functions can be assumed for the bony dorsal shield in the pelvic region of the male *Tragulus javanicus* and *T. napu* (Milne-Edwards, 1864: pl. IV, Fig. 2, 2a; Dubost and Terrade, 1970: Fig. 3).

Tragulids become sexually mature at 9–26 months (Dubost, 1975). The courting and mating behaviors are primitive in many respects, e.g., absence of "Flehmen" in males (curling of lips in response to urine licking) (Dubost, 1965; Ralls et al., 1975). In the female there is a so-called diffuse placenta similar to that of camels and pigs (Milne-Edwards, 1864: pl. VII, Fig. 1-2; Turner, 1876; Strahl, 1905) and unlike the cotyledonous placenta of ruminants. One infant is produced at a time, which does not follow its mother but hides in dense vegetation (Eisenberg and McKay, 1974). Mothers nurse in a unique position: they stand and raise the hind leg on the side toward the infant (Ralls et al., 1975). Tragulids live for 8–12 years in the wild; in captivity, a lifespan of 16 years and more has been known (Jones, 1993).

Tragulids search for food on the ground. They are unable to stand on their hind legs to browse on vegetation as higher ruminants may do (Dubost, 1978). Their food consists of easily digestible forage providing an extremely high percentage of protein (fallen fruit and seeds, flowers, leaves, shoots, petioles and stems, and mushrooms) (Nordin, 1978; Dubost, 1984). This feeding strategy indicates that tragulids are so-called "concentrate-selectors." *Hyemoschus* is also known to eat invertebrates, fish, small mammals, and carrion occasionally (Dubost, 1964).

Metabolic processes of tragulids differ markedly from those of higher ruminants (e.g., Nolan et al., 1995). Investigations have been made into body temperature (Whittow et al., 1977), food intake (Nordin, 1978), digestibility characteristics (Paden and Nordin, 1978), and body-water turnover (Kamis, 1981). The gross morphology of their stomach is similar to that of pecoran concentrate-selectors (Agungpriyono et al., 1992), but tragulids lack or have only a small third of the four chambers of pecorans, the omasum, a condition evaluated as primitive (Langer, 1974). The name-giving digestion strategy in Ruminantia, the chewing of the cud (Latin = ruminare), is performed by tragulids also. However, the rumen, the first chamber enlarged from a forestomach performing cellulose fermentation in symbio-

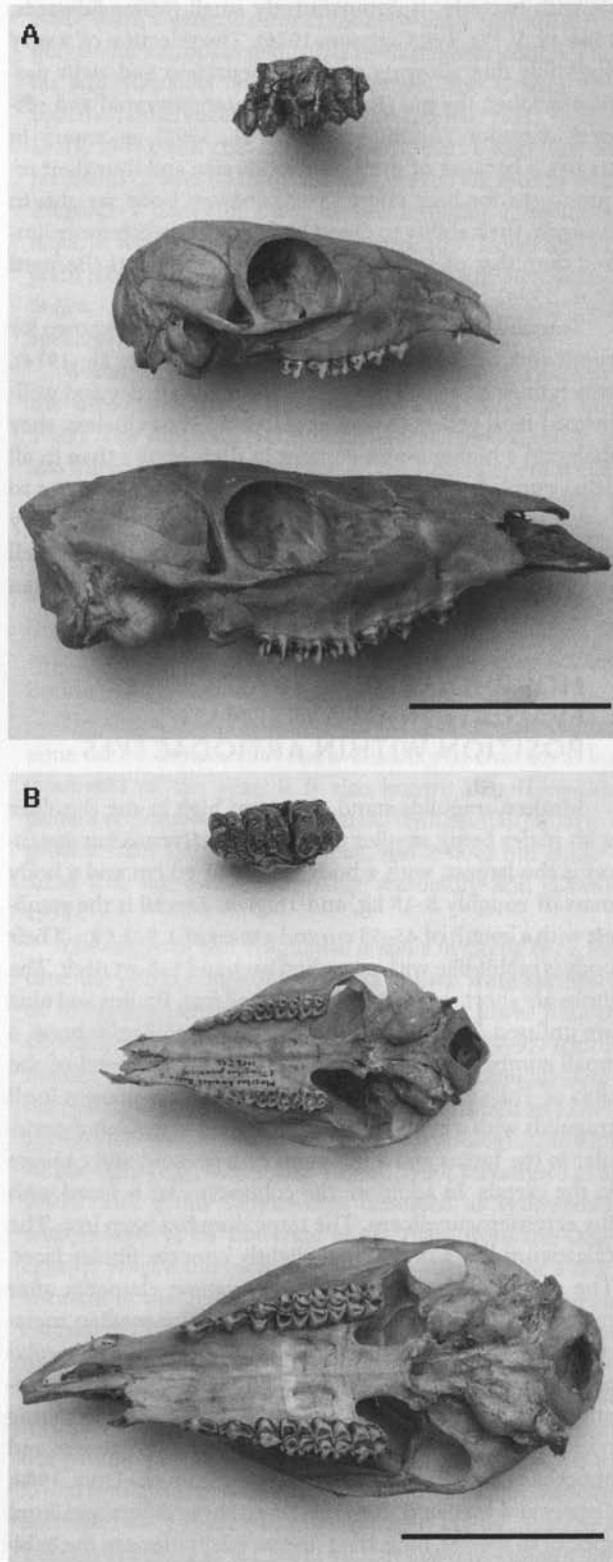


Fig. 16.3. (A) Lateral/labial view of skulls and upper dentition of fossil and extant tragulids. From above to below: *Dorcatherium crassum*, left upper molar row from the fossil site of Sandelzhausen (middle Miocene, Germany), Bayerische Staatssammlung für Paläontologie und Geologie in München 1959 II 4144; female *Tragulus javanicus*, provenance unknown, Bayerische Staatssammlung für Paläontologie und Geologie in München 1952 I 22; male *Hyemoschus aquaticus*, canines are missing, Makokou/Gabun, property of Gérard Dubost (Paris), H 30? 15-3-63 (photo by Georg Janssen). Scale bar equals 5 cm. (B) Ventral/occlusal view of the specimens from A (photo by Georg Janssen). Scale bar equals 5 cm.

sis with bacteria, is comparatively small (Milne-Edwards, 1864: pl. V, Fig. 1-5; Carlsson, 1926). The selection of a very digestible diet allowing rapid fermentation and swift passage through the gut (Kay, 1987) guarantees rapid and efficient digestion (Agungpriyono et al., 1992), necessary in tragulids because of their small body size and thus their requirement for high energy per kilogram body weight. In contrast, their ability to digest higher-fiber diets is more limited than that of larger, more derived ruminants (Bernard et al., 1994).

Tragulids exhibit the lowest daily water intake known for ruminants of the humid tropics (Macfarlane et al., 1974), which must be associated with their relatively dry and well-formed fecal pellets (Nolan et al., 1995). Nevertheless, they maintain a higher water content in their bodies than in all other ruminants (Panaretto, 1968). Tragulids are known to have a gallbladder and appendix. Their body contains very little fat and an extremely high percentage of muscle as well as specialized anatomical proportions (e.g., gut more than 25% of body mass) (Vidyadaran et al., 1983).

#### MORPHOLOGICAL TRAITS AND EVALUATION OF SYSTEMATIC POSITION WITHIN ARTIODACTYLS

Modern tragulids stand 20–40 cm high at the shoulder with males being smaller than females. *Hyemoschus aquaticus* is the largest, with a body length of 80 cm and a body mass of roughly 8–15 kg, and *Tragulus kanchil* is the smallest with a length of 45–55 cm and a mass of 1.5–2.5 kg. Their body is rabbit-like with an arched back and a short neck. The limbs are short, as well, with four-toed feet. Radius and ulna are unfused. The fibula is reduced to the malleolar bone, a small compact bone fused with the distolateral end of the tibia of *Tragulus*. Further fusions of bones are present in all tragulids with a cubonavicular formed of cuboid and navicular in the tarsus and a magnum of trapezoid and capitate in the carpus. In addition, the cubonavicular is fused with the ectomesocuneiform. The trapezium has been lost. The calcaneum has a nearly flat, slightly concave fibular facet. The metapodials comprise four complete elements after metacarpal and metatarsal I were lost. The median metatarsals (III and IV) are fused into a cannon bone. In *Tragulus* even metatarsals II and IV are fused as in pecorans. The relative proportions of metapodials and toes differ. In living tragulids they are longer and more slender in *Tragulus* and *Moschiola* compared with *Hyemoschus* (Smit-van Dort, 1989; Groves and Meijaard, 2005) and even show differences from species to species, indicating diverse adaptations to the habitat and locomotion. The side metapodials are completely present, slender in *Tragulus* and *Moschiola* and strong in *Hyemoschus*, but not functional except perhaps on swampy ground. A peculiarity is the bony dorsal shield of the male *Tragulus napu* and *T. javanicus* (Milne-Edwards, 1864, pl. IV, Fig. 2, 2a; Gray, 1869) above the pelvis, forming an internal turtle-like carapace.

The skull has nearly equal preorbital and postorbital proportions. The very large orbit has only one lacrimal foramen in its rostral rim. The postorbital bar is complete and primarily composed of the jugal. The snout is tapered. The auditory bulla is expanded and cancellous (with the exception of the hollow bulla of *Moschiola*). The closed plan of the facial skull lacks a lacrimal fossa in general. An antorbital vacuity is present in *Moschiola* and *Hyemoschus*. The premaxilla and nasal are in contact in *Tragulus* and *Moschiola* but separated in *Hyemoschus*. Cranial appendages are absent. The corpus of the mandible is low and without the shallow incision of the pecorans rostral to the angle.

Although the upper incisors are lost, the upper canine is saber-like and even enlarged in males, used for intraspecific combats (see above). Two-thirds of the canine is housed in a long maxillary alveolus, which curves back above the cheek tooth row, close to the nasomaxillar contact, to the level of P2 or P3. The lower canine is incisiform closely positioned to the third incisor. The cheek teeth are generally low crowned, lowest in *Hyemoschus* and a little higher in *Moschiola* and *Tragulus*. In the lower and upper premolar rows, the first tooth (P1 and p1) is totally lacking in extant species, but p1 is occasionally found in fossil species in which it has a premolariform crown, variable in length, with one or two conids and a bifurcated root (Gentry et al., 1999, Fig. 23.2). It is sometimes separated from the p2 by a small diastema. The other premolars are long and slender with one longitudinal main crest on the buccal side and a shorter lingual transverse crest that quickly turns to run toward the posterior end of the tooth. P4 is an exception, displaying a triangular shape. The crown of the molars is formed by four rounded to sickle-shaped cusps showing the so-called bunosenodont morphology. The lower molars show a special crest complex called the "Dorcatherium fold." It is formed by the bifurcation of the posterior slopes of the protoconid and the metaconid resulting in a "Σ" shape and named after a fossil tragulid. The upper molars are characterized by labially projecting styles and cones.

Many of the described tragulid features (short limbs with unfused full-length lateral digits II and V, and with unfused or partly fused central metapodials; incomplete distal keel on metapodials; elongate, relatively narrow astragalus with the distal articulation pulley medially deflected; short and peglike odontoid process of the axis; lower premolars without linguall projecting cusps) are evaluated as plesiomorphic (primitive) because they are found in the primitive ruminant families Amphimerycidae (Europe), Archaeomerycidae (Central Asia), Leptomerycidae, and Hypertragulidae (North America), which are all documented from middle to late Eocene deposits (Webb and Taylor, 1980; Janis, 1987; Gentry and Hooker, 1988). Because tragulids lack derived pecoran characters, they are placed at the most basal systematic position within living Ruminantia. Based on these plesiomorphic features, the appearance of living tragulids is considered to resemble that of early ruminants. The cubonavicular fusion and the incisiform lower canines

are shared derived features of all members of the suborder Ruminantia. Within this the infraorder Tragulina, including the family Tragulidae, is a paraphyletic assemblage of primitive ruminants (e.g., Webb and Taylor, 1980; Janis, 1987; Gentry and Hooker, 1988; Gentry, 2000a). The Tragulina is considered a sister group to the "higher" ruminants, mainly taxa bearing cranial appendages (deer, antelopes, cattle, giraffes, and pronghorns), which are today a highly diverse radiation grouped as the infraorder Pecora.

Unique (autapomorphic) features that separate the tragulids from all other ruminants are a malleolar bone fused with the distal end of the tibia, an ectocuneiform fused with the cubonavicular in the tarsus, no postglenoid process, a very small external exposure of the mastoid, as well as a closed postorbital bar. Exceptions are known in fossil tragulids, however (Gentry, 1978; pers. obs.).

A primitive status of tragulids within Ruminantia can be assumed not only from morphological features but also from aspects of the physiology, behavior, and ecology of the living representatives. Because similarities with peccaries are obvious (e.g., Milne-Edwards, 1864: 117; Janis, 1984), they comply with conditions for a transitional position between Suoidea and Ruminantia. This positioning is also supported by the observation that from peccaries through tragulids to ruminants, the forestomach common to all these groups increases in complexity (Langer, 1988). From an analysis of their muscle antigens, Duwe (1969) even concluded that the tragulids are most closely related to the tayassuids. If this is so, the loss of the upper incisors, the incisiform lower canine, and the cubonavicular would be traits developed in parallel with the pecorans, but much earlier.

Extensive descriptions of the tragulid skeleton and dentition can be found in Milne-Edwards (1864), Pilgrim (1910, 1915), Carlsson (1926), Mottl (1961), and Fahlbusch (1985).

### ORIGIN, PHYLOGENY, INTRAFAMILIAR SYSTEMATICS, BIOGEOGRAPHY, AND PALEOECOLOGY

In 1864 Milne-Edwards established the family Tragulidae within the Ruminantia based on the structure of the stomach, dentition, and feet. He separated the Asian *Tragulus* and African *Hyemoschus* from the Moschidae, another living ruminant group without cranial appendages.

Investigations of extant Tragulidae since the first half of the nineteenth century have served to establish the generic distinction between the African *Hyemoschus* and the Asian *Tragulus* (e.g., Gray, 1843; Milne-Edwards, 1864), based on clear morphological differences in the skeleton and dentition, still in common use. Although the monotypic status of *Hyemoschus* has not been challenged (however, three subspecies have been named), a constant disagreement about the taxonomic composition of the Asian representatives has persisted. Since the 1940s, the opinion has prevailed that the genus *Tragulus* comprises two species in Southeast Asia (*T. napu* and *T. javanicus*) and one species (*T. meminna*) in India.

Since then, a generic distinction between a Southeast Asian genus and an Indian genus has been recommended, *Tragulus* and *Moschiola* respectively (Groves and Grubb, 1987), based on differences in the skeleton (Flerov, 1931; Smit-van Dort, 1989), and coat color (Pocock, 1919). Recently, Meijaard and Groves (2004a) have recognized six species within *Tragulus* (*T. javanicus*, *T. williamsoni*, *T. kanchil*, *T. nigricans*, *T. napu*, *T. versicolor*) with 24 subspecies, and Groves and Meijaard (2005) followed on with three species in *Moschiola* (*M. indica*, *M. meminna*, *M. kathygre*) and a potential fourth species (?*Moschiola* sp.).

Within the extant tragulids, *Hyemoschus* is regarded as the most primitive (e.g., Carlsson, 1926; Smit-van Dort, 1989). The more slender limbs, higher crowned teeth, and less intense water dependence of the Asian genera seem to resemble the more pronounced adaptation of advanced artiodactyls to drier and more open landscapes. In addition, body, especially limb, proportions of *Tragulus* and *Moschiola* are different and correlate with different habitat conditions (Smit-van Dort, 1989; Groves and Meijaard, 2005). In any case, the relict aspect of tragulid disjunct geographic distribution reflects their complex history.

The restriction of extant tragulids to the tropical climate zone can be explained by the availability of fruit for at least 9 months of the year. It is also known that *Hyemoschus* prefers very low seasonality in areas with rainfall equal to or greater than 1,500 mm per year, and it does not occur in areas that are even moderately seasonally arid (Dubost, 1978).

The origin of the Tragulidae is still a mystery. For a long time the geologically oldest fossils known were specimens of the genus *Dorcatherium* (Fig. 16.4) from lower Miocene deposits of Africa and Europe (Gentry et al., 1999; Pickford, 2001a). Thus, the evolutionary history of tragulids before the early Miocene remained unknown, although an Eocene appearance has been anticipated by morphological and molecular data (e.g., Webb and Taylor, 1980; Miyamoto et al., 1993). The genus *Cryptomeryx* (assessed as synonymous with *Iberomeryx* by Bouvrain et al., 1986) from the Oligocene of France and India has been considered to be a direct ancestor of the Tragulidae (Schlosser, 1902) or even the oldest tragulid (Sudre, 1984). Some years later it was suggested that *Cryptomeryx* should be included in a new family named Lophiomerycidae (Janis, 1987), which is grouped in the infraorder Tragulina with the Tragulidae and Hypertragulidae (Webb and Taylor, 1980) and whose roots can be followed to the late middle Eocene (Guo et al., 2000). Recently described early ruminant material from the late Eocene of Thailand (Métais et al., 2001) includes two mandibles with brachyodont dentition of what has been claimed to be the oldest known member of the Tragulidae, *Archaeotragulus krabiensis*. It suggests that the origin of the family should be searched for in the middle Eocene of Southeast Asia (see Métais and Vislobokova, this volume). Moreover, together with early ruminants from the middle Eocene of Myanmar (Métais et al., 2000), *Archaeotragulus* testifies to a contempo-

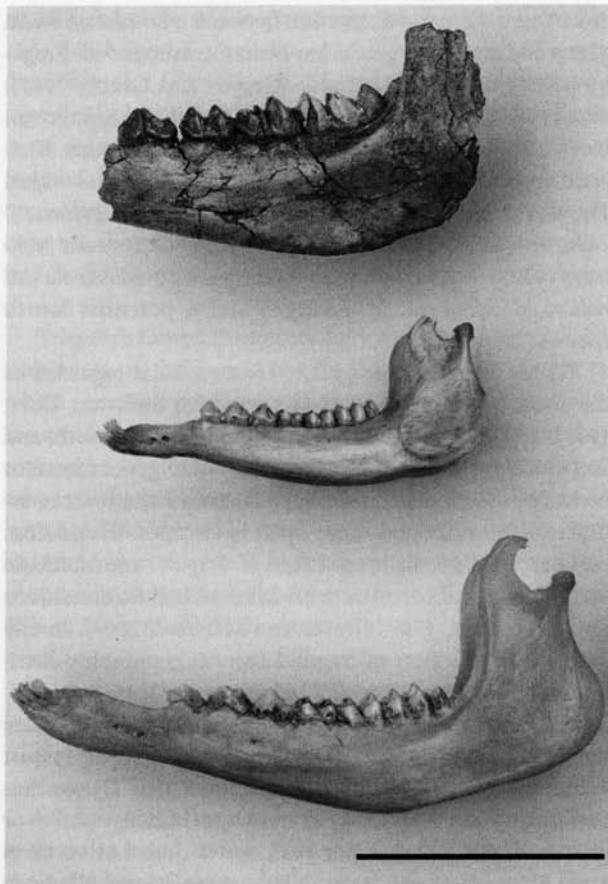


Fig. 16.4. Left jaws and lower dentition of fossil and extant tragulids. From above to below: *Dorcatherium crassum*, jaw fragment with fourth premolar to third molar from the fossil site of Sandelzhausen (middle Miocene, Germany), Bayerische Staatssammlung für Paläontologie und Geologie in München 1959 II 4146; female *Tragulus javanicus*, provenance unknown, Bayerische Staatssammlung für Paläontologie und Geologie in München 1952 I 22; male *Hyemoschus aquaticus*, Makokou/Gabun, property of Gérard Dubost (Paris), H 30? 15-3-63 (photo by Georg Janssen). Scale bar equals 5 cm.

aneous occurrence of a possible tragulid representative alongside lophiomerycids and opens the possibility of a common origin for both groups. This direction of thought is supported by a diverse, mainly undescribed fauna of early ruminants with still unknown familial affiliation from the middle Eocene of Myanmar and China, reflecting an early ruminant radiation (Métais et al., 2000; Tsubamoto et al., 2003; Métais et al., 2005). The same age of origin, or even earlier, has been proposed by recent molecular data (44.3–46.3 Ma; Hassanin and Douzery, 2003).

Apart from the Eocene *Archaeotragulus*, no tragulid fossils are known from the Paleogene. This fact still leaves a gap in the known evolution of tragulids until their sudden and widespread appearance in the lower Miocene of Southeast Asia (Mein and Ginsburg, 1997), Africa (Witworth, 1958; Hamilton, 1973), and Europe (Mein, 1989). The majority of fossil tragulids, including all of the European and African ones as well as some Asian forms, are referred to the genus *Dorcatherium*, established in the very first description of a fossil or living member of this family (Kaup, 1833) (Table

16.1). *Dorcatherium* comprises bunoselenodont to selenodont species of various body sizes. Its strong similarity with the extant *Hyemoschus* has often been mentioned (e.g., Gentry, 1978b), and the two genera have sometimes been combined. In fact, comparison of dentition and limb structure of *Dorcatherium* with those of extant tragulids shows a greater resemblance to *Hyemoschus* than to *Tragulus* or *Moschiola*, but it is not congruent in all details. Additionally, only a single *Dorcatherium* skull ever has been recorded (Kaup, 1933), and the taphonomic damage to this specimen obscures its original morphology and proportions, which makes it nearly impossible to compare cranial details pertinent to a synonymization with *Hyemoschus*. In its more selenodont cheek teeth, lacking p1 and a cingulum, more robust jaws, and lack of contact between premaxilla and nasals, *Hyemoschus* contrasts with *Dorcatherium*.

As yet the genus *Dorcabune* Pilgrim, 1910 is restricted to several Miocene Asian members of the family plus one Pleistocene species and a European probable occurrence in the late Miocene of Crete (Van der Made, 1997a) (Table 16.1). Blunt cusps of the cheek teeth were originally given as the diagnostic feature. The current morphological range in the genus resembles that of *Dorcatherium* in that there are bunoselenodont as well as selenodont species of different sizes. A revision of both genera is urgently needed. It would most probably result in two main lineages of Miocene tragulids with an obvious ecomorphological differentiation into bunoselenodont omnivores and selenodont herbivores (Mottl, 1961; Fahlbusch, 1985; Qiu and Gu, 1991), adaptations which might have appeared several times in parallel in different radiations producing a much more complex phylogenetic pattern. In fact, the interspecific relationships are difficult to reconstruct because usually we are faced with sudden appearances of tragulid assemblages of several sympatric species (Pilgrim, 1915; Mottl, 1961; Fahlbusch, 1985).

Two additional fossil genera, more recently established, show more similarities with the extant Asian genera. *Siamotragulus* is an early to middle Miocene genus from South and Southeast Asia (Thomas et al., 1990) with simpler lower premolars than *Dorcatherium* or *Dorcabune* and more advanced limb structures with completely fused median metapodials and more reduced side metapodials. Thus, it strongly resembles *Tragulus*, although it clearly differs by its still-separate isolated malleolar bone. These traits indicate a further Miocene but exclusively Asian lineage. Its relationship with the extant *Tragulus* has not yet been discussed. The Chinese *Yunnanotherium* (Han, 1986) of the late Miocene is characterized by small body size, upper cheek teeth with a weak cingulum, and an incompletely developed *Dorcatherium* fold; it thus also shares more features with the extant Asian tragulids and might belong to a lineage leading directly to them.

Unfortunately, Pliocene and Pleistocene tragulid specimens are nearly unknown and are more seldom described (e.g., Bakalov and Nikolov, 1962), which keeps the later history of the family in obscurity. An upper molar from the early Pliocene in Kenya recently referred to *Hyemoschus aquaticus* (Pickford et al., 2004) would be better placed in

Table 16.1. Tragulid species and their spatiotemporal distributions

| Species   | Distribution   |
|---|--|
| <i>Archaeotragulus krabiensis</i> Métais, Chaimanee, Jaeger and Ducrocq 2001        | Late Eocene, Thailand  |
| <i>Dorcatherium crassum</i> (Lartet, 1851)  | Latest early to late Middle Miocene, Europe                        |
| <i>Dorcatherium guntianum</i> von Meyer, 1846                                       | Latest early to middle middle Miocene, Europe                      |
| <i>Dorcatherium vindobonense</i> von Meyer, 1846 (= <i>D. rogeri</i> Hofmann, 1909) | Latest early to middle middle Miocene, ?early late Miocene, Europe |
| <i>Dorcatherium peneckeii</i> (Hofmann, 1893)                                       | ?Latest early Miocene, middle Miocene, Europe                      |
| <i>Dorcatherium nauai</i> Kaup and Scholl, 1834                                     | Late Miocene, Europe   |
| <i>Dorcatherium jourdani</i> (Déperet, 1887)  | Late Miocene, Europe   |
| <i>Dorcatherium puyhauberti</i> Arambourg and Piveteau (1929)                       | Late Miocene, Europe   |
| <i>Dorcatherium bulgaricum</i> Bakalov and Nikolov, 1962                            | ?Pliocene, Bulgaria  |
| <i>Dorcatherium pigotti</i> Whitworth, 1958   | Early to middle Miocene, Africa                                    |
| <i>Dorcatherium chappuisi</i> Arambourg, 1933                                       | Early to middle Miocene, Africa                                    |
| <i>Dorcatherium parvum</i> Whitworth, 1958  | Early Miocene, East Africa   |
| <i>Dorcatherium songhorensis</i> Whitworth, 1958                                    | Early Miocene, East Africa   |
| <i>Dorcatherium iririensis</i> Pickford, 2002                                       | Early Miocene, East Africa   |
| <i>Dorcatherium moruorotensis</i> Pickford, 2001                                    | Latest early Miocene, East Africa                                  |
| <i>Dorcatherium libiensis</i> Hamilton, 1973  | Latest early to earliest middle Miocene, North Africa, Arabia      |
| <i>Dorcatherium</i> sp. in Pickford, Senut and Mourer-Chauviré, 2004                | Early Pliocene, East Africa  |
| <i>Dorcatherium orientale</i> Qiu Zhanxiang and Gu Yumin, 1991                      | Middle Miocene, China  |
| <i>Dorcatherium minimus</i> West, 1980  | Earliest late Miocene, Pakistan                                    |
| <i>Dorcatherium nagrii</i> Prasad, 1970   | Late Miocene, Pakistan, India                                      |
| <i>Dorcatherium minus</i> Lydekker, 1876  | Late Miocene to early Pliocene, Pakistan, India, China             |
| <i>Dorcatherium birmanicus</i> (Noetling, 1901)                                     | Late Miocene to early Pliocene, Myanmar                            |
| <i>Dorcatherium majus</i> Lydekker, 1876  | Late Miocene, Pakistan   |
| <i>Dorcabune welcommi</i> Ginsburg, Morales, and Soria, 2001                        | Early Miocene, Pakistan  |
| <i>Dorcabune anthracotheroides</i> Pilgrim, 1910                                    | Late Miocene, Pakistan   |
| <i>Dorcabune nagrii</i> Pilgrim, 1915   | Late Miocene, Pakistan   |
| <i>Dorcabune sindiense</i> Pilgrim, 1915  | Late Miocene, Pakistan   |
| <i>Dorcabune progressus</i> (Yan, 1978)   | Late Miocene, China  |
| <i>Dorcabune liuchengense</i> Han, 1974   | Early Pleistocene, China   |
| <i>Siamotragulus sanyathanai</i> Thomas, Ginsburg, Hintong, and Suteethorn, 1990    | Middle Miocene, Thailand   |
| <i>Siamotragulus bugtiensis</i> Ginsburg, Morales, and Soria, 2001                  | Early Miocene, Pakistan  |
| ? <i>Siamotragulus indicus</i> (Forster Cooper, 1915)                               | Early Miocene, Pakistan  |
| <i>Yunanotherium simplex</i> Han, 1986  | Late Miocene, China  |
| <i>Tragulus javanicus</i> (Osbeck, 1765)  | Extant, Southeast Asia   |
| <i>Tragulus napu</i> (G. Cuvier, 1822)  | Extant, Southeast Asia   |
| <i>Tragulus williamsoni</i> Kloss, 1916   | Extant, Southeast Asia   |
| <i>Tragulus kanchil</i> (Raffles, 1821)   | Extant, Southeast Asia   |
| <i>Tragulus nigricans</i> Thomas, 1892  | Extant, Southeast Asia   |
| <i>Tragulus versicolor</i> Thomas, 1910   | Extant, Southeast Asia   |
| <i>Tragulus ?sivalensis</i> Lydekker, 1882  | Late Miocene, India  |
| <i>Moschiola indica</i> Gray, 1852  | Extant, India  |
| <i>Moschiola meminna</i> Erxleben, 1777   | Extant, Sri Lanka, Dry Zone  |
| <i>Moschiola kathygre</i> Groves and Meijaard, 2005                                 | Extant, Sri Lanka, Wet Zone  |
| ? <i>Moschiola</i> sp. in Groves and Meijaard, 2005                                 | Extant, Sri Lanka  |
| <i>Hyemoschus aquaticus</i> (Ogilby, 1841)  | Extant, West Africa  |

Note: Modified from Pickford (2001a).

*Dorcatherium* because of its strong cingulum, which is lacking in *Hyemoschus*.

The Tragulidae have always been an exclusively Old World family. Miocene occurrences are reported from Southeast and South Asia (e.g., Pilgrim, 1915; Forster-Cooper, 1915; Prasad and Satsangi, 1968; West, 1980a; Han, 1986; Thomas et al., 1990; Zhanxiang and Yumin, 1991; Gaur, 1992; Guo et al., 2000; Ginsburg et al., 2001), Southeast, West, and North Africa (e.g., Hopwood, 1929; Walker, 1969; Whitworth, 1958; Hamilton, 1973; Pickford, 2001a, 2002) as well as Europe (e.g., Kaup, 1833; von Meyer, 1846; Thenius, 1952; Rinnert, 1956; Mottl, 1961; Bakalov and

Nikolov, 1962; Hünermann, 1983; Fahlbusch, 1985; Ginsburg, 1989; Ginsburg et al., 1994; Rössner, 2004) and testify to an early geographic division between Eurasian and African family branches. Their disjunct distribution in the modern world is thereby revealed to be a breakup of an earlier, much wider distribution extending over vast regions of Eurasia and Africa. Additionally, they were more common and more diverse in paleocommunities than they are today, and recently an adaptive success of tragulids, as even serious competitors to higher ruminants, in occupying a newly present wetland area in the middle Miocene of Central Europe has been documented (Rössner, 2004). There the

tragulids used the drying Eurasian relict basins of the Paratethys, side arm of the Tethys, with limnofluvial environments to immigrate to Central Europe and were quantitatively much better represented than the Pecora.

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