Chapter 3
The Genus *Homo*: Origin, Speciation and Dispersal

Winfried Henke and Thorolf Hardt

Abstract The taxonomical interpretation of the fossil record of our own genus *Homo* is still highly controversial. In spite of obvious major advances concerning the acquisition, analysis and interpretation of the fossil specimens there currently remain unbridgeable disagreements concerning the origin, speciation and dispersal of our genus. The polarized positions result foremost from different methodological approaches for species recognition (e.g., Tattersall 1986; Wolpoff and Caspari 1997; Schwartz 2000a; Wiesemüller et al. 2003; Jobling et al. 2004; Rothe and Henke 2006). Beside the Multiregional Evolutionary Model (MRE) there are different Recent African Origin Models (RAOMs) with varying numbers of speciation. This contribution discusses the evolution and origin of 'early' *Homo*, the assumed speciation events and the validity and credibility of traditional, newly described or reinterpreted *Homo*-species and the hypothesized patterns of dispersal. We ask for an explanation of the tremendous evolutionary success as well as the triggers for the incomparable career of *Homo*. Finally we will try to decipher the speciation process and dispersal patterns of our forerunners and to unravel the traces of our fossil ancestors.

Though paleoanthropologists, who seek the doorways to the past, have recently been very successful in developing new sets of keys (Henke and Tattersall 2007), the species recognition within the genus *Homo* remains a permanent challenge of paleoanthropological research. As the evolutionary process was a single real-historic-genetical event it is not a matter of taste how many species there have been. There is a need for sound taxonomic units strictly based on phylogenetic systematics as a prerequisite for progress in evolutionary biology (Wägele 2000; Wheeler and Meier 2000; Rothe and Henke 2001, 2006; Wiesemüller et al. 2003).

**Keywords** Hominin taxonomy • Species recognition • Speciation processes

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Introduction

There are few problems in paleoanthropology that have been more continuously troublesome during the last century than defining the genus *Homo* because of its fragmentary hominid fossil record, the tendency to over-split hominid taxa and emphasize differences rather than similarities, and the lack of suitable methods to resolve the relative and absolute ages of fossil samples complained Howell (1978). Nearly a quarter of a century later Dunsworth and Walker (2002, p. 432) still bewail: "At the moment we are plagued with more questions than answers concerning the evolution of early *Homo*", and Smith's (2002, p. 456) conclusion in his review on the confusingly complicated patterns of migrations, radiations and continuity in Middle and Late Pleistocene humans is: "While these debates are not likely to end soon, there is clear evidence on several fronts that many participants practiced good science. […] Along with an increasing amount of data pertinent to the patterns of modern human origins, these evolving models are certain to enhance greatly our understanding of the radiations and evolutionary history of our genus *Homo*."

Even though the methods of dating paleoanthropological and archaeological processes or events (see Wagner 2007) underwent a rapid progress during the last few decades, it is unrealistic to expect that the boundaries of the genus *Homo* are currently well defined and that the aspects of speciation and intrageneric relationships are solved. On the one hand there is a great improvement of the time resolution of the process of human evolution, and on the other hand there is to recognize a tremendous increase of the human fossil record by systematic explorations and meticulous excavations of the relevant fossiliferous layers (see Etter 1994; Henke 2005; Henke and Rothe 1994, 1999a; Johanson and Edgar 2007; Tattersall and Schwartz 2000), but in spite of both positive trends we have to notice the paradox consequence that we run the risk in paleoanthropology because of different genus and species concepts and contradictory phylogenetic theories to miss the wood for the trees (Rothe and Henke 2001; Wheeler and Meier 2000; Wägele 2000; Wiesemüller et al. 2003; Collard and Wood 2007).
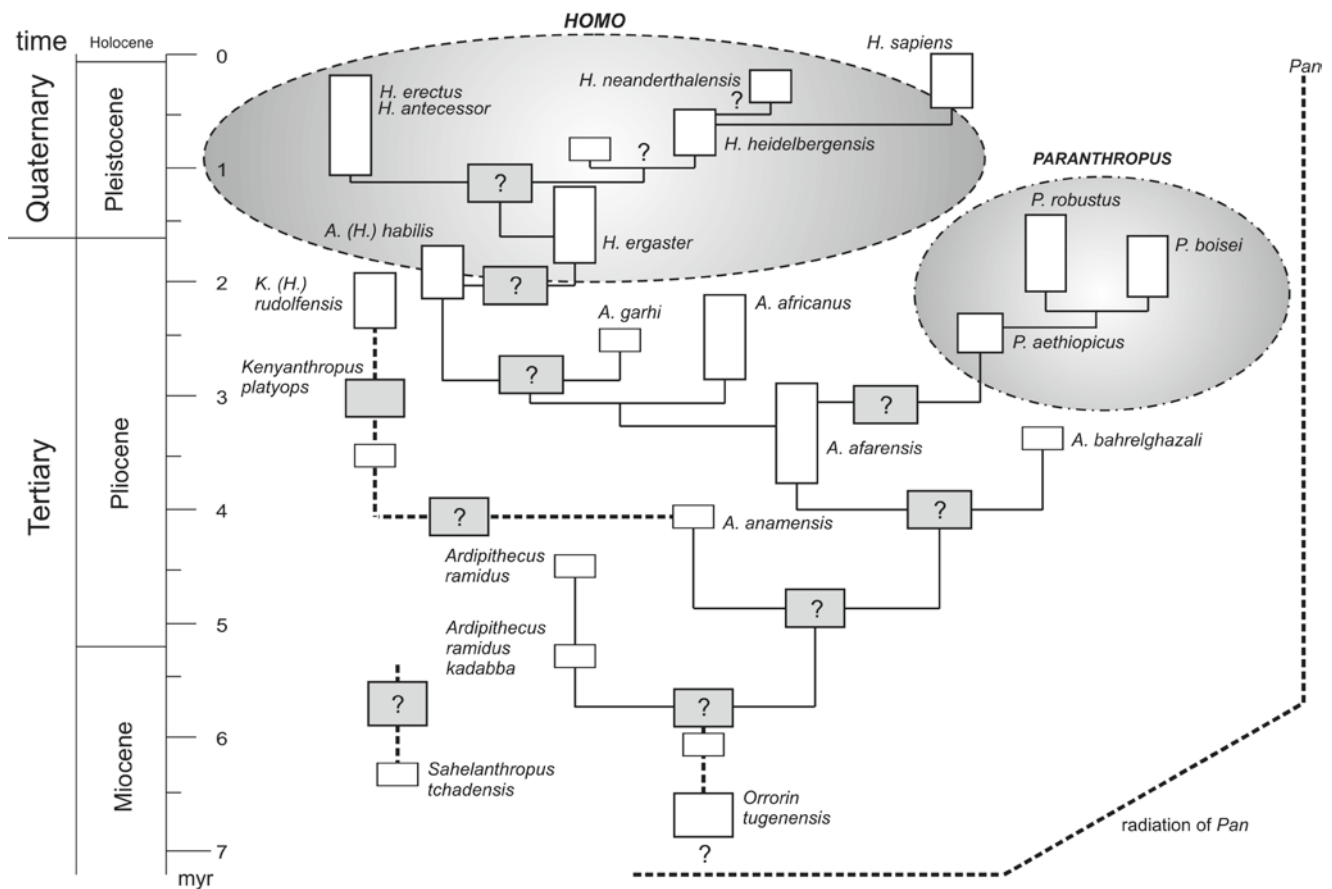
Fig. 3.1 Pedigree of hominin evolution following the extreme 'splitters' proposals that we do not favour – for further comments see text (Redrawn from Henke and Rothe 2003; Henke 2006a, modified)

Despite the rapidly increasing amounts of scientific data the controversies on human evolution are currently not minor than at that time when Clark Howell bewailed the over-split of hominid taxa, though the level has changed. While some commonly used junior synonyms like *Anthropopithecus* Dubois, 1892; *Pithecanthropus* Dubois, 1892; *Protanthropus* Haeckel, 1895; *Sinanthropus* Black, 1927, *Cyphanthropus* Pykraft, 1928; *Meganthropus* Weidenreich, 1945; *Telanthropus* Broom and Robinson, 1949 and *Atlanthropus* Arambourg, 1954, were dropped out and successively integrated in the genus *Homo* by a taxonomic revision during the sixties and seventies of the last century (e.g.. Groves and Mazák 1975), the number of *Homo*-species increased rapidly as well as the number of potential forerunners of the genus *Homo* (see pedigree in Fig. 3.1).

Due to the many different approaches ranging from evolutionary taxonomy (Simpson 1961; Mayr 1975) to numerical taxonomy or phenetics (Sneath and Sokal 1973) as well as phylogenetic systematics or cladistics (Hennig 1950; Wiley 1978; Ax 1984; Wägele 2000; Wiesemüller et al. 2003), we are actually far from a consensus concerning the taxonomically basic anthropological problem, how many fossil species of our genus have existed in the past and how

they were related to one another. Despite the rapidly growing number of hominid fossil specimens, the diversification of disciplines participating in paleoanthropology and an obvious progress in methodology during the second half of the last century (Henke and Tattersall 2007; Hardt and Henke 2007; see Fig. 3.2), it is still highly controversial and open to discussion whether the process of human evolution was smooth or jumpy (see Wolpoff 1996–1997, 1999; Wolpoff and Caspari 1997; Henke and Rothe 1999a, b, 2001, 2005; Campbell and Loy 2000; Tattersall and Schwartz 2000; Tattersall 2007; Henke 2003a, b; Rothe and Henke 2006). While some scientists suggest that new hominin species originated through a slow accumulation of small-scale changes in existing lineages, i.e. a phyletic process called gradualism or phyletic transformation, others support a model which has been described as punctuated equilibrium (Gould and Eldredge 1977). The latter currently more widely accepted model likens the evolution of hominins to a series of starts and stops, i.e. periods of genetic and phenotypic stasis are periodically interrupted by rapid speciation events, which are the starts of new species (see Campbell and Loy 2000; Jobling et al. 2004; Futuyama 2007). Even if one chooses to accept that the most appropriate metaphor for the
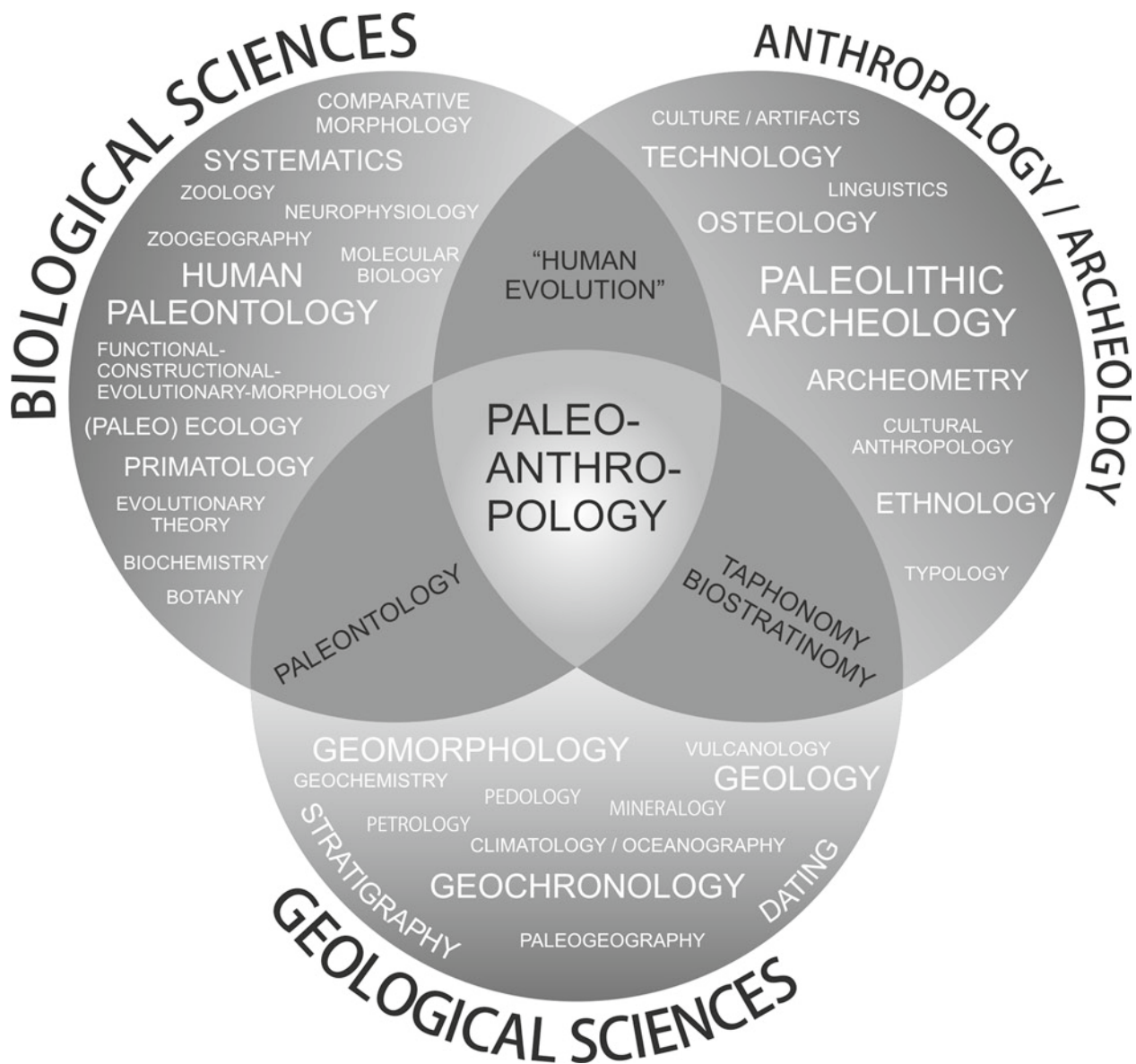
Fig. 3.2 VENN-Diagram presenting the participation of manifold scientific fields in palaeoanthropology (Modified after Delson 2000, from Henke and Tattersall 2007)

pattern of human evolution appears to be a branching bush, rather than a ladder to be climbed, one question still remains to be answered: How many hominin species were there?

This contribution aims to give an answer by reviewing the current alternative paleoanthropological ideas on the origin and diversification of the genus *Homo*. The review starts with a brief historical overview of the quests for centres of our generic origin, continues with the discussion on the earliest species of *Homo*, and asks for an explanation of the tremendous evolutionary success as well as the triggers for the incomparable career of our genus. Finally we will try to decipher the speciation process and dispersal patterns of our forerunners and to unravel the traces of our fossil ancestors.

Early Searches for the 'Cradle of Mankind'

The Neanderthal man from the Kleine Feldhofer Grotto in the Neander Valley near Düsseldorf was found by limestone workers in 1856 and described by the local teacher Johann Carl Fuhlrott (1803–1877). The fossil was the first early human specimen to be recognized as such. Discoveries like that from Engis (excavated in 1829) and another from Gibraltar (found in 1848) were made sooner, but their nature became evident much later. Fuhlrott's merit was that he had realized the significance of the fossils, which the limestone workers took for animal bones (Schott 1977, 1979; Schmitz and Thissen 2000). Fuhlrott fought, together with the anatomist Herrmann

Schaaffhausen (1816–1893), for their acceptance as ancient remains from the diluvial age (Zängl-Kumpf 1990). As the discovery of the fossil bones antedated the publication of Darwin's *Origin of Species*, this specimen has often been apostrophized as first proof for human evolution. (Bowler 1988; Desmond 1997; Corbey and Roebroeks 2001; Henke 2007). In his famous papers on *Evidences as to Man's Place in Nature*, Darwin's colleague Thomas Henry Huxley (1863) for the first time gave morphological arguments for our relationship with recent primates and pointed to the scarce fossil record known in his time. In spite of contrary statements by many historians, Huxley said virtually nothing about human origins but concentrated exclusively on demonstrating the physical resemblances of humans and apes. He concluded that humans were still sufficiently unique that they should be kept apart from the great apes, which he relegated to their own taxonomic group. Concerning the Neanderthal man from Germany, Huxley conducted a sophisticated comparison with anatomically modern skulls from Australian Aborigines and other aboriginal relicts, pioneering new ways of orienting and measuring skulls for easier comparison (Desmond 1997). He viewed the Neanderthals as a very "primitive race" of humans, "the most pithecoid of human crania yet discovered" (Huxley 1863, p. 205). The Huxley-biographer Desmond (1997) commented that Huxley was preparing the world for "ancient semihumans", which means that the idea of our early forerunners was at Darwin's time woolly and premature.

The Irish zoologist William King proposed in 1864 the species name *Homo neanderthalensis*, although his arguments for a separate species in the genus *Homo* were inadequate and imprecise. Since then, opinion has fluctuated as to whether the fossils should be considered as a separate species, *Homo neanderthalensis* or *Homo primigenius* or as a subspecies of *H. sapiens* (*H. sapiens neanderthalensis*). The "fate of the Neanderthals" (Brace 1962, 1964; Trinkaus and Shipman 1993) remained the trickiest controversy in paleoanthropology until now (Spencer 1984; Stringer and Gamble 1993; Tattersall 1995a, b; Krings et al. 1997, 2000; Henke and Rothe 1999a; Wolpoff 1999; Finlayson 2004; Henke 2006a, 2007; Harvati 2003, 2007).

What became very soon apparent in the second half of the penultimate century was the tremendous need for an extension of the fossil report – since that time colloquially termed as "missing links". Beyond it there was missing an improved comparative methodology to analyze and interpret the human fossils. As recently has been described by Henke (2006, 2007) and Henke and Rothe (2006) neither the Neanderthal fossils from the Feldhofer Grotto nor those from many other European sites had a path-breaking impact on the formation of paleoanthropology as biological science. Furthermore the discovery of the specimens from La Naulette (1866), Šipka (1880), Spy (1886), Taubach (1887) and the pivotal fossils and artefacts from Krapina (1899–1906) did not induce a paradigmatic shift in paleoanthropology though Dragutin Gorjanović-Kramberger's excavations had pushed the anthropological research in the right direction of detailed comparisons and hypothesis-testing (Gorjanović-Kramberger 1906; see Henke 2006b). Others asked whether Eugene Dubois' essential discovery of *Pithecanthropus erectus* in 1891 coincided with a paradigm shift in paleoanthropology (see Shipman and Storm 2002). The implication which could be derived from the fossils was that erect posture and bipedal walking antedated the process of encephalization, but even this finding was not convincing for the leading paleoanthropologists of that time. That paleoanthropology remained predominantly a highly narrative science in the early twentieth century became evident from the fatal Piltdown forgery (Spencer 1990a, b), named *Eoanthropus dawsoni*, and the fact that it took more than 40 years until John S. Weiner, Sir Kenneth Oakley, and Sir Wilfrid LeGros Clark jointly exposed the hoax, although we have to mention that there was much scepticism and rumour earlier (see Friederichs 1932; Weinert 1947). Whoever the players were in this black mark in science, they were aware of the attractiveness and fascination of fossils, and they obviously knew about the public appeal and the rare resources that help to decipher our place in nature (see Stringer and Gamble 1993; Foley 2001).

The embarrassing success of the Piltdown forgery unmasked the ethnocentrism and Euro-centrism of the European anthropologists of early twentieth century, in other words, hardly anybody of the protagonists of that time could image that our phylogenetic forerunners originated and lived in another continent than Europe the obvious centre of culture. The interpretation of the Piltdown fossil as a human precursor was partially responsible for the vehement dismissal of the first *Australopithecus* fossil from South Africa. Raymond Dart's interpretation of the Taung child as missing link between ape and man yielded a storm of controversy (Woodward 1925; Keith 1931). This is remarkable insofar as Dart's discovery matched the prophecy of Darwin (1871, p. 202): "It is, therefore, probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee: and, as these two species are now man's nearest allies, it is somewhat more probable that our progenitors lived on the African continent than elsewhere."

To the extent that these and other indications for an extra-European "cradle of humankind" were deliberately ignored, the Piltdown case is a telling example of cut and dried opinions (Spencer 1990a, b). Small wonder, that the scientific output of paleoanthropology during the first decades of the last century was far more redolent of stagnation than progress. The evolutionary biology at those times was characterized by Ernst Mayr as "chaotic" (Tattersall 2000a, p. 2). We can notice that even at the beginning of the twentieth century, Darwin's principles were widely misunderstood by

anthropologists, who persisted in orthogenetic biological thinking or insisted on the theoretical split between natural sciences and humanities (see Henke and Rothe 2003, 2005, 2006). Paleoanthropological theory and methodology were nascent, and it took a total change to a population genetical thinking and a modern Synthesis by Theodosius Dobzhansky, Ernst Mayr and Julian Huxley in the first half of the last century and an integrated primatological approach during the second half, introduced by Sherwood Washburn (1953) in the fifties of the last century, to establish the theoretical frame of an innovative paleoanthropological research (see Foley 1987; Henke and Rothe 1994, 2003, 2006; Henke 2007; Henke and Tattersall 2007).

After the discovery of the Taung child Africa came more and more into the focus of paleoanthropology, firstly with surprising fossils from South Africa [*Australopithecus* (*Plesianthropus*) *transvaalensis*; *Paranthropus crassidens*; *Paranthropus robustus*] and secondly from East Africa [*Paranthropus* (*Zinjanthropus*) *boisei*, *Paranthropus* (*Paraustralopithecus*) *aethiopicus* (further newly excavated and described taxa see pedigree Fig. 3.1)]. A paleoanthropological sensation was the discovery of a human fossil from Olduvai (F.L.K.N.N. Site – Bed I) which was classified as *Homo habilis* by Louis S. B. Leakey et al. (1964). Phillip Tobias (1989a, b, 1991) retrospectively called this fossil a premature discovery after Stent who defines that "… a discovery is premature if its implications cannot be connected by a series of simple logical steps to canonical or generally accepted knowledge" (Stent 1972, p. 84).

Actually there is a highly controversial discussion on the phylogenetical status of *H. habilis* as the hypodigm of this taxon has been successively enlarged during the last 50 years and exhibits an extremely large variation (Alexeev 1986; Hartwig-Scherer and Martin 1991; Collard and Wood 2007; Susman 2008). The fact that there is no agreement about the classification of the earliest evidence of *Homo* is on the one hand an indication for a severe theoretical deficit of our taxonomical approaches and on the other hand strong evidence that we are at the roots of our genus. Currently there is nearly no doubt that Africa is the cradle of *Homo* and that our genus conquered the Old World soon after its emergence. What was the "Rubicon" *Homo* had crossed to finally reach this incomparable success of our own species – and how many species of this genus went extinct (Foley 1991)? These are essential paleoanthropological questions to be answered.

The Earliest Evidence of Homo

Within the theoretical concept of an adaptive evolutionary change from archaic hominids to human-like ones the traditional expectations concerning the genus *Homo* are full

uprightness, successive reduction of the mastication apparatus as adaptation to changed food processing, improved encephalization, and evidence of cultural abilities. Whether the fossil species attributed to *Homo* had already developed a human-like society (Rothe and Henke 2006), a language, or art (Haidle 2007; Mithen 1998, 2007) can only be judged with great uncertainty, if at all. For example, allometrical effects may cover the real abilities, i.e., body sizes have to be taken into account to achieve an idea of the relative brain size (Hemmer 2007). Current research on cultural behaviors and underlying cognitive and linguistic competences in early hominins is a highly interdisciplinary enterprise (see Henke and Tattersall 2007), which gives only very rough information concerning the first appearance of the genus *Homo*.

We are of the opinion that there is a need for sound taxonomic units as a prerequisite for progress in evolutionary biology (Wägele 2000; Wheeler and Meier 2000; Rothe and Henke 2001, 2006; Wiesemüller et al. 2003), and do not agree with those who argue that discussions on species concepts are wasted effort. Though we are convinced that there is little hope that the discrepancies about the theory of speciation and the species concepts (e.g., biological species, chronological species, cladistic species, ecological species, evolutionary species, morphological species, phenetic species, phylogenetic species, reproductive species) will be eliminated in the near future and paleoanthropologists will reach a consensus on hominid systematics, we agree with those who regard taxonomy and systematics beside a thorough background in an increasingly broad spectrum of disciplines (see Fig. 3.2) as an essential prerequisite for phylogenetic discussions. Without an exact knowledge of the population genetical processes, a precise theory of speciation and an inter-subjective definition of taxonomic categories there is no chance to escape the narrative concepts of paleoanthropology and the image of an "Instant Science", as Kathy Chang labeled a paleoanthropology that knows the answers from the first glance (cited in White 2000).

Excurse

Here we will not step deeper into this discussion, but want to explain our viewpoint in brief. The most common definition of a species is the biospecies (Mayr 1969, 1975), i.e., a group of actually and potentially interbreeding natural populations, which is reproductively isolated from other species. Because this definition is applicable only to contemporaneous living organisms, alternative definitions have been proposed (Simpson 1961; Wiley 1978). Paleoanthropologists very often describe fossil species as morphospecies, based on morphological or anatomical similarity, or refer to temporally successive species in a single lineage, so-called paleospecies or chronospecies. We don't regard these species

concepts as valid approaches. The most accepted definition of a species is given by Wiley (1978, p. 18) as "…a single lineage of ancestral descent populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (see Wiesemüller et al. 2003; Henke 2005; Rothe and Henke 2006). The currently best method of choice to decipher phylogenies is the phylogenetic systematics or cladistics (see Hennig 1950; Wiley 1978; Ax 1984; Wägele 2000; Wiesemüller et al. 2003; Rothe and Henke 2006). A reconstruction of phylogenetic relationships is strictly based on the observation of synapomorphic traits. However we must be aware, paleoanthropologists are just modelling!

The Potential 'Candidates' for the 'Earliest' *Homo*

The discoverers of *H. habilis* (Leakey et al. 1964) described the *species nova* as being more advanced than *A. africanus* and not as humanized as *H. erectus*. But even 15 years after the species was labelled for the first time, the majority of competent scholars in the field did not accept *H. habilis* as a valid taxon. The reason was that there was a lack of 'morphological space' between *A. africanus* and *H. erectus*, as Stringer (1986) supposed in his article on "The Credibility of *Homo habilis*", i.e., the new species was strongly criticized in the beginning, for many experts argued that the Olduvai specimens could be classified within existing taxa. Meanwhile, there seems to be worldwide acceptance of the fact that specimens with smaller endocranial capacities need *not* be excluded from membership in *Homo* and that the fossils are not a normal variant of either the putative australopithecine ancestor or the putative descent *H. erectus*. Within the material, attributed to 'early *Homo*' (Wood 1992, 1996a, b), three species can be identified today, one of them resembles *Homo erectus* and is interpreted as either 'early African *Homo erectus*' or *Homo ergaster*, and the two other species are *Homo rudolfensis* and *Homo habilis* (*sensu stricto*).

Homo rudolfensis and Homo habilis (s. str.): Although Tobias (1991) made a strong case for only one species being represented among specimens attributed to *H. habilis*, other authors see evidence that there may be two species, one named *H. rudolfensis,* which was proposed in 1986 by the Russian anthropologist Valeri Alexeev for specimen KNM-ER 1470 (Alexeev 1986), and the other *H. habilis* [*s. str.*] (see e.g., Tobias 1989a, b; Wood 1992; Henke and Rothe 1994; Stringer 1996, 2001; Tattersall and Schwartz 2000; Collard and Wood 2007; Schrenk et al. 2007; Susman 2008), which are sister taxa within a monophyletic *Homo* clade. However, this phylogenetic interpretation is only a little more parsimonious than a polyphyletic one, explaining the features typifying each species as parallel developments (see

also Bilsborough 1992, p. 132; Kennedy 1999; Rightmire 2007). Anyway, whatever may be the correct taxonomic solution, there are strong arguments against a *H. habilis* [*sensu lato*] concept while the hypodigm remains unsure. *H. rudolfensis* shows, apart from an increased average brain size of c. 750 cc, features of the face and masticatory apparatus that parallel those of *Paranthropus*, e.g., marked orthognathy, broader midface than upper face, and large palate, but *H. habilis s. str.* shows a moderate average brain size of 610 cc and progressive features of cranium, face, and jaws.

The postcranium of *H. rudolfensis* is evidently more derived, like that of later *Homo*, although the association with the skull fragments is not confirmed. In contrast, *H. habilis s. str.* shows a very plesiomorphic, australopithecine-like physique. The described combination of australopithecine-like cranio-dental features with a derived postcranium in *H. rudolfensis* and of progressive cranium and dentition with primitive body proportions in *H. habilis s. str.* (a highly putative association) allows the conclusion that neither of the two species represents a reliable ancestor of later *Homo* (see *H. ergaster*), because every interpretation has to take very unlikely evolutionary changes into account to explain these unusual morphological mosaics.

Fossils representing *H. habilis* [*s. l.*] were first described from Olduvai, where they were uncovered from layers that have also yielded australopithecine skeletal material (Bed I and Bed II), but the largest contribution to the hypodigm comes from another site in East Africa, Koobi Fora, on the northeast shore of Lake Turkana. Further remains of the species have been recovered from Members G and H of the Omo Shungura Formation. From the western shore of Lake Turkana, a cranial fragment from the Nachukui Formation has been described, and a fragmentary skull, Stw 53, was recovered from the South African cave of Sterkfontein in Member 5. The attribution of hominin material from Member 4 of Sterkfontein to *H. habilis s. l.* is uncertain, although material from Swartkrans Member I (Sk 847, Sk 27) was confirmed as belonging to *H. habilis s. l.* In addition to the fossils from sub-Saharan sites, there are reports on *H. habilis s. l.* fossils from sites beyond Africa, the Near East and Asia, which have only little reliability and acceptance (Fig. 3.3). The actual hypodigm concentrates especially on East Africa. A mandible from Uraha (U 501, Malawi), which was attributed to *H. rudolfensis* by Bromage et al. (1995) forms a link to the more northern sample (Schrenk et al. 1993, 2007).

The recognition of *H. habilis s. l.* and the dating of some specimens from Olduvai to about 2.0 Ma was the first compelling evidence for the existence of Tertiary man in the sense of a species of the genus *Homo* (Tobias 1989a, b). Due to the improvement of dating methods and the discovery of new remarkable fossils, it is currently accepted that the genus *Homo* emerged before the end of the Pliocene. Earliest well-flaked
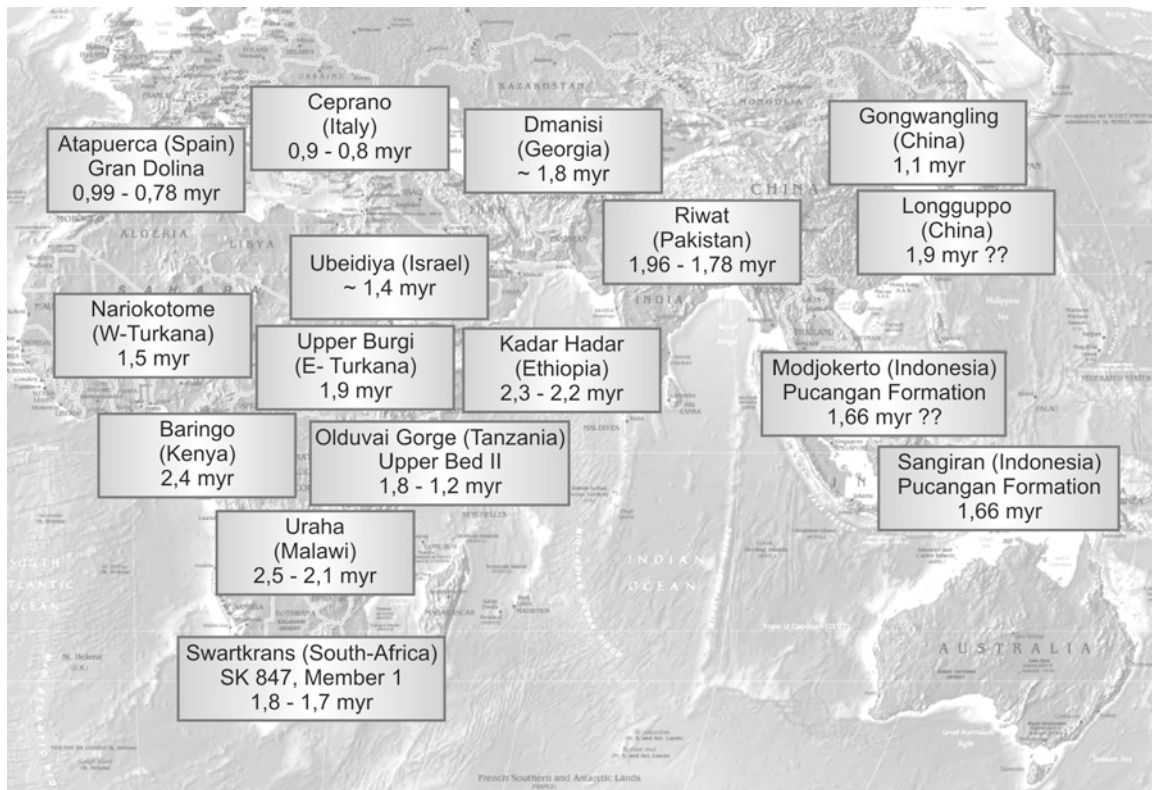
Fig. 3.3 Earliest traces of the genus *Homo* around the world with chronological setting (Henke 2003a, modified)

stone artefacts, identified as Oldowan-like in character, have been traced back to about 2.5–2.6 Ma (Semaw 2000); however, there is no proof that these implements testify to the presence of a particular hominin species. The definition of *H. habilis* is, essentially, an anatomical one, although ethological evidence may be added in support (Tobias 1989a, b, 1991). The most recent occurrences of *H. habilis* are from Olduvai Bed II, dating to about 1.6 Ma. The higher age of *H. rudolfensis* (2.5–1.8 Ma) in comparison to *H. habilis s. str.* (2.1–1.6 Ma) cannot be taken as evidence that this species is the better candidate for the direct *Homo* lineage, because the phylogenetic analysis has to be based on relevant diagnostic features (Table 3.1).

Tobias' (1991) review of the morphology of *H. habilis s. l.* lists the following critical morphological features of the first description, which have been strengthened and supplemented by subsequent studies.

The postcranium exhibits a very controversial morphological pattern: on the one hand there are distinct similarities with *H. sapiens* (e.g., clavicle, broad terminal phalanges, capitate metacarpophalangeal articulations, stout and adduced big toe, well marked foot arches) and on the other hand distinguished differences (e.g., scaphoid, trapezium, trochlea surface of the talus, robust metatarsal III). The partial skeleton OH 62, a *H. habilis s. str.*, which was found by Johanson et al. (1987),

Table 3.1 Diagnostic features of *Homo habilis s.l.*

- Absolute and estimated relative brain size (average 640 cc) with spectacular advance over australopithecines; exaggerated encephalization, brow ridges vertically thin
- Relatively open-angled external sagittal curvature to occipital
- Thin-walled braincase
- Light pneumatization of cranial bones
- Face moderately prognathous, but less marked than in *A. africanus*
- Retreating chin, with a slight or absent mental trigone
- Foramen magnum slightly in front of the basis cranii
- Large canines in comparison with australopithecines and *H. erectus*
- Canines large compared with premolars
- Petrous pyramid of the temporal bone lying in nearly transverse and coronal plane
- Cheek-teeth with reduced crown diameters and crown area in comparison to those of australopithecines
- Molar crowns small buccolingually and elongated mesiodistally
- Third molars tending to be smaller than second molars, especially P3, P4, M1 showing buccolingual narrowing of the crowns
- Lateral aspect of the frontal lobe exhibiting a pattern of sulci, typical of *Homo sapiens*
- Well developed bulges in Broca's area and in the inferior parietal lobule (part of Wernicke's area)
- Complex middle meningeal vascular pattern

Compiled by Tobias (1991)

has especially caused much discussion (Hartwig-Scherer and Martin 1991), because the estimated length and robustness of the humerus and forearm bones of OH 62 suggest that its proportions are remarkably ape-like, and the predicted weight/stature relationships are also more like that of Panini (Aiello and Dean 1990; Aiello 1996), but the phylogenetic status of 'Lucy's child' remains uncertain.

Although Tobias (1991) gave an extremely detailed description of *H. habilis s. l.*, listing 334 cranial, mandibular, and dental features, the question of what autapomorphic features define *H. habilis* remained controversial (Stringer 1986; Bilsborough 1992; Wood 1992; Henke and Rothe 1999; Grine 2001; Manzi 2001; Rightmire 2001a, b; Wood and Collard 2001, 2007). The main reason for the uncertainty in the interpretation of the diversity of early *Homo* is that the fossil hominin remains that are formally or informally allocated to *H. habilis* or declared to have affinities with this species vary from one author to another; in other words, there are multiple taxon solutions. The claimed heterogeneity of the *H. habilis s. l.* material from Olduvai (e.g., OH 7, 13, 16, 24), Koobi Fora (e.g., KNM-ER 1470, 1590, 1805, 1813, 3732), Omo (L894-1, Omo 75–14, Omo 222–2744), and Chemeron (KNM-BC1), as well as from Sterkfontein (e.g., Stw 53) caused different approaches to find a better supported classification, but the split into two species is taxonomically ambiguous (Wood 1996a, b; Henke and Rothe 1994, 1999). Cladistics has made little contribution to the search for distinctive features, or autapomorphies, of *H. habilis*. For example, Chamberlain and Wood (1987) concluded that when *H. habilis s. str.* and *H. rudolfensis* are separately included in a cladistic analysis, they are linked as sister taxa within a single clade defined by the feature states of elongated anterior basic-

ranium, higher cranial vault, mesiodistally elongated M1 inf. and M2, and narrow mandibular fossa. Wood and Collard (2001, p. 141) concluded "…that if *Homo habilis sensu stricto* and *Homo rudolfensis* are included in *Homo* that genus fails both the 'grade' and the 'clade' tests."

The most complex cladistic analysis of early hominin relationships was conducted by Strait et al. (1997) and Strait and Grine (2004). Several different approaches agreed in indicating that the robust australopithecines form a clade, that *A. afarensis* is the sister taxon of all hominins, and that the genus *Australopithecus*, conventionally defined, is paraphyletic. Concerning *H. habilis*, the relationships of *A. africanus* and *H. habilis* were unstable in the sense that their positions varied in trees that were marginally less parsimonious than the favoured one.

The paleoecological scenario that explains the observed phylogenetic pattern states the possibility that bipedalism (and hence, the earliest hominins) evolved in response to changing ecological conditions in Africa during the late Miocene and early Pliocene. Vrba's (1988) faunal reconstructions indicate that hominin diversity between 2.5 and 1.5 Ma was possibly associated with environmental desiccation. After 2.5 Ma, hominin diversity is represented primarily by two distinct lineages, *Paranthropus* and *Homo*, which reacted to such desiccation by following different evolutionary trajectories (i.e., hypermastication vs. hypercephalization) (Strait et al. 1997, p. 56). The morphological changes demonstrate that the masticatory apparatus increased moderately in the early stages of human evolution. Subsequently it increased markedly in *Paranthropus* and decreased in *Homo*, a dichotomy that almost certainly represents a divergence in trophic adaptations (Fig. 3.4).
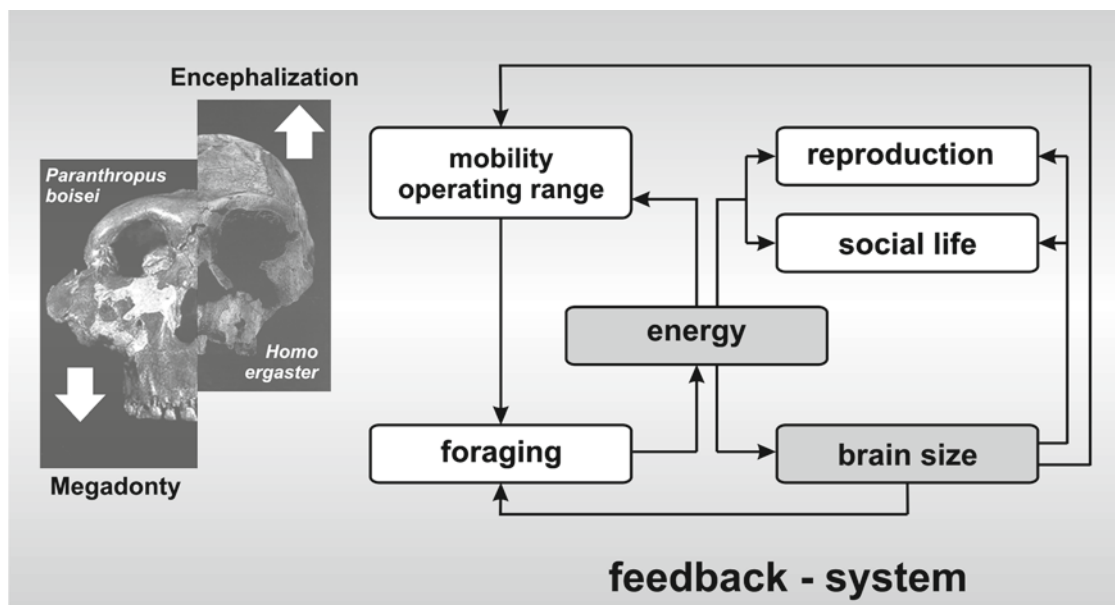
Fig. 3.4 Encephalization vs Megadonty: feedback-system, which describes the interdependencies of several components leading to the evolutionary 'success' of *Homo* (After Martin 1995; from Henke 2003a)

A cladistic analysis conducted by Wood and Collard (1999a, b) showed that neither *H. habilis* nor *H. rudolfensis* can be assumed with any degree of reliability to be more closely related to *H. sapiens* than they are to species allocated to other genera. In a recent contribution Collard and Wood (2007, p. 1575) confirmed their positions, concluding, that "…the available evidence still suggests that the adaptive strategies of *H. habilis* and *H. rudolfensis* were different from those operated by *H. erectus*, *H. ergaster*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*." Their proposal to remove *H. habilis* and *H. rudolfensis* from die genus *Homo* and to assign them to a different genus or pair of genera is not widely-accepted (e.g., Schrenk et al. 2007; Johanson and Edgar 2007; Susman 2008). However, the characterization of the *H. habilis s. l.* as "mysterious" hypodigm tells its own tale (Tattersall and Schwartz 2000).

Homo erectus (incl. Homo ergaster): At the end of the Basal Pleistocene (c. 1.5 Ma), *H. habilis* and *H. rudolfensis* disappeared from the fossil record, followed somewhat later by *P. robustus* and *P. boisei*. The exact reason for their extinction is not known, but there are indications from high faunal turnovers that climatic fluctuations may have caused dramatic ecological shifts. At the beginning of the Pleistocene, the first epoch of the Quaternary, which was characterized by a series of glacial and interglacial periods, a new hominin emerged, African *Homo erectus sive Homo ergaster*. There is a long-standing hypothesis that populations similar to this species were directly ancestral to the earliest members of the living species *H. sapiens*, whereas hypotheses concerning the link to hominin forerunners changed with the increase in the fossil record and are still under ongoing discussion (see e.g., Rightmire 1990; Henke and Rothe 1995, 1999; Henke 2003a, b, 2005, 2006a; Antón et al. 2007; Tattersall 2007; Hardt and Henke 2007).

The German zoologist Ernst Haeckel first linked humans to apes in a tree-like diagram in "General Morphology" from 1866 and suggested an Asian origin of humankind, based on the hypothesis of a near relationship to hylobatids (Haeckel 1866). The first fossil finds of *H. erectus* (formerly named *Pithecanthropus erectus*) were made in 1891 by Eugene Dubois in Central Java. The Dutch army doctor was convinced at that time that he had discovered the presumed 'missing link', the transitional form between apes and humans. The conviction that the new human taxon had been an erect bipedal creature resulted in the species name *erectus*. Because the Java man was the first non-European fossil in paleoanthropology, the discovery led to questioning of the European-centred world view that had so far been supported by the famous Neanderthal fossils. From now on, Asia was hesitantly accepted to be the place of human origin. South-East Asia and the Far East became in the first half of the twentieth century the centre of the search for the earliest human fossils, until it became evident that hominins of a *H. erectus* grade existed in the other continents of the Old World too.

During the last decades it became the favoured phylogenetic hypothesis that *H. erectus* (or a conspecific taxon named *H. ergaster*) originated in Africa from an earlier species of the same genus, *H. habilis s. l.*, forming an intermediate position in the human family tree between the ancient forerunner and 'archaic' *H. sapiens*. *H. erectus* was – sloppy verbalized – a sandwich-species. This species was said to be the conqueror of the Old World, the first hominin to emigrate out of Africa, successively reaching Asia and Europe. But its evolutionarily intermediate position in the human family tree has been questioned more and more during the last decades (e.g., Howell 1986, 1996; Franzen 1994a; Henke and Rothe 1995; Rightmire 1990; Tattersall 2000a, b, 2007; Schwartz and Tattersall 2002, 2003; Wood and Collard 2001; Henke 2003, Henke 2005, 2006; Henke and Rothe 2006; Antón et al. 2007; Harvati 2007).

Definitions of *H. erectus* (Dubois 1894) still rest on the Far Eastern fossils from Zhoukoudian and Java (Jacob 1975; Howells 1980; Weidenreich 1943). The species *H. erectus* came to replace a variety of contemporaneous geographically distinguished genera, including the genera *Pithecanthropus*, *Sinanthropus*, *Meganthropus*, and *Atlanthropus*. A taxonomic revision by Campbell (1965) deleted older genera and species, lumping these Early and Middle Pleistocene hominin taxa into a single species and separating them only on the subspecies level (*H. erectus erectus*, *H. e. modjokertensis*, *H. e. pekinensis*, *H. e. capensis*, *H. e. leakeyi*, *H. e. mauritanicus*, *H. e. heidelbergensis*, *H. e. ngandongensis*, *H. e. yuanmouensis*, *H. e. bilzingslebenensis*, *H. e. tautavelensis*, *H. e. georgicus*, and others). But this taxonomic approach was obviously not the complete solution to all problems, because the more fossils were found and the more precise the chronological dating became, the more complex the whole situation has become.

At the 100 years anniversary of "*Pithecanthropus*" Jens Lorenz Franzen (1994b, p. 9) asked among others the following burning questions: "What really is *Homo erectus*? Is it a good species? Behind which two or even more 'true' species may be hidden? – How can *Homo erectus* be defined, particularly if it is not the result of a speciation event but just a transitional phase of phylogenetic development on the way to modern man? – How can it be separated from 'archaic' *Homo sapiens*? – And then again, is *Homo erectus* the result of a cladogenetic event or is it the result of continuous transition? – Is it possible to distinguish between an Asian, and African and/or European branch of *Homo erectus*? – Should the African and European branches, if they really exist, be called species of their own?"

The answers were as diverse as the questions, by no means unexpected in paleoanthropology, especially in regard to the diversity and weaknesses in principal taxonomic approaches. Although some anthropologists regard *H. erectus* as a grade within a transitional phylogenetic

model (e.g., Frayer et al. 1993; Thorne and Wolpoff 1981, 1992; Wolpoff 1980, 1992, 1996–1997, 1999; Wolpoff et al. 1994a, b; Wolpoff and Caspari 1997, 2000), other authorities hold the view that *H. erectus* originated from a hominin branch of African origin – possibly *H. ergaster* – in Asia and remained restricted to the Far East (e.g., Tattersall 1995a, b, 2007; Tattersall and Schwartz 2000). Some experts claim that the Asian and African wings of *H. erectus* exhibit no autapomorphic features and that the early Europeans originated from an African species other than *H. erectus*, named *Homo heidelbergensis* (Rightmire 1990, 1998). Is it a phantom, a chimera?

The recent discussion on the question of whether *H. erectus* was an ancestor of our own species or an evolutionary side branch received new stimuli from exciting fossils from Dmanisi (Georgia). From this site at the gates of Europe, in 1991 a fossil mandible and since 1999 more or less complete skulls and postcranial material of an unexpected high age (most reliable date 1.75 Ma) and surprising morphology indicate a much earlier Eurasian dispersal of *Homo* than was believed before (Bräuer et al. 1995; Henke 1995; Henke et al. 1999;

Henke and Rothe 1999b; Gabunia et al. 2000a, b, 2001; Vekua et al. 2002; Rightmire et al. 2005).

Because early *Homo* fossil material from Africa that has been classified as *H. ergaster* (Groves and Mazák 1975; formerly attributed as 'African' *H. erectus*) has a maximum age of only c. 1.9 Ma, and the hominin fossils from Dmanisi (Gabunia et al. 2001; Vekua et al. 2002), Sangiran and Modjokerto (Java, Swisher III 1994; for discussion of the chronology see Langbroek and Roebroeks 2000), and Longgupo, China (Huang et al. 1995) may be of around the same age or a little younger, there is a severe problem of explaining the very early Eurasian dispersal and finding out which species was the pioneering emigrant (Fig. 3.5). The evidence from Longgupo Cave suggests by the given primitive nature of the premolar teeth, that the first hominid to occupy Asia may not have been *H. erectus*, but perhaps a variant of *H. ergaster* or even *H. habilis*. Etler et al. (2001) question this interpretation of the fossils from Longgupo. The mandibular fragment cannot be distinguished from penecontemporary fossil apes, especially the Late Micoene-Pliocene Chinese genus *Lufengpithecus*, while the incisor is indistinguishable
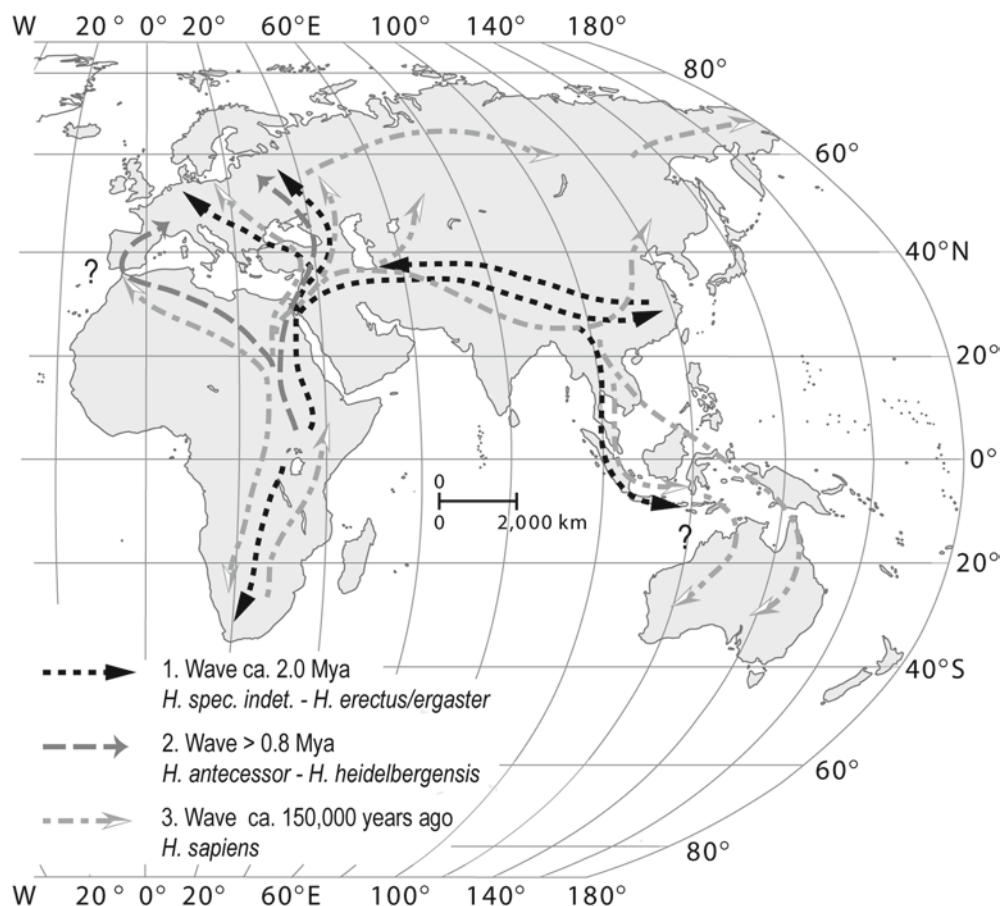
Fig. 3.5 Potential migration waves "Out of Africa" and periods of archaic *Homo* – populations supposed by several paleoanthropologists (After Hardt et al. 2007)

from those of recent land living east Asian people and may be intrusive in the deposit.

The Dmanisi mandible D 211 (Henke 1995; Bräuer et al. 1995) and the later excavated skulls with their small cranial capacities and plesiomorphic features (e.g., postorbital constriction) have been discussed as descendents of and "early" *H. ergaster* or an evolved *H. habilis* too (Gabunia et al. 2001). These specimens are actually the key fossils in the current discussion (Balter and Gibbons 2002) of the early *Homo*-dispersal from Africa. For a better understanding of the complex phylogenetic pattern and deciphering of the 'muddle in the middle', as Rightmire (1998) characterized the problems concerning Late Early and Middle Pleistocene human evolution, we have to analyze the regional and chronological hypodigm and discuss a possible African origin and early Asian dispersal (Henke and Rothe 1994, 1999a, b; Larick and Ciochon 1996; Wolpoff 1996–1997; Manzi 2001; Schwartz and Tattersall 2000, 2002). Only when species – in the sense of an evolutionary species (Wiley 1978) – have been adequately defined morphologically

appropriate comparisons can be made and the distribution of character states across species is used to generate phylogenetic hypotheses. But until now, we do not have any consensus of the *H. erectus* hypodigm, which means that we have no agreement on the question of which fossils belong to the taxon that has been defined as *H. erectus* (Howells 1980, 1993; Rightmire 1990; Franzen 1994a, b; Henke and Rothe 1995; Howell 1996; Antón 2003; Antón et al. 2007; Tattersall 2007). Chronological information concerning the earliest traces of the genus *Homo* in the Old World is given in Fig. 3.6. *Homo* fossils which indicate the earliest appearance of *H. erectus* (or *H. ergaster*) or an earlier *Homo*-species out of Africa are described from Asia (incl. Dmanisi; see Fig. 3.7), while Europe has been invaded much later by hominins which have been classified as potential *H. erectus* or as *H. antecessor* followed by *H. heidelbergensis*, and *Homo* (*sapiens*) *neanderthalensis* and modern humans (Fig. 3.8) (Ullrich 1998).

Because those hominins that were found in Java since 1891 (formerly *Pithecanthropus*) and at Zhoukoudian, near
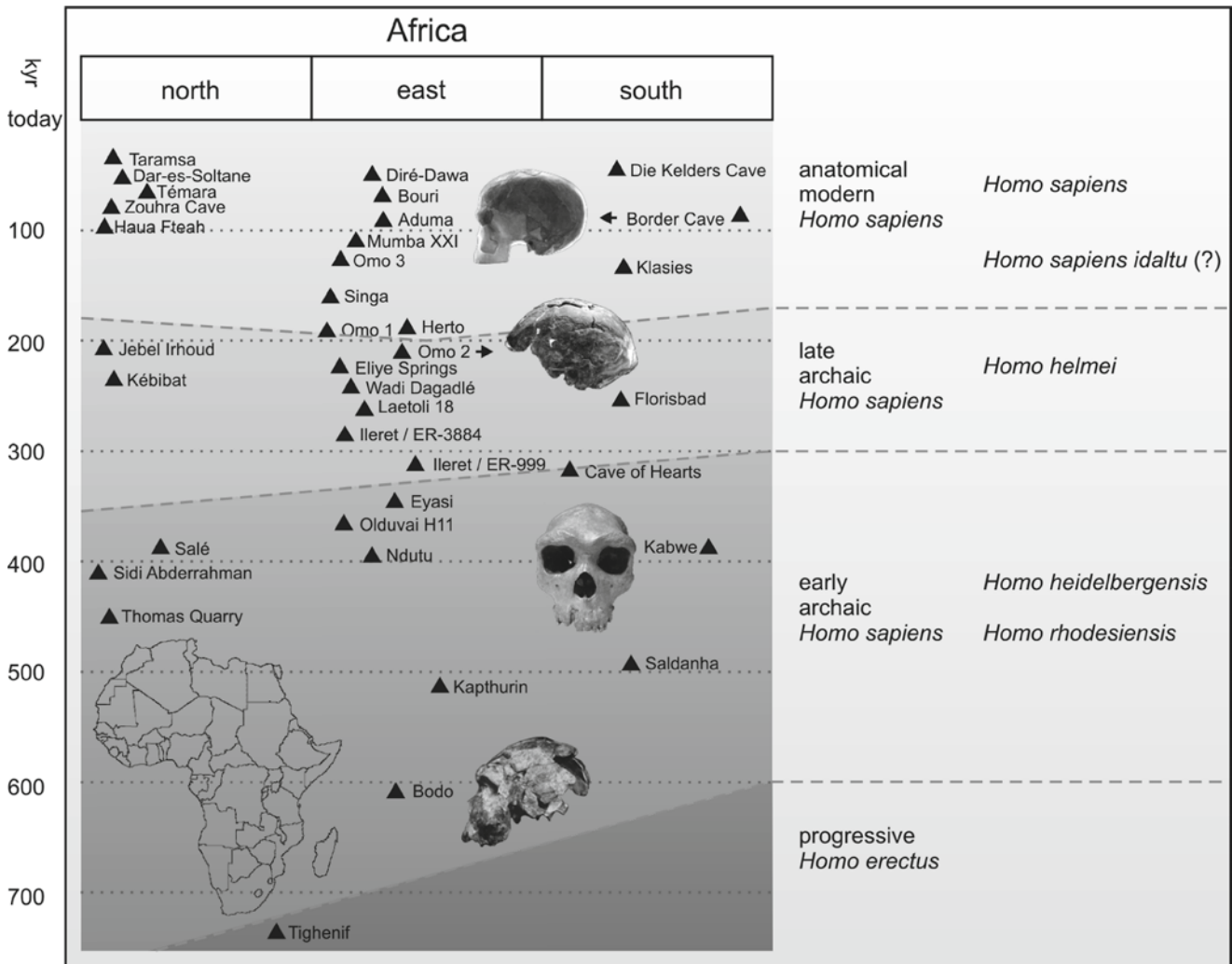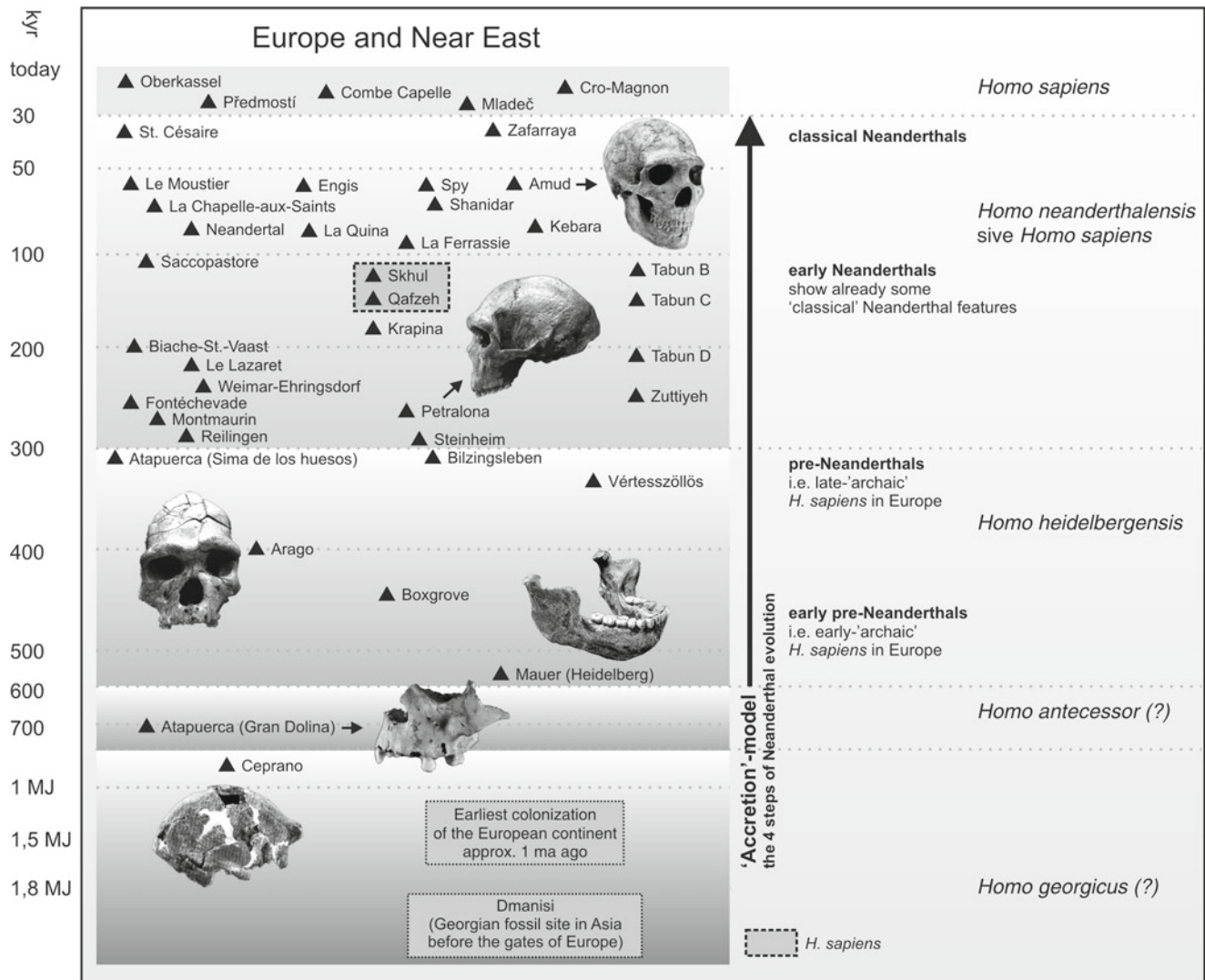

Fig. 3.6 Time scale of *Homo* fossils in Africa depicting taxa assignment and chronology (Hardt and Henke 2007)

Fig. 3.7 Time scale of important *Homo* fossils in Europe and the Near East in chronological order and attribution to the steps of the gradual 'Accretion model' and the 'Archaic *Homo* model' respectively (Hardt and Henke 2007)

Beijing, in the 1930s, now known as *H. erectus* (formerly attributed to the genus *Sinanthropus)*, were clearly more archaic than fossils from Europe (e.g., Mauer) and Northwest Africa (e.g., Ternifine), it was initially stated that *Homo* emerged in East Asia and dispersed westward. Since around 1960, when specimens from different localities in the eastern Rift Valley and South Africa were assigned to 'early *Homo*' for the first time, the picture has changed. Especially the hominin fossils around Lake Turkana (initially classified as *H. erectus* and currently termed *H. ergaster*) have proved to be the oldest ones and the more plesiomorphic forms too. Consequently, the actually preferred dispersal hypothesis sees the 'African *H. erectus*' or *H. ergaster* as the species which firstly immigrated to Asia and subsequently to Europe. Advances in dating methods and new finds from China and Indonesia indicate that early *Homo* may have arrived in East Asia by c. 2 Ma (Fig. 3.6). Alan Turner and O'Regan (2007)

recently stated that the effects of tectonic and climatic changes on the Levantine route during the Plio–Pleistocene suggests that a late Pliocene dispersal should be given serious consideration, because the *Homo* migration can be seen as part of the pattern of dispersion by members of the terrestrial mammalian fauna (Torre et al. 1992; Hemmer 1999; Vrba 2007).

Judged from current archaeological and paleoanthropological evidences Europe was reached not earlier than c. 1.3 Ma (Arzarello et al. 2007; Carbonell et al. 2008), but we have to remember the rule that 'absence of evidence is no evidence of absence.'

From a palecological view, there has been several times admonished that those hypotheses should not be neglected which propose that *Homo* may have reached Europe from Far East Asia and not directly from Africa *via* the Levant (or even the Gulf of Sidra or the Street of Gibraltar). To prove
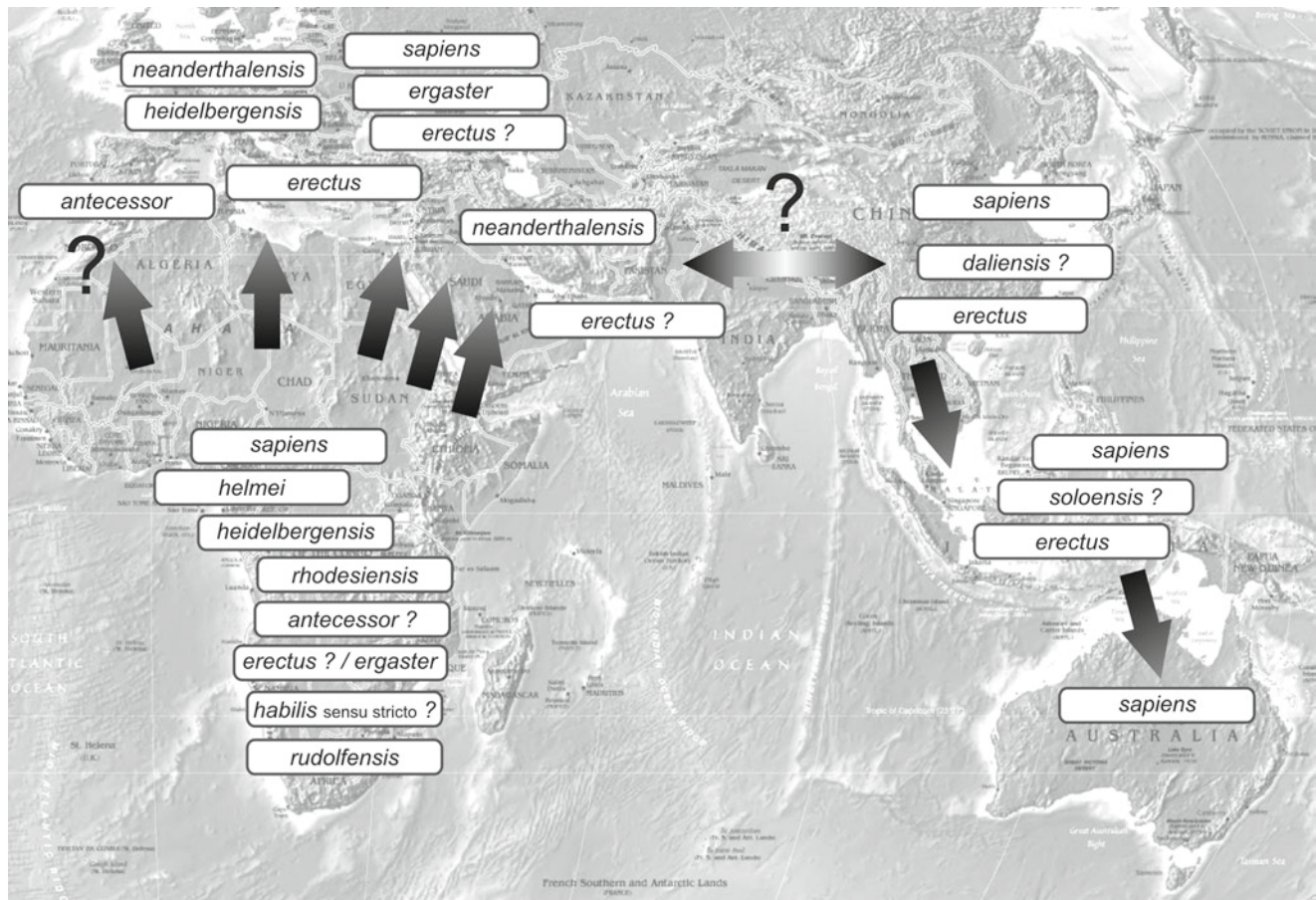
Fig. 3.8 Species of the Genus *Homo* ('splitters' view on dispersals out of Africa)

such dispersal scenarios, faunistic information should be taken much more into account, because of the co-evolution of hominin predators with carnivores (Felidae, Canidae). Further information can be gained from the dispersal pattern of the mammals that they scavenged or hunted (Henke et al. 1999; Torre et al. 1992; Turner and O'Regan 2007).

The regional fossil records of the Early and Middle Pleistocene hominins from Africa, Asia, and Europe demonstrate broadly similar morphological trends. There is – in the opinion of the gradualists – no convincing evidence to support a Middle Pleistocene speciation event leading to a distinct *H. sapiens* – quite the contrary, the proponents of the so-called multiregional theory of hominin evolution (see e.g., Wolpoff 1996–1997, 1999) point out that there is morphological continuity between *H. erectus* and *H. sapiens*. For example, the Ngandong skulls from Java, whose age may be no more than 34,000 years, have been described by some authors as *H. erectus* and by others as 'archaic' *H. sapiens* or a species of its own, *Homo soloensis*. Due to the repeated occurrence of fossil specimens exhibiting a morphologically intermediate pattern between *H. erectus* and *H. sapiens*, which is obviously incompatible with a punctuational interpretation of human evolution, there is cause for much debate

on stability and change in *H. erectus* and need for a critical assessment of the inflation-like splitting of the genus *Homo* as practised by some protagonists (e.g., Schwartz 2000a, b; Schwartz and Tattersall 2002, 2003; Tattersall and Schwartz 2000).

Anthropologists who argue that a speciation event took place within the genus *Homo* during the Early and Middle Pleistocene describe many morphological characteristics of *H. erectus* (incl. *H. ergaster*) (Table 3.2), but character states that are autapomorphic are obviously rare and controversial (Andrews 1984; Bilsborough and Wood 1986; Bräuer and Mbua 1992; Henke and Rothe 1994; Howell 1986; Howells 1980, 1993; Hublin 1986; Kennedy 1991; Rightmire 1990, 1998, 2007; Wolpoff 1996–1997; Tattersall and Schwartz 2000). The splitting of the *Homo* hypodigm on the species level is highly controversial. If one does not take the extreme position of so-called 'lumpers' like Wolpoff et al. (1994a, b), who explain the variability within *Homo* by polymorphism and polytypism and merge *H. erectus* within the evolutionary species *H. sapiens*, there are diverse proposals by so-called 'splitters' ranging up to a maximum of a dozen *Homo*-species. As it is quite obvious that some of these decisions are much more gut feeling than brain generated, we should

seriously ask for the reliability of the applied methodologies and the validity of the described taxa.

The following list describes some of the traits that set *H. erectus* apart from *H. habilis*/*H. rudolfensis* on the one hand and *H. sapiens* on the other hand. The schedule demonstrates the opinion of 'splitters', – so-called 'lumpers' do not accept these features as taxonomically valid (see also Henke and Rothe 1994, 1999a, b; Henke 2005; Table 3.2; Fig. 3.9).

Some anthropologists argue that *H. erectus* is an exclusively Asian taxon which possesses features not present in African specimens and in *H. sapiens* either. For this reason they see better arguments for an African than for an Asian origin of *H. sapiens*. Strong opposition comes from 'multiregionalists', because the supposed autapomorphic characters that seem to underline the uniqueness of the Asian sample are not truly independent characters, because they are correlated within functional units of adaptation. No anthropologist denies that there are differences between the Asian and African *Homo* samples under discussion, but the point is whether these differences are sufficient to warrant taxonomic recognition at the species level (see e.g., Bilsborough 1992; Henke and Rothe 1999a; Wiesemüller et al. 2003).

That *H. erectus* was fully upright and bipedal is still expressed by the species name, but until the virtually complete skeleton KNM-WT 15,000 (Walker and Leakey 1993) was discovered, we knew very little about the *H. erectus* postcranium. The skeleton of the c. 12-year-old boy from Nariokotome, West-Turkana, which has been dated to 1.6 Ma, enables us to reconstruct stature, limb proportions, locomotion, maturation, and gestation. In adulthood the young boy, who measured 1.68 m, would have been c. 1.80 m tall and weigh c. 47 kg. He was tall and thin, resembling

present-day equatorial Africans. Rogers et al. (1996) discussed the behavioral implications of the archaeological and paleogeographical record and early *H. erectus* anatomy. The described physiological changes (e.g., secondary altriciality, longer period of maturation, increase in need for food, increase in long-distance locomotor efficiency, and greater resistance to heat stress), combined with the implied behavioral changes (e.g., greater parental investment, larger home ranges) and the archaeological evidence for a changed behavioral ecology (e.g., lithic standardization by the reduction of single platform cores, use of large flakes for cores) suggests that the 'early' *Homo* of the Early Pleistocene was less constrained than earlier hominins by the natural distribution of resources. This makes him an ideal candidate for emigrating pioneers (see Fig. 3.10). For this reason and from the total morphological pattern, Wolpoff et al. (1994, p. 341) see "no distinct boundary between *H. erectus* and *H. sapiens* in time and space." They regard the lineage as a single evolutionary species, but other authorities describe different earlier and further speciation processes, stating that the emergence of *Homo* has not been a single linear transformation of one species into another, but rather a "meandering, multifaceted evolution" (see Tattersall 2000b; and the splitter's pedigree version given in Fig. 3.1). The crucial paleoanthropological puzzle is to find a sound answer to the question: How many speciation processes took place, when and where? (see Hardt and Henke 2007).

## Counting of Species – Purely a Matter of Taste?

How Many Homo-*Species Were There?*

Beside the lumper's model of gradualism there have been published many speciation models which interpret the hominin fossil record in quite different, obviously much more complex or even complicated ways ranging from moderate views of speciation to the view of extreme 'splitters'. As mentioned above, the currently preferred approach is the cladistic analysis. This method which has been developed by Hennig (1950) is based upon the presence and absence of larger numbers of traits or character states. Sister groups (adelphotaxa) are formed on the basis of sets of shared derived character states (synapomorphies), and species are defined on the basis of unique derived character states (autapomorphies). Similarities based on synapomorphic traits only are relevant for the reconstruction of a monophylum, a taxonomic group of organisms that has a single common ancestor (see also McHenry 1996; Wiesemüller et al. 2003; Rothe and Henke 2006). The cladistic principle sounds easy

Table 3.2 Diagnostic features of *Homo erectus*

- Cranial capacity ranging from 800 to 1,225 cc, thick brow ridge (torus supraorbitalis), especially in the later forms
- Special neurocranial proportions: wide cranial base, vault walls relatively vertical in their lower portions; long, flat, low braincase
- More arched than bell shaped contour of the braincase seen from the rear, occipital large and sharply angled
- Well marked nuchal plane bounded by a distinct nuchal ridge (occipital torus)
- Temporal lines distinct and slightly raised, especially anteriorly
- Dagittal keeling and parasagittal depression in Asian skulls only, occipital ankles
- The separation of the African sample from the Asian is highly questioned. Wood (1984) for example describes the following autapomorphies of the Asian *H. erectus*
- Occipital torus with sulcus above
- Angular torus and mastoid crest
- Sulcus on frontal behind torus
- Proportions and shape of occipital bone
- Relatively large occipital arc

Diagnostic features of *Homo erectus* as described by Groves and Mazák (1975) and others (see Henke and Rothe 1994)
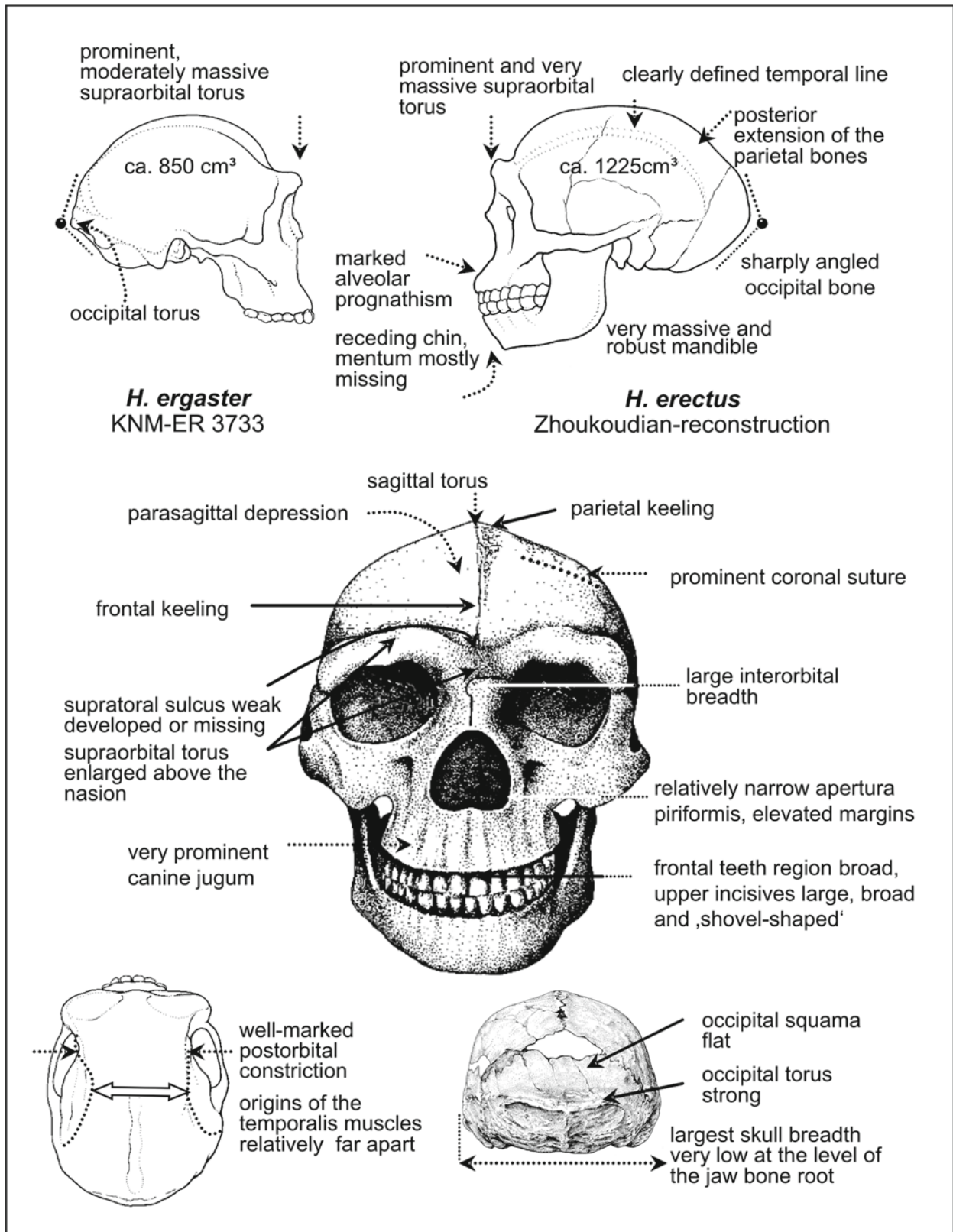
Fig. 3.9 Morphological features of the skull of *Homo ergaster* and *Homo erectus* demonstrated by the specimen KNM-ER 3733 and the reconstruction of the female *'Sinanthropus'* from Weidenreich (1943), Norma occipitalis of ZH XII (From Henke and Rothe 1999a, redrawn)

anatomical changes	physiological changes	behavioral consequences	archeological evidence
narrow hips and birth channel	secondary altriciality	increased parental investment	evidence for the transport of bone and stone; archeological traces of efficient environment using; hints for using fire
increased brain size	elongated maturation time	feeding supply by male? reciprocal food sharing fixed habitat?	
increasing body size	increased requirements for better food	expenditure of time to obtain food, greater dispersal; increase in food diversity? flesh consumption?	archeological record from very different ecological context, incl. open and arid biotopes; comprehensive archeological evidence for using stone tools to gain high-quality food; increase of cut-marks in bones
greater linearity in body shape	increasing strength, enhancement of the locomotory efficiency	greater home area greater daily migration decrease in population density	
decrease in mandibula and tooth size	higher resistance against heat-stress	greater ability for the production of gracile lithic tools; increase in preoral food preparation; increase in food quality? more efficient tools?	standardization of tool-types to organize manufacturing more efficient; Using of great flakes as cores
	reduction in masticatory capacity		

Fig. 3.10 Adaptational patterns of *H. erectus* (Rogers et al. 1996 modified)

but isn't, as the problems start with the choice and weighting of the characters, the scoring of character states and end with the arbitrariness of the principle of parsimony, the rule, that in the presence of two competing and otherwise equal explanations, the simpler of both should be considered the most likely. Ockham's razor, the theory regarding the simplest explanation as the best solution is highly controversial (Wiesemüller et al. 2003). Dilemmas are programmed and we have to solve them as we have to consider that the evolution of our own species has been a singular real-historic-genetical event and the paleoanthropological challenge is to reconstruct this unique phylogenetic incidence. Referring to

the different taxonomical schools (see above) we have to state that we can not expect consensus due to the underlying principals and the applied methodological approaches. For this reason we have to discuss the opposed phylogenetic models against the methodological background (Rothe and Henke 2006).

Once again: lumpers' combine facts and evidences into simple, highly variable categories; taxonomically they create taxa that include variable morphs that might – to a 'splitter' – be better allotted to several taxa. The 'splitters' are convinced that where distinct morphs can readily be identified it would seem most productive to assume they represent

Table 3.3 Hominine taxonomy

Genus *Homo* Linnaeus, 1758 [including the following genera: *Anthropopithecus* Dubois, 1892; *Pithecanthropus* Dubois, 1892; *Protanthropus* Haeckel, 1895; *Sinanthropus* Black, 1927; *Cypanthropus* Pycraft, 1928; *Meganthropus* Weidenreich, 1945; *Atlanthropus* Arambourg, 1954; *Telanthropus* Broom and Robinson, 1949]; earliest appearance in the Pliocene, world-wide distribution

Species name and	First description	Age	Dispersal
Homo antecessor	(Bermudez de Castro et al., 1997)	EP	W-Europe
Homo cepranensis	(Mallegni et al., 2003)	EP	Italy
Homo erectus	(Dubois, 1892; Weidenreich, 1940)	P	Africa and Eurasia
Homo ergaster	(Groves and Mazák, 1975)	P	Africa and Eurasia
Homo floresiensis	(Brown et al., 2004)	LP–EHol	Indonesia
Homo georgicus	(Gabunia et al., 2002)	EP	W-Asia
Homo habilis	(Leakey et al., 1964)	Pli–P	Africa
Homo heidelbergensis	(Schoetensack, 1908)	MP	Africa and Europe
Homo helmei	(Dreyer, 1935)	MP	N-Africa
Homo mauretanicus	(Arambourg, 1963)	MP	N-Africa
Homo modjokertensis	(Koenigswald, 1950)	EP	Indonesia
Homo neanderthalensis	(King, 1864)	MP–LP	Eurasia
Homo palaeojavanicus	(Sartono 1981)	MP	SE-Asia
Homo rhodesiensis (cf. *heidelbergensis*)	(Woodward, 1921)	MP	Africa
Homo rudolfensis	(Alexeev, 1986; Wood, 1992)	Pli–P	E-Africa and Malawi
Homo sapiens	(Linnaeus, 1758)	P–today	Worldwide
Homo soloensis	(Dubois, 1940)	MP	SE-Asia

Hominine Taxonomy: Species designations of the genus *Homo*; temporal and geographic ranges. Except *Homo sapiens* all the other taxa went extinct (Adopted from; Mai et al. 2005; see also Henke 2003a, b, 2005)
Hol Holocene, *P* Pleistocene, *Pli* Pliocene, *E* early, *M* middle, *L* late

species unless there is compelling reason to believe otherwise, (see Campbell and Loy 2000; Mai et al. 2005). Is species recognition purely a matter of taste? Are species constructions – or do they really exist? (for different views see Wiley 1978; Ax 1984; Willmann 1985; Tattersall 1986; Wolpoff and Caspari 1997; Schwartz 2000a; Wiesemüller et al. 2003; Rothe and Henke 2006; Futuyama 2007). The list given in Table 3.3 demonstrates that more than a dozen species of the genus *Homo* have been described with increasing tendency during the last decades. For this reason we must ask how reliable the tremendous splitting is and how valid the definitions are.

Opposing Views of Lumpers and Splitters

Scenario I: Multiregional Evolution Model (MRE)

Jan Jelínek, a life-long proponent of regional continuity, influenced by the theories of Franz Weidenreich and effected by his own broad anthropological and archaeological research in the Old World continents and Australia asked: "Have we any solid scientific grounds on which to consider Middle Pleistocene European finds, with earlier morphological cranial changes, as *Homo sapiens* and the extra-European finds evolving in the same direction but in somewhat different degree and time sequence of adaptation into different conditions as *Homo erectus*?"

His answer was that the evidences from the global perspective should lead us sink *H. erectus* into *H. sapiens* (Jelinek 1978). He stated his view more precisely in the eighties: "If the differential diagnosis between *Homo erectus* and *Homo sapiens* cannot be other than by convention, and […] this convention must be different for different geographical regions, then the value of such difference should be critically considered […] It is time to replace the paleontological species with a biological one. […] Paleontological taxonomy cannot be in contradiction with […] biological facts" (Jelínek 1981, p. 88; see also Wolpoff and Caspari 1997, p. 253).

Together with Milford Wolpoff et al. (1994, 341) he proposed "to merge *Homo erectus* within the evolutionary species *Homo sapiens*". Wolpoff and Caspari (1997, p. 255) point to the fact that the evolutionary species "… retains the essence of the biological species – reproductive isolation (the reason it can maintain its identity and has unique evolutionary tendencies) – while avoiding many of its deficiencies: lack of time-depth, absence of morphological criteria for diagnosis, and, perhaps most important, emphasis on reproductive ties alone as a major cohesive force."

The 'multiregionalists' interpret the fossil evidences within the rationales of the evolutionary species concept as Jelínek proposed in the 1960s: "No species splits occurred when *H. sapiens* is said to originate from *H. erectus*; there was no division of one species into two, and therefore no species birthing…" (Wolpoff and Caspari 1997; p. 256).

The multiregional evolution model (MRE) states that there is no basis for distinguishing a species called *H. sapiens*

from a species *H. erectus* (and other Middle and Late Pleistocene species); Fig. 3.11a reflects this gradualist view. The MRE traces all modern populations back to c. 2 Ma when humans migrated out of Africa for the first time. Since this phase there has been no speciation, but an interconnected web of ancient lineages existed in which the genetic contributions to all living peoples varied regionally and temporally (Thorne and Wolpoff 1981, 1992; Wolpoff 1999). We straighten

out here that the MRE is in contrast to otherwise uttered opinions no candelabra-model. The MRE has its historic base in the polycentric evolution hypothesis of Franz Weidenreich, proposing "that the conditions associated with the initial migrations of humans from Africa … created the central and peripheral contrasts that affected the early establishment of regional features at the peripheries of the human range" (Wolpoff 1992, p. 26).
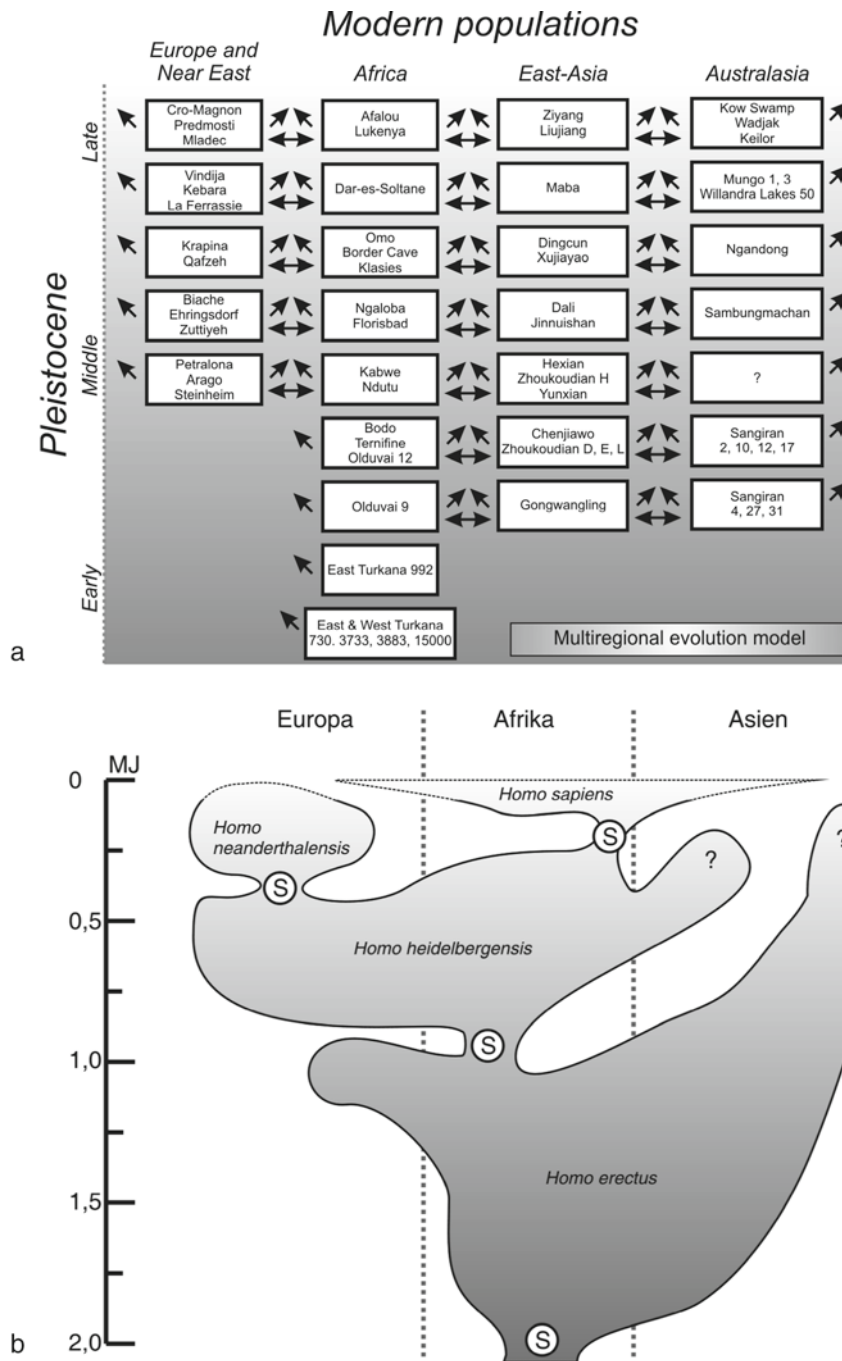
Fig. 3.11 (**a**) *MRE* (Multiregional evolution model) or the 'lumpers' view of human evolution (Frayer et al. 1993), (**b**) "Out of Africa"– model after Rightmire (2001a), (**c**) RAO-model after (Stringer 2002), (**d**) Out of Africa-model with hybridization after (Bräuer 2006, 2007)
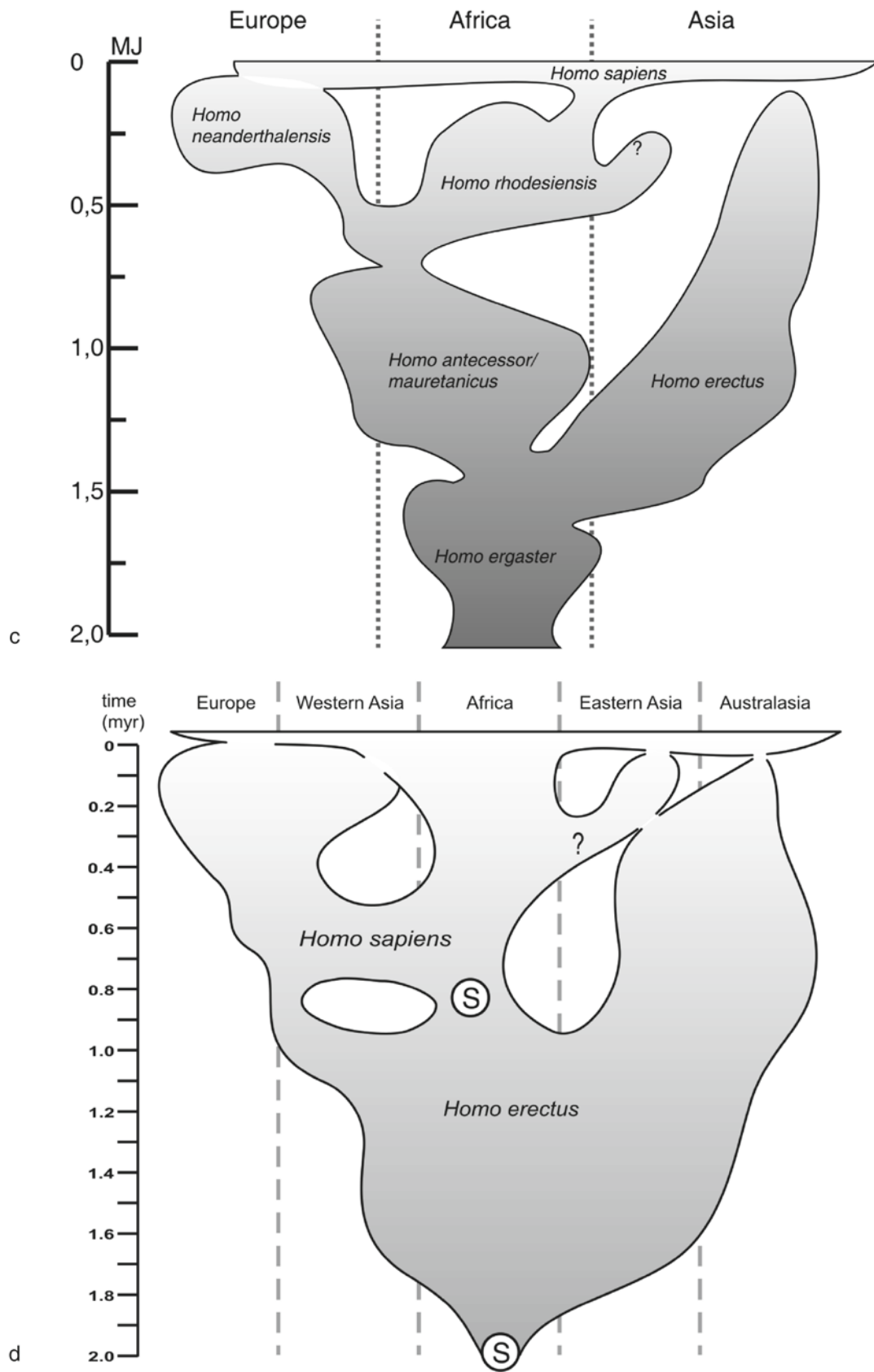
Fig. 3.11 (continued)

Scenario II: Recent African Origin Models (RAOM)

In opposite to the MRE all other phylogenetic models described here suppose at least one or more speciation events within the genus *Homo*. A widely accepted recent African origin model (RAOM) has been proposed by Rightmire (1998, 2001a, b; Fig. 3.11b). The pedigree describes three further speciations after the emergence of *Homo ergaster/erectus*. At around 0.8 Ma an evolutionary split in Africa is leading to *H. heidelbergensis*. While Rightmire leaves the phylogenetic role of *H. antecessor* in his model open (Rightmire 2001a), he recently discussed the hypothesis that this species could be a direct descent of *H. erectus* and the ancestor of *H. heidelbergensis* on the one side and *H. rhodesiensis* on the other side (Rightmire 2007; see also Stringer 2002, Fig. 3.11c, discussed below).

H. heidelbergensis, firstly described in 1907, has reached a reinterpretation during the last decade (Rightmire 1998). The hypothesis is that *H. heidelbergensis* has given on the one hand rise to *H. neanderthalensis*, who emerged in Europe, and on the other hand to *H. sapiens* or modern humans, who split in Africa and successively occupied all other continents. The traditional model of the sixties and seventies of the last century implied that *H. erectus* was a valid species in all the continents of the Old World. The small European hypodigm was divided in different subspecies such as *H. erectus heidelbergensis*, *H. erectus bilzingslebenensis*, *H. erectus tautavelensis* and some others. The subspecies-splitting was applied for the Asian and African branches of *H. erectus* as well (for scientific historical aspects see Groves 1989; Henke and Rothe 1994). With the rapid increase of the hypodigm during the eighties of the last century the validity of a European *H. erectus* taxon was more and more disputed (Henke and Rothe 1994, 1995; Rightmire 1998). However, meanwhile many paleoanthropologists believe that *H. erectus* never has reached Europe, but there are different causes for this change of view. While Wolpoff et al. (1994) – as just mentioned – and Wolpoff (1996–1997, 1999) do not believe that the taxon *H. erectus* is valid in any event, others regard those European specimens that were formerly discussed as belonging to *H. erectus* as a species of their own, which originated in Africa around 0.6 Ma. For taxonomic reasons it was named *H. heidelbergensis* (see Rightmire 1990, 1998; Lahr 1994; Groves and Lahr 1994; Condemi and von Koenigswald 1997; overview in Ullrich 1998; Wagner and Beinhauer 1997; Wagner et al. 1997; Hardt and Henke 2007). It is – as proponents of this classification claim – best described by specimens from Kabwe (formerly Broken Hill, Zambia), Bodo (Middle Awash, Ethiopia), Petralona (Greece), Arago (France) and Sima de los Huesos (Atapuerca, Spain) (more details see Figs. 3.6 and 3.7).

Concerning the validity of the derived features of *H. heidelbergensis* there is no consensus at all. Astonishingly enough, that the Kabwe/Broken Hill skull was formerly attributed to 'archaic' *H. sapiens* and some authorities adhere to this classification though the gradual split in 'early and late archaic' *H. sapiens* does not match with the rules of classification. However, this type of array is insofar of interesting importance as Kabwe 1 and Bodo are key fossils in all out-of-Africa hypotheses. Both specimens are recognised as representatives of the first appearance of people distinct from *H. erectus*. Rightmire (1998, p. 135) describes for *H. heidelbergensis* on the one hand a pattern of plesiomorphic *H. erectus*-like traits and on the other hand apomorphies like an evolved endocranial volume, more *sapiens*-like proportions of the frontal and temporal bone, as well as details of the nose and the palate as also present in the specimens from Elandsfontein (South Africa), Ndutu (Kenya) and European fossils from Petralona, Arago and others (see Figs. 3.6 and 3.7).

Newly unearthed fossils from Bouri (Middle Awash, Ethiopia) yield unique insights into unresolved spatial and temporal relationships of *H. erectus* and younger taxa. The hominin calvaria and postcranial remains from the Dakanihylo Member of the Bouri Formation are ~1.0 Ma; they are associated with abundant early Acheulean stone tools and a vertebrate fauna that indicates predominantly a savannah environment. Asfaw et al. (2002, p. 317) are convinced that the morphological attributes of the fossils "centre [them] firmly within *H. erectus*". They see strong indications "that African *H. erectus* was the ancestor of *Homo sapiens*." Furthermore, the new fossils from Bouri shed light on newly described c. 0.8 Ma fossils from the Gran Dolina of Atapuerca (Spain), which have been classified as *H. antecessor* (Bermudez de Castro et al. 1997; Arsuaga et al. 1999; Carbonell et al. 1999). The hypothesis that this *species nova* may have originated in Africa and given rise to *H. neanderthalensis*, which flourished between ca. 200 and 30 ka while *H. sapiens* evolved as adelphotaxon of *H. heidelbergensis* in Africa, is in our opinion a daring hypothesis. By new fossil evidence from Italy it is now even less reliable than before. Fresh arguments to drop the taxon *H. antecessor* come from the research of the 800–900 ka calvarium from Ceprano (Ascenzi et al. 2000a, b; Manzi 2001, 2004; Manzi et al. 2001, 2003; Bruner and Manzi 2007). The specimen exhibits a morphological pattern which separates it from archaic humans like *H. ergaster* and *H. erectus*. While Mallegni et al. (2003) consider the cranial features as indication for a separate species (*H. cepranensis*), others as Bruner and Manzi (2007) evaluate them as ancestral morphology of the *H. heidelbergensis/rhodesiensis* hypodigm. Both authors are pleasantly discrete when they state: "Nevertheless, a definite taxonomic interpretation of this fossil cannot be provided until more appropriate comparative fossil samples (both in terms of chronology and anatomical completeness) are recovered" (Bruner and Manzi 2007, p. 365).

As mentioned above, there are highly differing scenarios of the origin of 'anatomically' modern human beings. The irreconcilable standpoints of the proponents of the MRE and the RAOMs have been hardened by totally different species concepts. The reproach of Tattersall

(cited by Flanagan, taken from Wolpoff 1999, p. 397) is that the 'multiregionalists' are "linking everything from *H. erectus* to *H. sapiens* into 'one big happy family' […] Paleontologists do not give other animals such a special treatment." Is this really an appropriate argument if we consider the facts?

Wolpoff, the protagonist of the 'multiregionalists', comments on Tattersall's critique by quoting the evolutionary geneticist A. Templeton (2002): "We make far too much of our anatomical difference […] Biologists who study, say, fruit flies know that each population can look quite distinct […] and yet they are tempted to hastily split them into separate species. Why must we look at ourselves any differently?" (Wolpoff 1999, p. 397).

The crucial case of whether there was more than one *Homo*-species comes from the long-standing unsolved debate on the Neanderthal problem: in spite of contrary reports, especially comments on molecular biological results, there is in our opinion currently no solution to the problem by mtDNA (see Henke and Rothe 1999a, b) in spite of differing opinions and claims (Serre et al. 2004; Caramelli et al. 2006; Orlando et al. 2006; Krause et al. 2007), as the final decision can only be obtained by nDNA analyses. Recent conducted genomic research, studying the "phenotypic sweep" by Eswaran et al. (2005, p. 1) came to the conclusion "that as much as 80% of nuclear loci have assimilated genetic material from non-African archaic humans." These results coincide with those of Relethford (2001a) who regards a "Mostly out of Africa"-model, in which Africa contributes the most to accumulated ancestry in all regions, as the adequate MRE-version. In both cases there is no speciation accepted to explain the variability of Middle and Late Pleistocene *Homo*.

The different RAOMs suggests that the humankind descends from a very recent modern population that lived in Africa only around 200 ka and replaced early humans elsewhere. This hypothesis has been called by its opponents 'Garden of Eden model' because it pleads for a – very recent – single regional human origin. The main elements of this theory are derived from the chronological and morphological comparison of the African and non-African fossil specimens. The presence of regional continuity only in Africa and the first appearance of modern human features in this continent were taken as strong arguments for different replacement models (Afro–European *sapiens* hypothesis *with* hybridisation; Bräuer 1984; see further Bräuer 2006, 2007; Fig. 3.11d). Although Bräuer's hypothesis supported the idea of a replacement *with* admixture, other authorities advocated – in the beginning – for a *total replacement* from paleoanthropological (Stringer 1986; Stringer and Andrews 1988) or paleogenetic reasons (mtDNA research; Cann et al. 1987; Stoneking and Cann 1989; Wilson and Cann 1992). Especially those genetic studies, which revealed that an African woman from c. 200–150 ka– called Eve or 'Lucky Mother' – was our last common ancestor, gained much credit in public discussions and its populist summary 'we are all Africans'.

What we actually know about diversity and variability is that there is a great amount of *Homo* fossils from the late Middle and Late Pleistocene in Africa, Asia, and Europe whose morphology differs – in comparison to earlier specimens – only within a moderate range. The diachronic comparative analysis allows describing a trend to less massive faces and larger skullcaps, approaching step by step the pattern of [anatomically] modern humans in Africa. Because this gradual process is less convincingly verified in Asia and extremely controversial in Europe, so-called out-of-Africa hypotheses have reached a high rate of acceptance (Stringer 1982, 1992; Bräuer 1984; Cann 1992) compared to the gradualistic, anagenetic MRE (Thorne and Wolpoff 1992; Wolpoff 1996–1997; Wolpoff et al. 1984).

The debate has received a new dynamic by the results of evolutionary human genetic research. The results from mtDNA analyses of recent female samples (Cann et al. 1987; Cann 1992) were topped by sophisticated aDNA research on the classical Neanderthal specimens from Felderhofer Grotto (Krings et al. 1997), Mezmaiskaya Cave (Ovchinnikov et al. 2000), and other specimens (Pääbo et al. 2004; Serre et al. 2004). At least the popular science was convinced that the Neanderthal problem was solved by aDNA analyses; coverheadlines like "Neanderthals are not our ancestors" (see Krings et al. 1997) did not miss the target, the intended message that Neanderthal man belonged to a species of its own. But those who read the papers attentively will realize that these results do "not definitively resolve the question of a possible Neandertal contribution to the gene pool of modern humans since such a contribution might have been erased by genetic drift or by the continuous influx of modern human DNA into the Neandertal gene pool" (Serre et al. 2004, p. 0313).

In spite of contrasting assertions by the proponents of the different models and refining of the RAOMs by human demographic history (see Excoffier 2002), there is the conclusion that none of them is unequivocally supported by the available data, although the out-of-Africa model gained tremendous – in our judge highly undeserved – support by the aDNA results from Neanderthal fossils. The currently running Neanderthal Genome Project, a joint project of Germany's Max Planck Institute for Evolutionary Anthropology and Branford, Connecticut-based 454 Life Sciences Corp., to map the Neanderthal genome, or DNA code should be observed with critical scepticism. Of course can we expect very interesting genomic results; however, the prognosis is indicated that each taxonomic hypothesis will create new controversies. A cynic would say that those anthropologists who look for differences will find them; the crucial question will be how to evaluate them within taxonomical categories (Storch et al. 2001; Wägele 2000; Wiesemüller et al. 2003; Jobling et al. 2004; Rothe and Henke 2001, 2006; Futuyama 2007).

Clifford Jolly's (2001, p. 177) studies commemorate to circumspective interpretations. He looked for population

genetical analogies from the papionin monkeys and their implications for human evolution and concluded: "An overall similarity in depth of genetic diversity suggests that papionin taxa such as *Papio* baboons, rather than extinct humans, may present the better analogy for human population structure of the "prereplacement" era. Neanderthals and Afro-Arabian "premodern" populations may have been analogous to extant baboons (and macaque) allotaxa: "phylogenetic" species, but "biological" subspecies."

Within the current version of his replacement model with hybridisation Bräuer (2007) sees good support from different lines of evidence that the European, African and possibly the Asian Middle Pleistocene lineages too belonged to one polytypic species *H. sapiens* (see Fig. 3.11d). We see in his statement the logical taxonomic consequence of the RAOM *with* hybridization and replacement.

In addition, concerning the evolution of European hominids Hublin (1998, p. 301) suggested that "…the development of the Neanderthal morphology results from an *accretion* phenomenon beginning in the middle of the Middle Pleistocene, around 450,000 BP…" due to drastic climatic changes in the Pleistocene. Caused by processes of geographical isolation through ice sheets, genetic drift, and intense selection as a result of the extremely cold environmental conditions the Neanderthal features run through a gradual development until they reached their terminal status (Couture and Hublin 2005; Harvati 2007; contra see Hawks and Wolpoff 2001). The proposed "Accretion model" is divided into four parts ranging from Stage 1 "early pre-Neanderthals" over Stage 2 "pre-Neanderthals" and Stage 3 "early Neanderthals" to Stage 4 "classic Neanderthals" with their typical features fully expressed (see Fig. 3.7). Consequentially, this model also offers two possibilities, namely to assign Neanderthals as an outstanding species *H. neanderthalensis* within a chrono- or morphospecies concept or as a subspecies of *H. sapiens* within an anagenetic concept. Whatever decision will be made, they will raise several new questions pertaining to African and European Middle Pleistocene lineages of *H. heidelbergensis* and *H. rhodesiensis* respectively.

There seems to be much more overlap with the MRE as former discussions indicated (Smith and Spencer 1984; Akazawa et al. 1992; Bräuer and Smith 1992; Wolpoff 1999; Relethford 2001a, b; Tobias et al. 2001). There is to recognize a gradual approximation to the MRE, which hypothesizes that modern humans evolved throughout the Old World as a single species roughly 2–1 Ma. But by far not all paleoanthropologists agree that speciation is a special case, an elusive phenomenon as e.g. Brace (1993), Frayer et al. (1993), Wolpoff and Caspari (1997, 2000), Wolpoff (1999), Grubb (1999) assert. Quite the contrary seems to be the case, not only in paleoanthropology (see Table 3.3) but in primatology too. The growing proliferation of specific names should be regarded with high scepticism, that's why Loring Brace

(1993, p. 151) expressed in his paper with the hissing title "The creation of specific hominid names: Gloria in excelsis deo? or ego? or praxis?" the suspicion "that the vanity of the namer is frequently involved in the creation of new nomina". In any case, each inauguration of a new taxon must be based on agreed biological principles and a sound methodological concept, otherwise each further discussion is in vain, but as paleoanthropology is a fossil- and journalism-driven science there is little hope to escape this kind of discussions (White 2000; Henke 2006, 2007; for the general problem of popular sciences see Franck 1998). Unprofessional handling of the fossil specimens like LB 1 from Flores is a sad example how paleoanthropology is discredited to "paleopoesy" and looses its credibility. Neither such a fascinating discipline like paleoanthropology nor the rare specimens as witness of our evolutionary history merit this kind of para-scientific treatment in times where paleoanthropology has been grown up and consolidated as a serious discipline (see Henke and Rothe 1994, 1999, 2003; Henke and Tattersall 2007).

The "muddle in the middle" will continue as long as arbitrary species like *H. antecessor* are created by the analysis of very scanty fossil material. This kind of weak founded taxonomical proposals does not contribute to a consolidation of our diverse views on modern human origins The description of two lineages of species (*H. antecessor – H. heidelbergensis – H. neanderthalensis* and *H. antecessor – H. rhodesiensis – H. sapiens*) is extremely problematic as it describes no cladistic events but successive speciations. If one would exclude this kind of chronospecies and regard the changes as anagenetical process, it would be mere consistent to regard the European *H. heidelbergensis* as *H. neanderthalensis* (Stringer 1996; Arsuaga et al. 1997; Hardt and Henke 2007). Simultaneously *H. rhodesiensis* should be involved in the taxon *H. sapiens*.

Whether species like *H. helmei*, *H. soloensis* and *H. palaeojavanicus* which have been redefined by some authorities during the last years as well as the creation of the *species novae H. georgicus* (Gabunia et al. 2002), *H. cepranensis* (Mallegni et al. 2003) and especially *H. floresiensis* (Brown et al. 2004; see also Falk et al. 2005) are valid evolutionary species is to doubt, as a detailed description of their autapomorphies is missing.

Concluding Remarks

It is quite obvious that paleoanthropologists have, in spite of a tremendous increase of methodological approaches and facts, no clear picture of the speciation processes which took place in the genus *Homo*. Nevertheless most of them agree that our genus originated in Africa around 2 Ma. Soon after the first appearance of "early *Homo*" (most probably *Homo ergaster*) our forerunners immigrated into Asia and much

later into Europe. After the first dispersal around c. 1.8 Ma there followed a second expansion out of Africa between 840 and 420 ka, followed by a third expansion wave around 150–100 ka as shown in Fig. 3.5. That an out-of-Africa dispersal took place again and again is beyond doubt, but whether this was a demic diffusion or a successive exodus of separate taxa with hybridization or replacement of the archaic populations is still highly controversial. The core problem is that it is not a matter of taste how many speciation events took place in this scenario. As this is a long-lasting problem we are afraid that paleoanthropologists don't have or don't apply the right methodological instruments to figure out how many species there have been. The way we see it is much more near the lumpers' view, than those of the splitters', as there are good arguments from different kinds of sources that our polymorphic and polytypic species *Homo sapiens* has relatively deep roots and that the dispersal was an early single event, followed by a permanent, uninterrupted but in the intensity regionally and chronologically highly varying gene flow with movements out of Africa to Asia and possibly back again (at least from Asia; Wolpoff 1999; Relethford 1999, 2001a; Zilhão 2006). Quite unexpected after 25 years of heated discussion Bräuer's RAOM approaches the MRE though there remain principal discrepancies. Bräuer (2008) states "that the African Middle Pleistocene lineage represents the species *Homo sapiens* and that the European Neandertal lineage, which derived from early African *Homo sapiens*, belongs to the same species except that there would be unequivocal evidence that Neandertals and modern humans were too different to be one species". Also Relethford's (2001a) "mostly out of Africa" model based on a population genetical approach point to a kind of compromise, as it only causes confusion to call in a splitter's manner any unit a species. However, this may be a wishful thinking. Gilbert et al. (2003, p. 259) put it this way: "We do not know where the gene flow barriers were among the sampled populations, nor do we know about unsampled populations/lineages." Discussing the taxonomic status of *H. rudolfensis* and *H. habilis* Wood (1996b, p. 112) supplementary concluded that "we are aware from the more recent fossil record of the major morphological "components" of *Homo*, but we remain ignorant about their functional interrelationships, the order in which they arose, and their relationships to the environmental and ecological pressures and constraints prevailing around 2 Ma." This view is still valid and remains a challenge for the next decade.

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