Journal of Human Evolution 96 (2016) 134–138

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

News and views

Archaeological excavation of wild macaque stone tools

Michael Haslam [a,*], Lydia Luncz [a], Alejandra Pascual-Garrido [a], Tiago Falótico [a], Suchinda Malaivijitnond [b], Michael Gumert [a,c]

[a] School of Archaeology, University of Oxford, Dyson Perrins Building, South Parks Road, Oxford, OX1 3QY, UK
[b] Primate Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand
[c] Division of Psychology, School of Humanities and Social Sciences, Nanyang Technological University, Singapore, 637332, Singapore

ARTICLE INFO

Article history:
Received 17 February 2016
Accepted 4 May 2016
Available online 30 May 2016

1. Introduction

More than 3 million years of excavated archaeological evidence (Harmand et al., 2015) underlies most major insights into the evolution of human behaviour. However, we have seen almost no use of archaeological excavation to similarly broaden our understanding of behaviour in other animal lineages. The few published examples include recovery of a late Holocene assemblage of stones from the Ivory Coast, attributed to the agency of both humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes verus*) (Mercader et al., 2002, 2007), and exploration of the occupation sites of non-tool-using species such as penguins (Emslie et al., 2014) and other birds (Burnham et al., 2009). The development of viable methods for identifying and interpreting past non-human tool use landscapes is essential if we are to gain a better understanding of technological evolution within other animals, including our close relatives, the primates. Recently, the growth of primate archaeology has built on the close phylogenetic relationship between humans and other primates to begin filling in this lacuna (Haslam et al., 2009; Carvalho, 2011; Stewart et al., 2011; Haslam, 2012, 2014; Visalberghi et al., 2013; Haslam et al., 2014; McGrew et al., 2014; Benito-Calvo et al., 2015; Luncz et al., 2015; Kühl et al., 2016).

Here, we present the first report on an archaeologically excavated Old World monkey tool use site, which was created by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*) (Bunlungsup et al., 2016) during shellfish-processing activities in coastal Thailand. These macaques use stone and shell pounding tools to access a wide variety of coastal and inter-tidal resources, including shellfish, crabs and nuts (Fig. 1) (Malaivijitnond et al., 2007; Gumert et al., 2009, 2011; Gumert and Malaivijitnond, 2012; Tan et al., 2015), and previous work has demonstrated that use-wear on the stone tools permits reconstruction of past macaque activities (Haslam et al., 2013). Uncovering the history of this foraging behaviour opens up opportunities to study its evolution within the macaque lineage and, more broadly, to retrieve comparative data for researchers studying human and primate coastal exploitation (e.g., Marean, 2014; Russon et al., 2014).

2. Methods

The excavation site was designated Laem Son 5 (LS5), and is located on the small island of Piak Nam Yai (PNY), in Laem Son National Park, Thailand (N 9° 34.629, E 98° 28.239). This hilly island has an area of 1.7 km^2 and 5.4 km of coastline, which includes rocky areas, sandy beaches and mangroves. In December 2013, when this study was conducted, there were approximately 200 unhabituated macaques living in nine groups on PNY (Gumert et al., 2013). The excavations were conducted in sandy sediments on the east coast of PNY, close to Thao Island (Gumert et al., 2013) and facing a sheltered bay at the mouth of the Kapoe Estuary. The site was located in an area where two of the tool-using macaque groups – named the Mangrove and Bayside Groups – overlapped in their ranges (Gumert et al., 2013). There are no known human activities that employ stone tools at PNY.

The LS5 site was selected because it sits beneath an overhanging, large basalt boulder (Fig. 1). The boulder has abundant oysters on the underside that faces the water, giving potential for monkeys to drop oyster-processing tools at the site following their use. The boulder has a sloped upper surface, which may have resulted in any stone tools used on that surface (i.e., with the boulder as an anvil) also falling down and accumulating at the site. The boulder is inundated by high tides.

Excavation was by hand, using trowels and hand-shovels. All sediment was wet sieved through a 5 mm mesh in the adjacent Andaman Sea. All shell and stone recovered from sieving was collected for analysis. The site was excavated as three 0.5 × 0.5 m squares (designated LS5A, LS5B and LS5C, forming a 1.5 × 0.5 m

* Corresponding author.
E-mail address: michael.haslam@rlaha.ox.ac.uk (M. Haslam).

http://dx.doi.org/10.1016/j.jhevol.2016.05.002

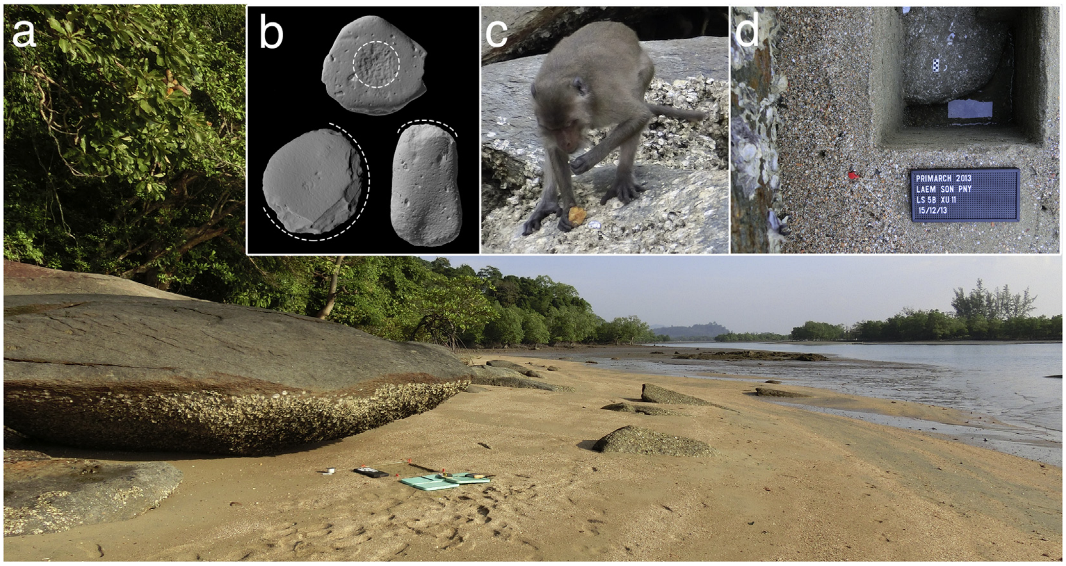

Figure 1. (a) Site LS5 at low tide, Piak Nam Yai, facing north along the island's east coast. The site is situated beneath the large boulder on the left. (b) Use-damage on tools collected after use by PNY macaques, showing (clockwise from top) pitting, crushing and fracture damage, with the use-wear highlighted by dashed white lines in each instance. Modified from Haslam et al. (2013, Fig. 4). (c) Burmese long-tailed macaque using a stone tool to open and eat oysters from an intertidal basalt boulder, Piak Nam Yai, Thailand. (d) LS5B during excavation, with a buried boulder visible at the base of the excavation (along with the rising water table), and the boulder that overhangs the site present at the left of the photograph. The scale on the buried boulder is 5 cm.

site) over three days in December 2013. This strategy was needed because the tide covers the site twice daily in a metre or more of water. We found that 0.25 m^2 was the maximum area that could be excavated to the water table in the time between exposure of the site by the receding tide, and intrusion into the site by the returning tide. Excavation stopped upon reaching the water table at approximately 60 cm depth each day.

Macaque tools were identified from among the stone debris at the site via their distinctive use-wear patterns, particularly pitting, crushing and fracture wear. We took a conservative approach in this study, whereby stones with no visible damage, or with damage that was superficial or not localized to specific parts of the stone, were not considered tools. As a means of quantifying the abundance of tools and non-tool stones, we counted all stones over 3 cm in maximum dimension from the tool-bearing levels, with the 3 cm cut-off chosen as it constitutes the lower size boundary for known macaque tools (Gumert et al., 2009; Haslam et al., 2013).

Employing the Use-Action Index (UAI) previously developed at PNY (Haslam et al., 2013) we reconstructed the most probable former use of each tool, by monkeys pounding open either (i) oysters (*Saccostrea cucullata*) attached to the rocky substrate, or (ii) unattached prey such as gastropods. For a full list of the more than 40 known prey species opened with tools by the PNY macaques, see Gumert and Malaivijitnond (2012). The UAI is applied to each tool by dividing it into 10 zones, and recording the intensity of use-damage (specifically, crushing damage) on the faces and narrow ends of a tool. At PNY, tools with greater damage to the face are considered hammers for opening unattached prey, and those with greater damage on the points have been found to be typically oyster processing tools (Gumert et al., 2009; Haslam et al., 2013). All tools were digitised using a NextEngine 3D laser scanner.

The National Research Council of Thailand and the Department of National Parks, Wildlife and Plant Conservation of Thailand provided permits to carry out research activities at Laem Son National Park. Methods for collecting stones used by the macaques were reviewed and approved by the NTU-Institutional Animal Care & Use Committee (IACUC) in Singapore (ARF SBS/NIE-A 0138 AZ).

3. Results

LS5 sediments consist of sub-horizontally stratified fine to coarse sands and shell grit, with the density of broken shell material varying between layers. The upper 45–50 cm of the site is brownish yellow sand (10YR 6/6, wet), while the basal ±10 cm is grey silty sand (10YR 5/1, wet). The basal sediments have a contribution of fine grey silt from a large basalt boulder (Fig. 1), which is weathering in situ, as well as an increased concentration of pebbles and cobbles. The full dimensions of the buried basalt boulder are unknown. The buried boulder had a similar covering of attached barnacle and oyster shells to boulders currently exposed by low tide at PNY, albeit the shells on the buried rock were empty and less numerous.

Oysters make up approximately 30–40% by weight of all shell debris from the surface down to 45 cm depth, increasing to 50–60% below this depth, partially as a result of oysters detached from the buried boulder in the basal levels. Non-tool stones follow a similar pattern, with total stone weights increasing from around 2–7 kgm^{-3} near the surface, to over 60 kgm^{-3} in the basal levels. From this distribution, we conclude that the basal material comprises a lag deposit of stones prevented from moving by surrounding boulders. Similar lag deposits can be seen around exposed boulders in the vicinity of the site today, where stones have been accumulated by the tides and the surrounding sands winnowed away.

Ten stones identified as macaque tools were recovered from the site (Table 1; Fig. 2; Supplementary Online Material [SOM]), one from 15 to 20 cm depth in LS5C, and the remaining nine from the grey basal sands at 50–60 cm depth in LS5B and LS5C. The mean weight of these tools is 48.3 g, and they include nine basalt tools and one quartz tool. Tools constituted 4.3% of recovered stones from tool-bearing levels (10 of 233), using a 3 cm size cut-off. None of the non-tool stones shows use-damage that could be attributed to macaque behaviour.

Applying the UAI (Haslam et al., 2013) indicated that the narrow ends of all but one of the stones had been used by monkeys to process molluscs (most probably oysters), the exception being a

Table 1
Macaque tools excavated from LS5, Piak Nam Yai, Thailand.

Tool ID	Square; depth (cm)	Material	Weight (g)	Length (mm)	Width (mm)	Thickness (mm)	UAI; Action[a]
PNY065	5C; 15–20	Basalt	45.8	43.7	31.9	31.6	3.62; A
PNY064	5C; 50–55	Basalt	70.8	69.0	60.8	14.4	−2.58; P
PNY075	5C; 50–55	Quartz	35.5	45.4	36.8	21.2	3.92; A
PNY076	5C; 50–55	Basalt	34.1	42.6	37.8	17.4	2.86; A
PNY077	5C; 50–55	Basalt	19.3	44.8	42.5	8.7	4.16; A
PNY079	5C; 55–60	Basalt	21.4	51.1	32.8	10.4	3.05; A
PNY080	5C; 55–60	Basalt	31.6	46.7	43.6	12.2	1.52; A/P
PNY081	5C; 55–60	Basalt	33.8	65.4	35.2	11.2	1.64; A
PNY082	5C; 55–60	Basalt	14.6	36.5	32.1	8.9	3.15; A
PNY062	5B; 55–60	Basalt	175.8	86.8	66.0	25.0	0.50; A/P

[a] UAI = Use-Action Index, see (Haslam et al., 2013) for details. Action: A = 'axe' hammering; typically using the narrow end of a tool to open sessile oysters; P = 'pound' hammering, typically using the broad face of a tool to open unattached prey such as gastropods.

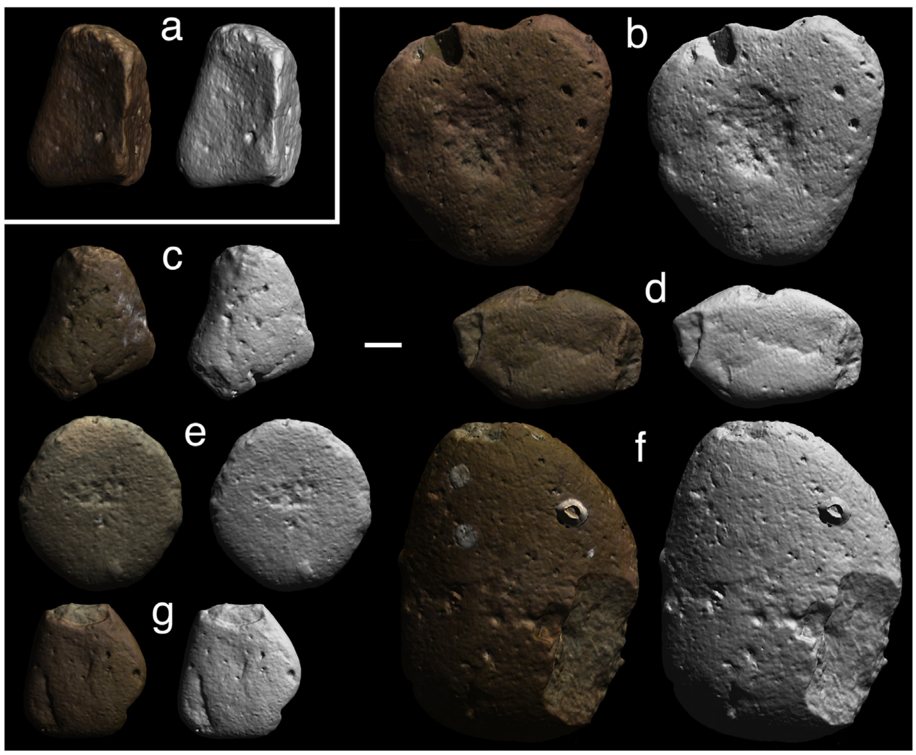

Figure 2. 3D scans of selected macaque tools excavated from LS5, Piak Nam Yai, Thailand: (a) PNY065, (b) PNY064, (c) PNY076, (d) PNY079, (e) PNY080, (f) PNY062, (g) PNY082. (a) and (c–g) have crushing and/or fracture wear on their narrow ends; (b) and (e–f) have pitting wear on the tool face. Each tool is shown with both a photorealistic and surface-only scan, to illustrate use damage. For further details on the tools see Table 1. The scale bar is 1 cm. For 3D models of the macaque tools recovered from LS5, see the SOM.

tool from the basal sediments that was most likely used to pound open unattached prey on a stone anvil. We anticipate that the UAI will misclassify tool function around 10% of the time (Haslam et al., 2013), however this does not affect our conclusion that the majority of the recovered tools from LS5 were most likely used in the past for oyster processing by wild macaques.

We obtained five radiocarbon ages on four undamaged oyster shells from LS5C, the square that yielded the majority of macaque tools (Table 2). All of the samples returned modern ages, i.e., post 1950. The sequence of coarse to fine sediments in the upper part of LS5 is consistent with reports of surface deposition from the major 2004 tsunami in Thailand (Kendall et al., 2006; Szczucinski et al., 2006), where such sediments averaged around 12 cm close to the coast. However, based on data from Ko Ra island south of Laem Son National Park, the location of LS5 on the protected east coast of PNY suggests that any impact was likely to have been minor (Kendall et al., 2006). In any case, the basal lag deposits and their enclosed tools at LS5 do not share any characteristics with reported tsunami sediments, indicating that their deposition is unrelated to, and therefore pre-dates, the 2004 tsunami.

4. Discussion

The recovery of buried stone tools used by wild macaques in the past demonstrates the validity and viability of an archaeological

Table 2
Radiocarbon ages obtained on oyster shells for LS5, Piak Nam Yai, Thailand.

Sample	Depth (cm)	Species	$\delta^{13}C$	Date[a]
OxA-29312	15–20	*Saccostrea cucullata*	0.01	1.03181 ± 0.00262
OxA-29313	50–55	*S. cucullata*	−0.31	1.03586 ± 0.00258
OxA-29314	50–55	*S. cucullata*	−0.26	1.02845 ± 0.00261
OxA-29315	55–60	*S. cucullata*	−0.09	1.04984 ± 0.00265
OxA-29316	55–60	*S. cucullata*	−1.31	1.02267 ± 0.00263

[a] Modern date (post 1950) reported as F14C (fraction of modern).

approach to Old World monkey tool use. The age of the excavated tools at 65 years or less does not extend the known antiquity of long-tailed macaque oyster processing, which currently stands at around 120 years (Carpenter, 1887), but they are the first Old World monkey tools to be archaeologically excavated from a secure context. Reconstructions suggest that sea-levels have been decreasing to their present level since an early-mid Holocene maximum (Horton et al., 2005; Scheffers et al., 2012). Sites in the current intertidal zone, like LS5, are therefore likely to have been either formed within the past thousand years, or be older than 7000 years, justifying further primate archaeological exploration of this zone.

As this is the first report of excavated macaque tools, and the first report of any Old World monkey archaeological excavation, we believe that it is useful to spend a little extra time outlining the reasons why we have identified these ten stones as macaque tools, rather than as naturally-modified stones. First, our conclusion is based on hundreds of hours of observation of the wild macaques on PNY island, including explicit focus on the tool use-damage that occurs, and comparisons between natural stones and macaque tools (e.g., Gumert et al., 2009). Second, prior to commencing excavations we formulated a use-wear protocol that allows us to reconstruct macaque tool behaviour with a high degree of accuracy (Haslam et al., 2013) (Fig. 1b). Third, we only considered stones that had repeated, localized damage visible to the naked eye (e.g., multiple pits, extensive crushing, or step-terminated fractures) as tools. Our conservative screening process excluded stones from the LS5 excavation that displayed either random or superficial damage, even though macaques conceivably may also have used those stones in the past. Fourth, we have conducted replication experiments with the PNY stones to observe how use-wear forms on previously undamaged stones, both from use as mollusc-opening tools and from movement within the tidal zone. The latter produces little to no damage, and none that can be mistaken for intensive macaque tool use, within the sandy environment surrounding LS5. In particular, repeated pitting on the centre of a stone's flat face (e.g., Fig. 2b, 2e, 2f), and crushing confined solely to the narrow ends of a tool (e.g., Fig. 2a, 2c, 2d, 2f, 2g) does not occur on the natural stones in the sandy beach area. The development of pitting, crushing and fracture wear on tools used by PNY macaques was illustrated in Haslam et al. (2013) and is reproduced in Figure 1b; note that the tools in this image were all observed in use by wild macaques immediately prior to their collection, and the identified damage was unambiguously caused by macaques.

The recovered tools fit within the size range of known oyster-processing tools on PNY (Gumert et al., 2009), although they fall at the lower end. Our knowledge of modern macaque tool use behaviour and transport (Gumert and Malaivijitnond, 2013) suggests that most of the tools from the basal deposits at LS5 were likely last used within a few metres of the location where they were found, although at present we cannot exclude their having been brought to the site from a wider radius. One tool (PNY064), identified via use-wear as most likely having been used to pound unattached prey, may have been used in a hammer–anvil combination with either the discovered boulder or other unknown buried boulders nearby. Given the debris build up around present-day macaque oyster sites on PNY, the increase in oyster debris in the basal LS5 sediments probably at least partially resulted from macaque use of stone tools to harvest these shellfish.

The lone oyster-processing tool found higher in the site sediments could not have been used in conjunction with the buried boulder. Instead, a monkey may have used it to obtain oysters from the boulder that currently overhangs the LS5 site. However, at this stage we cannot rule out the possible influence of tsunami or tidal forces on the upper parts of LS5, and we are cautious not to assign a precise behavioural narrative to these tools.

The role of coastal and aquatic foraging in human evolution has long been a topic of debate (Colonese et al., 2011; Archer et al., 2014; Thomas, 2015), with some even suggesting that coastal resource use spurred the development of modern human behaviour (Marean, 2014). We anticipate that the extension of the macaque archaeological record back into the past, of which this study is the first step, will help reveal how a non-human animal has developed a technological response to accessing prey in what can be an inhospitable and variably accessible environment. In conjunction with evidence of aquatic foraging from primates such as great apes (Russon et al., 2014) and Neanderthals (Cortés-Sánchez et al., 2011), the macaque record will eventually provide both a unique source of comparative data and a long-term record of how coastal environments may be exploited by technologically proficient animals other than modern humans.

Acknowledgements

This work was funded by a European Research Council Starting Grant (#283959) to MH. We thank Kathryn Reusch, Chelsea Budd and Hannah Mosley for assistance in the field.

Supplementary Online Material

Supplementary online material related to this article can be found at http://dx.doi.org/10.1016/j.jhevol.2016.05.002.

References

Archer, W., Braun, D.R., Harris, J.W., McCoy, J.T., Richmond, B.G., 2014. Early Pleistocene aquatic resource use in the Turkana Basin. J. Hum. Evol. 77, 74–87.
Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T., de la Torre, I., 2015. First GIS analysis of modern stone tools used by wild chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West Africa. PLOS ONE 10 e0121613.
Bunlungsup, S., Imai, H., Hamada, Y., Gumert, M.D., San, A.M., Malaivijitnond, S., 2016. Morphological characteristics and genetic diversity of Burmese long-tailed macaques (*Macaca fascicularis aurea*). Am. J. Primatol. http://dx.doi.org/10.1002/ajp.22512.
Burnham, K., Burnham, W., Newton, I., 2009. Gyrfalcon *Falco rusticolus* post-glacial colonization and extreme long-term use of nest-sites in Greenland. Ibis 151, 514–522.
Carpenter, A., 1887. Monkeys opening oysters. Nature 36, 53.
Carvalho, S., 2011. Extensive surveys of chimpanzee stone tools: from the telescope to the magnifying glass. In: Matsuzawa, T., Humle, T., Sugiyama, Y. (Eds.), The Chimpanzees of Bossou and Nimba. Springer, Dordrecht, pp. 145–155.
Colonese, A., Mannino, M.A., Mayer, D.B.-Y., Fa, D., Finlayson, J., Lubell, D., Stiner, M., 2011. Marine mollusc exploitation in Mediterranean prehistory: an overview. Quatern. Int. 239, 86–103.
Cortés-Sánchez, M., Morales-Muñiz, A., Simón-Vallejo, M.D., Lozano-Francisco, M.C., Vera-Peláez, J.L., Finlayson, C., Rodríguez-Vidal, J., Delgado-Huertas, A., Jiménez-Espejo, F.J., Martínez-Ruiz, F., 2011. Earliest known use of marine resources by Neanderthals. PLOS ONE 6, e24026.
Emslie, S., Polito, M., Brasso, R., Patterson, W., Sun, L., 2014. Ornithogenic soils and the paleoecology of pygoscelid penguins in Antarctica. Quatern. Int. 352, 4–15.
Gumert, M., Malaivijitnond, S., 2012. Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. Am. J. Phys. Anthropol. 149, 447–457.
Gumert, M., Malaivijitnond, S., 2013. Long-tailed macaques select mass of stone tools according to food type. Phil. Trans. R. Soc. B 368. http://dx.doi.org/10.1098/rstb.2012.0413.
Gumert, M., Kluck, M., Malaivijitnond, S., 2009. The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. Am. J. Primatol. 71, 594–608.
Gumert, M., Hoong, L.K., Malaivijitnond, S., 2011. Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). Am. J. Primatol. 73, 1–11.
Gumert, M., Hamada, Y., Malaivijitnond, S., 2013. Human activity negatively affects wild stone tool-using Burmese long-tailed macaques *Macaca fascicularis aurea* in Laem Son National Park, Thailand. Oryx 47, 535–543.
Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X., Quinn, R.L., Brenet, M., Arroyo, A., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315.
Haslam, M., 2012. Towards a prehistory of primates. Antiquity 86, 299–315.
Haslam, M., 2014. Primate archaeobotany: the potential for revealing nonhuman primate plant-use in the African archaeological record. In: Nixon, S.,

Murray, M.A., Fuller, D. (Eds.), The Archaeology of African Plant Use. Left Coast Press, Walnut Creek, CA, pp. 25–35.

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B.L., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W., Mercarder, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., Warren, R., 2009. Primate archaeology. Nature 460, 339–344.

Haslam, M., Gumert, M., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-wear patterns on wild macaque stone tools reveal their behavioural history. PLOS ONE 8, e72872.

Haslam, M., Cardoso, R.M., Visalberghi, E., Fragaszy, D., 2014. Stone anvil damage by wild bearded capuchins (*Sapajus libidinosus*) during pounding tool use: a field experiment. PLOS ONE 9, e111273.

Horton, B.P., Gibbard, P.L., Milne, G.M., Morley, R.J., Purintavaragul, C., 2005. Holocene sea levels and palaeoenvironments, Malay-Thai Peninsula, southeast Asia. The Holocene 15, 1199–1213.

Kendall, M., Paterson, G., Aryuthaka, C., Nimsantijaroen, S., Kongkaeow, W., Whanpetch, N., 2006. Impact of the 2004 tsunami on intertidal sediment and rocky shore assemblages in Ranong and Phnagnga provinces, Thailand. Phuket Marine Biology Centre Research Bulletin 67, 63–75.

Kühl, H.S., Kalan, A.K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Jones, S., Kehoe, L., Regnaut, S., Tickle, A., Ton, E., van Schijndel, J., Abwe, E.E., Angedakin, S., Agbor, A., Ayimisin, E.A., Bailey, E., Bessone, M., Bonnet, M., Brazolla, G., Buh, V.E., Chancellor, R., Cipoletta, C., Cohen, H., Corogenes, K., Coupland, C., Curran, B., Deschner, T., Dierks, K., Dieguez, P., Dilambaka, E., Diotoh, O., Dowd, D., Dunn, A., Eshuis, H., Fernandez, R., Ginath, Y., Hart, J., Hedwig, D., Ter Heegde, M., Hicks, T.C., Imong, I., Jeffery, K.J., Junker, J., Kadam, P., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K., Lapeyre, V., Lapuente, J., Lee, K., Leinert, V., Meier, A., Maretti, G., Marrocoli, S., Mbi, T.J., Mihindou, V., Moebius, Y., Morgan, D., Morgan, B., Mulindahabi, F., Murai, M., Niyigabae, P., Normand, E., Ntare, N., Ormsby, L.J., Piel, A., Pruetz, J., Rundus, A., Sanz, C., Sommer, V., Stewart, F., Tagg, N., Vanleeuwe, H., Vergnes, V., Willie, J., Wittig, R.M., Zuberbuehler, K., Boesch, C., 2016. Chimpanzee accumulative stone throwing. Scientific Reports 6. http://dx.doi.org/10.1038/srep22219.

Luncz, L., Wittig, R., Boesch, C., 2015. Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). Phil. Trans. R. Soc. B 370. http://dx.doi.org/10.1098/rstb.2014.0348.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., Hamada, Y., 2007. Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). Am. J. Primatol. 69, 227–233.

Marean, C.W., 2014. The origins and significance of coastal resource use in Africa and Western Eurasia. J. Hum. Evol. 77, 17–40.

McGrew, W.C., Matsumoto, T., Nakamura, M., Phillips, C., Stewart, F., 2014. Experimental primate archaeology: detecting stone handling by Japanese macaques (*Macaca fuscata*). Lithic Technology 39, 113–121.

Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rainforest. Science 296, 1452–1455.

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R.T., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proc. Natl. Acad. Sci. 104, 3043–3048.

Russon, A.E., Compost, A., Kuncoro, P., Ferisa, A., 2014. Orangutan fish eating, primate aquatic fauna eating, and their implications for the origins of ancestral hominin fish eating. J. Hum. Evol. 77, 50–63.

Scheffers, A., Brill, D., Kelletat, D., Bruckner, H., Scheffers, S., Fox, K., 2012. Holocene sea levels along the Andaman Sea coast of Thailand. The Holocene 22, 1169–1180.

Stewart, F., Piel, A., McGrew, W.C., 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. J. Hum. Evol. 61, 388–395.

Szczucinski, W., Chaimanee, N., Niedzielski, P., Rachlewicz, G., Saisuttichai, D., Tepsuwan, T., Lorenca, S., Siepak, J., 2006. Environmental and geological impacts of the 26 December 2004 tsunami in coastal zone of Thailand – overview of short and long-term effects. Pol. J. Environ. Stud. 15, 793–810.

Tan, A., Tan, S.H., Vyas, D., Malaivijitnond, S., Gumert, M., 2015. There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. PLOS ONE 10 e0124733.

Thomas, K.D., 2015. Molluscs emergent, Part II: themes and trends in the scientific investigation of molluscs and their shells as past human resources. J. Archaeol. Sci. 56, 159–167.

Visalberghi, E., Haslam, M., Spagnoletti, N., Fragaszy, D., 2013. Use of stone hammer tools and anvils by bearded capuchin monkeys over time and space: construction of an archeological record of tool use. J. Archaeol. Sci. 40, 3222–3232.