

The unravelled LB1 (*Homo floresiensis*) riddle? Some critical comments on the morphology of LB1

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Foreword by the editors. Alfred Czarnetzki passed away on 20 May 2013 in Tübingen. After his death, his widow Roswitha Blank-Czarnetzki found a number of almost finished publication projects. Although some of them can no longer be published without the author's input, others are so far advanced that it appears to be sensible and appropriate to publish them posthumously. Czarnetzki's most recent draft of the following paper was dated 7 May 2012. It has been reviewed by us as usual and is otherwise published as found. Since the research relating to LB1 did not stop in 2012, we editors, with grateful thanks to Winfried Henke, have supplemented the text at the end with some literature references for important studies published since then which Alfred Czarnetzki was no longer able to take into account.

Introduction

The unrivalled combination of morphological features of the LB1 specimen of Flores that are described in the literature and discussed at special workshops has given rise to several publications. In the meantime there are some indications (BROWN, 2004; CULOTTA, 2007; LIEBERMANN, 2004; TOCHERI ET AL. 2007; JUNGERS, 2009) that LB1 exhibits some ape-like features. This was the reason for us to undertake a very intensive study of the morphological features of modern and fossil Asian *Homoidea* together with microcephalics (WEBER, 2006), but excluding the metric data, and to reappraise these with those of LB1. Furthermore, we ascertained that only the remains of the fossil orangutan led to the misinterpretation of some fossil hominoid specimens belonging to the human phylogeny such as *Ramapithecus* (LEWIS, 1934; SIMONS, 1964) or *Sivapithecus indicus* (PREUSS, 1982) or Plitdown (WOODWARD ET AL., 1912). Schwartz (1988) ascertained: "not chimpanzees or other African apes that are humankind's closest cousins, but Asian orangutans". And in his revised and updated publication (SCHWARTZ, 2005) he presents additional evidence for his contention that orangutans share significantly more morphological similarities with humans than any other great ape. "The knowledge of the aforementioned examples, the high variability within the species orang-utan (*Pongo*)" first mentioned by Selenka (1898) or, last but not least, by CULOTTA ET AL. (2007) when she noted: "an (unsuccessful) hunt for living "orang pendek"", or Lieberman's overcautious allusion to this problem: "This cave woman ... so unlike

modern humans", gave rise to the question as to whether the skeletal remains of LB1 could be a local variant of the genus *Pongo* or a product of isolation on an island, and awakened our interest in examining the variability of special morphological features of the genus *Pongo*.

Material and method

We utilised the published data of LB1, a cast of the skull at the Rheinisches Landesmuseum Bonn, the morphology of 23 skulls and 9 endocasts of microcephalic modern humans (VOGT, 1867) together with the endocasts of 9 microcephalics out of a private collection. Our knowledge is further based on the examination of more than 5,000 modern human skulls from all over the world and comparative original orangutan skulls in the State Collection of Anthropology and Palaeoanatomy, Munich, together with data of the cited publications. We (i) investigated the details of the special morphological features of the skull and the postcranial skeleton very intensively. Additionally, (ii) CTs were produced owing to our experience that metric data can describe the real morphological similarities or dissimilarities only within different populations, but not between them. We therefore preferred the most exact observations and descriptions of the shape of the morphological features that are relevant for the analysis of the LB1 problem.

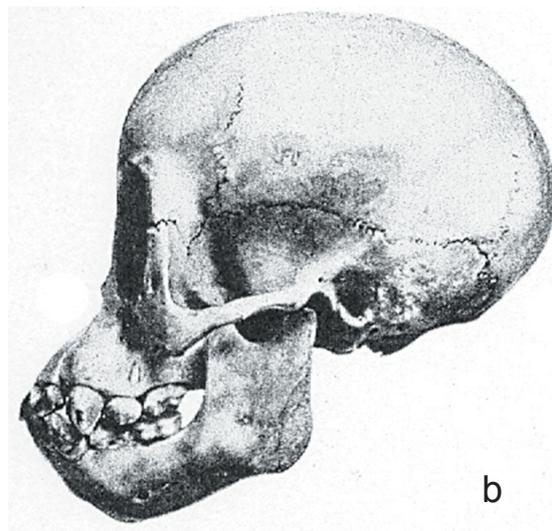
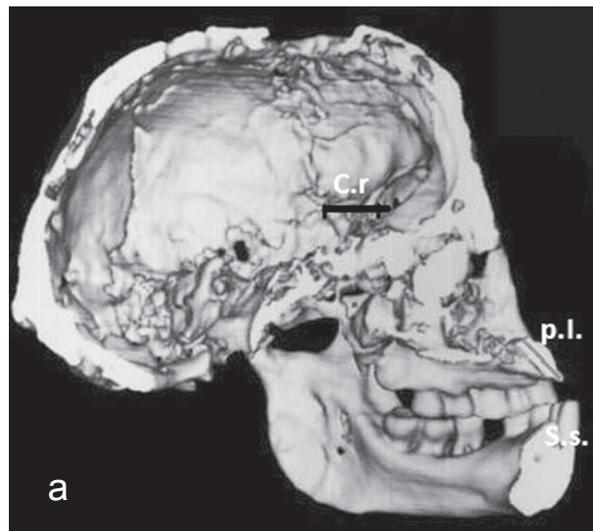
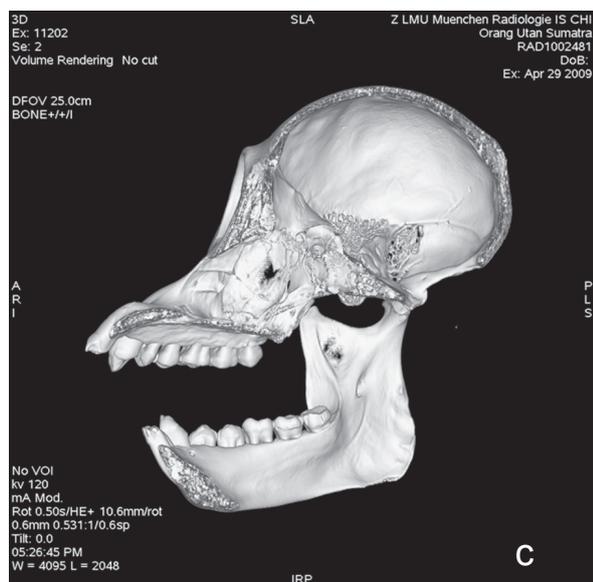


Fig. 1 Mediansagittal section of LB1 (a); a juvenile *Pongo pygmaeus* (b) according to Selenka (1898), and a mediansagittal CT section of a female *Pongo pygmaeus* (c) from Sumatra (see also Fig. 5).



Results

First of all we noted (i) the special course of the oblique line of the lower jaw (Linea obliqua mandibulae) compared to *Pithecanthropus*, *H.s.s.*, *Pongo pygmaeus* and LB1 (**Fig. 1 a-c**); and (ii) the rounded shape of the orbits (**Fig. 4b**, frontal view) and the extremely well-developed roots of the upper canine. But there are further features that bear a striking resemblance only to Pongo, but not to other hominoids, and not to *Homo s.s.* or its antecedents, and only to three modern microcephalics.

Some features are not in good agreement with one another. These are:

1. the low degree of dental prognathism
2. unfused frontal suture (Sutura frontalis)
3. partially unfused sphenoccipital synchondrosis (Synchondrosis sphenoccipitalis) in contrast to fully developed dentition.

As can be seen in **Table 1**, the features no. 1, 2, 3, 4, 8 - 16 are identical in *Sivapithecus indicus* (PREUSS, 1982), too. All these 13 are comparable features of these two specimens. Such a high number of analogue features or more can normally be observed only within a species, or between *Pongo* and LB1, but never between different species of other Pongidae. The features no. 3, 5, 7, 17 are also comparable with microcephalics of modern humans. Owing to the tendency of microcephalics to develop atavisms, we were able to ascertain through our studies that features can exist like a flat frontal, a very faint supraorbital torus (Pongo-like, **Fig. 3a**), a supramastoid crest, a lateral position of the mandibular fosse, the very low brain size and facial asymmetry (**Fig. 4a, b**). The similarities between *Pongo* and microcephalics that we could identify within the 32 features are comparable to those between LB1 and *Pongo* (**Fig. 6**). They are all identical within the LB1 specimen and orangutans (**Fig. 7**). This also holds true for the 13 comparable features (**Fig. 6 - 8**) between LB1 and *Sivapithecus*, but not for all the other homininae. The big toe was, in addition, relatively short. The other toes were very long and curved and therefore like those of Pongids.

	Features	LB1	Pongo	Sivap.	P.e.e.	H.s.s.	Microc.
1.	Less developed supraorbital torus	+	+	+	-	-	-
2.	Supraorbital torus runs along the supraorbital margin	+	+	+	-	-	-
3.	Supraglabellar depression	n.p.	+	+	-	-	+
4.	Rounded orbits	+	+	+	-	-	-
5.	Shape of the occipital bone in lateral view	+	+	n.p.	-	-	+
6.	Straight squamosal suture	+	+	n.p.	+	±	-
7.	Transition from the occipital squama to the basoccipital	+	+	n.p.	-	-	+
8.	Protrusion of the upper incisors	+	+	+	-	-	-
9.	Failure of the anterior nasal spine	+	+	+	-	-	-
10.	Flat cheek bone	+	+	+	-	-	-
11.	Double rooted P3	+	+	+	-	-	-
12.	P3 with 4 cusps	+	+	+	-	-	-
13.	Root of the canine extremely elongated and strong	+	+	+	-	-	-
14.	Simian shelf	+	+	+	-	-	-
15.	Deep digastric fossa	+	+	+	-	-	-
16.	Curvature of the Linea obliqua	+	+	+	-	-	-
17.	Asymmetry of the endocranium and the face	+	+	n.p.	-	-	+
18.	Low degree of humeral torsion	+	+	n.p.	-	-	-
19.	Bar-like humeral diaphysis	+	+	n.p.			
20.	Elongation of the coronoid process of the ulna	+	+	n.p.	-	-	-
21.	Articulation of the wrist	+	+	n.p.	-	-	-
22.	Shape of scaphoid and trapezoid	+	+	n.p.	-	-	-
23.	Straight femoral diaphysis	+	+	n.p.	-	-	-
24.	Extremely faint development of the gluteal tuberosity	+	+	n.p.	-	-	-
25.	Medial epicondyle of the femur extremely developed and	+	+	n.p.	-	-	-
26.	Clearly stepped medial epicondyle of the femur						
27.	Very smooth attachment of muscles of the posterior aspect of the femur	+	+	n.p.	-	-	-
28.	CT Cross-section of the femoral cervix	+	+	n.p.	-	-	-
29.	CT Cross-section of the femoral diaphysis	+	+	n.p.	-	-	-
30.	CT Cross-section of the tibial diaphysis nearly rounded	+	+	n.p.	-	-	-
31.	Lack of the arch of the foot	+	+	n.p.	-	-	-
32.	First toe short	+	+	n.p.	-	-	-
33.	Other toes long and curved	+	+	n.p.	-	-	-
34.	Intracranial capacity measured in ccm	417	425	n.p.	1000	1300	426

Table 1 Features of LB1 and their concordancy with other species or variants.

Pongo= Orangutan, Sivap. = Sivapithecus, P.e.e. = Pithecanthropus erectus, H.s.s. = Homo s.s., Microc. = Microcephalics of modern humans. + = synapomorphic features, - = apomorphic features, n.p. = not preserved features, ± = as well as

While processing the CTs of the orangutan skulls we observed an extremely low degree of humeral torsion in LB1. It was compared with the data of 9 other Pongids (MARTIN, 1914). The values

of LB1 (110°) can be observed only in Hylobatids and Pongids, while all the others exhibit a higher degree, especially *H.s.s.* (151.05° ± 8.64). The torsion value of LB1 spans the range of -3σ

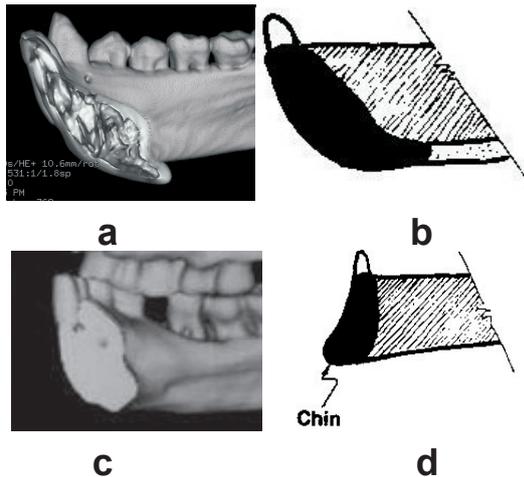


Fig. 2 Negative chin and simian shelf of *Pongo pygmaeus* (a) and LB1 (b). Schematic drawing of a simian shelf (b) and the positive chin of modern man (c). Notice the overlay of the simian shelf by the mandibular torus and the different diameters of the simian shelf. Very tiny in a modern *Pongo pygmaeus* (Fig. 1a) and very massive in LB1.

H.s.s. The data of the latter are based on the sum of 1,054 individuals out of 30 local samples. The body height of LB1 was determined by the known

formulae for modern man (BREITINGER, 1937; TROTTER & GLEESER, 1958). For a femoral length of 280 mm, the averages must be between 128.0 and 132.8 cm (body height orangutan: 90-100 cm). This body height is actually extremely low for modern humans and suggests dwarfism in modern man or that it may belong to other *hominoidea*. The CT cross-section through the femoral cervix, the middle of the femoral shaft as well as the tibial diaphysis is identical in LB1 and modern Pongo, but is never identical with modern humans (Fig. 8). On the basis of this unrivalled summary of Pongo-like features these skeletal remains should be assigned to the more gracile variant from Sumatra, *Pongo abelii floresiensis*.

- Ordo:** Primates, Linnaeus, 1758
- Subordo:** Anthropeoidea, Mivar, 1864
- Superfamilia:** Hominoidea, Gray, 1825
- Familia:** Pongidae, Gray, 1825?
- Tribus:** Pongini, Gray, 1825
- Genus:** Pongo, Linaeus, 1758
- Species:** *Pongo abelii*
- Subspecies:** *Pongo abelii floresiensis*

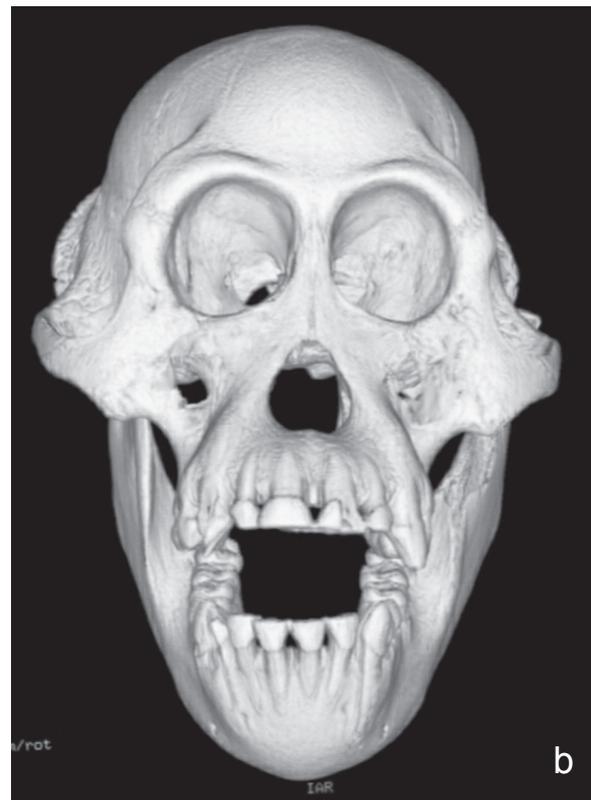
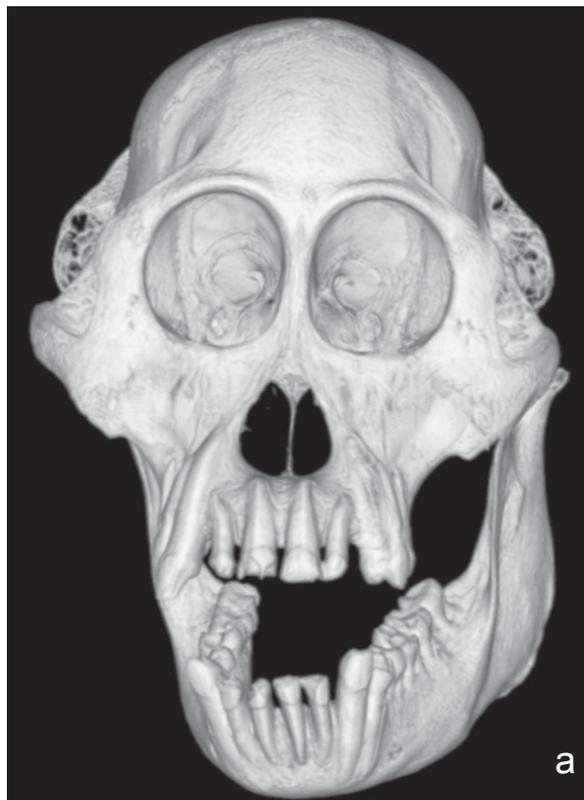


Fig. 3 Local variations in female orangutan skulls from Sumatra (a) and Borneo (b).
a: With almost completely rounded orbits, well-developed canine roots (both as in LB1), but a weakly developed supraorbital torus and distinct temporal lines.
b: The typical completely rounded orbits, a relatively well-developed supraorbital torus and canine roots, less developed temporal lines and a rounded neurocranium as in LB1.

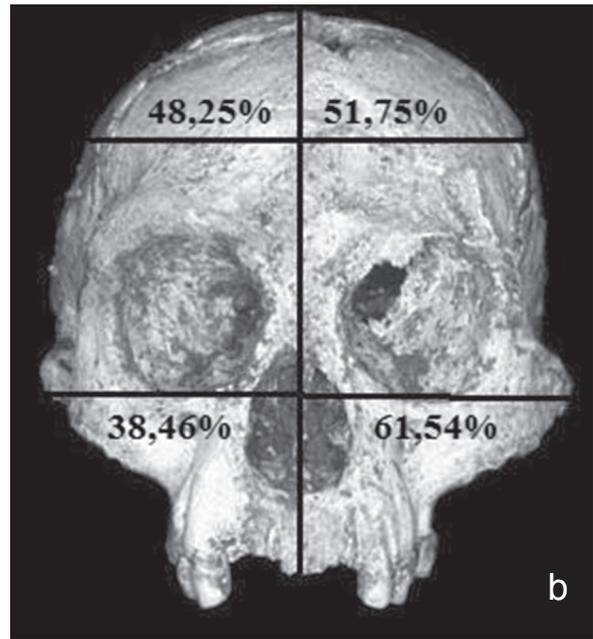
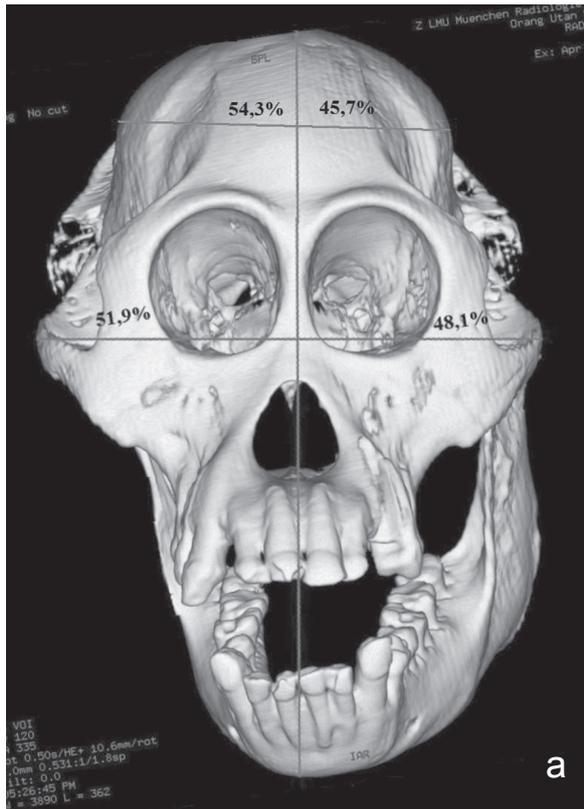


Fig. 4 Asymmetry of the skull of an orangutan from Sumatra (a) and LB1 (b).

a The normal right-left asymmetries of a skull
b LB1 with the uncommon left-right asymmetry especially of the face, possibly an effect of restoration and deformation by embedding.

Discussion

First of all, one has to consider that the reconstruction of the skull of LB1 is (i) based on a heavily deformed and extremely rain-sodden skull. The sphenoid especially is highly compressed after reconstruction (**Fig. 4b**; **Fig. 5**). Moreover, the part of the socket for the incisors (premaxillary bone) is missing due to weathering (**Fig. 4**). This is demonstrated by the 3D figure of the midsagittal section published by BROWN ET AL. (2004, Fig. 4). Additionally, he listed 14 morphological features that are “distinct from *Homo*”. Furthermore, the studies of Schwartz (1988), as mentioned above, ascertain that the morphological similarities between *Pongo* and *Homo* can be observed much more frequently than those between *Homo*, *Pan* and *Gorilla*. This can, for example, easily be demonstrated by the features listed in Tables 5-1 and 5-3 of Schwartz (1988). The traits used by SCHWARTZ (1988) differ only in two cases (9.4%) between *Pongo* and *Homo*, while *Gorilla* and *Pan* share only 9.4% with *Pongo* and *Homo*. This result supports our comparison as demonstrated in Table 1. Additionally, *Pongo* seems to very easily develop local or isolation variants, both within the different biotopes of Borneo alone as well as between Borneo and

Sumatra (SELENKA, 1898). LB1 could therefore be such a variant caused by isolation and/or the “Island rules” (BROMHAM ET AL., 2007) that takes hold through the development of new variants of a specific species. Furthermore, this special variant could represent a juvenile stage of development at an adult age (paedomorphism). Such morphological changes originate from the well-known phylogenetic process of neoteny (paedogenesis).

Only the morphology of the braincase and the facial skeleton of LB1 are very similar to those of juvenile or female orangutans (**Fig. 6**). The contrast between the tiny stature and the big foot fits well with the straight femoral diaphysis, and the nearly rounded one of the tibia with the morphological proportions of a Pongid. Even the straight diaphysis of the femur can never be observed in the genus *Homo*, including microcephalics, but in all Pongids and Hylobatids (CZARNETZKI, 1966; GIESELER, 1926) as a normal morphological feature of their adaptation to their specialised locomotion. This applies especially to the condyle tangent angle of the distal epicondyles of the femur (GIESELER, 1926) that can be observed only in non-human primates, but never in humans, and to a great extent to the values of the torsion of the humerus. Furthermore, it is well known

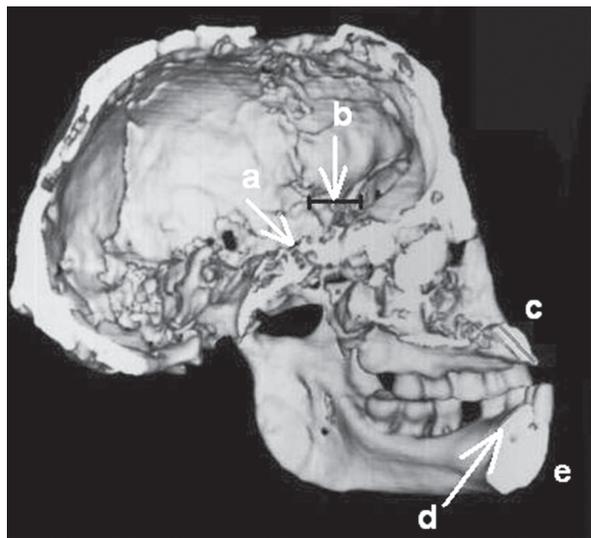


Fig. 5 Non-human features of LB1. a: incompletely fused synchondrosis spheno-occipitalis; b: compressed major wing (ala major) of the sphenoid bone; c: extreme protrusion of the incisors; d: simian shelf; e: negative chin.

since the discussion about the upright walk of Lucy at the “Ancestors: The hard evidence” Symposium (New York, 1984) that the bones of the feet of the great apes are much more similar to those of real human bipedalism than those of the hands. Recently, LIEBERMAN (2009) pointed out that the foot of LB1 is only very similar but never the same as the human foot. The CT cross-section through the femoral cervix and through the middle of the femoral and tibial diaphysis are identical in modern *Pongo* and in LB1, as is well known from functional analyses of the femur and the tibia (PREUSCHOFF, 1970), the cross-section of the diaphysis depending directly on the direction of the acting and reacting forces. Taking into account the biomechanical principles one can conclude that similarities between these features give an indication of the similar functional adaptation of the anatomy of the muscles and the resulting kind of locomotion. This means that the morphological features of the extremities of LB1 are in good agreement with a primate-like locomotion and therefore very different to modern humans (CZARNETZKI ET AL., 1998). The differences in the articular surface of the wrist bones can, in contrast to the similarities of the scaphoid and capitatum between *Pongo* and LB1 (TOCHERI ET AL., 2007), never be an argument for a species-specific differentiation, because it is known that these features vary even within a species, e.g. the occipital condyle of modern humans varies from

circle-like and smooth to bean-like and curved within a human population. Only the position and the overall shape of the wrist bones are therefore essential for a precise definition of the species.

Conclusion

The comparison of the available morphological features of LB1 with 23 skulls of microcephalic modern humans, nearly 5,000 modern humans from all over the world, and from Palaeolithic to modern times, the orangutan skulls of the State Collection of Anthropology and Palaeoanatomy, Munich, *Sivapithecus*, *Pithecanthropus erectus* specimens from the Far East, and further data of other hominoidea added from literature, led to a surprising result. The analysis of the morphological meaning of LB1 was as precise as possible and (i) took into account the fact that the skeletal elements were more distorted or less distorted depending on the time they had been embedded in very moist soil and therefore (ii) had had to be reconstructed by the authorised person imagining what the real morphology should be. Taking into account all these postulates together with the knowledge of phylogenetic principles like paedomorphism, neoteny, island rules, high variability within the genus *Pongo*, the high number of affinities (30 out of 31) with the genus *Pongo* and all comparable 13 features of *Sivapithecus indicus* (PREUSS, 1982), the phylogenetic positioning of LB1 could only result in a position close to or within the variability of the genus *Pongo*. In particular, the features of the extremities like the big foot with its short big toe (see SCHWARTZ, 2005, p. 94), the small femur and tibia of LB1, its low degree of humeral torsion, and the elongation of the coronoid process of the ulna, are in best agreement with the laws of functional anatomy for the locomotion of a pongo-like *Hominoid*.

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Fig. 6 Skull of LB1 (see above) compared to a juvenile Pongo (below).

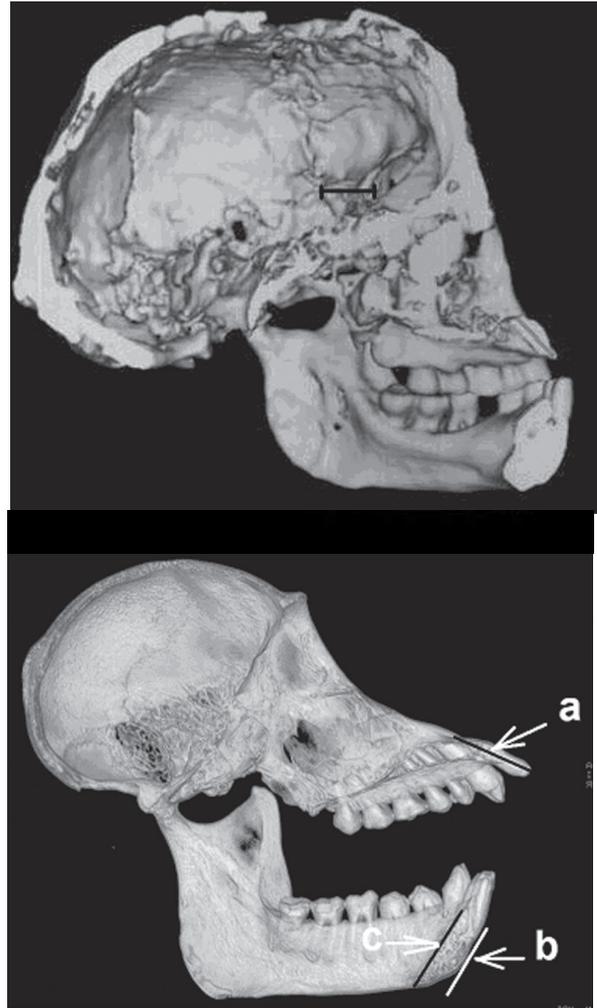


Fig. 7 Skull of LB1 (see above) in comparison with an orangutan of Sumatra (below). The common features of both are: the protrusion of the incisors (a), the negative chin (b) and the simian shelf (c)

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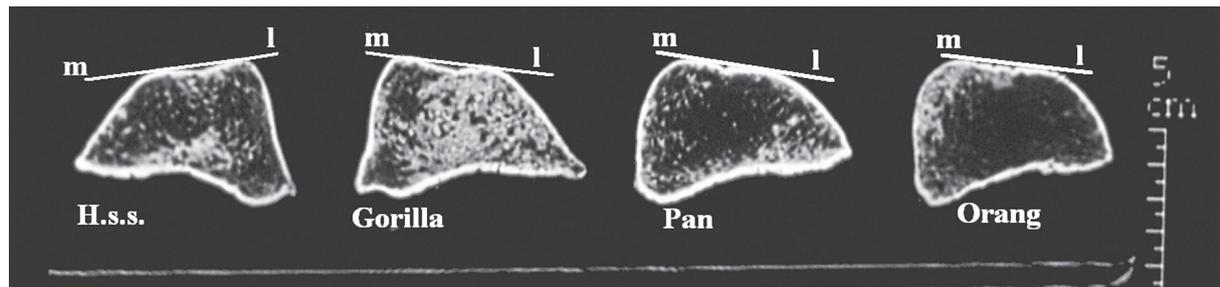


Fig. 8 CT cross-section of the distal femur of a H.s.s., Gorilla, Pan and Orangutan. Note the characteristic different inclination of the condyle-tangent-angle of the distal femur between modern humans and all three Ponginae.

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