

---

Volume 85

Issue 1 *Special Issue on Revisiting the "Negrito"  
Hypothesis*

Article 1

---

2013

# Introduction: Revisiting the "Negrito" Hypothesis: A Transdisciplinary Approach to Human Prehistory in Southeast Asia

Phillip Endicott

*Musée de l'Homme, Paris, France, endicott@mnhn.fr*

Follow this and additional works at: <http://digitalcommons.wayne.edu/humbiol>



Part of the [Biological and Physical Anthropology Commons](#)

---

## Recommended Citation

Endicott, Phillip (2013) "Introduction: Revisiting the "Negrito" Hypothesis: A Transdisciplinary Approach to Human Prehistory in Southeast Asia," *Human Biology*: Vol. 85: Iss. 1, Article 1.

Available at: <http://digitalcommons.wayne.edu/humbiol/vol85/iss1/1>

---

# Introduction: Revisiting the "Negrito" Hypothesis: A Transdisciplinary Approach to Human Prehistory in Southeast Asia

## **Abstract**

The "negrito" hypothesis predicts that a shared phenotype among various contemporary groups of hunter-gatherers in Southeast Asia - dark skin, short stature, tight curly hair - is due to common descent from a region-wide, pre-Neolithic substrate of humanity. The alternative is that their distinctive phenotype results from convergent evolution. The core issues of the negrito hypothesis are today more relevant than ever to studies of human evolution, including the out-of-Africa migration, admixture with Denisovans, and the effects of environment and ecology on life-history traits. Understanding the current distribution of the negrito phenotype dictates a wide-ranging remit for study, including the articulation of the relationship between foragers and farmers in the present, the development of settled agriculture in the mid-Holocene, and terminal Pleistocene population expansions. The consensus reached by the contributors to this special double issue of Human Biology is that there is not yet conclusive evidence either for or against the negrito hypothesis. Nevertheless, the process of revisiting the problem will benefit the knowledge of the human prehistory of Southeast Asia. Whether the term negrito accurately reflects the all-encompassing nature of the resulting inquiry is in itself questionable, but the publication of this double issue is testament to the enduring ability of this hypothesis to unite disparate academic disciplines in a common purpose.

## **Keywords**

Southeast Asia, Negritos, Hypothesis, Workshop, Transdisciplinary

---

## ***Introduction: Revisiting the “Negrito” Hypothesis: A Transdisciplinary Approach to Human Prehistory in Southeast Asia***

PHILLIP ENDICOTT<sup>1</sup>\*

*Abstract* The “negrito” hypothesis predicts that a shared phenotype among various contemporary groups of hunter-gatherers in Southeast Asia—dark skin, short stature, tight curly hair—is due to common descent from a region-wide, pre-Neolithic substrate of humanity. The alternative is that their distinctive phenotype results from convergent evolution. The core issues of the negrito hypothesis are today more relevant than ever to studies of human evolution, including the out-of-Africa migration, admixture with Denisovans, and the effects of environment and ecology on life-history traits. Understanding the current distribution of the negrito phenotype dictates a wide-ranging remit for study, including the articulation of the relationship between foragers and farmers in the present, the development of settled agriculture in the mid-Holocene, and terminal Pleistocene population expansions. The consensus reached by the contributors to this special double issue of *Human Biology* is that there is not yet conclusive evidence either for or against the negrito hypothesis. Nevertheless, the process of revisiting the problem will benefit the knowledge of the human prehistory of Southeast Asia. Whether the term negrito accurately reflects the all-encompassing nature of the resulting inquiry is in itself questionable, but the publication of this double issue is testament to the enduring ability of this hypothesis to unite disparate academic disciplines in a common purpose.

This special double issue of *Human Biology* resulted from a workshop, titled “Revisiting the ‘Negrito’ Hypothesis, an Inter-disciplinary Synthesis of the Prehistory of Southeast Asia,” which was convened by *Human Biology* in Paris during September 2012 after a chance conversation with the editor, Franz Manni, about a dormant idea to have a similar edition dedicated to African “pygmies.” I put it to him that the rainforest foragers of Southeast Asia equally deserved focused

<sup>1</sup>Musée de l’Homme, Paris, France.

\*Correspondence to: Phillip Endicott, Museum National d’Histoire Naturelle, 57 rue Cuvier, Paris, 75005 France. E-mail: phillip.endicott@gmail.com.

*Human Biology*, February–June 2013, v. 85, no. 1–3, pp. 7–20.

Copyright © 2013 Wayne State University Press, Detroit, Michigan 48201-1309

academic attention, and that a transdisciplinary approach to the subject would act as a platform from which to discuss human evolution outside of Africa in a broader perspective. The rainforest foragers of Southeast Asia, who share phenotypic traits of small stature and dark skin color with African pygmies, had been central to early anthropological theory, but the subject has become somewhat unfashionable in the postmodernist age.

From the beginning, the aim was to have contributions from as many branches of anthropology and associated disciplines as possible. In this issue, social, cultural, linguistic, biological, and physical anthropology all have contributions, as well as population genetics, archeology, and geographic information systems (GIS). I also invited Stanley Ulijaszek from the University of Oxford to attend to lead discussion on the various topics, and his overview appears at the end of this double issue. The first drafts of each manuscript were submitted for circulation prior to the meeting in September 2012, where they were presented and discussed by the participants. The manuscripts were subsequently revised, in the light of the interactive discussions, and subjected to the process of peer review. Sadly, before these preparations were completed, one of our number passed away. Abe Padilla will be missed by his family and colleagues, and his unfinished manuscript is included as a testimony to his participation despite serious illness.

There are many ways to write an introduction to such an issue, but after some reflection I decided on a personal synthesis of the subject, based mostly, but not solely, on the collected manuscripts. In doing so, the aim is to follow the intention of the workshop to arrive at a more informed view on the validity of the negrito hypothesis through transdisciplinary cross-fertilization. As the only person who read all the manuscripts in all their different stages of evolution, I have tried to “join the dots” between what I see as some of the most salient and important points raised. Whether the whole has become greater than the sum of its constituent parts I will leave to the reader to decide. I have also tried to outline some future directions that a truly transdisciplinary approach to human evolution might take. Throughout this introduction, the terms *hunter-gatherer* and *forager* are used interchangeably to refer to a way of life based predominantly on mobile resource procurement and small-scale social organization.

## The Hypothesis

The formation of the negrito hypothesis is intertwined with the inception of anthropology as an academic discipline in the second half of the nineteenth century. Reports concerning isolated populations in Southeast Asia were prominent among those sent to European institutions from colonial postings during this time. Many of these populations exhibited some physical characteristics in common that were rare among their neighbors. The most important of these were short stature, dark complexion, and tightly curled “peppercorn” hair. Populations answering this description could be found in and around the forests of Peninsular and Island Southeast Asia, the most widely reported being those of the Andaman Islands,

Malaysia, and the Philippines. The emerging sense of “otherness” was reinforced by the fact that most of these groups followed a way of life based on small mobile bands and practiced a wide range of resource procurement, including hunting and foraging.

The concept of a common origin for all groups of a similar phenotype in the region quickly emerged. The term *Negrito*, coined to refer to these isolate populations of Southeast Asia, was derived from *negrito*, the Spanish diminutive for “black,” a term first used to describe the hunter-gatherers of the Philippines. Based on their fragmented distribution across the region, “Negritos” were presumed to derive from an early substrate of humanity in Southeast Asia, whose former distribution may have included parts of New Guinea and Australia—and possibly even as far as Japan—but were either absorbed, or replaced, by later migrants (Barnard-Davis 1867; de Quatrefages 1895; Radcliffe-Brown 1922). This proper noun is still in popular and academic usage, yet the concept of an ancestral region-wide population with a common phenotype remains a hypothesis to be proven, hence the use of lowercase *negrito*.

### **Ancestral Connections: The Physical Evidence**

During the last 150 years, support for the negrito hypothesis has waxed and waned, but the prehistory of Peninsular and Island Southeast Asia remains a subject of considerable interest to studies of human evolution. A late Pleistocene out-of-Africa migration of humans is now well established, with Southeast Asia considered to be the main route taken to reach Australia and Melanesia at least 45 kya. For the out-of-Africa scenario to accommodate the negrito hypothesis, it would be reasonable to anticipate evidence for short stature in the fossil record. There is irrefutable evidence for a small-bodied hominin on the island of Flores during the late Pleistocene, but this is widely considered to be another species (Brown et al. 2004). Possible evidence for a hominin of short stature in the early paleoanthropological record of the northern Philippines does exist but is limited to a single meta tarsal, whereas later human remains indicate a mosaic of both gracile and robust phenotypes (Dizon et al. 2002; Détroit et al. this issue).

A second expectation of placing the negrito hypothesis within an out-of-Africa scenario is that there should be some degree of shared retention of phenotype among other populations, in particular the African pygmy groups. Comparing postcranial measurements of Aeta (Philippines) and Andamanese with African, Asian, and Australian hunter-gatherers suggests that the phenotypic variation does not support the existence of a generic pygmy or negrito phenotype, past or present (Stock this issue). Similarly, analysis of cranial morphology and dental traits for Malaysian, Philippine, and Andaman negrito populations is equivocal for a common phenotype, with mixed, regionally specific affinities displayed (Bulbeck this issue). These findings do not rule out an ancestral connection between these populations, but any account of the negrito hypothesis has to explain this amount of physical variation.

## Convergent Evolution and Life History

An alternative explanation for the negrito phenotype is that of convergent evolution, whereby similar physical traits developed independently among multiple populations. The traditional explanation for dark complexion is a need to dissipate heat, but this is not convincing because dark-bodied radiation is similar for all colors. Protection from ultraviolet light is another reason evinced for dark skin, yet tropical sunlight requires only a light brown skin color to be an effective prophylactic in this respect, and life in the rainforest reduces the need still further. Living in tropical rainforests is also suggested to contribute to a reduction in stature due to locomotory adaptation to the environment. One such adaptation—typical of both negrito and African pygmy populations—is aboreal foraging, which leads to considerable stresses on the lower limb joints. Although the ankle morphology of nonhuman primates in the wild and captivity accurately predicts the amount of climbing they engage in, the same plasticity is not detected among human climbing populations (Venkataraman et al. this issue). If aboreal foraging has been significant throughout prehistory, it is also possible that tree climbing itself favors a short stature, by way of reduced mortality rates.

A related explanation for the existence of short stature is that it evolved as a life-history trade-off favoring early reproduction and cessation of adult growth in the face of high mortality rates, but this hypothesis is as yet unproven (Migliano et al. 2007). Genome-wide scans of genotype data on African, Philippine, and Papuan populations of short stature indicate recent positive selection at different loci associated with growth and sexual development (Migliano et al. this issue). There is, however, no evidence for direct selection acting on genes associated with height regulation, which might be expected in the case of locomotory adaptation. Although these results can be interpreted as supporting the hypothesis of convergent evolution for some aspects of phenotype in the *recent* past, this analysis would not necessarily be able to detect selection associated with short stature if it was the ancestral condition of all populations in the region.

In New Guinea, the secular trend over a 20-year period is for an increase in height of ~4 cm, proof that significant change in the mean stature of a population occurs over a short timescale (Tommaseo-Ponsetta et al. this issue). This increase is actually much higher for individuals younger than 30 years of age, due to recent changes in nutrition and disease regimes, indicating that both of these factors could have contributed to short stature in the past. If convergent evolution is the source of a common negrito phenotype, understanding the biological mechanisms underlying both reductions and increases in human stature is important. The field of immunological ecology provides a way to study epigenetic factors involved in stature at an intergenerational level. Aeta mothers in the Philippines are observed to nurse higher-birth-order infants for more months than their older siblings. This increases levels of milk compounds ingested, capable of communicating past infectious disease environments to the child, which could lead to accelerated life-history attributes (Bernstein and

Dominy this issue). Although this research did not obtain a positive result, it provides an excellent model for future research.

## **Neolithic Entanglements—Evidence from Language**

There is no doubt that major demographic changes occurred during the mid-Holocene with the advent of agriculture. This process is widely associated with the migration of peoples speaking Austroasiatic and Austronesian languages into Peninsular and Island Southeast Asia, respectively (Bellwood 1993). The ancestral hunter-gatherers of Malaysia and the Philippines must have been in close contact with these newcomers because there has been widespread language shift. During this process, they were either absorbed by the incoming population or marginalized to ecological zones not under pressure from the ensuing development of agriculture. It is clear from both historical linguistics and distribution maps that this is an ongoing process (Padilla this issue; Reid this issue). The Andamanese are exceptions to this rule as they maintained both their isolate languages and their hunter-gatherer existence across the entire archipelago until the time of British occupation in 1856, when they were devastated by exposure to a suite of novel pathogens. To what extent the Neolithic transition resulted in similar demographic declines elsewhere is not known, but any movement toward a sedentary existence would lead to a proliferation of density-dependent infectious diseases.

Although the languages formerly used by extant negrito populations in Malaysia and the Philippines have been lost, comparative and historic analysis of each language family provides important inferences about past social interactions with agriculturists since the mid-Holocene. In the case of the Philippines, it is clear that negrito languages have features that generally distinguish them as being either first-order members of their subgroup or isolates within the Malayo-Polynesian language family (Reid this issue). These features indicate that many languages were adopted soon after the arrival of the ancestors of today’s agriculturists at least 4 kya (Gray et al. 2009) but that the intensity of contact between groups occupying these different ecological niches has not been maintained (Reid 1987; Reid this issue). The word used to describe the ancestral foragers in Proto-Malayo-Polynesian can be reconstructed as the preexisting indigenous word for “person” in northern Luzon, which was then glossed as “dark-skinned person” (Reid 1994; Reid this issue). If this is correct (for an alternative reconstruction, see Blust this issue), then the dark complexion component of the negrito phenotype already existed in the Philippines at this time.

In contrast, most Peninsular Southeast Asian negrito groups (Kensiw, Kentaq, Jahai, Menriq, and Batek) speak languages that form a single clade nested *within* the Northern Aslian branch of the Austroasiatic language tree. The exception is the Lanoh, who speak a language from Central Aslian and follow a more diverse range of resource procurement (Benjamin this issue). This Northern Aslian branch, spoken by the absolute majority of negrito populations, appears to have developed about 2 kya, substantially after the transition to agriculture in the region (Dunn et

al. this issue). The timing of this language shift could be linked to the existence of transpeninsular trade routes, which operated along lowland river systems of Malaysia and southern Thailand, whose current location closely matches the distribution of negrito groups. The ancestors of today's groups are likely to have played a crucial role in the operation of these portage routes, due to their intimate knowledge of the interior, vital to the movement of goods and the supply of forest products to the coastal communities (Benjamin this issue).

### **Social Relations between Foragers and Farmers**

A feature of foraging groups with the negrito phenotype is that the rules governing their normative social and economic behavior patterns tend to reinforce the distinction between nomadic and sedentary modes of existence (Benjamin this issue). The boundaries being maintained are not always the same; for example, the Lanoh and Batek both deviate from the traditional foraging mode of resource acquisition and have elements of societal organization that differ from other negrito groups. Among the Batek, this diversification and modification of socio-economic arrangements reflects a flexible approach to risk-reduction strategies. This helps to buffer them from an unpredictable future, by maintaining a wide range of potential exchange partners and, through them, access to widely scattered resources (Lye this issue).

Insights into the prehistory of social relations between foragers and agriculturists are helpful for understanding how a negrito phenotype might develop and/or be maintained through time. This is because both cultural choice and environment can affect genetic and epigenetic mechanisms. The potential for change in the recent past in Peninsular Southeast Asia seems predominantly in the direction of a sedentary lifestyle (Benjamin this issue). The key question is whether the negrito phenotype existed everywhere prior to the Neolithic, or whether it developed as a consequence of marginalization. If the negrito phenotype arose independently, in both Peninsular Southeast Asia and the Philippines, *after* the arrival of agriculturists, then its universal presence throughout the Andaman archipelago is more difficult to explain, when the surviving languages show no indication of past contact with agriculturist communities (Blust this issue).

### **Evidence for Diffusion of Cultural Beliefs**

Despite the widespread language shift witnessed across the region, evidence persists for a common preagricultural belief system among negrito groups of Peninsular Southeast Asia, the Philippines, and the Andamans (Blust this issue). It takes the form of distinctive traits connected with beliefs about punitive thunderstorms, recorded by anthropologists during the last century. Surprisingly, this nexus of beliefs, which are highly distinctive in a global perspective, are also found among non-negrito Malayo-Polynesian speakers in the Philippines, Peninsular Southeast Asia, neighboring Sarawak, eastern Indonesia, and



southeastern New Guinea (Blust 1991; Blust this issue). This suggests that the belief system may have been part of the original cultural package associated with the Malayo-Polynesian dispersal.

An origin for this cultural complex among the common ancestors of negrito populations is more plausible than diffusion from Proto-Malayo-Polynesian speakers. This is because the same nexus of beliefs is not reported from Taiwan, which allows for it to have been acquired by Proto-Malayo-Polynesian speakers from the ancestors of today’s foraging groups in the Philippines. Moreover, the Peninsular Southeast Asian negrito populations were not part of the Malayo-Polynesian sphere of influence. Without a common language, it is also difficult to explain the required recent diffusion to the Andamans (Blust this issue). This fascinating conundrum highlights the potential of using historical data and raises the possibility of a region-wide belief system prior to the Neolithic.

Articulation between the societal types of Proto-Malayo-Polynesian speakers and the ancestors of the negrito populations of the Philippines undoubtedly led to transformations in the way of life of the foragers. The common belief system concerning punitive thunderstorms reinforces the hints from language that the cultural complex of early Proto-Malayo-Polynesian speakers in the Philippines evolved as a mixture of their own preexisting beliefs and knowledge and those found among the indigenous groups they encountered. This view is enhanced by the reconstruction of referents for tropical fruits and tubers in Proto-Malayo-Polynesian (Blust 1994). These sources of nutrition were encountered in the latitudes south of Taiwan by people whose preexisting resource base included maritime foraging. Knowledge of novel resources was most likely acquired locally, initially with sufficient intensity of interaction to cause widespread language shift among the indigenous foraging groups.

## **Alliance and Marriage between Farmers and Foragers**

This assimilation of cultural belief systems, as well as practical knowledge of the environment and ecology, included sustained demographic movements into groups of Proto-Malayo-Polynesian speakers from the ancestors of today’s negrito populations. A system of marriage by capture is unlikely to have been the basis for this admixture due to evidence for the assimilation of cultural traits. Marriage and alliance are more likely to have been facilitated through a cross-cultural compatibility of kinship systems between different societal types (Turner this issue), as is witnessed in Malaysia today (Benjamin this issue; Lye this issue). The ancestral kinship system for Proto-Malayo-Polynesian speakers is reconstructed to include symmetrical exchange, and a preference for cross-cousin marriage, involving a focus on the brother-sister bond (Turner 2007). Yet, the equivalent components of kinship and marriage among both the foraging and sedentary populations of the Philippines are now rather different. The general direction of changes in categories observed is consistent with the principles of evolutionary kinship theory (Allen 2004), but it is the nature of the changes in the Philippines that merits particular attention.

The reconstructed ancestral focus on the bond between brother and sister has been replaced by an emphasis on the one between husband and wife (Turner this issue). Combined with a move away from prescriptive marriage rules, the resulting system of kinship uses both parental lines to determine the status of descendants and excludes marriage with known blood relations. The most parsimonious explanation for the origin of these categories and rules is either that they existed among the ancestors of Philippine negrito populations, before the arrival of Proto-Malayo-Polynesian speakers, or that they emerged during the ensuing amalgamation of societal types. This adaptation of kinship and marriage systems may help explain the subsequent rapid spread of Malayo-Polynesian speakers across the region.

### **Gene Exchange in the Philippines**

It is reasonable to anticipate that this admixture of early farmers and foragers in the Philippines should leave traces in the genetic diversity of contemporary populations. Applying the phylogeographic method with the haploid systems of mitochondrial DNA (mtDNA) and Y-chromosomal DNA indicates that sedentary communities usually contain more female than male lineages derived from hunter-gatherers (Delfin et al. 2011). This is a two-way street, however, and the contemporary genetic diversity of the hunter-gatherers in northern Luzon also preserves both maternal and paternal lineages thought to have originated with the speakers of Proto-Malayo-Polynesian (Heyer et al. this issue).

The ancestral postmarital residence rule in Proto-Malayo-Polynesian society is reconstructed as matrilocal, which can lead to a female-biased sex ratio in effective population sizes (Turner 2007; Jordan et al. 2009). However, although female-biased patterns of admixture are observed in Malayo-Polynesian-speaking societies of eastern Indonesia (Cox et al. 2010; Xu et al. 2012), the general Philippine population is sex neutral in this respect (Cox et al. 2010). Among Philippine negrito groups in northern Luzon, both male- and female-biased effective population sizes are observed (Heyer et al. this issue). It may be significant that the elevated male effective population sizes—something that is quite rare globally—are found among the two Agta ethnolinguistic groups, because these harbor Y-chromosomal DNA lineages thought to be external to the Philippines at a frequency of 50%. Measures of autosomal genetic diversity among, and within, the Agta and Aeta ethnolinguistic groups are high, consistent with the maintenance of high long-term effective population sizes, and different demographic histories (Heyer et al. this issue).

### **Inferences of Regional Demography and Genetic Continuity using mtDNA**

During maximal glacial conditions in Southeast Asia, the exposed continental shelf created a single land mass, known as Sundaland, that included most of the islands west of Bali and the peninsula. The exceptions were the Andaman and Nicobar

archipelagoes, which always required a short sea crossing. The region east of Bali was not united, but during this time the land area was significantly increased and sea crossings between islands were reduced. From ~20 to 10 kya, there are consistent signals for an increase in the effective population size of females throughout the region, peaking around 16 kya (Gunarsdottir et al. 2011; Jinam et al. 2012; Guillot et al. this issue). By the start of the Holocene, there is a strong trend for a decline in female population sizes (Guillot et al. this issue), likely associated with the loss of land area and climate change as the sea level rose, substantially lowering the overall carrying capacity of the environment.

The fossil record for the terminal Pleistocene and early Holocene is rather patchy but displays considerable variation in phenotype, through both time and space, with no obvious candidates for an ancestral negrito population (Higham this issue). But the substantial population growth of the terminal Pleistocene does coincide with the appearance of Hoabinhian stone tool types across Mainland Southeast Asia, whose known distribution includes the Sunda Shelf region but does not extend east of the Wallace Line (Higham this issue). Hoabinhian tools are usually reported from rock shelters and caves, which were only seasonal in their use. This leads to a strong bias in reporting because of the vast lowlands associated with the expanses of the Sunda Shelf and the widespread use of open-air sites by hunter-gatherers, which are underrepresented in the archaeological record (Higham this issue).

Ideally, ancient DNA would be recovered from pre-Neolithic human remains and compared with today’s negrito groups to test hypotheses about genetic continuity, but the postmortem preservation of DNA in a tropical climate is seldom sufficient for this type of analysis. The best that might be hoped for is ancient mtDNA—due to it being present in much greater numbers relative to nuclear DNA—but even if the negrito populations from the Andamans, Malaysia, and the Philippines were part of a larger metapopulation in the late glacial period, subsequent admixture with agriculturists would make it difficult to interpret the results in a meaningful way. Certainly, the mtDNA diversity of today’s negrito populations—as well as those of New Guinea and northern Australia—exhibits more affinity with immediate neighbors than between negrito groups themselves (Barik et al. 2008; Delfin et al. 2011; Jinam et al. 2012; Heyer et al. this issue; McAllister et al. this issue; Migliano et al. this issue; Tommaseo-Ponzetta et al. this issue).

## **Searching for Connections using Genome-wide Nuclear Data**

Analyzing much larger numbers of markers from the nuclear genome on a regional scale with principal component analysis (PCA) clearly indicates the similarity between Jehai and Kensui negrito populations in Malaysia (Jinam et al. this issue). PCA analysis of nuclear data also reveals an axis involving Malaysian negritos, Malayo-Polynesian speakers, and Philippine negritos (Jinam et al. 2012). Evidence for a deep common ancestry within the eastern part of the region also emerges in a study including Australians, two paleogenomes, and three negrito populations

(Reich et al. 2011). Of particular interest to the current topic is that the Malaysian and Andaman negrito groups demonstrate clear common ancestry in this study. A second clustering involves Philippine negritos, New Guinea, and Australia, purportedly due to ancient admixture with another species of hominin designated “Denisovans” (Reich et al. 2011). According to this interpretation, any shared ancestry between the three regionally distinct negrito groups has to be older than this admixture event.

When a more comprehensive range of populations representing all the relevant major language families of Southeast Asia is analyzed, a slightly different perspective on the genetic structuring of groups emerges (Chaubey and Endicott this issue). The affinity between the negrito populations of the Andamans and Malaysia is confirmed, as is the weaker attraction to the Philippines; but the Onge of Little Andaman, together with their nearest genetic neighbors the Great Andamanese, also have substantial amounts of their genomes related to groups ancestral to (a) South Asia and (b) Melanesia. Interestingly, a signal for admixture with Denisovans was also found among the Onge, equivalent to 20% of the level found in some Philippine negrito populations (Reich et al. 2011), which is consistent with the substantial component of their genomes attributed to the ancestors of Melanesians (Chaubey and Endicott this issue). Regarding the ancestral South Asian component, an earlier nuclear data study suggested that the Onge were related to the ancestors of southern Indians and had experienced a significant reduction in genetic diversity since this ancient split (Reich et al. 2009). The inclusion of Southeast Asian and Melanesian populations for comparison, however, reveals a scenario whereby the Onge and Greater Andamanese were already a mixture of all three components prior to settlement of the archipelago (Chaubey and Endicott this issue).

This finding may have a bearing on the presence of an ancestral South Asian genetic component among northern Australians, which is attributed to an admixture event ~4 kya (Pugach et al. 2012). Given the lack of evidence for recent admixture among the Onge (Reich et al. 2011), together with the presence of this signal in other populations across Southeast Asia (Chaubey and Endicott this issue), it may be more parsimonious to suggest that this ancestral South Asian component was already distributed across the Sunda Shelf by the time of marked declines in population sizes at the end of the Pleistocene (Guilliot et al. this issue). These and other hypotheses will no doubt be revised further once improved data sets are used with more realistic demographic models.

## Conclusion

The identification of weak affinities between contemporary populations with a negrito phenotype using population genetic markers is somewhat paradoxical in the sense that these markers are screened to ensure that they are not under selection. Therefore, although genetic affinity may indicate common ancestry within an ancestral metapopulation, it cannot inform directly about phenotype in the past. Nevertheless, it does suggest that the surviving hunter-gatherer populations of the

region have maintained sufficient separation from their agricultural neighbors for this deeper genetic connection to be detected. These are not grounds, however, for continuing with unchallenged assumptions about genetic and cultural isolation of negrito populations, either in the past or in the present.

Rather, it is the *process* of articulation between different human groups that is the key to understanding the prehistory of today’s negrito populations and the region as a whole. In order to develop this approach, it is necessary to build testable models by integrating detailed ethnographic knowledge and anthropological theory with population genetic inference. Those components of culture dependent on linguistics will need to focus predominantly on the Neolithic onward, but, in principle, the evolution of some cultural traits, such as kinship systems, can be projected further back in time.

A deeper understanding of recent demographic processes and cultural choices can also inform continuing research into the genetic and epigenetic influences on the origin and maintenance of phenotype among Southeast Asian foraging populations. With the current price of whole genomic sequencing, it is likely that the data necessary for discovering the genetic pathways involved will soon be at hand. These data can also provide large numbers of markers for model-based approaches to human demographic inference. The utility of whole genome data for studies of selection will also require the development of novel methods for analysis and a deeper understanding of the sometimes complex downstream processes affecting the expression of phenotype. Ultimately, to realize the full potential of this research, there will need to be a continuing focus on life-history traits and their interdependence with environmental, ecological, immunological, and cultural factors.

To the panel of contributors assembled for this special double issue of *Human Biology*, it was clear by the end of the workshop that there is very little support for the negrito hypothesis in its original form. The visually seductive features of phenotype can equally be attributed to convergent evolution, but this alternative explanation must also remain a hypothesis until sufficient evidence is accumulated to explain the similarities and variation in phenotype. The vision of a future approach that emerges is one that includes both the synchronic and diachronic study of the entire region of Southeast Asia and beyond. So, perhaps it is time to reconsider the use of the term *negrito* altogether, given that it is no longer the sole focus of the investigation. As with all symbols, the success of the negrito hypothesis as a convenient shorthand is precisely because the word can mean something different to each individual, while allowing everyone concerned to believe they share a common belief. In the end, perhaps it is this quality that was responsible for the success of the workshop.

## Literature Cited

- Allen, N. J. 2004. Tetradic theory: An approach to kinship. In *Kinship and Family: An Anthropological Reader*, R. Parkin and L. Stone, eds. Hoboken, NJ: Wiley-Blackwell, 221–235.
- Barik, S. S., R. Sahani, B. V. R. Prasad et al. 2008. Detailed mtDNA genotypes permit a reassessment of the settlement and population structure of the Andaman Islands. *Am. J. Phys. Anthropol.* 136:19–27.
- Barnard-Davis, J. 1867. *Thesaurus Craniorum: Catalogue of the Skulls of the Various Races of Man, in the Collection of Joseph Barnard-Davis*. London: printed for the subscribers.
- Bellwood, P. 1993. Cultural and biological differentiation in Peninsular Malaysia: The last 10,000 years. *Asian Perspect.* 32:37–60.
- Benjamin, G. 2013. Why have the peninsular “negritos” remained distinct? *Hum. Biol.* 85:445–484.
- Bernstein, R. M., and N. J. Dominy. 2013. Mount Pinatubo, inflammatory cytokines, and the immunological ecology of Aeta hunter-gatherers. *Hum. Biol.* 85:231–250.
- Blust, R. 1991. On the limits of the “thunder complex” in Australasia. *Anthropos* 86:517–528.
- Blust, R. 1994. The Austronesian settlement of mainland Southeast Asia. In *Papers from the Second Annual Meeting of the Southeast Asian Linguistics Society*, K. L. Adams and T. J. Hudak, eds. Tempe: Program for Southeast Asian Studies, Arizona State University, 25–83.
- Blust, R. 2013. Terror from the sky: Unconventional linguistic clues to the negrito past. *Hum. Biol.* 85:401–416.
- Brown, P., T. Sutikna, M. J. Morwood et al. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1,055–1,061.
- Bulbeck, D. 2013. Craniodental affinities of Southeast Asia’s “negritos” and the concordance with their genetic affinities. *Hum. Biol.* 85:95–134.
- Chaubey, G., and P. Endicott. 2013. The Andaman Islanders in a regional genetic context: Reexamining the evidence for an early peopling of the archipelago from South Asia. *Hum. Biol.* 85:153–172.
- Cox, M. P., T. M. Karafet, J. S. Lansing et al. 2010. Autosomal and X-linked single nucleotide polymorphisms reveal a steep Asian-Melanesian ancestry cline in eastern Indonesia and a sex bias in admixture rates. *Proc. Biol. Sci.* 277:1,589–1,596.
- Delfin, F., J. M. Salvador, G. C. Gayvelline et al. 2011. The Y-chromosome landscape of the Philippines: Extensive heterogeneity and varying genetic affinities of negrito and non-negrito groups. *Eur. J. Hum. Genet.* 19:224–230.
- de Quatrefages, A. 1895. *The Pygmies*. New York: Appleton and Company.
- Détroit, F., J. Corny, E. Z. Dizon, and A. S. Mijares. 2013. “Small size” in the Philippine human fossil record: Is it meaningful for a better understanding of the evolutionary history of the negritos? *Hum. Biol.* 85:45–66.
- Dizon, E., F. Détroit, F. Sémah et al. 2002. Notes on the morphology and age of the Tabon Cave fossil *Homo sapiens*. *Curr. Anthropol.* 43:660–666.
- Dunn, M., N. Kruspe, and N. Burenhult. 2013. Time and place in the prehistory of the Asian languages. *Hum. Biol.* 85:383–400.
- Gray, R. D., A. J. Drummond, and S. J. Greenhill. 2009. Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* 323:479–483.
- Guillot, E. G., M. K. Tumonggor, J. S. Lansing et al. 2013. Climate change influenced female population sizes through time across the Indonesian archipelago. *Hum. Biol.* 85:135–152.
- Gunarsdottir, E. D., M. Li, M. Bauchet et al. 2011. High-throughput sequencing of complete mtDNA genomes from the Philippines. *Genome Res.* 21:1–11.
- Heyer, E., M. Georges, M. Pachner, and P. Endicott. 2013. Genetic diversity of four Filipino negrito populations from Luzon: Comparison of male and female effective population sizes and differential integration of immigrants in Aeta and Agta communities. *Hum. Biol.* 85:189–208.
- Higham, C. 2013. Hunter-gatherers in Southeast Asia: From prehistory to the present. *Hum. Biol.* 85:21–44.

- Jinam, T. A., L.-C. Hong, M. E. Phippes et al. 2012. Evolutionary history of continental southeast Asians: “Early train” hypothesis based on genetic analysis of mitochondrial and autosomal DNA data. *Mol. Biol. Evol.* 29:3,513–3,527.
- Jinam, T. A., M. E. Phipps, N. Saitou, and The Hugo Pan-Asian SNP Consortium. 2013. Admixture patterns and genetic differentiation in negrito groups from West Malaysia estimated from genome-wide SNP data. *Hum. Biol.* 85:173–188.
- Jordan, F. M., R. D. Gray, S. J. Greenhill et al. 2009. Matrilocal residence is ancestral in Austronesian societies. *Proc. Biol. Sci.* 276:1,957–1,964.
- Lye Tuck-Po. 2013. Making friends in the rainforest: “Negrito” adaptation to risk and uncertainty. *Hum. Biol.* 85:417–444.
- McAllister, P., N. Nagle, and R. J. Mitchell. 2013. The Australian Barrineans and their relationship to Southeast Asian negritos: An investigation using mitochondrial genomics. *Hum. Biol.* 85:485–494.
- Migliano, A. B., I. G. Romero, M. Mespalu et al. 2013. Evolution of the pygmy phenotype: Evidence of positive selection from genome-wide scans in African, Asian, and Melanesian pygmies. *Hum. Biol.* 85:251–284.
- Migliano, A. B., L. Vinicius, and M. M. Lahr. 2007. Life history trade-offs explain the evolution of human pygmies. *Proc. Natl. Acad. Sci. USA* 104:20,216–20,219.
- Padilla, S. G., Jr. 2013. Anthropology and GIS: Temporal and spatial distribution of the Philippine negrito groups. *Hum. Biol.* 85:209–230.
- Pugach, I., F. Delfin, E. Gunnarsdottir et al. 2012. Genome-wide data substantiate Holocene gene-flow from India to Australia. *Proc. Natl. Acad. Sci. USA* 110:1,083–1,088.
- Radcliffe-Brown, A. R. 1922. *The Andaman Islanders*. Cambridge: Cambridge University Press.
- Reich, D., N. Patterson, M. Kircher et al. 2011. Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. *Am. J. Hum. Genet.* 89:516–528.
- Reich, D., K. Thangaraj, N. Patterson et al. 2009. Reconstructing Indian population history. *Nature* 461:489–495.
- Reid, L. A. 1987. The early switch hypothesis: Linguistic evidence for contact between negritos and Austronesians. *Man Culture Oceania* 3:41–59.
- Reid, L. A. 1994. Possible non-Austronesian lexical elements in Philippine negrito languages. *Ocean. Linguist.* 33:37–72.
- Reid, L. A. 2013. Who are the Philippine negritos? Evidence from language. *Hum. Biol.* 85:329–358.
- Stock, J. T. 2013. The skeletal phenotype of “negritos” from the Andaman Islands and the Philippines relative to global variation among hunter-gatherers. *Hum. Biol.* 85:67–94.
- Tommaseo-Ponzetta, M., S. Mona, F. Calabrese et al. 2013. Mountain pygmies of Western New Guinea: A morphological and molecular approach. *Hum. Biol.* 85:285–308.
- Turner, J. W. 2007. Alternative pasts: Reconstructing Proto-Oceanic kinship. *Ethnology* 46:235–270.
- Turner, J. W. 2013. Kinship matters: Structures of alliance, indigenous foragers, and the Austronesian diaspora. *Hum. Biol.* 85:359–382.
- Venkataraman, V. V., T. S. Kraft, J. M. DeSilva, and N. J. Dominy. 2013. Phenotypic plasticity of climbing-related traits in the ankle joint of great apes and rainforest hunter-gatherers. *Hum. Biol.* 85:309–328.
- Xu, S., I. Pugach, M. Stoneking et al. 2012. Genetic dating indicates that the Asian-Papuan admixture through eastern Indonesia corresponds to the Austronesian expansion. *Proc. Natl. Acad. Sci. USA* 109:4,574–4,579.



PHILLIP ENDICOTT entered academia as a mature student in 1996 to study anthropology and archaeology at the University of Oxford (UK), where he was introduced to the concept of transdisciplinary research. This strong foundation was followed by master's degrees in material culture and biological anthropology. He graduated from Magdalen College, Oxford, after completing a doctoral dissertation on the genetic prehistory of Island Southeast Asia. Dr. Endicott holds a permanent research position at the Musée de l'Homme (National Museum of Natural History) in Paris, France, where his responsibilities include genetic research on the anthropological collections. Past and current research projects include the population history of the Andaman archipelago, regional genetic prehistory of Sahul and Southeast Asia,

the settlement of Polynesia, and Bayesian approaches to the genetic dating of human prehistory. Dr. Endicott has been awarded a Wenner-Gren Foundation grant to study hominid genetic diversity (2011–2012), and, within the European Union's Seventh Framework Programme for Research (FP7), he coordinates an international collaboration (2012–2016) with the University of Auckland (New Zealand) and the Estonian Biocenter (Tartu, Estonia) to develop statistical methods for studying the coevolution of genes and culture.