

E E P

Asiatic Equids

HUSBANDRY GUIDELINES

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2 HEMIONES: PLURIDISCIPLINARY QUEST OF THEIR IDENTITIES AND RELATIONSHIPS

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2.1 The Conservation Problem

2.1.1 Introduction

There are three different studbooks for regional populations of the hemione¹, one for Persian Onager (*Equus hemionus onager*, fig. 17), one for Turkmenian Kulan (*E. h. kulan*, fig. 18), and one for Eastern Kiang (*E. h. holdereri*, fig. 20).

To have three captive breeding programmes for populations of a single species is rare in general, and unique for zoo-living equids. Onager and Kulan are very similar phenotypically, and zoo visitors might be unable to distinguish them. A widespread opinion therefore questions if two different breeding programmes would not constitute a redundant duplication of efforts. Thus the profile of Onager and Kulans in zoos dwindles, sharpened by the competition for space by the more recently imported Kiang. Decreased fertility in an increasingly overaged population means the risk of longer-term extinction of the Onager herd in zoos. On the other hand, the Onager and Kulan studbook herds are based on fair founder numbers, each from well-defined geographic localities, and the survival of both populations is endangered in the wild too. The Onager, whose survival in zoos is jeopardised for the waning interest among keepers, is one of the most seriously endangered equids indeed. Hemiones breed without problems in zoos if keepers want them to do so. The bulk of the captive Onager herd is kept in west European zoos who therefore have a global responsibility for its management. Onagers were among the first ungulates to be imported in fair numbers from a well-defined locality to initiate an ex-situ breeding programme documented in a studbook. Now, the low profile of the Onager when "competing" with other species for attention by keeping institutions is likely to result in the end of that ex-situ programme which had proven successful over five decades.

2.1.2 The Approach

There is agreement that rational decisions on how to continue the captive management of *E. hemionus* are urgent. Doubts about the actual distinctness of Onager and Kulan contributed to the low profile of the former. In order to refresh the understanding of the systematic differentiation of the hemiones, the Equid Taxon Advisory Group (TAG) considered the launching of a pluridisciplinary research project, in which the Zoological Institute of Heidelberg University and the Musée National d'Histoire Naturelle-CNRS in Paris were to

¹ Hemiones are treated in this report as a single species (Formenkreis), *Equus hemionus*. The frequently applied term "Asiatic Wild Ass" is avoided in this report because a zoological-systematic sister group relationship of Hemiones and African true wild asses (*Equus africanus*) is questionable. Moreover, Hemione is preferred by us over the otherwise welcome suggestion by Schlawe (1986) to use the name "Kulan" as designation for the species *Equus hemionus*, because in Zoological Gardens (e.g. in the international studbook) "Kulan" designates the Hemiones from Turkmenistan only.

Fig. 17 Onager female (*Equus hemionus onager*) on the left side, Przewalski's horse stallion (*Equus ferus przewalskii*) on the right side. The difference in the body size of both species is obvious.

Fig. 18 Kulan stallion (*Equus hemionus kulan*)

Fig. 19 Khur stallion (*Equus hemionus khur*)

Fig. 20 Kiang group (*Equus hemionus holdereri*)

contribute an overview on this subject, and to supply new data filling existing gaps in air of knowledge.

Within this project, W. Zimmermann, co-chairperson of the Equid TAG, coordinated the activities initiated by her, and provided data on the population history and on the reproductive biology of the studbook herds. V. Eisenmann from the Muséum National d'Histoire Naturelle-CNRS in Paris studied hemione osteology and palaeontology and authored the osteology and palaeontology chapters. A. Schreiber from the Zoological Institute of Heidelberg University contributed genetic data obtained from the analysis of samples supplied by many zoos, analyzed the taxonomic relevance of the herds' reproductive seasonality, and authored the draft version of the present report (other than the morphometric and palaeontological sections). The final edits and conclusions rest on the discussion among all authors.

This work is based on the contributions, and insights, of additional persons. Peter Fakler (Heidelberg) assisted with competence in the investigation of the RAPD-DNA data. L. Schlawe (Berlin) kindly presented historical illustrations and unpublished notes on his views of hemione systematics for study. Dr. Gertrud Neumann-Denzau (Essen), Mr. Schlawe, and Dipl.Biol. Claus Pohle critically read the manuscript. Mr. A. Johannes, member of the expedition team to capture the Hagenbeck Onager herd, kindly provided unpublished maps and notes on this capture. Michel Baylac (Paris) helped with the statistical analyses of the osteological data, and Ralf Engelhorn critically reviewed the statistics of reproductive seasonality. Cecilia Rodriguez Loredó (Paris) helped to realize the map (Figure 22). Table 1 benefitted from the suggestions of Gertrud and Helmut Denzau.

The following zoos and game parks contributed samples for the genetic investigation: Germany: Augsburg, Berlin (Tierpark), Berlin (Zoo), Cologne, Mundenhof, Munich, Nürnberg, Rostock, Stralsund, Stuttgart. Great Britain: Marwell, Whipsnade. Switzerland: Basel, Oberwil. Netherlands: Rotterdam. France: Paris (Vincennes Zoo). Finland: Helsinki. Czech Republic: Usti nad Labem. Saudi Arabia: Taif.

The osteological material studied is preserved in the following collections:

France: Muséum National d'Histoire Naturelle-CNRS, Paris, Laboratoire d'Anatomie Comparée and Laboratoire des Mammifères et Oiseaux; Muséum d'Histoire Naturelle, Lyon. Germany: Zoologisches Museum der Humboldt-Universität, Berlin. Museum Alexander Koenig, Bonn; Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt; Zoologisches Institut und Zoologisches Museum, Hamburg; Institut für Haustierkunde, Universität Kiel; Zoologische Sammlung des Bayerischen Staates, Munich. Great Britain: British Museum (Natural History), London. India: Material collected by Dr. Nita Shah, studied at Dehra Dun. Iran: Faculty of Sciences of the University of Teheran, material partly collected by Marjan Mashkour. Netherlands: Zoologisch Museum, Amsterdam. Rijksmuseum van Natuurlijke Historie, Leiden. Russia: Zoological Museum of the Moscow University; Zoological Institute, St. Petersburg. Switzerland: Naturhistorisches Museum, Basel; Muséum d'Histoire Naturelle, Genève. Czech Republic: National Museum (Natural History), Praha. United States of America: Field Museum of Natural History, Chicago; Museum of Comparative Zoology, Harvard University, Cambridge. American Museum of Natural History, New York. Smithsonian Institution, Washington. Peabody Museum, Yale.

The Cologne Zoo funded the laboratory consumables, and travel costs to the museums of Bonn, Hamburg, Kiel, and Praha. Grants from various organizations to Heidelberg University are acknowledged too.

2.1.3 Hemiones Briefly Introduced

Horses and hemiones are the only modern representatives of Palaeartic equids. Hemiones are the swiftest-running equids existing, and used to have a very large distribution. Before anthropogenic fragmentation of their range into isolated patches, they roamed in the steppes and semideserts of east Europe, Anatolia, the Middle East, Central Asia and Tibet. Even now, they inhabit ecologically extreme habitats, like summer-hot and winter-cold deserts, salt pans, or even mountainous regions above 5000 m altitude. Being grazers which also take herbs and succulents, hemiones perform regular or opportunistic migrations in search of pasture and water, or to evade high snow cover. The latest comprehensive overview on hemione biology, including impressive photographs of free-living specimens, herds, and habitats, has been published by Denzau (1999).

Populations have declined since early historic times (Duncan 1992), and less than 2000 Turkmenian Kulans now survive, chiefly in one single sanctuary, the Badkhyz Reserve of Turkmenistan (with a few small reintroduced herds elsewhere), some 2000 Khurs in one single location in the Little Rann of Kutch Sanctuary of northwest India, and probably less than 800 Onagers in two populations occur in Iran. Only the Dziggetai of the Gobi desert (fig.4), estimated at several thousand individuals, and the Kiang, estimated at 60 000 – 70 000 specimens (Schaller 1998), remain in fair numbers.

Hemiones are traditional zoo animals and have been bred in captivity since the 19th century. However, none of the survivors of World War II was among the founder stock of the current studbook herds. From 1954 on, 55 Onagers from Iran, 120 Kulans from Turkmenistan, and 14 Kiangs and two Dziggetais from China were imported into European and American zoos. In 1954 Carl Hagenbeck organized an expedition to capture 20 Onagers near Chabeiky/Abarqu and Marvast in east-central Iran (Mohr 1961, Johannes pers. comm.). The seven founder animals of the Hagenbeck line produced most Onagers of the studbook population, while another 13 specimens were distributed to the zoos of Rotterdam, Munich, Chicago, Philadelphia and the Catskill Game Farm. Subsequent imports from Iran reached the zoos of Paris, Tilburg, Tel Aviv, New York and San Diego. The last wild-caught pair arrived at the Kabul Zoo in 1973. The first Onager foal after World War II was born at Hagenbeck's zoo in Hamburg where 77 Onagers have been bred until this date. All 120 founders of the Kulan zoo population originated from the Badkhyz Reserve in Turkmenistan. Turkmenian Kulans were imported, with but few exceptions (Whipsnade, Kolmarden), to zoos in east Europe (e.g. Moscow, Prague, St. Petersburg, Askania Nova, Leipzig, Tierpark Berlin). The last wild-caught Kulan arrived in 1987. Today, a few herds can be seen in west European collections too (e.g. Antwerp, Helsinki, Madrid, Nürnberg, Rome). In America, Kulans are restricted to the Canyon Colorado Equid Sanctuary (New Mexico, U.S.A.), where they number more than 100. The most famous breeding place is the Falz-Fein Biosphere Reserve <Askania Nova> in the Ukraine (more than 200 Kulans bred). The first captive Kulan foal was born at the Prague Zoo. Tierpark Berlin and the zoos of Riga, Moscow, Munich and San Diego imported 14 Kiangs

between 1957 and 1990. Riga Zoo was the first of these collections to breed Kiangs in captivity, and has produced 82 Kiang foals till date.

In 1998 the "International Studbook of Asiatic Wild Asses" (Claus Pohle, Tierpark Berlin) registered 371 Turkmenian Kulans in 58 collections, 146 Iranian Onagers in 28 collections, and 93 Eastern Kiangs in 15 collections. The Onager and Kulan populations rose until the early 1980s when the interest of zoos in these equids began to flag (fig.21). Maximum numbers of captive births occurred in 1982 (68 Kulans) and 1984 (28 Onagers), but zoo herds have been stagnant or slightly decreasing ever since. Only the Kiang population has been increasing up to date in captivity, with the maximum birth number of 18 Kiang foals observed in 1998. The interest in breeding captive hemiones (other than Kiangs) has waned during the 1990s. The Onager studbook herd certainly cannot survive if this neglect continues.

2.2. Available Taxonomic Schemes

2.2.1 First Descriptions and Arrivals in Zoos

Some authors assume that hemiones were domesticated to draw chariots across Southwest Asia (Mesopotamia, Anatolia, Iran, Turkmenistan) between 6000 B.P. and 2.000 B.P., since when they were replaced by horses. This opinion is not altogether accepted but the use of more or less tame hemiones to breed hybrids with asses or horses is discussed (Clutton Brock 1992). Artistic representations and bones do not tell much on this subject. Thus the genetic composition of extant wild populations may, but need not, have been altered by human interference (e.g. by feral specimens).

The extinct Anatolian and/or Syrian hemiones were apparently still known to several ancient Greek naturalists, who designated them with the same name, hemiones (half-asses), as the domestic mules, although they were aware that these "free-living mules" were fertile. Despite this ancient acquaintance with the species, hemiones were (re)discovered for science by Peter Simon Pallas only in 1775. Shortly after describing *Equus hemionus* from a Dziggetai obtained in the Daurian steppes (Transbaikalian Siberia), Pallas reported on hemiones from Kasbin (Qazvin) in north Persia of which two had been sent to the St. Petersburg Zoo (one mare arrived alive), zoos have been instrumental in the scientific recognition of hemiones and in studies of their genetic diversity. After various reports not meeting the prerequisites of a taxonomic description, Boddaert finally coined the technical name *Equus onager* for this north Persian population in 1785.

In 1832 two Khur stallions were imported from India to London Zoo, and shortly after three Indian Khur arrived at the Ménagerie du Jardin des Plantes in Paris, where a successful breeding group was established. Two other specimen were kept at the Knowsley Menagery in England. *Equus khur* (fig. 19) was described by Lesson as a third species.

The Syrian hemione arriving at the London Zoo in 1854 was the first of a small number kept there over the years; offspring was given to Amsterdam Zoo (L. Schlawe unpubl., pers. comm.). Two female Syrian hemiones from the desert between Baghdad and Palmyra were sent to the Ménagerie at Paris, and served for the description of a fourth species, *Equus*

Demographic data of Equus hemionus between 1949 - 1999

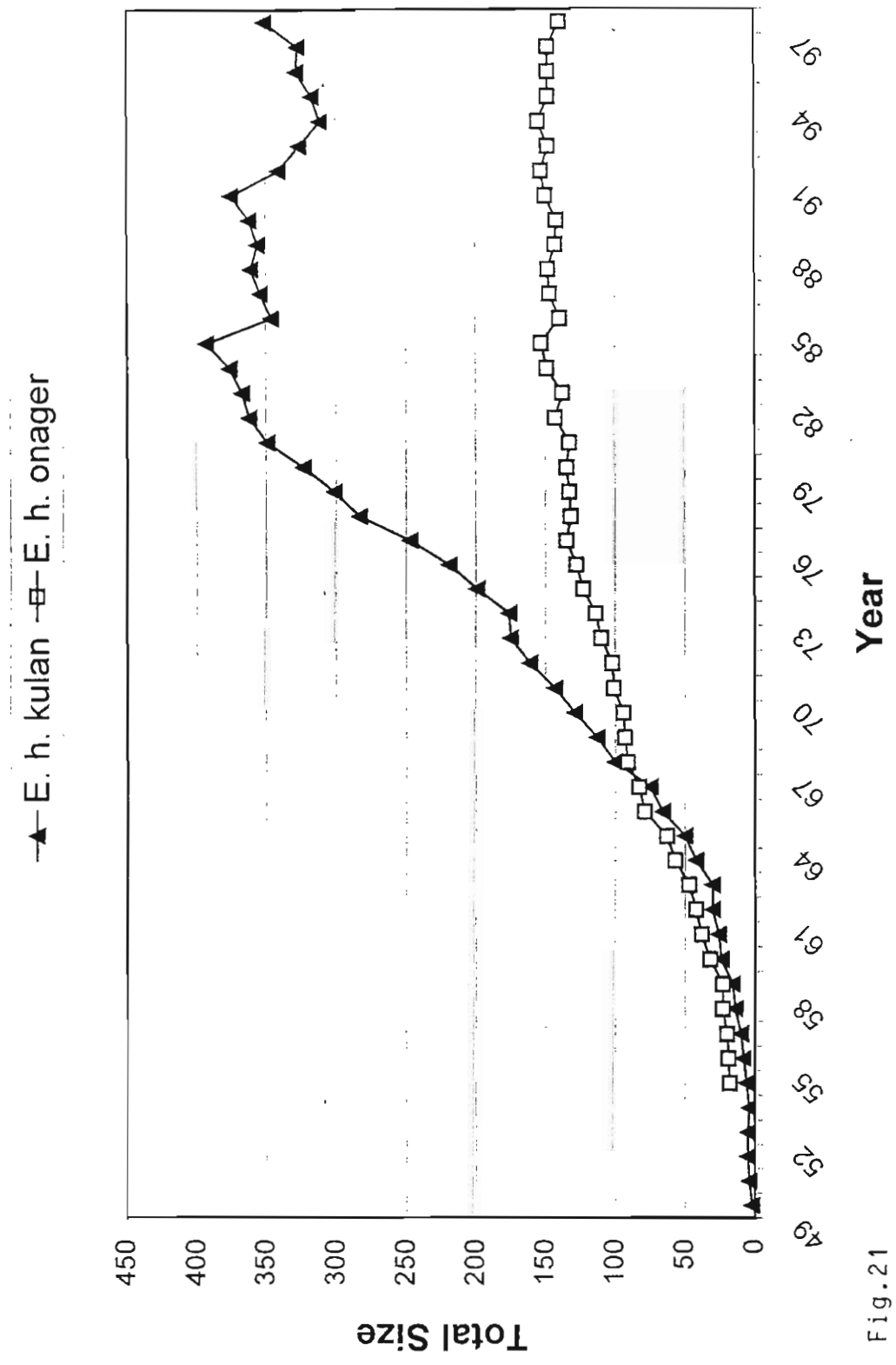


Fig. 21

hemippus (half-horse), by I. Geoffroy St. Hilaire. Other Syrian hemiones went to Schönbrunn Zoo (Vienna), where a small group was kept in the period of the 1850s-1870s. A single specimen, caught near Aleppo and imported to Schönbrunn before World War I, became the last survivor of Hemippe; it died at Vienna in 1927.

Single Dziggetais were kept in Hagenbeck's Menagery at Hamburg and in the zoos at Hamburg, Frankfurt, Askania Nova and Woburn Abbey around the turn of the 19th/20th centuries (Schlawe 1986). Since World War II, Dziggetais have been confined to Chinese zoos with very few exceptions (e.g. Berlin, Halle). Dziggetais were among the rarest hemiones exhibited in zoological gardens, which imported about the same number of them than of the now extinct Hemippe.

Since the publications by Moorcroft (1841) and Hué (1850), the existence of the Tibetan Kiang was known to European zoologists. In 1894 the Duke of Bedford imported four Kiangs to Woburn Abbey, England, and sent offspring to Philadelphia Zoo, the first New World collection (1909) to keep Kiangs. Other zoo Kiangs lived in Amsterdam, Berlin, Munich, Paris, Vienna, and New York (L. Schlawe unpubl., pers. comm.).

2.2.2 Systematic Concepts and Revisions

We are aware that to ask anyone to enter into the details of hemione taxonomy is to ask for great concentration and patience. In consequence we propose two levels of reading the present chapter, the first exposition being a kind of abstract of the second part which is documented in greater detail. At both levels, we hope that the schematic map (fig. 22) and the synoptic historico-taxonomic overview (Table 1) will help the reader through this labyrinth.

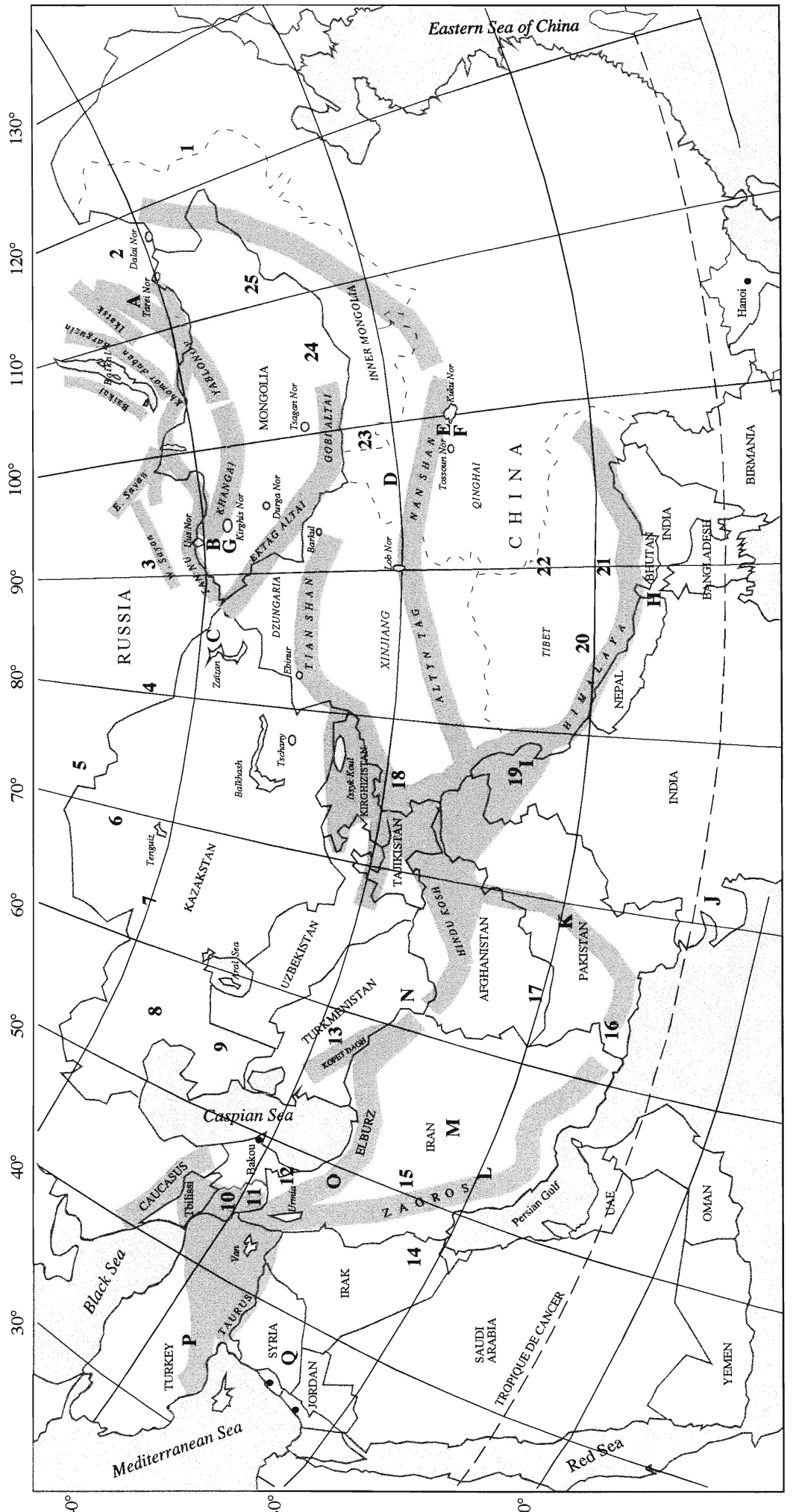
2.2.2.1. Overview

A cursorial look at the map (Fig. 22) will show that the historical distribution of hemiones covered an area ranging between at least 30° to 50° N and 40° to 110°E. A look at Table 1 and Table 2 will show that at least 17 specific or subspecific names have been proposed. These taxa were at various times referred to the genus *Equus*, *Hemionus* and *Microhippus*, and at other times to the genus *Asinus*. In that case, they were usually referred to as Asiatic wild asses to distinguish them from the true African wild asses.

In order to avoid, at least just for now, cumbersome trinomial nomenclature and taxonomical discussions, we will refer to each hemione by a vernacular name with geographical specifications. Thus, Eastern, Southern, and Western Kiangs are those hemiones who presently inhabit the mountains of Tibet, Sikkim, and Ladakh, in three disjunct populations. We use the name of Dziggetai for hemiones living in Mongolia east of the Dzungarian Gates, and the name of Kulan for hemiones living west of the Dzungarian Gates, down to the east of Caspian Sea. The name of Khur is used for the Indian hemione of the Little Rann of Kutch desert, and the name of Onager for all hemiones from Iran. The extinct Syrian hemione is referred to as Hemippe.

Figure 22. Type localities (A-Q) and extreme historic localities (1-25) of hemionus, with references on the pages of Stielers' Atlas (1908) where they can be found.

- A. *E. hemionus hemionus*, Tarei nor, 50°115° (Matschie 1911, Stielers, p. 58)
 B. *E. hemionus castaneus*, Kirghiz nor = Khyargas = Hyargas, 49°93° (Matschie 1911, Stielers, p. 57)
 C. *E. hemionus finschi*, NE of Zaissan = Saissan nor, 48°84° (Bannikov 1981, Stielers, p. 57)
 D. *E. hemionus luteus*, Suring gol, between Chami and Su-tschou, 40°30'96° (Matschie 1911, Stielers, p. 62)
 E. *E. kiang tafeli*, NE of Tossun nor, 37°97° (Bannikov, 1981, Stielers, p. 64)
 F. *E. kiang holdereri*, SW of Koko nor, 37°100° (Matschie 1911, Stielers, p. 62)
 G. *E. hemionus bedfordi*, Kobdo province = Hovd, 49°93° (Matschie 1911, Stielers, p. 57)
 H. *E. kiang polyodon*, N Sikkim, S of Himalaya, 27°89° (Bannikov 1981, Stielers, p. 63)
 I. *E. kiang kiang*, Ladakh province, 34°77° (Matschie 1911, Stielers, p. 62)
 J. *E. hemionus khur*, Little Ran of Kutch, 23°71° (Matschie 1911, Stielers, p. 63)
 K. *E. hemionus blandfordi*, Sham Plains, 29°20'69°40' (Pocock, 1947)
 L. *E. hemionus hamar*, Fars province, 29°53° (Matschie 1911, Stielers, p. 61)
 M. *E. hemionus babrum*, Yazd = Jesd, 32°55° (Matschie 1911, Stielers, p. 61)
 N. *E. hemionus Kulan*, Badkhyz, 35°50'61°40' (Groves & Mazak, 1967)
 O. *E. hemionus onager*, Qasvin area = Kaswin, 36°50° (Matschie 1911, Stielers, p. 61)
 P. *E. hemionus anatolicus*, Anatolia (Haltenorth & Trense, 1956)
 Q. *E. hemionus hemippus*, deserts between Palmyre and Bagdad, 34°37° (Matschie 1911, Stielers, p. 52-61).
1. Nonni river (Dauren), 48°124° (Solomatin 1973, Stielers, p. 58)
 2. Argun river, N of Dalai nor, 50°118° (Matschie 1911, Stielers, p. 58)
 3. Minussinsk, 54°92° (Solomatin 1973, Stielers, p. 57)
 4. Kulundin steppe, 53°80° (Solomatin 1973, Stielers, p. 57)
 5. Barabin steppe, 55°74° (Solomatin 1973, ° Stielers, p. 57)
 6. Koktschetau mountains, 53°70° (Solomatin 1973, Stielers, p. 58)
 7. Turgai province, 50°62° (Bannikov 1981, Stielers, p. 58)
 8. Left bank of Ural river, 47-51°53° (Bannikov 1981, Stielers, p.47-49)
 9. Ust Urut, 43°56° (Bannikov 1981, Stielers, p. 49)
 10. N of Ararat, 40°44° (Bannikov 1981, Stielers, p. 49)
 11. Middle Arax river, 39°46° (Bannikov 1981, Stielers, p. 49)
 12. Talysch, 38°48'30' (Bannikov 1981, Stielers, p. 49)
 13. Kopet Dag mountains, 39°56° (Matschie 1911, Stielers, p. 61)
 14. ³Irak Arabi², 32°46° (Matschie 1911, Stielers, p. 61)
 15. N of Kohrud mountains, 33°51° (Matschie 1911, Stielers, p. 61)
 16. Coasts of Oman and Persian Gulf (Matschie 1911)
 17. Hilmend = Helmand province, 31°64° (Matschie 1911, Stielers, p. 61)
 18. Kashgar, 39°76° (Solomatin 1973, Stielers, p. 62)
 19. W Tibet, 33°77° (Denzau 1999, p. 50)
 20. SW Tibet, 30°85° (Denzau 1999, p. 50)
 21. S Tibet, 28°90° (Denzau 1999, p. 50)
 22. Central Tibet, 33°90° (Denzau 1999, p. 50)
 23. 42°99° (Denzau 1999, p. 46)
 24. Gurbun Saikhan, south of, 43°30'105° (Andrews, 1933)
 25. SE Mongolia, 45°114° (Bannikov, 1981)



Although the very names of hemione and Hemippe indicate morphologies intermediate between asses and horses respectively, there are persisting tendencies to lump hemiones and asses inside the genus *Asinus* (Sclater 1862, Schwarz 1930, Groves and Mazak 1967). Most authors, however, and in particular most of those who concentrated on osteology (George 1869, Orlov 1968, Eisenmann this study), insist on a generic (or at least sub-generic) separation between asses and hemiones.

Fig. 22, and Tables 1 and 2, show that it is the contact zones between taxa that generated most discussions among taxonomists. Indeed, the external phenotypes of geographically adjacent hemione populations, as well as their osteological characters, seem either to intergrade or to present a mosaic of features. When there are sharp differences of size or coloration, and relatively extended geographic distances separating populations (as in the case of the Hemippe and the rest of the hemiones), there is hardly any controversy.

Discords and confusion usually result from incorrect geographical interpretations (see below for the case of two names, *castaneus* and *bedfordi*, given to Dziggetais presumably inhabiting closely adjacent sites), and/or from mistaking the different colours of summer and winter coats for racial differences, and from various interpretations of poorly known, and somehow possibly transitional forms connecting two "good" subspecies (in particular *finschi*, *hamar*, and *blandfordi*), or even from incorrect associations between museum skins and wrongly associated skulls (in the case of the Nepal Kiang).

Whatever the generic name, the number of species recognized from morphological revisions varies from one (George, Schwarz, Antonius, Orlov, Solomatin, Bannikov; Eisenmann) or two (Lydekker, Groves and Mazak) up to four (Sclater, Bourdelle). Even taking the odd type specimens of questionable taxa into consideration, opinions diverge as to the internal grouping of species or subspecies. Ancient papers and reviews based on osteology (Gray, Sclater, Schwarz, Orlov, Eisenmann) insist on the close similarity between Kiangs and Dziggetais (or at least between Kiangs and the easternmost and southernmost Dziggetais). This similarity is not just a matter of larger body size. Moreover, Bannikov (1981) and Orlov (1968) reject absolutely the idea of a specific distinction between Kiangs and Dziggetais.

Concerning the central issue of this paper, i.e. the degree of similarity between Onagers and Kulans, Matschie, Lydekker, Schwarz, Groves and Mazak, Denzau, and Eisenmann (this study) distinguished Kulans and Onagers as subspecies, some earlier authors even at a specific level (e.g. Matschie and Lydekker, see Table 1). For Eisenmann (this paper), skulls of Khurs segregate better than skulls of other hemiones.

Thus, revisions of the genetic diversity of hemiones resulted in different taxonomic schemes. These differences partly reflect the transition of systematic zoology from the binomial to the trinomial nomenclature (i.e. the advent of the subspecies category), or the preference, in any one historical period, of either structuralistic zoology (accepting many taxa in its attempt to reflect the order of nature in names) or functional biology (stressing the biological cohesion of all actually or theoretically interbreeding individuals). Such changes will not be commented upon in detail, because they are not relevant for understanding real population genetic patterns. Other changes refer to the (sub)generic classification of the species in the (sub)genera *Equus*, *Asinus*, *Asinohippus*, *Hemionus* or *Microhippus*, which again are not informative for

nepalensis 1959 nep	polyodon 1847 p	kiang 1841 k	holdereri 1911 ho	tafeli 1922 t	hemionus 1775 hem or h.	luteus 1911 l	bedfordi 1911 bed	castaneus 1904 c	finschi 1911 f	kulan 1967 kul	onager 1785 ona or o.	bahram 1947 ba	hamar 1841 ha	blandfordi 1947 bl	khur 1827 kh	hemippus 1855 hp
Gray 1849, 1852	Equus onager															
Slater 1862	Asinus onager															
George 1869 (Osteology)	Equus hemionus															
Matschie 1893	Equus															
Lydekker 1904	Equus hemionus															
Matschie 1911, 1922	Equus hemionus															
Schwartz 1930	Equus hemionus															
Antonius 1933, 1938	Equus hemionus															
Pocock 1947a, 1947b	Equus hemionus															
Bourdelle 1948, 1955	Equus hemionus															
Groves & Mazak 1967	Equus hemionus															
Orlov 1968 (Craniology)	Equus hemionus															
Solomatin 1973	Equus hemionus															
Bannikov 1981	Equus hemionus															
Denzau & Denzau 1999	Equus hemionus															
Eisenmann (Osteology)	Equus hemionus															

Table 1

Evolution of hemione taxonomy from 1849 to modern times. This historical overview is not exhaustive but intends to present a sample of concepts proposed by various authors. The purely or predominantly osteological works are specified. According to the opinion of each author, taxa are separated by bold lines when they are distinguished at the specific level, by plain lines when the distinction is subspecific, and by dots when the authors mention marked resemblances or intergradations. Question marks refer to not studied or doubtful taxa. A rejected taxon is indicated by a cross. Most abbreviations are easy to understand or explicit inside the uppermost boxes. *M* is for *Microhippus*.

understanding population evolution. Still other opinions evidently have but limited relevance because authors had not seen sufficient specimens of most taxa.

Table 2: Taxonomic descriptions of hemiones (*Equus hemionus*, Pallas 1775). The names marked by an asterisk were considered as designating valid taxa in the revision by Groves and Mazák (1967).

Taxon	Author
* <i>Equus Kiang</i>	Moorcroft 1941, Travels in the Himalayan Provinces 1, 312
* <i>E. polyodon</i>	B.H. Hodgson 1847, Calcutta J., N.H. 7, 469
* <i>E. Kiang holdereri</i>	P. Matschie in Futterer, K. 1911: Durch Asien 3, V. Zoologie (Nachtrag), 21
<i>Microhippus tafeli</i>	P. Matschie, Sitzungsber. naturforsch. Freunde Berlin 1922, 68
<i>Asinus equioides</i>	B.H. Hodgson, 1842, J. Asiatic. Soc. Bengal 11, 287
<i>Asinus kyang</i>	Kinloch 1869, Large Game shooting in Tibet, 13
<i>Asinus equuleus</i>	H. Smith in Jardine W.: The Naturalist's Library, Mammals, Volume 12
<i>Hemionus Kiang nepalensis</i>	E. Trumler 1959, Säugetierkundl. Mitt. 7, 23
* <i>Equus hemionus</i>	P.S. Pallas, 1775 Nov. Comm. Acad. Sci. Imp. Petropolit. 19, 394-417
<i>Equus Onager castaneus</i>	R. Lydekker, Novit. Zool. 11, 1904, 520
* <i>Equus hemionus luteus</i>	P. Matschie in Futterer K., 1911: Durch Asien 3, V. Zoologie (Nachtrag), 24
<i>E. hemionus bedfordi</i>	P. Matschie in Futterer K., 1911: Durch Asien 3, V. Zoologie (Nachtrag), 23
<i>Equus hemionus finschi</i>	P. Matschie in Futterer K., 1911: Durch Asien 3, V. Zoologie (Nachtrag), 24
* <i>Asinus hemionus Kulan</i>	C.P. Groves, V. Mazák 1967, Z. Säugetierkunde 32, 321
* <i>Equus Onager</i>	Boddaert 1785, Elenchus Animalium 1, Rotterdam, 160 P.S. Pallas 1780, Acta Acad. Sci. Imp. Petropol. 1 P.S. Pallas, 1781, Neue Nord. Beytraege 2, 22 Hablizl 1783, Neue Nord. Beytraege 4, 89-92
<i>Asinus hamar</i>	H. Smith in Jardine W.: The Naturalist's Library, Mammals, Volume 12, 351
<i>A. Dziggetai</i>	Wood 1879, Natural History (London), 138
<i>Microhippus hemionus bahram</i>	J. Pocock 1947, J. Bombay Nat. Hist. Soc. 47, 143
<i>Microhippus hemionus blanfordi</i>	J. Pocock 1947, J. Bombay Nat. Hist. Soc. 47, 143
* <i>Equus Khur</i>	Lesson 1827, Manuel de Mammalogie,
<i>Asinus indicus</i>	W.L. Sclater 1862, Proc. Zool. Soc. London
<i>Equus indicus</i>	George 1869, Ann. Sci. Nat. Zool. 12
* <i>Equus hemippus</i>	I. Geoffroy St. Hilaire 1855, Compt. Rend. Acad. Sci. Paris 41, 1214
* <i>E. hemionus var. syriacus</i>	M. Milne-Edwards 1869, Nouv. Arch. Mus. Hist. Nat. Paris 5, 40

2.2.2.2 Detailed History

Naturalists (e.g. Gustav Radde, Otto Finsch, and Alfred Brehm) travelling through Central Asia and seeing Kulans east of the Caspian Sea before their extermination, affiliated them with Dziggetais rather than with Persian Onagers (cf. Radde and Walter 1889). It is impossible to judge how far this opinion was influenced by incorrect assumptions of the 18th century zoologists: the original diagnosis of *Equus hemionus* and *E. onager* suggested the presence of a dark shoulder cross in *E. onager* but not in *E. hemionus*, which in reality is a polymorphic character observed in several regional populations (though perhaps in different frequency). However, Radde (1862; Radde and Walter 1889) had met considerable numbers of wild hemiones, and thus his statements on the extinct regional populations from Turkestan² might be of interest. Von Eversmann (cited by Lichtenfeld 1878) described Kulans imported from the region between the Caspian Sea and Lake Aral to Orenburg. These Kulans were said to lack shoulder stripes, and to differ as to the breadth of the white lateral areas bordering the dark dorsal stripe. Such white lateral borders of the dorsal stripe are characteristic of Onagers, but are absent from Dziggetais, which, according to Radde (1862), extended westwards to the Caspian Sea. The members of an expedition by German zoologists to west Siberia in summer 1876, during which Otto Finsch had purchased the hides near Lake Zaysan, and which later became the type of the subspecies *finschi* (see below), were also convinced that the Kulans of that location were rather westerly Dziggetais.

M. George's (1869) early monograph stands out of its time for details and depth, which paved the way for later studies, although formal subspecies were ahead of that time. He insisted particularly on a sharp distinction between hemiones and asses.

Paul Matschie (1893) suggested six "local races" which were however designated by binomial nomenclature. The Turkmenian half-asses were lumped with the Mongolian ones as *E. hemionus*, and separated from the two Persian races, *E. onager* (north Persia) and *E. hamar* (Fars province in SW Persia). From the geographic ranges Iran was the contact region where the Mesopotamian *E. hemippus*, the Indian and Baluchistan *E. indicus*, and the north *E. onager* met.

Richard Lydekker (1904) introduced subspecific names and described a new subspecies of Dziggetai (*castaneus*) from a locality just east of the Dzungarian Gates. The confusion around *castaneus* will be discussed below. For Lydekker (1904) Kiangs, Dziggetais (but not the new subspecies) and Kulans were subspecies of *Equus hemionus*. Surprisingly enough, the second species, *Equus onager*, included his new subspecies of Dziggetai (*E. o. castaneus*) together with *E. o. onager* (NW Iran), *E. o. indicus* (India, Baluchistan, Afganistan, and Eastern Iran), and *E. o. hemippus*. Moreover, Lydekker discussed a specimen from Baluchistan (British Museum 1891-5-13-1) that was later to be made the type of a new subspecies (*Microhippus hemionus blanfordi*) by Pocock (1947). This specimen was considered to be a hybrid of Kiang and Khur by Groves (1963), and ultimately as a representative of a transitional population

²**Turkestan**: dry, mountainous region of Central Asia, extending from the Caspian Sea (55°E) to the Gobi (Lop Nor; 90°E). **Western** (Russian) **Turkestan**: Kzakhzstan, Kyrgyzstan, Tajikistan, Turkmenistan, Uzbekistan, NE part of Afghanistan. **Eastern** (Chinese) **Turkestan**: Xinjiang Uygur Autonomous Region of China

between Khur and Onager (Groves and Mazak 1967). Eisenmann, however, sees this enigmatic form as fitting quite well the pattern of an Indian Khur.

Matschie's second revision (1911), based on new material collected in east Kazakhstan and central east Asia, modified his previous concept (see above) of one very widespread race *hemionus* for all Turkmenian and Mongolian-Chinese populations. An eastern Kiang, *holdereri*, was distinguished. The Kazakh population was separated from the Mongolian Dziggetai as a new subspecies *finschi*, based on two specimens collected from Zaysan Nur, just west of the Dzungarian Gates. According to the collectors of these two Kulans, O. Finsch and A. Brehm, the Kazakhstan Kulans resembled Dziggetais rather than Persian Onagers. The Dziggetai range within Mongolia (*hemionus*) was reduced by introducing the subspecies *luteus* for provenances from Gansu Province, just north of Nan Shan (China), and *bedfordi* for a specimen from west Mongolia which ultimately was inferred to originate from exactly the same site as the taxon *E. o. castaneus* of Lydekker (just east of the Dzungarian Gates) and should be considered as a younger synonym of it. Later, Matschie (1922) suggested even more Kiang taxa (cf. Table 2) which did not, however, gain acceptance of subsequent zoologists.

Lydekker (1916) modified his first classification into a three-species concept comprising *E. kiang*, *E. hemionus* and *E. onager*. *E. hemionus* was now restricted to Mongolia. *E. onager castaneus* was still recognized as a disjunct, unexplained outpost of its species. Solomatin (1973) admitted a transitional form between Dziggetais and Kulans but wrongly synonymized *castaneus* with *finschi* (a later synonym). Denzau (1999) also recognized *castaneus* (including *bedfordi* and *finschi*) and commented on its closer resemblance to Kulans than to Dziggetais, although Bannikov (1981) speculated that the intensively reddish-brown *castaneus* was a Dziggetai in bright summer coat.

Ernst Schwarz (1930) reported on a stallion imported to Berlin zoo from southern Iran. This specimen was thought to resemble the Khur more closely than the Onager. For Schwarz the single species *Asinus hemionus* was subdivided into six subspecies: the Syrian *A. h. hemippus*, the eastern *A. h. khur* (including hemiones from India, Baluchistan, and south Iran), *A. h. onager* (northwest and central Iranian plateau), *A. h. kiang*, *A. h. hemionus* (eastern, southern, and western Dziggetais), and *A. h. bedfordi* (the synonym of the westernmost Dziggetai *castaneus*) covering all Kulans (including the easternmost population *finschi*). Two specimen from Askabad and Merv (Merw, Mary) in southern Turkmenistan, close to the Iranian boundary, are included into this Kulan concept. Thus the Kulan ranged from the northern rim of the Iranian plateau through Western Turkestan up to the Altai foothills. Somewhere in southern Iran the Hemippe and the Khur were thought to meet.

Otto Antonius (1932), the director of Schönbrunn Zoo, Vienna, was in a perhaps uniquely privileged position, having bred and observed different hemione subspecies (Syrian, Persian, Turkmenian, Tibetan). This practical experience included hybridization experiments with other equid species (Antonius 1940, 1944, 1951). From that background, Antonius (1932) addressed the problem of the Kulan's identity in some detail. He conceded that Kulans from Turkmenistan differed phenotypically from the central Persian Onagers he knew, but deemed this difference as insufficient to justify taxonomic separation ("Standortsformen beschränkter Verbreitung"). The phenotypic differences perceived are reviewed below (Chapter 3.1). Antonius compared this situation with the transition of Burchell's zebras to other Plains zebras

in south Africa, and lumped all hemiones from north and east Iran, Western Turkestan and NW India into one subspecies, *E. hemionus onager*. The contact zone of this taxon (comprising all Khurs, Onagers and Kulans) with the Mongolian Dziggetai is unknown because the contact populations had been exterminated before investigations began. The south-west provinces of Iran were inhabited by *E. h. hemippus*, as concluded from the comparison of a hemione imported from southwest Iran to Schönbrunn Zoo (which appeared to have combined certain characters of both Onager and Hemippe), with an undoubted Hemippe imported to Vienna from the desert north of Aleppo (Syria). The latter was the last Hemippe kept in a zoo, and probably the last survivor of that subspecies. Antonius (1932) thus recognized only four subspecies of hemiones, *E. h. kiang* and *E. h. hemippus* for the two more clearly deviant and geographically terminal populations, and *E. h. hemionus* and *E. h. onager* for the ones inhabiting the area in between. His classification uses the fewest taxonomic names of any recent revision. However, Antonius was explicitly aware of phenotypic differences within those subspecies, and within the broad taxon *E. h. onager* in particular. His taxonomic philosophy thus differed from other early authors who aimed to designate each phenotype separately.

Frederick Harper (1940, 1945) listed the Kulan as *Asinus hemionus finschi*, reviving Matschie's name for the Kazakh population. *Asinus hemionus onager* was restricted to the western part of the Persian plateau, and the transition to the adjacent subspecies was considered uncertain. Southeast Iran was provisionally reserved for *Asinus hemionus khur*.

Edouard Bourdelle's studies of zebras, asses, and horses were based not only on skeletons and skins, but also on internal anatomy (dissections of digestive, respiratory, and other organs, published from 1932 to 1941). Unfortunately, he did not publish on the internal anatomy of hemiones. In 1948, he clearly distinguished three groups of hemiones: Hemippes, Kiangs - Dziggetais (including castaneus), Onagers - Khurs. In his contribution to the *Traité de Zoologie de Grassé* (1955), he eventually separated the Kiangs at a specific level (*Hemionus kiang*).

Eberhard Trumler (1959) defended the opinion that the Kiang was a distinct species, *Hemionus kiang*. In addition to recognizing the described subspecies *H. k. kiang* and *H. k. holdereri*, he introduced *H. kiang nepalensis* subsp. nov., supposedly living on the southern slopes of the Himalaya. Unfortunately this new subspecies was described on the basis of a skin of a southern Kiang (probably not from Nepal) wrongly associated with skulls of Tibetan ponys, as clearly demonstrated by Groves and Mazak (1967).

Vladimir Heptner et al. (1961, translated 1989) distinguished three groups of hemiones, the geographically terminally distributed *E. hemionus hemippus* and *E. h. kiang*, and the geographically intervening group containing *E. h. hemionus*, *E. h. finschi* and *E. h. onager*. Heptner et al. (1961) felt unable to subdivide the intermediate group, chiefly from a lack of material. Like Antonius (1932) they lumped Onagers, Khurs, and Kulans from the Badkhyz Reserve into one subspecies, *E. h. onager*. The enigmatic, poorly documented Kulans from Kazakhstan were tentatively recognized as *finschi*, and supposed to resemble the Badkhyz Kulans rather than the Dziggetai, an opinion later confirmed by Denzau (1999). Badkhyz Kulans were included in *E. h. onager*, because all alleged phenotypic differences from Persian Onagers were said to be covered by individual variation entirely. Somewhere in the north of

Badkhyz, Onagers defined as this must have met the *finschi*-population of the larger-bodied *hemionus*-group, but the locality of this zone was obscure.

Erna Mohr (1961) described the Hagenbeck import herd of Onagers from the perspective of an experienced mammal systematist. She emphasized the phenotypic polymorphism of this herd which was the most important founder group for the Onager studbook in zoos. Head shape, ramnoses, the breadth of the dark dorsal stripe, and several other characters were said to differ among the individuals of that herd in a manner which could provoke the idea that different "geographical races" were represented.

The museum revision by Colin Groves and Vratislav Mazak (1967) is most commonly used as the modern reference on hemione systematics. Two species are distinguished, based on exterior characters and partly on osteology: *Asinus kiang* (three subspecies) and *Asinus hemionus* (five subspecies). *A. kiang* is subdivided into the western Kiang *A. k. kiang*, the eastern Kiang *A. k. holdereri*, and the southern Kiang *A. k. polyodon*. *A. h. hemionus* includes the easternmost and one of the westernmost Dziggetais (*castaneus*) together with the easternmost Kulan *finschi*. *A. h. luteus* includes the southernmost Dziggetai and the synonym of *castaneus*. *A. h. onager* includes all hemiones from Iran, *A. h. khur* is the Indian form, and *A. h. hemippus* the Syrian population. *A. h. kulan* is formally described as a good subspecies based on material from the Badkhyz Reserve in Turkmenistan (close to the Iranian border), and includes Kulans from Turkmenistan and northwest Afghanistan, but explicitly not the easternmost *finschi* from Kazakhstan. Apart from details of body pigmentation (larger white muzzle field, white jaw angle), the elongated occiput of Kulan skulls and the lower position of their orbitae, when compared with Onagers, are mentioned as diagnostic characters. Groves and Willoughby (1981) and Groves (1986) eventually accepted the conservative view of a single genus *Equus*, with hemiones grouped in the subgenus *Hemionus* Stehlin and Graziosi, 1935. In that subgenus there are two species, *Equus (H.) hemionus* and *E. (H.) kiang*. A single specimen from Baluchistan, originally described as a new subspecies (*Microhippus hemionus blanfordi*) by Pocock (1947), and interpreted by Groves (1963) as a hybrid between Kiang and Khur, was later perceived (Groves 1986) as an intergrade between Khur and Onager.

Georges Dennler de la Tour (1975) commented that the habitat of the hemiones was bisected by the high-altitude central Asiatic mountain chain running from the Sibero-Mongolian border mountains, and the Altai, southwards to the Hindukush. The eastern Dziggetai-plus-Kiang-population was thus somewhat isolated from the Turkmenian Kulan (and the other southwest hemiones too). This argument, remarkably never published before, will be discussed in connection with the Pleistocene glaciations of these mountains in chapter 3.7. Dennler de la Tour (1975) recognized a distinct subspecies of hemiones, living to the west of the supposed mountain divide (Dzungarian Gates), but used for them the newer name *Kulan* (created for the hemiones from Turkmenistan and northwest Afghanistan by Groves and Mazák 1967), instead of the earlier designation *finschi* available for the hemiones from Kazakhstan (see above).

Andrej Bannikov (1981) explicitly negated the view that the Badkhyz Kulans were taxonomically distinct from the Persian Onagers, but retained *E. hemionus hemippus*, *E. hemionus finschi* and *E. hemionus khur* along with three subspecies of Kiang and *E. hemionus hemionus* (including *luteus* and *castaneus*).

Lothar Schlawe (1986, and unpublished manuscripts) compiled numerous historical notes on hemiones, and investigated the history of Dziggetais in zoological gardens. He favoured to compare within-population with between-population variation, and to understand the

population structure of a continuously distributed species, rather than to subdivide the hemione species into subspecies. In the case that subspecies names were found indispensable for practical purposes, Schlawe favoured the concept by Antonius (1932).

Peter Grubb (1993) recognized, in his treatment of Equidae for the "World List of Mammalian Species", three species again, *Equus kiang*, *E. hemionus* and *E. onager*, following the results of a cladistic approach to *Equus* phylogeny by Bennett (1980) whose basic material and data were unfortunately never published.

There is thus no consistent use of taxonomic names, neither is there a clear trend over time. Apart from formal discussions as to whether the hemiones comprise one, two, or three species, or more, there is at least agreement on the subdivision of the small and medium-sized hemiones from the area west of the Dzungarian Gates, India, and the Middle East for which the number of proposed taxa has varied from one to eight (Tables 1, 2).

2.3. The Evidence Augmented and Reconsidered

2.3.1 Body Size - External Appearance

There are three body size groups in hemiones: The extinct Hemippes were the smallest (shoulder height: 97-100 cm); Khurs (fig. 19,) Persian Onagers (fig. 17) and Turkmenian Kulans (fig. 18) have intermediate size (shoulder height: 108-127 cm); Dziggetais (fig. 2) and Kiangs (fig. 20) are largest (shoulder height: 117-141 cm). Broad samples of body size measurements in the medium-sized population group appear not to be available, but estimations from limb bone measurements will be provided in chapter 3.2.3.

There are more descriptions published on the colouration and externally visible body markings³ of hemiones than on their internal anatomy or genetics, and these characters provided arguments in favour of, or against, the validity of controversial subspecies. However, this literature actually has limited use for microtaxonomy. Most early authors generalized peculiarities of individual phenotypes as being diagnostic for whole populations. Some presumably confused winter and summer coats with pigmentation differences at the population level, although winter coats are often more greyish (and longer-haired) than summer coats are. Other authors dismissed the validity of subspecies only because the external phenotypes were individually polymorphic, and did not distinguish each and every individual from two regional populations. Both opinions are not compatible with a population biological approach: pigmentation patterns and body stripes are subject to genetic polymorphism just as molecular markers or chromosomes are (see below), and are influenced, in principle, by natural selection, genetic drift, and gene flow and introgression. This means that in genetically variable,

³ Body markings which have been discussed as possibly diagnostic for certain populations include: Pigmentation intensity, extent of white areas bordering the dark dorsal stripe, presence of dark shoulder stripe and rufous transversal leg stripes, breadth and length of dorsal stripe, etc.

cursorial-migratory and phylogenetically young species qualitative population markers distinguishing each and every specimen from two adjacent geographical populations cannot be expected (just as differently fixed genotypes of polymorphic genes, proteins or chromosomes cannot be). Genetic divergence starts by changing the frequencies of polymorphic traits.

Some authors stated that Persian Onagers were especially variable in their external phenotypes (Antonius 1932, Heptner 1961, Mohr 1961). This greater polymorphism would coincide, if pertinent, with the greater craniometric variation documented for Persian Onager than for any other regional hemione population (Eisenmann and Shah 1996, and unpubl. data).

Having expressed this limitation, a few accounts still are of interest. Shoulder crosses were reportedly more common in some populations from central Iran than from further north or east, although numerical frequency data are absent (Morier 1818, Antonius 1932, Goodwin 1940, Radde and Walter 1889). Mohr (1961) emphasized, however, the individual variation of that character. Onagers from northwest Iran were said to be generally lighter, the whitish underparts reaching further upwards, or, as otherwise stated, the dorsal field of darker pigmentation not descending as far down on the lower body parts, and the legs, than in more northerly populations (Antonius 1932). Morier (*A Second Journey through Persia*, London 1818; cited by Lichtenfeld 1878) reported that shoulder stripes were particularly common in Onagers from east Persia, whereas those from the steppes around Teheran had transversal brown leg bands instead. Mohr (1961) reported that these leg stripes were not easily detected in winter coats. The general hue of Persian Onagers was reported as being more reddish than in the more brownish Turkmenian Kulans (Denzau 1999). In that regard, Turkmenian Kulans would somewhat approach the Mongolian Dziggetais. The pigmented field on the lower jaw was said to follow the jaw's contour in Onagers, but to leave a triangular white jaw angle in Kulan instead (Groves 1986, Denzau 1999). This pattern appeared to us less visible in the Onager lineage imported to Paris Zoo, possibly originating from the Touran region in northeast Iran, than in the Hagenbeck herd originating from another site in central Iran. The longitudinal extension of the dorsal stripe, whether it ends at the tail basis or continues to the tail tuft, may distinguish Khurs from Onager and Kulans (Groves and Mazák 1967). Kulans and Dziggetais have shorter ears (165-178 mm) than Khurs (187-210 mm) (Groves 1986), but the specimen numbers on which these measurements rest are unknown. Hemippes had much shorter ears than the other populations with certainty. The different ear lengths of Kulans and Khurs might be reflected in the larger auditory orifices in the skulls of the latter (cf. below).

A useful tabulation of the external appearance of various hemione populations by Denzau (1999) provides further information on this subject. Of the subspecies accepted by Groves and Mazák (1967), the Iranian Onagers and the Badkhyz Kulans display the by far greatest similarity, in fact it is doubtful if they can be distinguished at all on the basis of external characters.

2.3.2 Osteology

2.3.2.1 Skulls

A multivariate (factorial correspondence) study of quantitative and qualitative characters of 350 skulls of all living equid species, including 56 hemiones (Eisenmann 1979, 1980) revealed gradual differences between six major groups, i.e. horses, hemiones, asses, Mountain zebras, Grevy zebras, and Plains zebras. Although discrimination is possible at a level of more than 90%, craniometric differences are slight, and individual variation such that there are few qualitative or quantitative characters distinguishing each and every individual of one of the six species groups from each and every of another group. No segregation was found among the hemiones, except that Kiangs had some tendency to cluster separately in one of the analyses. hemione skulls were found to be morphologically intermediate between horses and asses, but closer to the latter. The sample numbers, however, were poor.

Principal component analyses were recently performed on 160 skulls of hemiones (35 Kiangs, 29 Dziggetais, 32 Kulans, 37 Onagers, and 27 Khurs) and of 17 Somali wild asses, using various combinations of sub-samples. When all hemiones and asses were analysed together, size differences separated Somali wild asses, Dziggetais, and Kiangs as one group from all the other, smaller-bodied taxa. Moreover, Somali wild asses and Khurs were the only taxa to segregate perfectly on some axes. When only hemiones were analysed, Khurs were again the only population to segregate well, better so than Kiangs (to which they appeared, unexpectedly, close to along the second axis). Onagers and Kulans tended to form distinct clusters, but only on the 5th and 6th axes which explained only a small portion of the total variance. Other analyses of different subsamples confirmed the relatively good segregation of Khurs. The Kiang subspecies could not be distinguished other than by the slightly larger size of eastern Kiangs (the sample sizes were, however, not satisfactory). Size differences apart, Kiang and Dziggetai skulls did not differ markedly, and Kulan skulls resembled Dziggetai crania more closely than they resembled Onager skulls. In summary, Onager and Kulan skulls were very close to each other but could still be distinguished as groups.

Discriminant analyses of form, and discriminant analyses using log-shape ratios (performed by M. Baylac, National Museum of Natural History, Paris), revealed a clear gap between asses and hemiones. Among hemiones, the skulls of Khurs and Onagers were closest to Somali wild asses'. Mahalanobis distances (overall indices of morphological similarity between two groups, synthesizing differentiation into numerical scores) were smaller between Kiangs and Dziggetais, and between Kulans and Dziggetais, than between Kulans and Onagers.

Kiangs and Dziggetais have higher faces than the other hemione taxa, sometimes they looked 'ram-nosed'. That could be viewed as an adaptation to breathing cold and dry air (like in Saigas) or to eating hard vegetation (Orlov 1968). Data confirming these ideas are, however, absent. Mohr (1961) observed ramnoses as an individually polymorphic trait in the Hagenbeck Onager herd imported to Hamburg Zoo. Khurs (like Somali wild asses) have larger external auditory orifices, wider supra-occipital crests, and longer crania and choanae (inner openings of the nasal cavity into the mouth cavity). Large ears may support the temperature regulation (export of excess heat) of animals living in very hot climates. If the interpretation proposed by Orlov (1968) is correct, the relatively longer crania of Kiangs and Khurs (and of Hemippes)

can be functionally explained by the more important development of the temporal muscle relative to the masseter. In reverse, the shorter crania of Onagers relative to Kulans would indicate a preeminence of the masseter muscle over the temporal which may have some implication in the processing of food. Other differences are less easy to interpret functionally. Khurs (like Somali wild asses) have wider supra-occipital crests, and longer choanae. Onagers differed from Kulans by having longer muzzles and narrower supra-occipital crests. The long choanae of the Khurs and Somali wild asses could perhaps be related to the volume of the nasal cavity, again a potentially adaptive feature in fast-running animals. But what about the relatively short, but wide, choanae of Onagers, Kulans, and Dziggetais? Measurements of the volume of the nasal cavity are not available for any hemione population, and any possible relationship between the position, and the shape of the choanae and their implications on respiration and thermoregulation volume remains speculative. Kulans connected Onagers with Dziggetais in skull shape, but there were no qualitative markers in skull morphology to recognize each Kulan and Onager skull. Skull polymorphism produced scatter and overlap among the regional populations which could be identified statistically from series of skulls rather than on an individual basis.

Onager skulls (originating from any place in Iran) appeared more polymorphic than those from each other population. Iran has been reported as the meeting place for up to three subspecies (cf. above). Although most of our skulls were from zoo-bred Onagers, there is thus a possibility that skulls from geographically adjacent subspecies, e.g. Onager, Khur and Hemippe, or from transition zones among these, had been mixed into the Onager skull sample of the present investigation. The suggested range boundaries, and the supposed transition zones in Iran have never been mapped, and many of the Onager skulls collected in the wild had no precise origin, thus there was no way to circumvent this possible problem, or to remove its possible influence in retrospect.

2.3.2.2 Teeth

Tooth size, and protocone lengths, of the upper molars (cheek teeth) differed less among hemione populations than their skulls or limb bones did. The dentition characters of all populations (excluding the Hemippe) overlapped (Eisenmann and Mashkour 2000). The same was true for the lower cheek teeth, but one peculiar pattern of the double knot seemed to be relatively frequent in Kiangs, Dziggetais, and Kulans, but very rare in Khurs and Onagers.

2.3.2.3 Limb Bones

The main differences between hemiones are purely a matter of size (Eisenmann and Mashkour 2000). All variables of Kiangs, Dziggetais, and Kulans were larger than the corresponding variables of Onagers; all the variables corresponding to the Hemippes were smaller; Khurs were intermediate. Hemippes were so much smaller than all the other subspecies that there would be "room" for another subspecies in between. It is interesting to note that the fossil *E. hemionus binagadensis* (Eisenmann and Mashkour 1999) fills this size gap.

Hemione populations can reach markedly different shoulder heights. Body size generally follows a north-south cline. As mentioned before (Chapter 3.1), good data on shoulder height are rare or absent. Therefore, their extrapolation from the limb bone measurements appeared to be of interest. Unfortunately, the evaluation of shoulder height from limb bone measurements is a rather awkward matter. From experience, the absolute values do not appear reliable. One may, however, trust with some confidence the relative differences between 'absolute' values calculated in the same way. Such estimations were attempted, using the average lengths of metacarpals and metatarsals of five Hemippes, 29-32 Onagers, 13 Kulans, 2-3 Khurs, 7-10 Dziggetais, and 9-10 Kiangs. The individual data on the shoulder heights and metapodials of seven Onagers were used too. Assuming that Hemippes reach shoulder heights of 100 cm and Kiangs maximum heights of 142 cm, the interpolations for the other populations suggested the following values: Kulans average at about 130 cm shoulder height, and Onagers at about 124 cm. The mean heights thus appear to differ by 6 cm; the maxima, however, would be the same. Khurs appear to be smaller (about 110 cm ?) than Onagers.

The relative sizes of different bones are not altogether identical for all hemiones. Dziggetais exhibit relatively short proximal segments (Humerus, Femur, Radius, and Tibia) in comparison to the more distally located elements (MC III, MT III, PhI A and P). Dziggetais thus appear to be more 'cursorial' than the other hemiones.

Another obvious, but perhaps not significant, difference was observed in the third phalanges: these were relatively wide in Kiangs and Kulans, but relatively narrow in Dziggetais, Khurs, and Hemippes. Wide third phalanges might augment the contact surface of the hooves with the substratum on which an animal walks, and could thus be adaptative when walking or running on soft soils (e.g. on mud, snow or sand). Snow and/or sand are indeed part of the natural environments of Kiangs (Groves, 1974, 91-92) and of Kulans (Bannikov, 1981, 36, 41-42). Bannikov (1981, 40), however, stated that the biotopes were similar for Kulans and Dziggetais, and Denzau (1999, p. 45) provided the illustration of a very impressive Dziggetai track in sand. Accordingly, one would rather expect Dziggetais to have as wide third phalanges as Kiangs and Kulans have, if the above-mentioned interpretation were pertinent. Unfortunately, only small sample series of phalanges are available (three Hemippes, twenty Onagers, ten Kulans, three Khurs, four Dziggetais, and seven Kiangs). Morphological differences in mechanically stressed bones, as phalanges in a cursorial animal are expected to be, could well be due to the modificatory influence of the soil substratum, rather than to genetic adaptation.

2.3.2.4 Critical Evaluation and Conclusions

In general, museum collections include a greater number of isolated skulls than complete skeletons. Therefore the present data are rather poor as far as limb bones are concerned. They are even dramatically limited for Khurs and Hemippes. In Khurs, the database could be augmented in principle because the Khurs are still extant. For the extinct Hemippes, the only possible increase of the sample basis could be expected from the still unstudied specimens preserved in the museum at Vienna (Austria). Onagers and Kulans exemplify other problems. Nearly all of the few Kulan skeletons in museums originated from one locality, the Badkhyz Reserve, and this restricted geographic sample could result in an underestimation of the morphometric variance (similarly, almost all Khur skeletons originated from the Kutch

Reserve). By contrast, nearly all Onager bones in museums are from zoo-bred specimens: although relatively numerous samples are available for study, skulls and limb bones could have suffered from the old age of the zoo specimens, and from life under zoo conditions. Accordingly, their variation may be artificially inflated. Denzau (1999) and several other authors (see above) pointed to the possibility of genetically different hemione populations in Iran. If so, the larger osteological variation of the Onager museum sample could also be due to overlooked microtaxonomic heterogeneity. For Dziggetais and Kiangs, yet other difficulties arise. Apart from the problem of tracing the exact origin of samples, there is regionally unbalanced material: no Dziggetai skeletons at all, and only few skulls were studied from northern Mongolia or Transbaikalian Siberia, and of the perhaps subspecifically distinct southern Kiang. Last but not least, Hemippes must be omitted from discussion due to the present state of osteological knowledge.

These limitations notwithstanding, the present osteological database supports a single-species concept for all hemiones (other than Hemippes), and a closer resemblance (especially of Khurs and Onagers) to asses than to horses. Still, hemiones do appear clearly distinct from asses. Bergmann's law might explain the obviously larger body size of Kiangs and Dziggetais, and the slightly larger size of Kulans, when compared with Onagers and Khurs. Within the hemiones, Khurs are the regional population segregating best from the others by cranial morphology; unfortunately there are almost no data on their limb bones. Onagers and Kulans are rather similar, but osteology does not suggest to lump these populations into one and the same subspecies.

2.3.3 Chromosomes

Equidae display an impressive example of fast cytogenetic evolution. Therefore karyotypes are of interest when comparing two similar, weakly divergent populations.

In zoo-living Onagers and Kulans Ryder (1978, 1986, 1990) observed three different karyotypes of $2n = 54$, $2n = 55$ and $2n = 56$. This polymorphism was due to a centromere-centromere fusion reducing chromosome numbers, i.e. all karyotypes might belong to the same translocation polymorphism. The present evidence may well indicate different cytotype frequencies at the population level, i.e. the common karyotype of the Badkhyz Kulans could be the rarer chromosomal pattern in Onagers, and vice versa. This hypothesis needs confirmation in a larger sample series. If so, population differences among Kulans and Onagers would be supported by chromosomal data.

Five eastern Kiangs revealed karyotypes of $2n = 51$ and $2n = 52$ chromosomes (Ryder and Chemnick 1990). This polymorphism involved the same elements that participated in the polymorphic system of Onagers and Kulans.

2.3.4 DNA, Proteins

2.3.4.1 The Evidence Introduced

This report does not intend to review the molecular evolution of equids, but focuses on the question of differentiation of Onager and Kulans. Various authors have addressed the molecular phylogeny of *Equus* species. Among others, George and Ryder (1986) and Oakenfull and Clegg (1998) provided a comparison of mtDNA and globin genes respectively, and also reviewed the pertinent literature. Various phylogenetic scenarios have been proposed, which agree on an earlier divergence of horses from hemiones/asses/zebras, the order of radiation of the latter proving difficult to unravel. Despite agreement on some sister-group relationships, e.g. the separation of horses from a group containing hemiones, asses and zebras, a complete and robust resolution of the species phylogeny of *Equus* is still absent.

George and Ryder (1986) did not observe different restriction endonuclease cleavage maps when the mitochondrial DNA of Onagers and Kulans were compared. The same kind of analysis separated Przewalski's horses from Domestic horses. A. Oakenfull (pers. comm.) compared sequence haplotypes of mitochondrial DNA (control region) in Onagers and Kulans, and did not observe qualitative differences either.

2.3.4.2 RAPD-DNA

On account of the rather low genetic divergence even among *Equus* species, a multi-locus approach has been chosen for the present subspecies/population analysis. The idea behind this choice rests on the fact that evolution proceeds by the accumulation of new genetic variants in few to some genes first, which gradually spread over the whole genome if divergence times are sufficient. Weakly divergent populations, especially in a young, actively speciating genus like *Equus*, cannot be expected to reveal genetic differences in each and every single locus which happens to be elected by the investigator. A multi-locus approach thus appears to be more representative to spot weak population divergence. Apart from assaying several segments of the genome, the selection of fast-evolving portions of the nucleic acids offer greater likelihood for detecting population divergence than phylogenetically more conservative loci do. Therefore, the method based on RAPD-DNA was chosen as being best suited for the present case (P. Fakler and A. Schreiber, unpubl. data). The RAPD approach (RAPD = "Randomly Amplified Polymorphic DNA") rests on the visualization of many stochastically selected loci spread over the genome, which happen to bind the generalized PCR (Polymerase Chain Reaction) primer sets used. The major portion of the DNA consists of non-coding sequences which mutate and evolve more rapidly than coding sequences (genes) do. Random samples from the total DNA, as assayed with the RAPD approach, refer to more rapidly-evolving, non-coding portions with greater probability than to transcribed genes. These are advantages of the RAPD approach for addressing the present problem. However, the RAPD approach produces DNA markers of unknown location and function in the genome.

When RAPD fragments which fulfilled certain prerequisites of reproducibility were assayed, Onagers and Kulans from the two studbook herds could be separated on the population level indeed.

Specifically, the following facts were revealed: each individual of the equids in our sample panel (hemiones, Somali wild asses, Grevy's zebras, Plains zebras, Przewalski's horses) was correctly referred to its species, and two domestic donkeys tightly clustered with Somali wild asses. All hemiones clustered together inside the tree based on the genetic distances between individuals of all the mentioned species: within the single hemione clade, one exclusive Onager group contained 30 Persian Onagers (out of 37 investigated), but no single hemione from another population. It clustered with a sister group within the hemione clade which contained 11 Kulans and two Onagers. The five Kiangs resided together in another subclade of the hemione group, but in common with one Kulan and three Onagers which did not fit the general pattern of the majority of their relatives. Two of these oddly-grouping Onagers belonged to the Paris-Zoo herd which had been imported from a different locality in Iran than the Hagenbeck herd. Three more oddly-grouping Kulans represented the lowest divergence in the hemione clade; these three odd Kulan samples originated from one zoo where Kulans and Onagers may (or may not) have been mixed in the past, no certainty being available any more.

When all interindividual genetic distances based on the RAPD-DNA markers were averaged, the mean Onager-Kulan-distances was higher than the mean genetic distances observed between individuals within the Onager or Kulan herds respectively. This means that the genetically most deviant Onager was less distinctly separated from the other Onagers than the Onagers as a group were from the Kulans. Ingroup variability (which cannot be expressed as heterozygosity in RAPD markers however) was higher in Onagers or Kulans than in Kiangs. This finding could indicate less genetic diversity in Kiangs, although larger sample sizes should be studied before this observation merits generalization.

2.3.4.3 Allozymes

A study of allozymes representing up to 25 biochemical-genetic loci in 136 equids from all species and several subspecies, including 38 Onagers, 17 Kulans, 6 Kiangs (and several Somali wild asses, Grevy's zebras, Plains zebras from two subspecies, Hartmann's Mountain zebras, and Przewalski's horses) revealed fair genetic polymorphism in *Equus hemionus*. The genotype distribution within and between hemione populations showed that: Heterozygosity (ingroup variation) in the herds of Onagers, Kulans and Kiangs was in the same order of magnitude; the allozyme-genetic distance between the Onager and Kulan samples, based on allele frequencies, was but a very small fraction of the genetic distance between the Kulan/Onager sample and Kiang; all hemiones emerged as one group; the three included hemione populations showed distances in accordance with their geographical proximity, i.e. Kiangs were closer to Przewalski's horse than Onagers or Kulans were, but Kiangs were more distant to the Somali wild asses than were Kulans or Onagers. There were no allozyme alleles in our sample to permit the identification of Kulans or Onagers on the basis of qualitative markers.

More subtle statistical approaches (e.g. heterogeneity analysis of genotypes) did reveal different genotype distributions among Onagers and Kulans, but these could be influenced by captive breeding in two studbook herds. Overall, allozymes are unable to discriminate Onagers and Kulans safely.

2.3.4.4 Conclusions from Molecular Studies

In summary, genetic comparisons thus far did not reveal qualitative molecular differences between Onagers and Kulans. This result could be expected from the rather low overall species differentiation in *Equus*. Broader DNA approaches based on the comparison of many, and presumably rapidly-evolving, segments of the genome showed some genetic differences between Onagers and Kulans. Unfortunately, there are presently no data which would allow any insight into the temporal scale of this divergence in RAPD-DNA. Thus the systematic meaning of these findings is very difficult to assess at the moment, until more data are available on the intraspecific population differences of other equid species.

Moreover, the controversial species phylogeny of *Equus* implies that the phylogenetic polarity of molecular markers (as for morphological characters) is difficult to estimate. Thus nobody knows at present which characters are phylogenetically primitive (plesiomorphic) and which ones derived (apomorphic). Rhinoceroses and tapirs are too distantly related to equids to provide useful outgroup comparisons to recognize which alleles were the plesiomorphic ones in equids, and which were acquired later by some or one equid species/subspecies only.

Finally, those population-ecological characters of equids which presumably influence rates of molecular evolution (and thus help to understand the taxonomic meaning of molecular or biochemical-genetic distances) are unknown or poorly known. These factors include dispersal rates and patterns, sex-specific dispersal, the severity of population crashes (e.g. by droughts), the relative inbreeding in populations by social structure and mating preferences, etc. All of these factors determine the evolution of genetic polymorphisms, and, by synergism or antagonism, may accelerate or decelerate the fixation of polymorphic alleles in different populations, depending on their population ecology and behaviour. If the overall genetic differentiation is as subtle as found among the Onager and Kulan populations by this study, the consequences of such ecological differences may well overlay the time-dependent acquiring of new genetic information by the mutation-selection process.

Therefore, the main conclusion of the available genetic data is to demonstrate very weak molecular differences between Onagers and Kulans on the population level, whose taxonomic meaning is not easily interpreted without a broader database on the population biology and genetics of free-ranging equid populations.

2.3.5 Reproductive Biology

Equids are polyoestrous species whose reproductive season is not narrowly confined. While most Onager and Kulan foals are born in late spring, offspring in fact might have good chances for survival if born during the summer months (see also chapter 3.6). From 1968 on, an interesting experience was made in the Hai-Bar Arava Wildlife Reserve (Israel). 3,3 Onagers and 2,3 Kulans originating from the wild came to Israel after having spent a certain time in Westeuropean and Easteuropean zoos, and were allowed to interbreed. However, the extent to which both founder groups actually contributed to the herd is unknown. Bill Clark, Chief Curator of the Reserve reported 1983 that "the onagers which occur naturally in Iran, made several biological adjustments to the Israeli environment, particularly its earlier spring and

hotter summer. The Israeli onagers now shed winter coats a month earlier than their Iranian counterparts, and the foaling season has also shifted nearly a month earlier". Until 1993 the population was growing and no fertility problems could be recognized. The simulation programme used by David Salz & Daniel Rubenstein (1995) predicted an expected population size of 250 adult females within 20 years, which is very high. At least this example shows that Onagers and Kulans may successfully build up a viable population. These specific results do not suggest a genetically determined foaling season in those concerned subspecies. If so, it would provide a strong argument for the separate management of the two studbook herds.

Zoo-living Kulans give birth earlier in the year, on average, than Onagers do: Kulan births peaked in May, and Onager births in June (Pohle 1972). This statistically highly significant difference is confirmed on the basis of a much larger sample basis of births documented in the studbooks by the 1990s (unpubl. data of the present study), which reveals differences of 15 days between the means of foaling peaks of the two studbook herds.

However, closer statistical analysis reveals that most of this apparent seasonal difference is due to the inclusion inside the Kulan birth date sample of the large breeding group of Kulans kept at Askania Nova, Ukraine, which is kept and bred under semi-natural steppe conditions. The birth seasonality of Kulans at Askania Nova follows a lognormal distribution having its peak considerably earlier in the year than most zoo herds do. By contrast, all Kulans and Onagers from city zoos display a rather irregular birth distribution over the year, which does not fit in most cases into a lognormal distribution (or any kind of regular statistical distribution). The variance of birth distribution around the year can be extremely high in many zoos. Evidently, only the Askania Nova herd approaches natural birth patterns. Removing the birth data from Askania Nova, zoo-living Onagers still give birth earlier than Kulans on average, but the difference reaches much lower statistical significance.

The birth dates of hemionids in zoos are to some extent influenced by climate. That is demonstrated in statistical tests by the influence of the geographical position of a breeding station within the European west-east gradient. This gradient of increasingly continental climate towards the east, measured by the geographical longitudes of the 37 breeding stations considered, is a demonstrable factor for the seasonality of Kulan and Onager births in zoos, but it explains but a minor portion of the total variance.

Our attempts to detect heritability of birth seasonality failed for Onagers, their birth dates of F1-generation not correlating with the birth dates of their parents at all.

In summary, Kulans give birth, on average, well before Onagers in any year, although this difference should be evaluated separately for city zoos and the steppe-enclosure at Askania Nova. This difference has only a doubtful genetic basis. Climate does have an influence, but most variance might be due to stochastic factors implied in the management practice of the keeping institutions (e.g. periodical separation of stallion from mares).

2.3.6 Palaeontology

For a palaeontologist, hemiones, as indeed any other animals, can only be defined on teeth and bone characters. Skulls are exceedingly rare and must be reasonably well preserved to be of any use. Thus, the determination of a fossil hemione usually relies on the morphology of upper and lower cheek teeth and limb bones. All modern hemiones have slender limb bones and most have long protocones on the upper cheek teeth (like horses) and shallow ectoflexids on lower molars (like asses). It is interesting to note, however, that the only mandible from Kazakhstan (Turgai) we were able to see has deep ectoflexids on the lower M1 and M3. A few other teeth and bone morphologies are characteristic but even less constant.

Skull characters of modern and fossil equids support the hypothesis of a common origin for all extant species of *Equus* not much earlier than the Lower Pleistocene, about 1 or 1.5 Ma ago (Eisenmann and Baylac, 2000). Hemiones certainly existed in North America during the Middle Pleistocene, about 0.7 Ma ago (Eisenmann 1992). The oldest Eurasian skull that could (very tentatively) be referred to a large hemione was found in the (Lower ?) Pleistocene of Yakutia and described as *E. colimensis* (Lazarev 1980). A large hemione is definitely attested at Tologoj (Transbaikalia, 15 km SW of Ulan Ude) by teeth and limb bones. Its age could also be Lower Pleistocene (Vogt et al. 1995). In the Middle Pleistocene, about 0.4 Ma ago, and up to the Neolithic about 5,000 years ago or even later (Willms 1983), the enigmatic and poorly represented *Equus hydruntinus* had limb bones as slender as hemiones, but its teeth were very small, the protocones of its upper cheek teeth were short, and the ectoflexid of the lower molars were deep. This form had a wide range and reached even Northern Europe. When limb bones of *E. hydruntinus* are found unassociated with teeth, they can hardly be distinguished from hemiones. Thus, the presence of true hemiones in Europe is still a matter of controversy.

The recent description of the fossil *E. hemionus binagadensis* (including skull material) from the Middle-Upper Pleistocene of Azerbaidjan, about 0,13 Ma ago, and its possible presence in the Holocene (less than 10,000 years ago) of Qazvin Plain in Iran (Eisenmann and Mashkour 1999), suggests the past existence of another subspecies of hemione intermediate in size between Onagers and Hemippes.

During the Upper Pleistocene, according to Forsten (1998), hemiones are frequent in northern and northeastern China (Neimongol, Gansou, Shaanxi, Shanxi, Hebei, Beijing Municipality-Choukoudian, Liaoning, Jinin, and Heilong-jiang). Thus in China hemiones occupied an area situated roughly north of 35° and were found as far east as Dalian (122°E, 39°N) about 20,000-40,000 years ago (Zhou Xuexin et al. 1990). The fossils referred to *E. nipponicus* in Japan, however, do not belong to a hemione but to a small horse (Forsten 1998).

According to Kuzmina (1997), hemiones were also found during the Upper Pleistocene as far north as the island of Begichev, east of Tajmyr (110°E, 75°N) and in Yakutia. The fossil remains of a rather large hemione, found in Holocene (third-fifth millenia BC) deposits on the left bank of Lower Volga and North of Caspian Sea, were referred to *E. h. finschi* by Kuzmina (1997).

2.3.7 Zoogeography

Evidence on the palaeo-ecology of many portions of the hemione range is poor, but a few aspects are probably relevant. First, the central Asiatic system of parallel mountain chains bisects the range of *E. hemionus* into one eastern group (Dziggetai, Kiang) and one southwest Asian group (Kulan, Onager, Khur, Hemippe). These chains have been repeatedly glaciated during the Pleistocene (Granö 1910, Reinig 1937). Eastern and southwestern populations of Hemiones could communicate mainly by the Irtysh Valley, south of Altai (about 47°N, 85°E), and by the Dzungarian Gates, south of Tarbagatai (about 45°N 83°E).

It seems that the climate was too dry to allow these two passes to be blocked by glaciers (Velichko 1993). But the degree to which periglacial conditions were or were not an impediment to the communication between eastern and southwestern populations is uncertain. A single isolation event or repeated occurrences of evolution in isolation are, however, probable and may explain the major genetic gap within *E. hemionus* between the large-sized eastern and the smaller-sized southwestern populations. A Holocene evolution of Kiang and Dziggetai is considered unlikely. A secondary contact zone with genetic introgression between previously isolated Eastern and Western hemiones must be postulated somewhere in the region from where the animals were exterminated by hunting during the last centuries.

In Kazakhstan dry conditions prevailed during the whole Pleistocene (Velichko 1993) although levels and extensions of the Caspian and Aral Seas have notably fluctuated during the Upper Pleistocene. During interglacials the classical mammoth fauna and the palynology bear evidence of steppe landscapes with islands of forests of birch and pine forest. During cold periods these forests disappeared and gave way to steppes. Heptner (1938, 1940) concluded from the range patterns of endemic rodents that what was then designated as Russian Turkestan was an old evolutionary center for desert mammals, especially psammophilous (sand desert) species.

The periglacial landscape history in Turkmenistan and Iran is much more poorly investigated, but glaciers were locally confined to single montane sites (von Klebelsberg 1922, Bobeck 1937). East Iran and Turkmenistan were never separated by glaciers. Still, Iran is covered largely by Quaternary sediments, and is known to have experienced a succession of pluvial phases, when deserts had retreated and lakes and forests had expanded (Butzer 1958). For example, some salt deserts in East and Central Iran (i.e. the area where the Hagenbeck onagers had been captured in the 1950s) were covered by lakes a couple of thousand of years ago (Bobeck 1961, Huckriede 1962). Contemporary relict populations of moisture-dependent plants, amphibians and snails found at sheltered sites (gorges, springs) amidst semidesert landscapes indicate that forest had spread into what now is semidesert during moister climate periods (Huckriede 1962, Scharlau 1964). There is insufficient evidence to produce maps of the previous vegetation belts in Iran, but the compiled evidence from geomorphology, soil science, zoogeography, vegetation history and traces of human agriculture in current desert regions indicate that the current hemione habitat throughout east Iran and Turkmenistan could have been fragmented into regional pockets of unknown extent and limits. Geomorphology (Scharlau 1958) suggests small-scale, regional diversity of Pleistocene climates, with glacial conditions on the north slope of the Elburz Mountains (and locally on the Zagros Mountains), patches with real pluvial climate, and areas with fluvio-pluvial or fluvial sedimentation regimes

where rivers reached the Central Iranian plateau from higher-rainfall source regions in bordering mountain chains. Today only fossil river beds remain. Plants (Rechinger 1951) and small mammals (Heptner 1940) endemic to the Persian region show small-scale mosaic-like, regional patterns in Iran, making this country a floristically and faunistically complex, small-structured biogeographical unit.

De Lattin (1957) identified the centres of endemism for the animal species of temperate-zone broad-leaved forests, and of open steppes and semideserts, at the southern fringe of the Palaearctic. These centers of endemism are interpreted as the refugial areas where either forest or dry land species could persist during climatically unfavourable periods during the Pleistocene and early Holocene. Of particular interest is the fact that each refugial area, recognized as one distinct center of endemic steppe/semidesert beetles, birds or mammals as identified by de Lattin (1957), was inhabited by one distinct hemione subspecies, as recognized by Groves and Mazák (1967):

1. Syroeremisches Zentrum - Syrian Hemippe,
2. Iranoeremisches Zentrum - Persian Onager,
3. Turanoeremisches Zentrum - Turkmenian Kulan,
4. Sindhoeeremisches Zentrum - Indian Khur,
5. Mongoloeremisches Zentrum - Dziggetai,
6. Tibetoeremisches Zentrum - Western Kiang, and
7. Sinoeremisches Zentrum - Eastern Kiang.

Of the subspecies recognized by Groves and Mazák (1967), only the range of the Southern Kiang (subspecies *polyodon*) does not correspond to one of these centres of endemic biota identified by de Lattin (1957). These centres of regional endemism might suggest contraction and subsequent re-expansion of arid land ecosystems during the pluvial moist phases, and the intermittent arid phases, accompanying in the Middle East and Central Asia the Pleistocene ice age fluctuations of more northerly latitudes. These centers are not equal in the degree (taxonomic depth) of the endemism they contain.

The close correspondance of subspeciation in *E. hemionus* with the refugial areas of the Pleistocene Asiatic desert fauna is a strong argument to claim a causal relationship. Probably these populations became isolated during pessimal ecological phases and regained population contact (and started to interbreed once more) when conditions grew more arid again. The pluvial phases of Iran continued well into the Holocene, thus any putative fragmentation of Onager habitats could be of relatively young date. Range fragmentation and subsequent re-expansion could provide a plausible explanation for understanding the, albeit weak, genetic difference among regional populations of a mobile, migratory large mammal without present-day barriers intersecting the range.

Eisenmann and Mashkour (1999) referred fossil bones from Transcaucasia and the Qazvin plain in Iran (being the area from where the original *Equus onager* Boddaert, 1785 had been obtained) to three different hemione-like animals in close spatial and stratigraphic-temporal proximity to each other (and with a horse species): the extinct and enigmatic *Equus hydruntinus* which had also roamed in Europe, the modern onager (*E. hemionus onager*) and a hemione intermediate in size between hemippe and onager, *E. hemionus binagadensis*. The

finding of two kinds of hemiones in the same general area suggest that taxonomic differences existed within short time periods across very small geographic distances.

2.4. Synthesis

2.4.1 Some Reasons for the Taxonomic Controversies and Uncertainties

Insufficient data on hemiones themselves: Not a single museum or other collection possesses a meaningful sample series from each population, thus taxonomists describing new (sub)species, and probably most of the early revisors too, had only partial personal acquaintance with the actual species diversity. Skeletons of some hemiones in particular are very few or completely lacking. No work whatever has been done on the eco-physiology, parasitology, disease resistance, etc., nor even on thermal regulation of hemione populations, although they are the swiftest-running equids on earth, and some populations live in some of the hottest and driest climates existing. Most portions of hemiones' range are among the zoologically least explored areas in the world; some populations inhabit political borderlands offering security problems until the recent past, or today. The problem is still more complicated by the next factor, i.e. the extinction of several populations, in particular those geographically intermediate between Transcaspia and Mongolia: There is no chance to decide whether the southwest Asian populations and the Mongolian Dziggetai were connected by populations displaying clinal character continuity, or separated by an abrupt step of character divergence indicating secondary population contact.

Extinction of geographically northern & central populations: Hemiones from Anatolia, Ukraine, Russia, and most portions of Kazakhstan and Transcaspia were exterminated without a detailed documentation of their phenotypes. The Badkhyz population is the only surviving herd of this central portion of the species's range, in between Iran and Mongolia, and it is located at the southernmost fringe. Even so, there are no good samples in museums for it either. Only few published illustrations of Turkmenian/Transcaspian kulans remain: One stallion from Askabad was mentioned (Zoolog. Jb. 4, 1889) and depicted (Sammlung Kaukas. Mus. 1, 1899) by Gustav Radde; a foal from Tedschen kept at Moscow was depicted by Pfizenmayer (C. Hagenbeck's *Illustr. Tier- und Menschenwelt* 4,2), and a ,stallion from Merw' (Merv, Mary) in southern Turkmenistan, kept at Berlin Zoo, by Heck and Hilzheimer (in Brehms *Tierleben*, 1915, Vol. 12). Schwarz (1930) provided another photo from that individual, but L. Schlawe (unpubl., pers. comm.) objected that this photo probably refers to an Onager mare bred at the Berlin Zoo from parents with questionable geographic origins. Finally, Antonius (1932) photographed a female foal imported from the Dascht i Chul desert, southeast of Merv (Merw, Mary), to Vienna Zoo. The zoos at Berlin and Munich kept further Kulans imported from the southern region of the former Soviet Union between 1929-1951. Of these, one specimen at least (i.e. the first mare of this group imported to Berlin) was repeatedly illustrated in zoo publications.

Taxonomic philosophies: Hemiones taxonomists had very different scientific aims and backgrounds. In general, the late 19th century authors have aimed to designate each discernible phenotype as a taxon of its own, a couple of them in a rather excessive manner. Later revisors, e.g. Antonius (1932) designated them as subspecies population groups, allowing for internal

(intra-subspecific) differentiation. Different taxonomies may even originate from formal, purely nomenclatorial obligations: taxonomic rules permit three names for a taxon at most (but not four). It is thus impossible to formally designate two hierarchical levels of population divergence within one species. If the more distinctively divergent Kiangs are just a subspecies of *Equus hemionus*, the minor divergences among the regional populations in the Middle East and India can hardly justify similarly ranking subspecific distinctions. From some publications it appears that the population group of southwest Asia (Onager, Kulan, Khur) and all or some segments of the larger-bodied Mongolian/Tibetan population group (Kiang, Dziggetai, etc.) have been separated as distinct, fully-fledged species, only to resolve that problem of equality at the level of smaller-ranked taxa.

Lack of phylogenetic insight: Ideally, systematists do not just describe and discuss the extent and subdivision of variation observed in a taxon, but aim at reconstructing the phylogenetic history of a species, including the spatial and temporal frame of its origin and dispersal. By demonstrating how the present biodiversity evolved, and how deeply the populations are divergent, they enable zoo curators to understand the background of the natural diversity they have to manage. Unfortunately, the phylogeny of the extant equid species has, despite many attempts, never been clarified. No phylogenetic tree suggested over the decades is robust, whether inferred from anatomy or molecules. There might be not one single sister-group relationship between two equid species on which all zoologists would agree. In the case of hemiones, it is in general impossible to recognize which subspecific characters are plesiomorphic (= primitive) and which are apomorphic (= derived), and thus to recognize polarities in their population histories. When characters are clearly adaptive and accordingly probably apomorphic, they may also be subject to parallel evolution and thus of awkward use in phylogenies.

Interpopulation variation can, as presumably body size does, follow bioclimatical rules like Bergmann's rule, evidencing adaptive response to climatic selection. The mountain-dwelling Kiangs are largest, the northern population group of hemiones is larger than the southern, and according to data on limb bones (Eisenmann and Mashkour 2000), Kulan are larger than Onagers. A fossil subspecies of size intermediate between the (smallest) Syrian Hemippes and the Onagers has also been documented. Natural selection by continuous ecological or climatic clines is expected to result in smooth morphological clines if the selecting agent is continuous. Other characters may also be adaptive, like the ramnose of Kiangs and Dziggetais (see above) or the long ear of the Khur, possibly the longest of all subspecies (although data are lacking for several other populations). This observation could be related to Allen's rule, body appendages becoming longer in populations needing to export excess body heat. The Khur is the only population to reach tropical latitudes (hot deserts in summer, frost-free during winter). Anyway Khurs, which are craniologically closest to Somali wild asses and better segregated than other hemiones, have in common with asses not only a larger external auditory orifice, but also wider supra-occipital crests, and longer crania and choanae. Pigmentation is certainly somehow correlated with the environment at the macrogeographic level, the desert and steppe populations being less intensively pigmented than the Kiang from cooler high-altitude habitats (Gloger's rule). In other cases, the adaptive nature of characters is quite hypothetical, although longer crania could be related to a preeminence of the temporal muscle over the masseter (Orlov 1968).

Quite a number of characters, however, have no evident explanation. Moreover the lack of understanding of the mechanisms of evolution obliges us to deal with a mosaic of data (osteological, external, biological, genetic, etc.) the relation and the functional meaning of which are unclear. When separate sets of data do not give concordant results, it is very difficult, and frequently impossible to rate which ones are the most important.

Insufficient data on the palaeoenvironments: Lack of insight into the phylogeny of a species may in some way be compensated by external information on habitat availability through time. The dynamic succession of (sub)humid and arid periods in the Pleistocene and early Holocene is likely to have affected the range continuity of inhabitants of dry lands, but both the temporal frame and the consequences for vegetation belts are very poorly known.

Therefore, disagreement on the validity of hemione subspecies is not necessarily due to an observed lack of population divergence, but rather to the problems inherent in retracing evolution in a young and rapidly-evolving genus. Many characters, whether anatomical or molecular, are well-conserved throughout *Equus*. Weak differences even at the species level between, e.g. a zebra and an ass, do not necessarily mean that this zebra is conspecific with that ass. On the other hand, different phenotypes do not necessarily imply different species. And clearly, subspecies are still more delicate to delimit and recognize than species are.

2.4.2 Proposed Frame of Reference

In the present state of our knowledge, there is sufficient evidence to conclude that the vast range of *E. hemionus* was, probably repeatedly, split into several range patches in the past, even before the anthropogenic extermination of that species began. Climatic changes during the Pleistocene and early Holocene have successively isolated and reunited again distinct populations. All hemione populations, including the Kiang, produce fertile population hybrids. In consequence, zones of secondary population contact might mean the evolution of hybrid zones and the mutual transgression of genes among the reunited regional populations. Our comparison of the craniometric, DNA, and protein differences between the regional populations of hemiones suggest that differentiation proceeded in a mosaic pattern, rather than into one unidirectional cline. This is compatible with a large degree of stochastic evolution.

The cursorial equids might have rather extensive gene flow, although no empirical data are available. If two phenotypically and genetically distinct populations are interconnected by transitory populations in areas of contact, any subspecies allocation must be somewhat arbitrary. Local populations, though different, may rather be stations within a genetic continuum which still can imply fair genetic divergence among the terminal populations along that cline.

Current mainstream taxonomy is not inclined to recognize zonal subspecies. But this practice of course means that really-existing genetic differentiation is not necessarily reflected in subspecies names, which by consequence cannot be directly used when zoo curators seek the units for breeding management. E.g. Bannikov (1981) claimed that the eastern Kiang (*E. h. holdereri*) and the Dziggetai (*E. h. hemionus*) met and intergraded till the 1930s to the extent that observers felt problems when deciding if that contact zone was inhabited by Dziggetai or

Kiang. This gradual transition in one region might mean that clear subspecies or even species allocation is senseless in that respective contact zone at least. Craniological studies by Orlov and Eisenmann found also but little if any differences between Kiangs and Dziggetais. There is no doubt, however, that Kiangs and Dziggetais are two different units for conservation management.

2.4.3 How Different are the Hemione Populations from Iran and the Badkhyz Reserve ?

The results of our research indicate that the investigated Persian Onagers and Badkhyz Kulans are differentiated at the population level by RAPD-DNA markers and skull shape, but not in genetic distances derived from allozyme frequencies. More subtle differences in protein genotypes could be due to captive breeding, and thus are difficult to interpret. The skull markers may or may not have adaptive value. Polymorphic karyotypes (Ryder 1978, 1986, 1990) may diverge on the frequency level, but mitochondrial DNA seems to be largely conserved, however (George and Ryder 1986; A. Oakenfull in litt.).

RAPD-DNA are chiefly based on individually undefined DNA segments, chosen randomly from the DNA by amplification primers with which these segments selectively bind. Since the major part of the genome seems to consist of non-coding sequences (different from genes, which are transcribed into proteins and influence the metabolism), randomly chosen fragments might represent, by and large, chiefly non-coding sequences. These represent the most rapidly-evolving portion of nucleic acids, and it is these markers that differ. Chromosomes are notoriously fast-evolving traits in equids, and it might be no spurious coincidence that their numbers appear to differ also between Onagers and Kulans, though only at the population frequency level. The divergence of skull characters, our example of polygenically inherited traits, is evident by multivariate statistics only, i.e. again at the population level, while there are no qualitative markers for regional stocks. Skulls as polygenic characters, which reflect the concerted action of many genetic loci, might be particularly good markers for weak phylogenetic separation, because initial divergence starts in few loci, but not necessarily in those pragmatically chosen when electing one or few genes to assess phylogenetic population divergence.

The possible weak differences in the outward appearance have been discussed above; these alone would not justify any separation of the Hagenbeck Onagers and the Badkhyz Kulans. However, the latter appear, from morphometric extrapolations, to be larger (shoulder height).

The reproductive seasonality is significantly different among the studbook herds of Onager and Kulan, but largely disappear when the Kulan herd at Askania Nova is removed from the comparison of the city zoo breeding groups. Still, there is a tendency for Onagers and Kulans to give birth, on average, at different times. This may or may not be important: heritability cannot be proven for that difference from the studbook pedigrees which however suffer from the enormous stochastic variance due to management. This variance may easily obfuscate subtle, natural patterns.

Thus the most plausible hypothesis is to view Onager and Turkmenian Kulan as populations which have evolved weak genetic differences by historical isolation. Both inhabit distinctive

centers of endemism identified by de Lattin (1957) from other organisms (other mammals, birds, beetles). Within the Middle East population group of medium-sized hemiones, the population differences are less evident between the Persian Onagers and Badkhyz Kulans than for example between Onagers and Khurs, suggesting either less stringent isolation in the past, or more efficient gene flow since the time when range continuity had developed again. Badkhyz reserve, the home of the extant Kulan, is located at the southernmost rim of its historical range, not very far (300 km) from Touran, and gene flow among the northeast Iranian and Badkhyz herds can be taken for granted under the currently prevailing climatic conditions. In any case, Onager and Kulan might be the least differentiated subspecies pair of the southwest Asiatic small races recognized by Groves and Mazák (1967).

2.4.4 Conclusions

Considering the theory-dependance of evolutionary biology, the definition of management units for breeding projects by simply accepting the nomenclatorial concepts of an author who happens to be the most recent one implies much risk of chance decision. E.g. Grubb's (1999) taxonomy of equids, in the "World List of Mammalian Species", is in fact a return to the two-species concept of *E. onager* and *E. hemionus* proper (and another, third species *E. kiang* for Tibetan hemiones) which sounded very up-to-date in the century of P.S. Pallas, the scientific discoverer of the hemione in the 18th century, but had fallen into complete disregard during the two centuries in between.

Considering the balance of all evidence, this report follows the conclusions by Antonius (1932), Bannikov (1981), and Schlawe (1986), who recognized one subspecies, *E. h. onager* for the north Iranian and Turkmenian populations, leaving open where and how this subspecies met or intergraded (secondary contact zone ?) with the Dziggetai (Antonius, however, had included in this concept the Khur, which appears quite distinct on the basis of its craniology and remains unstudied genetically). This view contains subjective judgement from a broad, but not entirely satisfactory database. Onager and Kulan are, however, clearly differentiated genetically on a population level, evidently more so than could be expected from breeding them in two studbook herds alone. Subspecies are concepts of zoologists which, like species too, designate quite different population genetic networks in different groups of animals.

Taking into consideration all the factors enumerated above, the aim of a rational decision as to the conservation value of local populations can be approached, but not completely provided, by our work.

Anyway, the question whether to continue studbook breeding cannot really be answered by taxonomists but rests, as a conservation political decision, as the responsibility of those who decided to import and exhibit hemiones from Iran and from Turkmenistan for conservation purposes, and to create two studbook herds which can be neatly traced to two areas within the spatio-genetical system of *E. hemionus*. Both herds have been founded by more wild-caught specimens than many other captive breeding programmes, and both represent the result of a decade-long breeding effort of many people which aimed to conserve available segments of biodiversity. Future generations with different views of evolutionary processes may or may not prefer different theoretical frameworks to interpret the evolution of equids. There remains a

scientific fact that evolution proceeds in populations, and two populations from the population-genetical network of what is presently called *Equus hemionus* by most authors have been secured till date by the investment of scientists and practitioners in several zoos. In a way, Carl Hagenbeck was a remarkable pioneer of what became known later as ex-situ conservation. Reviewing the history of *Equus hemionus*, zoos were instrumental in getting to know several subspecies, and to date contributed the greatest share of knowledge on the biodiversity of those equids. Several museum specimens on which this work was based are zoo-bred hemiones, and all genetical insights, were possible because zoos provided the population samples for study. Without zoos, this equid would be almost unknown to the scientific world indeed. In a way, Hagenbeck's Onager import to Hamburg Zoo, and the subsequent breeding of a fairly large captive Onager population in many zoos, is a remarkable success story for conservation and zoological gardens, comparable to few others. Therefore, the low profile of the endangered hemiones which are living proof of this success story is astonishing. It looks almost like a denial of what zoological gardens are actually able to contribute to conservation.

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