Demographic Transitions and Migration in Prehistoric East/Southeast Asia Through the Lens of Nonmetric Dental Traits

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ABSTRACT The aim of this study is to examine and assess the nonmetric dental trait evidence for the population history of East and Southeast Asia and, more specifically, to test the two-layer hypothesis for the peopling of Southeast Asia. Using a battery of 21 nonmetric dental traits we examine 7,247 individuals representing 58 samples drawn from East and Southeast Asian populations inhabiting the region from the late Pleistocene, through the Neolithic, Bronze Age, Iron Age, and into the historic and modern periods. The chief data reduction technique is a neighbor-joining tree generated from the triangular matrix of mean measure of divergence values. Principal findings indicated a major dichotomization of the dataset into (1) an early Southeast Asian sample with close affinities to modern Australian and Melanesian populations and (2) a very distinct grouping of ancient and modern Northeast Asians. Distinct patterns of clinal variation among Neolithic and post-Neolithic Mainland Southeast Asian samples suggest a center to periphery spread of genes into the region from Northeast Asia. This pattern is consistent with archaeological and linguistic evidence for demic diffusion that accompanied agriculturally driven population expansion in the Neolithic. Later Metal Age affinities between Island and Mainland coastal populations with Northeast Asian series is likely a consequence of a South China Sea interaction sphere operating from at least 500 BCE, if not from the Neolithic. Such results provide extensive support for the two-layer hypothesis to account for the population history of the region. Am J Phys Anthropol 155:45–65, 2014. © 2014 Wiley Periodicals, Inc.

East, including Southeast, Asia is believed to have been initially occupied by anatomically modern humans (AMH) by at least 60,000 BP (e.g., Bräuer, 2008; Oppenheimer, 2009; Demeter et al., 2012), followed by near simultaneous dispersals into subcontinental Sahul (e.g., Hudjashov et al., 2007; Rasmussen et al., 2011; Sémah and Sémah, 2013) and near Oceania (e.g., Kayser, 2010; Cox, 2013). There appears to have been a hiatus before AMH moved into the Western Hemisphere, likely occurring sometime after the last glacial maximum (between 26,500 and 19,000 years ago, Clark et al., 2009; e.g., see Schurr and Sherry, 2004; O'Rourke and Raff, 2010; Stoneking and Frederick, 2010; Drake and Oxenham, 2013).

The skeletal record is sparse for the earliest phases of late Pleistocene AMH colonization of Northeastern Asia, making the Upper Cave crania recovered from Zhoukoudian (Weidenreich,1939) particularly important. Dating of these crania has not been resolved satisfactorily (see Kamminga and Wright, 1988; Cunningham and Wescott, 2002). Absolute dates range from as late as 10,000 BP (An, 1991) to 23,000–26,500 BP (Hedges et al., 1992), to as early as 29,000–34,000 BP (Chen et al., 1989). This uncertainty in dating has contributed to a diversity of views on the relationship of the Upper cave crania to modern populations. For instance, affiliations with Australian Aborigines (Coon, 1962; Kamminga and Wright, 1988; Stringer, 1999), Easter Islanders (Wright, 1992; Cunningham and Wescott, 2002) and even Paleo-Indian and Arctic populations (Weidenreich, 1939) have all been suggested. Turning to Island Northeast Asia, the well-preserved Minatogawa series (c.18,000 BP) from Oki-

nawa in the Japanese archipelago are argued to demonstrate affinities with Southeast Asian AMH, including Liujiang, Wajak, and Niah (e.g., Suzuki and Hanihara, 1982; Wu 1990; Baba and Narasaki, 1991; Kaifu et al., 2011). Other scholars have treated both the Minatogawa and Zhoukoudian series as simply representative of late Pleistocene archaic AMH globally, with no particular specific affinities with any modern populations (e.g., Brown, 1999; Wolpoff, 1999).

Apart from the Upper Cave crania, the earliest dates for AMH occupation of this region derive from Southeast Asia. The Liujiang specimen from Guangxi province in southern China (see Woo, 1959; Wu, 1990) has been dated to at least 68,000 BP and as early as between 111,000 and 139,000 BP (Shen et al., 2002). However, the specimen has not been directly dated and its relationship to the dated deposits remains unresolved

(Rosenberg, 2002). Problematic Liujiang aside, the fragmentary Laibing specimen, also from Guangxi Province, is dated to between 38,000 and 44,000 BP (Shen et al., 2007). Moving south, a range of other late Pleistocene specimens from Niah Cave in Malaysia (Brothwell, 1960; Kennedy, 1977; Barker et al., 2007), Tabon Cave in the Philippines (Macintosh, 1978; Dizon et al., 2002; Détroit et al., 2004), and Wajak in Indonesia (Dubois, 1922; Storm, 1995; Storm et al., 2013) have secure dates ranging from 40,000 to 16,000 BP. Most recently, the Tam Pa Ling specimen from Laos has been dated to at least 47,000 BP (Demeter et al., 2012). Finally, hominin material has been dated to 67,000 years BP at Callao Cave, northern Luzon in the Philippines (Mijares et al., 2010), although it is unclear whether these remains belong to AMH or an earlier form. What is clear is that while these various specimens have value in dating the initial appearance and subsequent spread of AMH in eastern Asia, their often fragmentary nature means they are somewhat less useful for clarifying genealogical relationships with modern populations in the region.

Terminal Pleistocene and early to mid-Holocene assemblages in Southeast Asia have proven to be of considerable value in elucidating genealogical relationships, with early work suggesting genetic links between these early populations and present-day Australo-Melanesians (e.g., Callenfels, 1936; Mijsberg, 1940; Von Koenigswald, 1952; Coon, 1962; Jacob, 1967). Analysis of more recent finds (e.g., Gua Gunung Runtuh, Moh Khiew, and Hang Cho) support the view that Southeast Asia was occupied at least until the preceramic period by descendants of the first colonists of late Pleistocene Sundaland (Matsumura and Zuraina, 1999; Bulbeck, 2000a; Matsumura and Pookajorn, 2005; Matsumura, 2006; Matsumura et al., 2008a,b, 2011).

Two models have been proposed for AMH origins in Northeast and Southeast Asia. Using recent DNA research, proponents of one model maintain that Southeast Asia was the primary source of all North and East Asian populations (e.g., Li and Bing, 2000; Capelli et al., 2001; HUGO Pan-Asian SNP Consortium, 2009). Proponents of the opposing model assert that contemporary Northeast/Southeast Asian populations are the result of a deep history of multiple gene flow events originating in the west (Lahr, 1996; Underhill et al., 2001; Hanihara, 2006, 2008; Stoneking and Harvati, 2013). Indeed, one recent study suggests Australian aboriginal populations can trace their descent back to the earliest AMH human dispersal into Southeast Asia approximately 80,000 years BP, while a subsequent dispersal more than 40,000 years later gave rise to modern Asians, even though there is evidence for gene flow between the original migrant populations prior to the divergence of Native Americans (Rasmussen et al., 2011).

Whatever may be the case in the late Pleistocene, the picture is muddied further by major demographic changes in the region concomitant with the development and adoption of agriculture and subsequent increase in population growth and mobility. In East/Southeast Asia major human dispersals have been correlated with the movement of major language groups (e.g., Austroasiatic on the mainland and Austronesian throughout Island Southeast Asia and the Pacific) concurrent with expanding food-producing populations during the Neolithic (Higham, 2001, 2013; Bellwood, 2005, 2013; Sagart, 2008). Linguistic data suggest that Southern China and Taiwan provided the ultimate sources of many of the existing language families of Southeast Asia, while archaeology places the origins of Neolithic farming societies in the Yangzi River Basin during the early Holocene (Crawford and Chen, 1998; Chen, 1999; Zhang and Hung 2010), prior to subsequent expansion from southern China into Southeast and eastern Asia (Bellwood, 2005; Lu, 2006).

For some time the "immigration" or "two-layer" hypothesis (Jacob, 1967), which suggests that modern Southeast Asian populations are a product of Northeast Asian-derived demic diffusion, coupled with varying levels of genetic exchange with extant indigenous local populations into the region as part of the expansion of food producing populations southward from, ultimately, a Yangtze basin homeland, has been the favored model. Nevertheless, this model has been challenged, and the primary basis for such challenges has been the difficulty in distinguishing between changes in skeletal morphology due to modernization from changes due to gene flow (Bulbeck, 1982; Harvati, 2009; Hubbe et al., 2011). The modernization interpretation holds that a relaxation in masticatory stress, due to the adoption of new food processing technologies, triggered a range of morphological adaptations (not the least being a reduction in dentofacial size or robusticity) (e.g., Brace, 1963; Dahlberg, 1963; Wolpoff, 1999). So the key question are the clear morphological changes seen in the mid-Holocene due to demic diffusion fueled by expanding Neolithic populations into Southeast Asia, or are the changes a consequence of local microevolutionary histories, which were for the most part in response to local adaptation scenarios? One way to address this impasse is to explore the issue with a suite of morphological traits that are both genetically conservative over time and robust to environmentally induced evolutionary pressures: dental nonmetric traits, which are argued to be formed under strong genetic control and free of environmental influence (e.g., Bowden and Goose, 1969; Townsend and Brown, 1978; Hanihara and Hanihara, 1989), are ideal in this context.

Turner's "Sundadont/Sinodont" tooth classification (Turner, 1989, 1990), based on nonmetric dental trait frequencies, is often cited as one of most useful tools available for investigating population origins and mobility in Eastern Asia and the Americas. Turner argued that Southeast Asians were characterized by what he termed the Sundadont dental complex, in contrast to the more derived Sinodont complex in Northeast Asia, with the implication that Northeast Asians were derived from Southeast Asian migrants. This placement of Southeast Asia at center stage for the origins of modern East Asian populations is consistent with the "regional continuity," or "local evolution," model for Southeast Asian population origins, which stands in opposition to the two-layer model, as well as genetic studies supportive of a single wave scenario for the colonization of Southeast Asia.

Turner's model is not without its critics (Kamminga and Wright, 1988). Indeed, Matsumura and Hudson (2005), using a broad suite of dental traits, demonstrated that gene flow occurred in the opposite direction; that is, from Sinodontic northeast Asian to Sundadontic Southeast Asian populations. Consequently, the local evolution model is no longer a viable alternative. Other critiques of Turner's model have had mixed success. For instance, Hanihara's (2008) global survey of nonmetric tooth traits, using R-matrix and Fst comparisons, found relatively larger levels of intraregional variation among

present-day Northeast Asians than Southeast Asians. This finding led him to support Turner's Sundadont local evolution theory for Southeast Asia on the one hand, while favoring a multiple origin model for Northeast Asia on the other. As far as Northeast Asians are concerned, Hanihara assumed avenues of gene flow across Siberia from the west and from Southeast Asian populations to the south.

The aim of this article is to build on Matsumura and Hudson's (2005) work with a significantly larger dataset of nonmetric dental traits, which includes early, middle, and late Holocene sequences in East and Southeast Asia, in an effort to provide the most comprehensive, geographically extensive and temporally exacting test of the two-layer hypothesis to date.

MATERIALS AND METHODS

The materials used in this study include 58 samples totaling 7,247 individuals from Northeast and Southeast Asia, Oceania, the Pacific, and the America (see Tables 1 and 2, and Fig. 1). In some cases, geographically adjacent and culturally contiguous samples were combined to deal with small individual sample sizes, such as materials from an array of early Holocene Hoabinhian/Mesolithic forager sites (see Matsumura et al., in press). The dataset includes samples from the late Pleistocene, early to mid-Holocene, Neolithic (defined as farming populations, see discussion in Oxenham and Matsumura, 2011), Bronze, and Iron Age through to proto-Historic, Historic, and modern samples. Space precludes a review of each sample in the dataset, however, the references in Table 1 provide details on the majority of samples used here. All assessments of dental morphology trait expression were carried out by the first author (HM) in an effort to eliminate the issue of interobserver error, which is particularly problematic in nonmetric dental studies.

An enormous number of dental traits have been examined and their value in exploring phylogenetic relationships have been discussed in some detail since early last century (e.g., Hrdlička, 1920; Dahlberg, 1963; Hillson, 1996; Scott and Turner, 1997; Hanihara, 2008). This study uses a battery of 21 nonmetric dental traits (see Table 3), which has proven particularly effective in teasing out phylogenetic relationships in previous work (see Matsumura, 1995, 2002, 2006, 2011; Matsumura and Hudson, 2005; Matsumura and Dodo, 2009; Matsumura et al., 2011). All traits were scored as present or absent for ease in describing the various samples and to facilitate statistical comparisons. Both sexes were combined due to the observation that there is low to minimal sexual dimorphism in the expression of these traits (Turner et al., 1991). As a general rule, observations were performed on teeth from the right side, with antimere substitution where necessary.

Unrooted tree diagrams using the neighbor-joining (NJ) method (Saitou and Nei, 1987, software package provided by Huson and Bryant, 2006) were generated from the triangular matrix of pairwise mean measure of divergence (Smith's MMD: Berry and Berry, 1967) values to aid in the interpretation of interpopulation phenotypic affinities. To facilitate statistically meaningful comparisons, samples were pooled into regional groups (e.g., Northeast Asian, Southeast Asian, etc.) prior to arcsine transforming trait frequencies and testing for significant differences in trait frequencies between geographic regions with ANOVA. Finally, post hoc tests

(Tukey and Kramer method) were performed across regional groupings to assess any differential effects of individual aggregate samples on the overall distribution of these groups.

RESULTS

Frequencies for the 21 nonmetric dental traits, excluding data published elsewhere (see Tables 1 and 2), are provided in Table 4. Figure 2 is an unrooted tree using the NJ method applied to the computed Smith's MMD values using the 21 dental traits. This diagram displays an array of recent Northeast Asian samples, comprising modern and historic Japanese and Chinese, at the top of their respective trees. The Native American, including subarctic, samples form a subcluster closely connected with the Northeast Asian array. An early Southeast concentration of samples (Early Vietnam and Laos, Early Flores and Malay including Mesolithic/Hoabinhian specimens) groups with Melanesian samples, including Loyalty, New Guinea, and New Britain Islanders. Australian Aborigines and Andaman-Nicobar are also very closely linked with this array of samples.

It is also worth noting that a majority of the modern Southeast Asian samples are scattered between the two main arrays. Many of the Mainland and Island samples (Aboriginal Taiwanese, Philippines, Hainan, Vietnam, Myanmar, and Thai) are situated somewhat closer to the Northeast Asian and Western Hemispheric grouping of samples. Sunda Islanders and Philippine Negritos, conversely, align with the cluster of Australo-Melanesian and early southeast Asian samples. Turning to the Neolithic and Metal Age samples, their allocation varies considerably between the two main aggregates. Neolithic Man Bac and Bronze/Iron Age Dong Son (northern Vietnam), Iron Age Southern Vietnam, some samples from Neolithic-Bronze Age Thailand (Khok Phanom Di, Ban Non Wat 1), Iron Age Thailand (Ban Non Wat 2, Noen U-Loke) and Iron Age Leang Codong Sulawesi Islanders branch out near the top of the tree. Conversely, Iron Age Phum Snay (Cambodia) and Tanegashima (Yayoi, Japan) are adjacent to the aggregation of early Holocene Southeast Asians and Australo-Melanesians. Other Neolithic samples, such as the Jomon (Japan), and Non Nok Tha, Ban Lum Khao, Ban Chiang, Ban Na Di from Thailand occupy intermediate positions relative to the main clusters.

Trait frequency data is profiled in Figure 3, to better visualize affinities and differences among the samples. Samples were combined into major geographical units with arcsine transformed frequency data to facilitate statistical comparisons. Overall, 15/21 original traits suggest significant geographic clines or anomalies. Statistical significance of differences in comparisons of trait frequencies between geographical units is given by F values calculated with ANOVA. Table 5 gives the results of post hoc tests (Tukey and Kramer method) which were performed across major regional East/Southeast Asian groups and others, to determine which of the geographic units drive the difference.

Shovel-shaped (Shoveling) incisors appear with considerably lower frequency among early Southeast Asians (Hoabinhian/Mesolithic), whereas their frequency increases in more recent Southeast Asians and is quite high among Northeast Asians. While not as clear as shoveling, other geographical and/or chronological clines are evident. For instance, the interruption groove of the
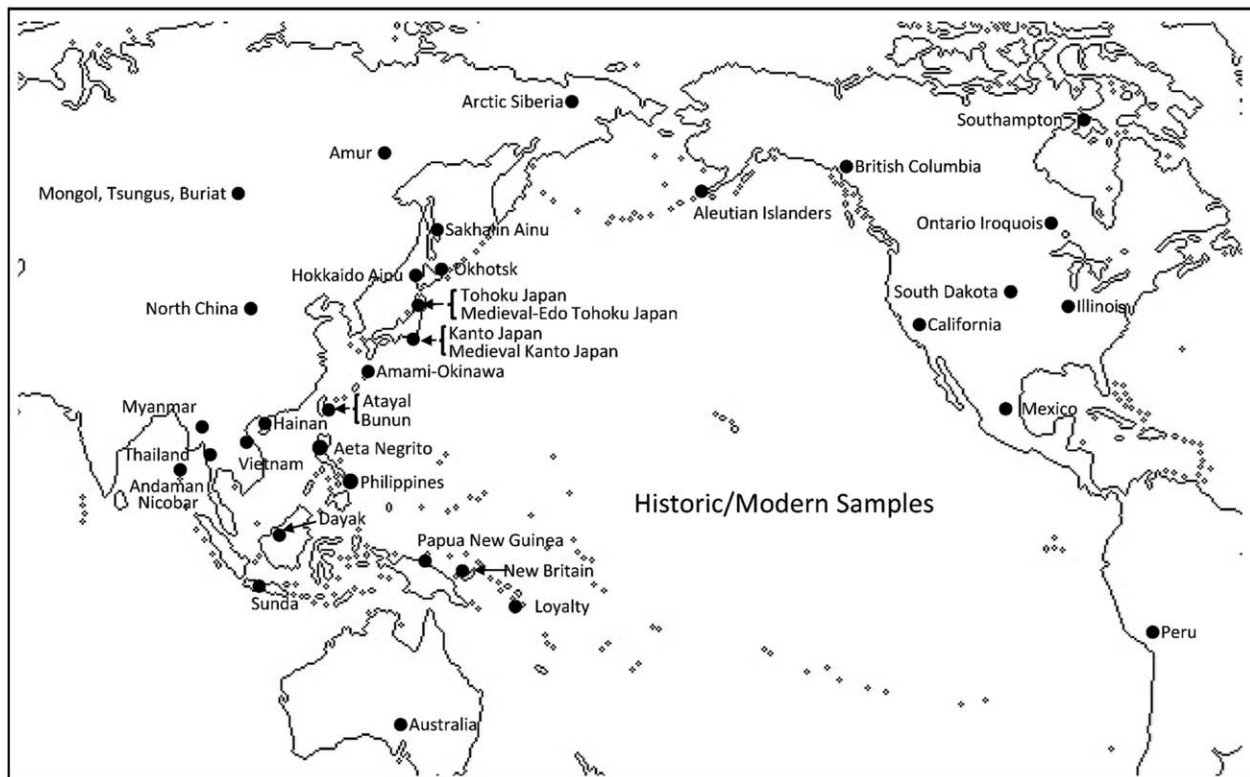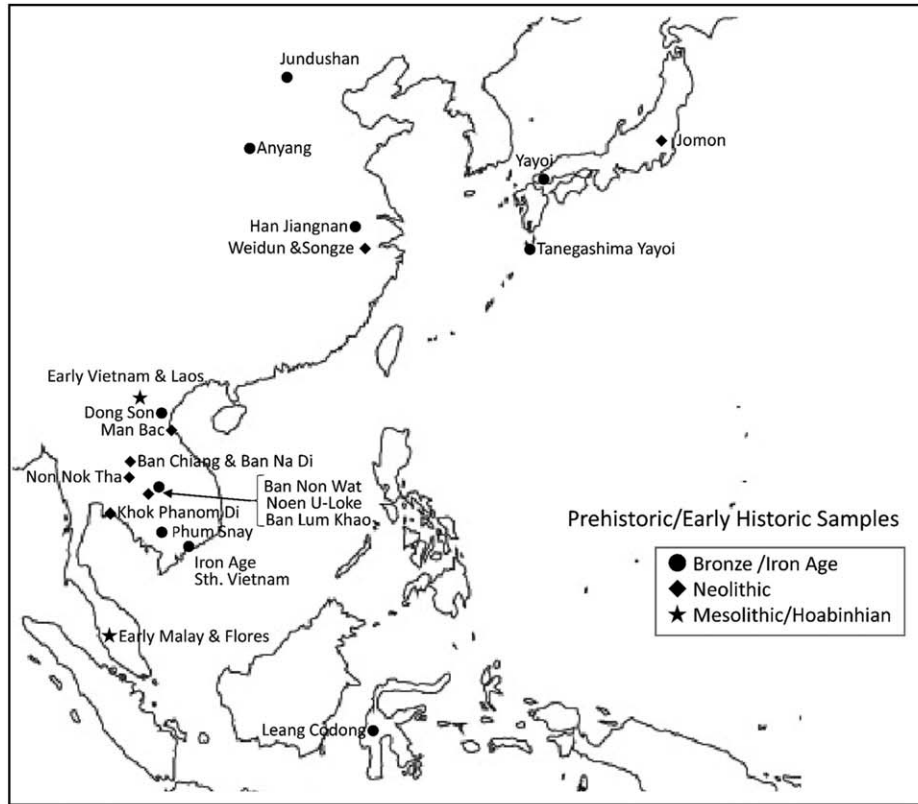
Fig. 1. Locality map of population samples used (upper map: prehistoric and early historic samples, lower map: comparative non-Asian samples, and historic and modern East/Southeast Asian samples).

TABLE 1. Comparative early population samples

Sample	Locality	Period	Remarks	References	N[a]	Storage[b]	Data Published
Late Pleistocene - Early Holocene samples							
Early Vietnam and Laos	Vietnam, Laos	Hoabinhian culture (c. 16,000–8,000 BP) and post-Hoabinhian or contemporary Mesolithic preagricultural sequence (Bac Son culture = c. 9,000–7,000 BP; Da But culture = c.5,000–6,000BP)	Hoabinhian Cultural Sites of Lang Bon, Lang Gao, Mai Da Nuoc, Mai Da Dieu, Dong Truong, Du Sang, Hang Dang and Hang Cho, Bac Son Cultural sites of Pho Binh Gia, Lang Cuom, and Cua Gi, and Da But Cultural sites of Da But and Con Co Ngua in Northern Vietnam, and sites of Tam Hang and Tam Pong in Laos	Mansuy and Colani (1925); Colani (1927a,b, 1939); Huard and Saurin (1938); Cuong (1986); Thuy (1990); Bui (1991); Cuong (2003); Matsumura et al. (2008a); Demeter et al. (2009, 2012); White (2011)	94	CSPH, IAH, LAPM, MHO	
Early Flores and Malay	Malaysia, Indonesia	Hoabinhian and post-Hoabinhian or contemporary Mesolithic preagricultural sequence (c. 14,000–4,000 BP)	Sites of Gua Cha, Guar Kepah, Niah in Malaysia, and sites of Liang Momer, Linag Toge, Liang X, Gua Alo, Aimere, Sampung and Gua Nempong in Flores Island	Callenfels (1936); Mijsberg (1940); Sieveking (1954); Verhoeven (1958); Trevor and Brothwell (1962); Harrison (1967, 1975); Jacob (1967); Bulbeck (2000a)	79	BMNH, CAM, NNML, UCB, UNLV, USM	
Neolithic (-Bronze Age) samples							
Ban Chiang and Ban Na Di	Thailand	Neolithic-Bronze Age (c. 3,500–2,300 BP)	Site in Udon Thani Province, Ban Chiang (Burial Phase EPI-EPV, MP VI-MPVII; N = 78, Ban Na Di N = 23	Gorman and Charoenwongsa (1976); Higham and Kijngam (1984); White (2011);Pietrusewsky an Douglas (2002); Boonlop and Bubpha (2011)	101	UHW, SAC, FAD	
Non Nok Tha	Thailand	Neolithic-Bronze Age (c. 3,500–3,000 BP)	Site in Khon Kaen Province	Solheim et al. (1966); Bayard (1971); Pietrusewsky and Douglas (2002)	53	UNLV	
Ban Non Wat 1	Thailand	Late Neolithic -Bronze Age (c. 3,800–2,400 BP)	Site in Khorat Province	Higham and Kijngam, (2009, 2010, 2012a, 2012b)	128	FAD	
Ban Lum Khao	Thailand	Terminal Neolithic -Bronze Age (c. 3,250–2,600 BP)	Site in Khorat Province	Higham and Thosarat (2004)	38	FAD	
Khok Phanom Di	Thailand	Late Neolithic (c. 3,800–3,500 BP)	Site in Chonburi province	Higham and Thosarat (1993); Tayles (1999)	58	FAD	
Man Bac	Vietnam	Late Neolithic (Phung Nguyen Culture, c. 3,800–3,500 BP)	Site in Ninh Binh Province, Northern Vietnam	Matsumura et al. (2008b); Oxenham et al. (2011)	43	IAH	Matsumura, (2011)
Weidun and Songze	China	Neolithic (Majiabang Culture, c.7,000–5,000 BP)	Sites in Jiangsu Province along Yangtze River in Southern China	Nakahashi and Li (2002)	111	NJM, SMNH	Matsumura (2002)
Jomon	Japan	Neolithic (specimens dated to c. 5,000–2,300 BP)	Sites in all over Japanese archipelago	Habu (2004)	711	UTK, KTU, SMU, NMNHT	Matsumura (1995)
Iron Age Samples							
Noen U-Loke	Thailand	Iron Age (c. 400 BC–AD 400)	Site in Khorat Province	Higham and Kijngam (2007)	43	FAD	
Ban Non Wat 2	Thailand	Iron Age (c. 420 BC–AD 600)	Site in Khorat Province	Higham and Kijngam (2009, 2012b)	60	FAD	
Iron Age South Vietnam	Vietnam	Iron Age (c. 300 BC–AD 300)	Sites of Giong Ca Vo in Ho Chi Minh City (N = 34) and Hoa Diem in Khanh Hoa Province (N = 42)	Cuong (1996); Thang and Hien (1997); Yamagata and Hoang (2013)	76	HCHM, LAPM, KHPM	

TABLE 1. Continued

Sample	Locality	Period	Remarks	References	N[a]	Storage[b]	Data Published
Phum Snay	Cambodia	Iron Age (c. 350 BC–200 AD)	Site of Phum Snay in Preah Neat Orey District, West Cambodia	O'Reilly et al. (2006, 2008); Domett and O'Reilly (2009); Matsumura et al. (2011)	209	RUFA, WBSR, WLPS	Matsumura et al. (2011)
Leang Codong	Indonesia	Iron Age	Site in Sulawesi Island	Verhoeven (1958); Jacob (1967); Bulbeck (2000a,b)	100	NNML	
Yayoi	Japan	Yayoi Period (c. 800 BC–AD 300)	Sites of Doigahama, Nakanohama, Kanenokuma and others in Northern Kyushu and Yamaguchi Districts, Western Japan	Nakahashi (1989); Hudson (2013)	212	KSU	Matsumura (1995)
Tanegashima Yayoi	Japan	Yayoi Period (c. 800 BC–AD 300)	Site of Hirota in Tanegashima Island, Southern Japan	Kokubu and Morizono (1958)	60	KSU	Matsumura (1995)
Anyang	China	Yin (Shan) Period (c. 1,500–1,027 BC)	Site in Henang Province in Northern China	Institute of History and Institute of Archaeology (1982)	81	AST	
Jiangnan	China	Eastern Zhou–Former Han Periods (770 BC–AD 8)	Sites in Jiangnan Province along Lower Basin of Yangtze River, Sothern China	Nakahashi and Li (2002)	68	NJM	Matsumura (2002)
Jundushan	China	Spring and Autumn Period (c. 500 BC)	Site in Yanqing Prefecture near Beijing	Beijing Cultural Relic Institute (2007)	57	PKU	

[a] N, number of individuals.
[b] Abbreviations of sample storage: AMNH, American Museum of Natural History, New York; NMP, National Museum of the Philippines, Manila; AST, Academia Sinica of the Republic of China in Taipei, Taiwan; NNML, National Natuurhistorisch Museum, Leiden; BMNH, Natural History Museum, London; NTW, Department of Anatomy, National Taiwan University; CAM, Department of Biological Anthropology, University of Cambridge; PKU, School of Archaeology and Museology, Peking University; CMCQ, Canadian Museum of Civilization, Quebec; RUFA, Fine Arts of Department, Royal University of Fine Arts, Phnom Penh; CSPH, Center for South East Asian Prehistory, Hanoi; SAC, Princess Sirindhorn Anthropology Centre, Bangkok; FAD, Fine Arts of Department, Thailand; SI, National Museum of Natural History, Smithsonian Institution; HCHM, Ho Chi Minh Historical Museum; SMNH, Shanghai Museum of Natural History; HKU, Hokkaido University, Sapporo; SMU, Department of Anatomy, Sapporo Medical University; HMUC, Phobe Hearst Museum, University of California; STMU, Department of Anthropology, St. Marianna University, Japan; IAH, Institute of Archaeology, Hanoi; THU, Department of Anatomy, Tohoku University, Japan; KHPM, Khanh Hoa Provincial Museum, Vietnam; UHW, Department of Anthropology, University of Hawaii; KSU, School of Social and Cultural Studies, Kyushu University; UMPH, Univ. of Medicine and Pharmacy at Ho Chi Minh City; KTU, Department of Anthropology, Kyoto University; UNLV, Department of Anthropology, University of Nevada; LAPM, Long An Provincial Museum, Vietnam; UPSD, Ward Museum, University of Pacific School of Dentistry, California; MAES, Museum of Anthropology & Ethnography, St Petersburg; USM, Centre for Archaeological Research, University of Sains Malaysia; MAL, Museo Amano in Lima; USYD, J.L. Shellshear Museum, University of Sydney; MDU, Department of Anatomy, Mahidol University, Bangkok; UTK, University Museum, University of Tokyo; MHO, Musée de l'Homme, Paris; UTOR, Department of Anthropology, Erindale College, University of Toronto; MNAP, Museo Nacional de Antoropologia y Arqueologica, Lima; WBSR, Wat Bo, Siem Reap, Cambodia; NJM, Institute of Archaeology, Nanjing Museum; WLPS, Wat Leou, Pham Snay Village, Cambodia.

TABLE 2. Comparative non-Asian samples, and historic and modern East/Southeast Asian samples

Sample	Locality	Period	Remarks	N[a]	Sample storage[b]	Data published
Safur and India						
Australia	Australia	Modern		101	BMNH, CAM	
Papua New Guinea	Melanesia	Modern	Including samples from Torres, Vanuatu and Solomon Islands	111	CAM, USYD	
Loyalty	Melanesia	Modern		62	MHO	
New Britain	Melanesia	Modern	New Britain Island	201	CAM, SI	
Andaman and Nicobar	India	Modern	Andaman and Nicobar Islands	88	BMNH, CAM	
Southeast and East Asia						
Vietnam	Vietnam	Modern	Northern and Southern Vietnam	99	MHO, UMPH	Matsumura et al. (2011)
Thailand	Thailand	Modern	Residents in Bangkok	110	MDU	Matsumura et al. (2011)
Myanmar	Myanmar	Modern		88	BMNH, CAM	
Sunda	Indonesia	Modern	Java, Bali, Timor, Celebes, Moluccas, Banca, Sumbawa, Sumatra and Mentawei Islands	121	AMNH, BMNH, CAM, SI	
Dayak	Malaysia	Modern	The State of Sarawak in Borneo Island	91	BMNH, CAM	
Philippines	Philippines	Modern	Non-Negrito	69	UTK, NMP	
Aeta Negrito	Philippines	Modern	Ethnic group of Aeta in Luzon Island	41	MHO, UTK	
Atayal	Taiwan	Modern	Taiwan Aborigines	79	NTW	
Bunun	Taiwan	Modern	Taiwan Aborigines	45	NTW	
Protohistoric Kanto Japan	Japan	Kofun Period c. 300–600 AD	Kanto District, Central Japan	287	KSU, KTU, NMNHT, UTK	Matsumura (1995)
Medieval Kanto Japan	Japan	Kamakura Period 1,192–1,336 AD	Kanto District, Central Japan	364	NMNHT, UTK	Matsumura (1995)
Okhotsk	Japan	c.400–1,000 AD	Sites of Okhotsk culture in Hokkaido, Japan and in Sakhalin Island, Russia	136	HKU, SMU	Matsumura et al. (2009)
Kanto Japan	Japan	Edo Period 1,603–1,868 AD	Kanto District, Central Japan	254	NMNHT, UTK	Matsumura (1995)
Tohoku Japan	Japan	Modern	Tohoku District, Northern Japan	103	THU	Matsumura and Dodo (2009)
Medieval-Edo Tohoku Japan	Japan	Muromachi - Edo Period 1,392–1,868 AD	Tohoku District, Northern Japan	82	THU, STMU, UTK	Matsumura and Dodo (2009)
Amami-Okinawa	Japan	Modern	Amami and Okinawa Islands, Southern Japan	166	KTU, UTK	
Hokkaido Ainu	Japan	Early Modern c. 1,300–1,900 AD	Hokkaido District, Northern Japan	61	SMU, UTK	Matsumura (1995)
Hainan	China	Modern	Hainan Island in Southern China	128	NTW	
North China	China	Modern	Manchuria in Northern China	104	UTK	Matsumura (1995)
Amur	Russia	Modern	Ethnic groups of Nanay, Negidal, Ulch and Nivkh in Lower Amur River Basin	86	MAES	Matsumura et al. (2009)
Sakhalin Ainu	Russia	Modern	Sakhalin Island	36	KTU	Matsumura et al. (2009)
Arctic Siberia	Russia	Modern	Chukchi Peninsula	122	MAES, MHO	Matsumura et al. (2009)
Mongol, Tsungus, Buriat	Mongol, Russia	Modern	Ulaanbaatar (Mongol), Toriskosavsk, Kalmyk, Yakutsk, Evenki (Russia)	175	BMNH, MAES, MHO, SI	Matsumura et al. (2009)
America						
Aleutian	USA	Modern	Kodiak, Kagamil, Kanagai, Atka and Amchitka Islands in the State of Alaska	146	SI	Matsumura (1995)
Southampton	Canada	AD 566–1,290	Site of Sadlemit site at Native Point in Southampton Island (Collins, 1956)	194	CMCQ	Matsumura (1995)
Ontario Iroquois	Canada	Modern	Peel Simocoe in Kleinberg Ossuary	272	UTOR	Matsumura (1995)

TABLE 2. Continued

Sample	Locality	Period	Remarks	N[a]	Sample storage[b]	Data published
British Columbians	Canada	c. 500–1,600 AD	Greenville in the State of British Columbia (Cybulski, 1992)	70	CMCQ	Matsumura (1995)
South Dakota	USA	Modern	Site of Arikara in the State of South Dakota	156	SI	Matsumura (1995)
Illinois	USA	Modern	Native Americans in the State of Illinois	163	SI	Matsumura (1995)
California	USA	Modern	Native Americans in the State of California	218	HMUC	Matsumura (1995)
Mexico	Mexico	Modern		69	UPSD	Matsumura (1995)
Peru	Peru	Pre-Inca–Inca c.500 BC–1,400 AD	Sites of Chancay, Pachacamac, Ancon and Paracas	108	MNAP, MAL	Matsumura (1995)

[a] *N*, number of individuals.
[b] Abbreviations of sample storage: see foot notes of Table 1.

TABLE 3. Criteria for the presence in the 21 nonmetric dental characteristics

Trait	Tooth	Description	Criteria	Presence	Remark
Shoveling	UI1, UI2	Hanihara et al. (1970)	Depth of Lingual Fossa (DFL)	DLF >= 0.5mm	(ASUDAS 3–7)
Double shoveling	UI, UI2	Suzuki and Sakai, 1973	-(none), +(weak), ++(moderate), +++(strong)	++, +++	(ASUDAS 3–6)
Dental tubercle	UI, UI2	Turner et al. (1991)	0(none), 1(faint), 2(trace), 3(strong ridging) −6(strong cusp)	3–6	
Spine	UI1	Dahlberg's P-plaque	0(none),1(single), 2(double), 3(triple)	1–3	
Interruption groove	UI2	Turner et al. (1991)	0(none), M(mesial), Med(central),D(distal)	M,D,MD,Med	
Winging (bilateral)	UI1	Enoki and Dahlberg (1958)	0(straight), 1(counter wing), 2(bilateral wing), 3(uni-counter wing), 4(uni-lateral wing)	1	
De Terra's tubercle	UP1	Saheki (1958)	0(none), +(faint ridging), ++(small cusp), +++(large cusp)	++,+++	
Double roots	UP1, UP2	Turner et al. (1991)	1(single), 2(double), 3(triple)	2–3	
Carabelli's trait	UM1	Dahlberg's P-plaque	a(none), b(furrow), c(pit), d(double grooves), e(Y-shape), f(small cusp), g-h(large cusp)	d–h	(ASUDAS 3–7)
Hypocone reduction	UM2	Dahlberg's P-plaque	3(none), 3+(faint cusp), 4-(small cusp), 4-(large cusp) 4(full size cusp)	3 and 3+	(ASUDAS 0–1)
Sixth cusp	LM1	Turner et al. (1991)	0(none), 1(small cusp)- 5(large cusp)	1–5	
Seventh cusp	LM1	Turner et al. (1991)	0(none), 1(faint), 2(small cusp)−4(large cusp)	2–4	
Protostylid	LM1	Dahlberg's P-plaque	0(none), p(pit), 1(curved groove), 2(slight secondary groove), 3(secondary groove)−5(free apex)	3–5	(ASUDAS 5–6)
Deflecting wrinkle	LM1	Turner et al. (1991)	0(none), 1(faint), 2(moderately deflect), 3(L-shape)	2–3	
Groove pattern Y	LM1	Jørgensen (1955)	Y, +, X	Y	
Groove pattern X	LM2	Jørgensen (1955)	Y, +, X	X	
Hypoconulid reduction	LM2	Turner et al. (1991)	4(no hyld), 5(hyld present), 6(6th cup present)	4	

U:Upper, L:Lower, I:Incisor, C:Canine, P:Premolar, M:Molar.
ASUDAS = Arizona State University Dental Anthropology System.

upper lateral incisors, De Terra tubercle of the upper premolars, and the X type groove pattern in the lower second molars all display very low frequencies within the Austro-Melanesian, Andaman/Nicobar, and Early Holocene Southeast Asian samples in comparison to northern populations. Further, the frequency of incisor

TABLE 4. Frequencies of the 21 nonmetric dental traits for comparative population samples (unpublished series)

		Early Viet.and Laos		Early Malay and Flores		Ban Chiang and Ban Na Di		Non Nok Tha		Khok Phanom Di		Ban Non Wat 1		Ban Non Wat 2	
		p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n
Shoveling	UI1	38.7	31	36.1	36	64.9	37	60.6	33	84.2	19	72.9	59	75.0	32
Shoveling	UI2	15.4	26	15.4	26	45.2	42	40.0	25	57.1	21	55.9	68	57.1	28
Double shoveling	UI1	0.0	35	2.8	36	14.0	43	10.8	37	23.8	21	17.3	75	11.6	43
Double shoveling	UI2	0.0	32	0.0	28	4.3	47	3.4	29	13.6	22	1.3	80	5.4	37
Dental tuberculum	UI1	18.8	32	11.4	35	9.1	44	16.7	36	14.3	21	13.8	80	23.8	42
Dental tuberculum	UI2	3.6	28	27.6	29	16.0	50	17.9	28	22.7	22	19.8	86	19.4	36
Spine	UI1	32.3	31	41.2	34	17.9	34	27.3	33	66.7	21	23.5	68	27.0	37
Interruption groove	UI2	7.1	28	11.1	27	35.7	42	17.9	28	50.0	22	36.4	77	28.1	32
Winging (bilateral)	UI1	16.2	37	0.0	15	12.2	41	8.0	25	17.4	23	12.1	66	11.1	27
De Terra's tuberculum	UP1	9.1	44	16.1	31	10.3	29	18.2	22	13.6	22	19.5	41	23.1	26
Double rooted	UP1	69.2	39	61.9	21	54.1	37	55.5	27	24.1	29	33.3	15	53.8	13
Double rooted	UP2	11.1	27	16.7	18	20.0	25	20.0	10	0.0	26	4.2	24	0.0	8
Carabelli's trait	UM1	15.3	59	8.8	34	32.5	40	9.3	43	39.4	33	24.7	77	23.1	39
Hypocone reduction	UM2	33.3	66	10.5	38	7.3	55	10.4	48	7.1	42	7.8	90	11.4	44
Sixth cusp	LM1	5.1	39	32.4	34	16.2	37	14.6	41	26.2	42	31.4	51	13.3	30
Seventh cusp	LM1	7.3	41	5.3	38	6.5	46	15.0	40	2.1	48	11.6	69	8.6	35
Protostylid	LM1	2.1	47	2.8	36	5.4	37	11.6	43	0.0	43	1.9	54	6.5	31
Deflecting wrinkle	LM1	21.1	19	34.8	23	31.0	29	31.6	19	41.9	31	28.9	38	52.2	23
Groove pattern Y	LM1	87.9	33	76.5	34	62.5	32	80.0	35	68.4	38	70.2	47	76.9	26
Groove pattern X	LM2	32.8	58	20.9	43	21.3	47	21.7	46	23.9	46	27.1	59	25.9	27
Hypoconulid reduction	LM2	50.9	53	51.4	35	40.0	40	44.2	43	31.1	45	37.0	54	41.7	24

		Ban Lum Khao		Noen U-Loke		Iron Age Sth. Vietnam		Dong Son		Leang Codong		Anyang		Jundushan	
		p (%)	n	p (%)	n	p(%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n
Shoveling	UI1	52.6	19	82.4	17	73.1	26	61.1	18	86.7	30	86.4	59	87.5	32
Shoveling	UI2	45.0	20	64.3	14	65.5	29	52.4	21	70.3	64	78.1	64	77.1	35
Double shoveling	UI1	18.2	22	22.7	22	25.9	27	37.9	29	29.0	31	14.7	68	35.3	34
Double shoveling	UI2	9.5	21	0.0	18	30.0	30	0.0	28	7.8	64	1.4	71	0.0	35
Dental tuberculum	UI1	0.0	22	19.0	21	30.8	26	7.7	26	10.0	30	5.9	68	8.8	34
Dental tuberculum	UI2	9.1	22	47.1	17	31.0	29	13.8	29	8.2	61	2.9	70	2.9	35
Spine	UI1	14.3	21	33.3	21	69.2	26	17.4	23	20.0	60	23.8	63	18.2	33
Interruption groove	UI2	33.3	21	68.8	16	53.8	26	37.9	29	58.1	31	27.3	66	41.2	34
Winging (bilateral)	UI1	15.8	19	21.4	14	0.0	13	0.0	29	0.0	0	9.2	65	13.6	44
De Terra's tuberculum	UP1	5.9	17	43.8	16	12.1	33	36.7	30	14.4	90	49.0	51	59.3	27
Double rooted	UP1	42.9	14	60.0	10	62.5	16	50.0	16	27.5	40	40.7	27	27.6	29
Double rooted	UP2	9.1	11	0.0	11	0.0	14	0.0	15	24.1	54	4.5	22	3.2	31
Carabelli's trait	UM1	29.2	24	22.2	27	24.4	45	9.8	41	14.7	75	18.3	71	38.2	34
Hypocone reduction	UM2	12.0	25	4.3	23	11.9	42	11.6	43	5.6	90	14.5	76	22.0	41
Sixth cusp	LM1	9.1	22	6.7	15	22.7	44	29.6	27	45.2	84	40.5	37	27.6	29
Seventh cusp	LM1	8.7	23	15.8	19	2.0	51	5.4	37	2.4	84	9.1	44	10.5	38
Protostylid	LM1	5.6	18	6.3	16	12.8	47	2.9	35	3.6	84	2.4	42	8.6	35
Deflecting wrinkle	LM1	6.7	15	50.0	10	28.1	32	30.8	26	32.7	55	26.1	23	25.0	20
Groove pattern Y	LM1	75.0	16	50.0	12	55.0	40	77.8	27	71.4	84	73.5	34	63.6	22
Groove pattern X	LM2	10.5	19	31.6	19	12.2	41	27.5	40	42.0	100	34.1	44	21.2	33
Hypoconulid reduction	LM2	62.5	16	64.7	17	27.5	40	24.4	41	39.0	100	14.0	43	29.4	34

		Andaman and Nicobar		Papua New Guinea		Loyalty		New Britain		Australia		Myanmar		Sunda	
		p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n
Shoveling	UI1	26.7	15	45.5	22	38.9	18	56.0	50	50.0	30	80.0	15	54.5	33
Shoveling	UI2	28.6	21	27.3	44	41.7	24	35.2	71	38.2	34	54.2	24	43.2	37
Double shoveling	UI1	0.0	15	13.0	23	11.1	18	0.0	65	2.9	34	5.9	17	0.0	28
Double shoveling	UI2	0.0	21	0.0	43	4.3	23	0.0	93	0.0	45	3.4	29	0.0	37
Dental tuberculum	UI1	33.3	15	28.6	21	26.3	19	22.7	75	34.4	32	5.9	17	21.1	38
Dental tuberculum	UI2	30.0	20	9.5	42	16.0	25	9.2	98	6.8	44	0.0	26	11.9	42
Spine	UI1	71.4	14	54.5	22	55.6	18	45.2	62	40.0	30	28.6	14	21.2	33

TABLE 4. Continued

		Andaman and Nicobar		Papua New Guinea		Loyalty		New Britain		Australia		Myanmar		Sunda	
		p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n
Interruption groove	UI2	10.0	20	13.2	38	13.0	23	20.7	87	23.7	38	4.3	23	20.5	39
Winging (bilateral)	UI1	15.4	26	14.3	84	11.1	18	20.8	72	12.1	33	3.3	60	12.0	75
De Terra's tuberculum	UP1	7.9	38	9.8	51	12.9	31	8.7	104	12.5	48	29.5	44	15.7	70
Double rooted	UP1	65.7	67	55.2	67	51.9	27	69.0	87	68.4	38	50.7	75	44.2	77
Double rooted	UP2	16.9	59	19.7	66	10.7	28	23.5	81	22.2	27	13.6	66	15.1	73
Carabelli's trait	UM1	16.4	73	27.4	84	14.3	42	24.4	164	16.4	73	20.0	75	32.7	107
Hypocone reduction	UM2	36.8	68	12.5	80	7.3	41	4.3	162	3.6	83	12.5	72	16.3	104
Sixth cusp	LM1	10.8	37	21.1	38	27.6	29	43.7	119	42.0	50	32.0	25	18.8	69
Seventh cusp	LM1	11.4	44	12.2	41	18.8	32	11.5	138	7.4	54	15.6	32	5.5	73
Protostylid	LM1	2.4	41	9.5	42	0.0	33	12.3	138	1.9	53	3.4	29	4.2	71
Deflecting wrinkle	LM1	33.3	27	30.0	30	10.0	30	44.6	92	43.8	32	33.3	21	27.5	51
Groove pattern Y	LM1	83.3	36	77.8	36	64.0	25	88.1	135	78.8	52	73.7	19	68.2	66
groove pattern X	LM2	20.9	43	18.9	37	11.8	34	16.7	156	36.9	65	39.4	33	22.4	85
Hypoconulid reduction	LM2	71.8	39	67.6	37	69.7	33	55.7	140	30.8	65	38.7	31	51.3	80

		Dayak		Philippines		Aeta Negrito		Atayal		Bunun		Hainan	
		p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n	p (%)	n
Shoveling	UI1	80.0	5	84.2	19	66.7	27	79.3	29	85.7	14	85.0	20
Shoveling	UI2	25.0	8	56.5	23	75.0	28	76.2	21	50.0	8	60.0	25
Double shoveling	UI1	0.0	8	21.1	19	0.0	31	22.6	31	26.7	15	20.0	20
Double shoveling	UI2	0.0	10	4.3	23	0.0	31	0.0	21	0.0	9	4.0	25
Dental tuberculum	UI1	0.0	9	26.3	19	12.0	25	29.0	31	14.3	14	5.0	20
Dental tuberculum	UI2	9.1	11	8.3	24	8.0	25	9.5	21	14.3	7	0.0	25
Spine	UI1	25.0	8	33.3	18	37.9	29	70.0	30	7.1	14	15.0	20
Interruption groove	UI2	11.1	9	19.0	21	50.0	30	47.6	21	14.3	7	36.0	25
Winging (bilateral)	UI1	15.4	39	27.8	18	0.0	27	16.1	31	13.3	15	9.1	44
De Terra's tuberculum	UP1	11.4	35	25.0	32	3.3	30	24.5	53	23.3	30	18.3	71
Double rooted	UP1	54.2	72	63.9	36	57.1	7	48.1	52	19.4	36	40.9	93
Double rooted	UP2	12.3	73	8.8	34	16.7	12	17.8	45	2.8	36	6.7	89
Carabelli's trait	UM1	29.4	68	19.5	41	24.3	37	24.6	69	22.2	36	26.7	105
Hypocone reduction	UM2	13.8	65	14.9	47	14.3	28	41.0	61	19.4	31	21.2	104
Sixth cusp	LM1	28.2	39	38.9	18	14.8	27	44.0	50	17.2	29	14.3	77
Seventh cusp	LM1	9.8	41	0.0	20	10.0	30	1.9	52	2.8	36	11.6	86
Protostylid	LM1	4.9	41	14.3	21	6.7	30	9.4	53	8.3	36	1.2	84
Deflecting wrinkle	LM1	22.6	31	25.0	16	14.8	27	15.9	44	7.1	28	18.3	60
Groove pattern Y	LM1	66.7	36	64.3	14	54.2	24	54.9	51	61.3	31	44.4	63
Groove pattern X	LM2	37.8	37	23.8	21	16.1	31	50.0	50	12.9	31	26.8	71
Hypoconulid reduction	LM2	37.8	37	50.0	22	48.1	27	22.4	49	53.3	30	42.1	76

p, frequency of presence, *n*, number of specimens.

dental tubercles is relatively high among early Southeast Asian populations, while somewhat rare in modern Southeast Asians and/or Northeast Asians.

Other traits can be seen to be somewhat regionally specific in terms of trait frequencies. These include winging of the maxillary incisors and deflecting wrinkle in the lower first molars of Native Americans, Carabelli's cusps of the upper first molars among early and modern Southeast Asians, hypocone reduction of the upper second molars among Sub Arctic and Andaman-Nicobar populations and low frequency of the Y-groove pattern in modern Southeast Asian lower first molars. In summary, a comparison of spatial and chronological variability in nonmetric dental traits indicates clearly the close affinities between: (a) early Southeast Asians and Australo-Melanesians; (b) Northeast Asians and Native Americans; and (c) significant dissimilarity between these two identified aggregates.

DISCUSSION

The earliest well-dated AMH in the region occur in Southeast Asia, suggesting initial AMH colonization via India rather than a more northerly and transcontinental dispersal through Siberia. Moreover, these first colonists shared a common ancestry with the earliest settlers of continental Sahul. Indeed, there is a long history of scholarship suggesting morphological similarities, with implied genetic relatedness, between Australian Aborigines, Melanesians, and pre-Neolithic samples in Southeast Asia (e.g., Tabon in Philippines; and Niah, Gua Cha, Guar Kepha, and Gua Kerbau in Malaysia), particularly with respect to dolichocrany with protruding glabellae, massive jaws with relatively large teeth, alveolar prognathism, and long slender limbs (e.g., Evans, 1918; Duckworth, 1934; Mijsberg, 1940; Trevor and Brothwell, 1962; Macintosh, 1978). More recent studies, based on

Fig. 2. An unrooted neighbor-joining (NJ) tree analysis applied to the Smith's mean measure of divergence matrix based on a battery of 21 nonmetric dental traits. Italicized samples are from Southeast Asia Symbols (see dialog box in Figure 1).

the morphological analysis of new skeletal discoveries from a number of Hoabinhian sites, also support this scenario (e.g., Gua Gunung Runtuh, Moh Khiew, and Hang Cho sites: see Matsumura, 2006; Matsumura et al., 2011). The current analysis of a more extensive dental dataset finds further support for close affinities between early Southeast Asians, including Hoabinhian/Mesolithic samples, and Australian and Melanesian groups, as well as Andaman and Nicobar Islanders. These observed close phenetic affinities, linking the inhabitants of Sahul, early Southeast Asia and the Eastern Indian islands, are consistent with a scenario of migrants who may have dispersed out of Africa along the southern rim of the Eurasian continent through South and Southeast Asia.

Modeling the population history of the region

Perhaps the most critical issue in understanding the population history of East/Southeast Asia involves clarifying the genealogical relationships between current populations and samples representative of the earlier occupants of the region. In this context two models, using skeletal and/or dental morphology or genetic approaches, have traditionally been applied. These include the two-layer model and the regional continuity model. Proponents of the two-layer model advocate an initial AMH colonization (first layer) of Southeast Asia by populations akin to Australo-Melanesians. Subsequent demic expansion into Southeast Asia (second layer) originating in Northeast Asia led to migration into the region and genetic exchange with local indigenous populations, the descendants of the first colonizers of the region, ultimately leading to the morphological and genetic makeup of present day Southeast Asian populations (Coon, 1962; Jacob, 1967). The two-layer model is strongly corroborated by both linguistic and archaeological evidence (Blust, 1977; Glover and Higham, 1996; Bellwood, 1997, 2005; Higham, 1998, 2001; Bellwood and Renfrew, 2003; Diamond and Bellwood, 2003; Sagart, 2008; Zhang and Hung, 2010).

While the two-layer model is quite robust and supported by multiple lines of evidence, issues remain with respect to the timing, source, and scale of the demic expansion (second layer). Some genetic and skeletal studies estimate the scale of gene flow due to agriculturally driven population movement to be negligible, resulting in a scenario that differs little from the regional continuity model, in which all modern populations, both in East and Southeast Asia, are the result of longstanding evolutionary continuity within each region without significant, if any, genetic interaction with each other, or with populations in other adjacent regions (Turner, 1990; Hanihara, 2006; Pietrusewsky, 2010). This model
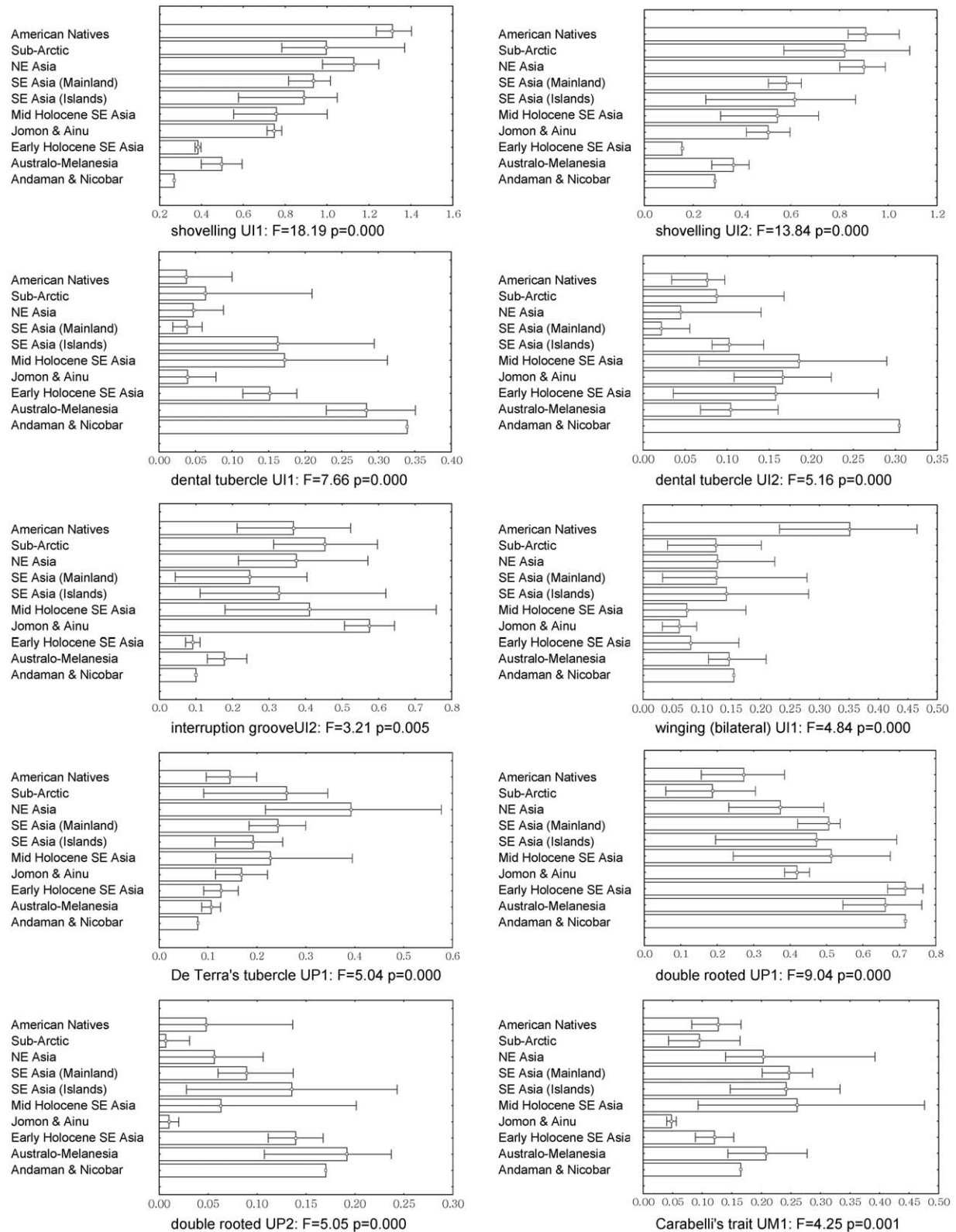
Fig. 3. Arcsine transformed frequencies of nonmetric dental traits with significant geographic clines or anomalies. *F*-values and probabilities calculated using ANOVAs for significances of regional variances. NE: Northeast, SE: Southeast, Early Holocene SE Asia combines all the pre-Neolithic samples including Mesolithic/Hoabinhian series, Mid Holocene SE Asia combines Neolithic/Metal Age samples.
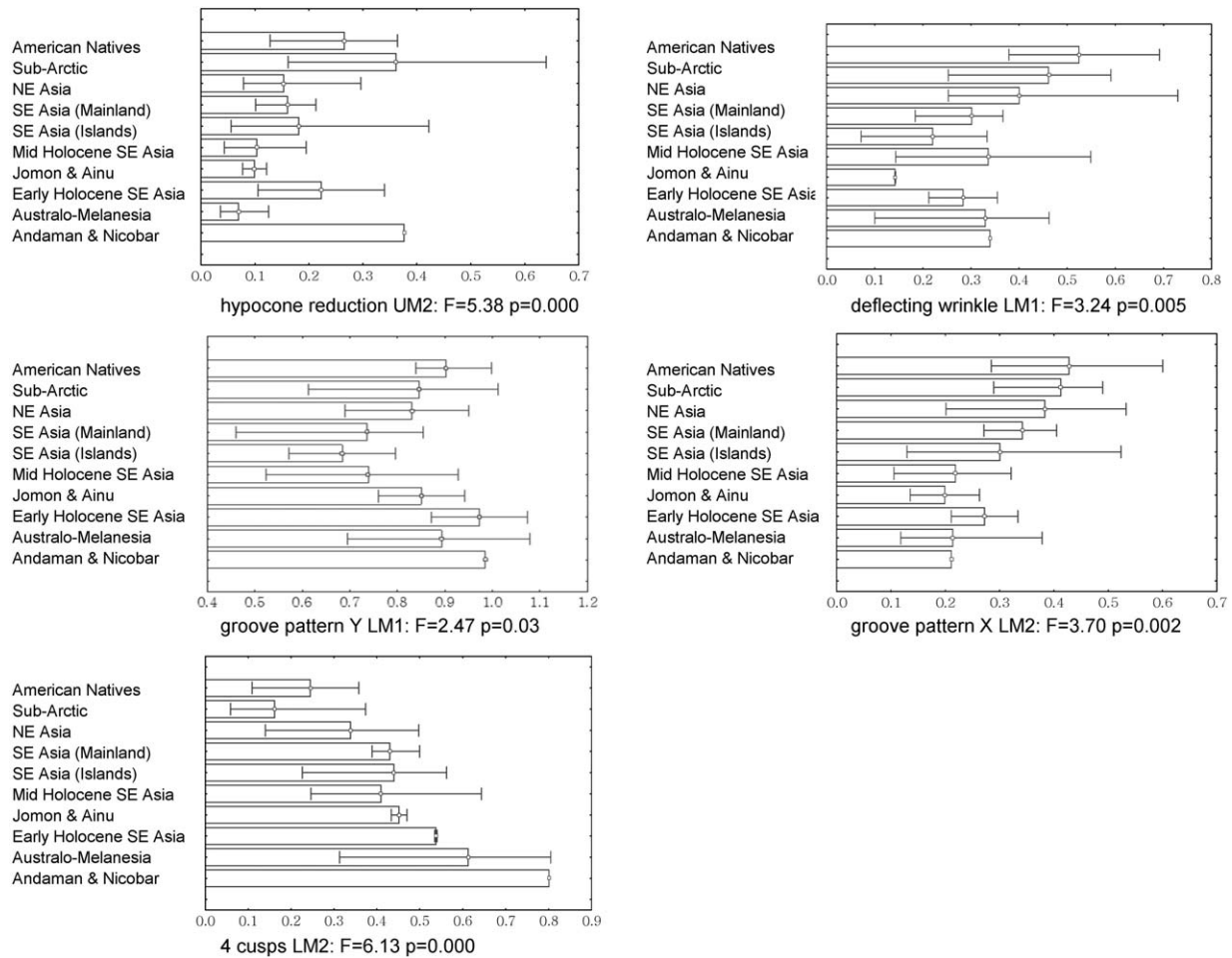
Fig. 3. (Continued)

has recently received further support from broad-stroke genetic approaches (e.g., Hill et al., 2007; Soares et al., 2008; Tabbada et al., 2010, Y-chromosome: Capelli et al., 2001; HUGO Pan-Asian SNP Consortium, 2009).

Fundamental problems with the regional continuity model are twofold. The first problem is the fact that much of its ostensible support derives from present-day population sample datasets. The second problem is a lack of samples dating prior to the agriculturally driven population dispersals of the Neolithic. One of the significant advances in this study is the inclusion of dental datasets spanning the pre-Neolithic (Hoabinhian/Mesolithic) through Neolithic and into the early Metal Age periods. Our own results show that there is a discontinuity in dental morphology between pre-Neolithic samples and the majority of later period samples, including both the Neolithic and the Bronze Age. Nonetheless, some later samples do not clearly separate from earlier populations, with Iron Age Phum Snay from Cambodia and contemporary Tanegashima Yayoi from Japan being clear examples. The most marked differences are seen when comparing Neolithic and post-Neolithic Vietnamese samples to pre-Neolithic (Late Pleistocene/early to mid-Holocene) samples from Vietnam. The close dental affinities of the vast majority of Neolithic/Bronze-Iron Age samples to present day East Asians (see Fig. 2) indicates intense levels of agriculturally driven demic expansion into

northern Vietnam since the beginning of the Neolithic (e.g., Man Bac), with source populations located somewhere in what is now geographically defined as China. This finding is corroborted by craniometric analyses using the same samples (Matsumura et al., 2011).

When examining other samples in mainland Southeast Asia, the NJ tree shows a clinal pattern in the degree of demic diffusion. Inferred gene flow gradually extends into the western inland parts of the region with significantly less evidence for genetic diffusion into northeast Thailand (e.g., Ban Chiang, Ban Na Di, Non Nok Tha, and Ban Lum Khao) relative to what is seen in northern Vietnam. This pattern is potentially explained by topography, for the northeast Khorat plateau is bordered by a series of rugged mountain ranges (Phetchabun and Dong Phaya Yen to the west and Annamese Cordillera to the north and east), that likely imposed significant topographic barriers, in contrast to the topographical ease of movement between southern China and northern Vietnam. Nevertheless, Ban Chiang cranial morphology is similar to that of Northeast Asians, suggesting a measurable degree of gene flow from the north. Indeed, later Iron Age inhabitants of this area, such as Noen U-Loke and Ban Non Wat 2, also display a shift to East/Northeast Asian dental morphology—a shift implying gradual gene flow into this area that stands in marked contrast to the rapid influx of East/Northeast Asian genes seen in Neolithic and post-Neolithic samples from northern Vietnam

TABLE 5. Results of post hoc multiple comparison test for ANOVAs of Figure 3, based on Tukey–Kramer method

Nonmetric toothtrait	Significantly diffrencial population from the major groups of East/Southeast Asia	Early Holocene Southeast Asia	Middle Holocene Southeast Asia	Island Southeast Asia	Mainland Southeast Asia	Northeast Asia
Shoveling UI1	Australo–Melanesia			**	**	**
	Mid Holocene SE Asia	*				**
	Island SE Asia	**				*
	NE Asia	**				
	American Natives	**	**	**	**	
Shoveling UI2	Australo–Melanesia					**
	Early Holocene SE Asia		*	**	*	**
	Mid Holocene SE Asia					**
	Island SE Asia					**
	Mainland SE Asia					**
	Sub-Arctic	**	**			
Double roots UP1	Australo–Melanesia					**
	NE Asia	*				
	Sub-Arctic	**	**	**	**	
	American Natives	**	*			
Dental tubercle UI1	Australo–Melanesia				**	**
	Mid Holocene SE Asia				*	**
	Island SE Asia					*
	American Natives		*			
4 Cusps LM2 (hypoconulid reduction)	Sub-Arctic	*	**	**	*	
	American Natives		*			
Hypocone reduction UM2	Sub-Arctic		**	*	*	**
Dental tubercle UI2	Mid Holocene SE Asia			*	**	**
	Sub-Arctic		*			
Double roots UP2	Australo–Melanesia		**			**
	Sub-Arctic			**		
De Terra's tubercle UP1	NE Asia	*	**	**		
Winging (bilateral) UI1	American Natives	**	**	**	**	**
Carabelli's trait UM1	Sub-Arctic		**	*		
	American Natives		*			
Groove pattern X LM2	Mid Holocene SE Asia					*
	Sub-Arctic		**			
	American Natives		*			
Deflecting wrinkle LM1	Sub-Arctic				*	
	American Natives				**	

Sequence of nonmetric tooth traits are in descending order of *F* value given in Figure 3 (significantly nondiffrencial tarits from Asian samples are not given in this table).

Asterisk mark is probability of Tukey–Kramer test: * significant at 5% level, ** 1% level.

Thailand is not solely characterized by gradual morphological and genetic transformation, for the earliest Neolithic sample from Thailand, Khok Phanom Di, shows evidence of Northeast Asian genetic influences. The site of Khok Phanom Di was colonized by the 18th or 19th century BCE (Higham and Thosarat, 2004; Higham et al., 2011) and is similar, in terms of technology and subsistence orientation, to other coastal Neolithic sites, such as Man Bac (Oxenham et al., 2011), that while displaying evidence for farming and extensive regional trade networks, also engaged intensively in marine foraging activities. The most parsimonious explanation for the phenetic affinities between Khok Phanom Di and East/Northeast Asian dental samples is that Khok Phanom Di represents the results of an early coastally mobile population that quickly tracked down the eastern seaboard of Southeast Asia, settled and intermixed with local indigenous peoples in the sheltered Gulf of Siam.

Metal age mobility

As the example of Khok Phanom Di suggests, the movement of people, genes, language and culture could just as readily use sea lanes as land routes. Indeed, a South China Sea interaction zone stretching from coastal Vietnam southward of Hue in the west to northern Borneo in the south, the central Philippines in the east, and as far north as Taiwan came into existence from at least 500 BCE (Solheim, 1959, 1964, 2006; Hung et al., 2013). The Vietnam Iron Age sample in this study comprises series from the ostensibly Sa Huynh site of Hoa Diem and Giong Co Vo in the Mekong Delta, sites with extensive evidence for interaction with contemporaneous communities in the central Philippines (Yamagata and Hoang, 2013, Hung et al., 2013). The very close affinity seen between the Philippine and Vietnamese Iron Age dental series in this study are consistent with the archaeological evidence for extensive maritime trade networks linking these geographically discontinuous areas, as well as arguments for the early establishment of Chamic languages in Vietnam being sourced from Austronesian speaking migrants (Hung et al., 2013). Furthermore, close affinities between the Leang Codong sample and other mainland Southeast Asian series, including Iron Age Vietnam, is not unexpected given the southeastern most extent of the South China Sea interaction sphere includes Sulawesi in the Indonesian archipelago (Hung et al., 2013).
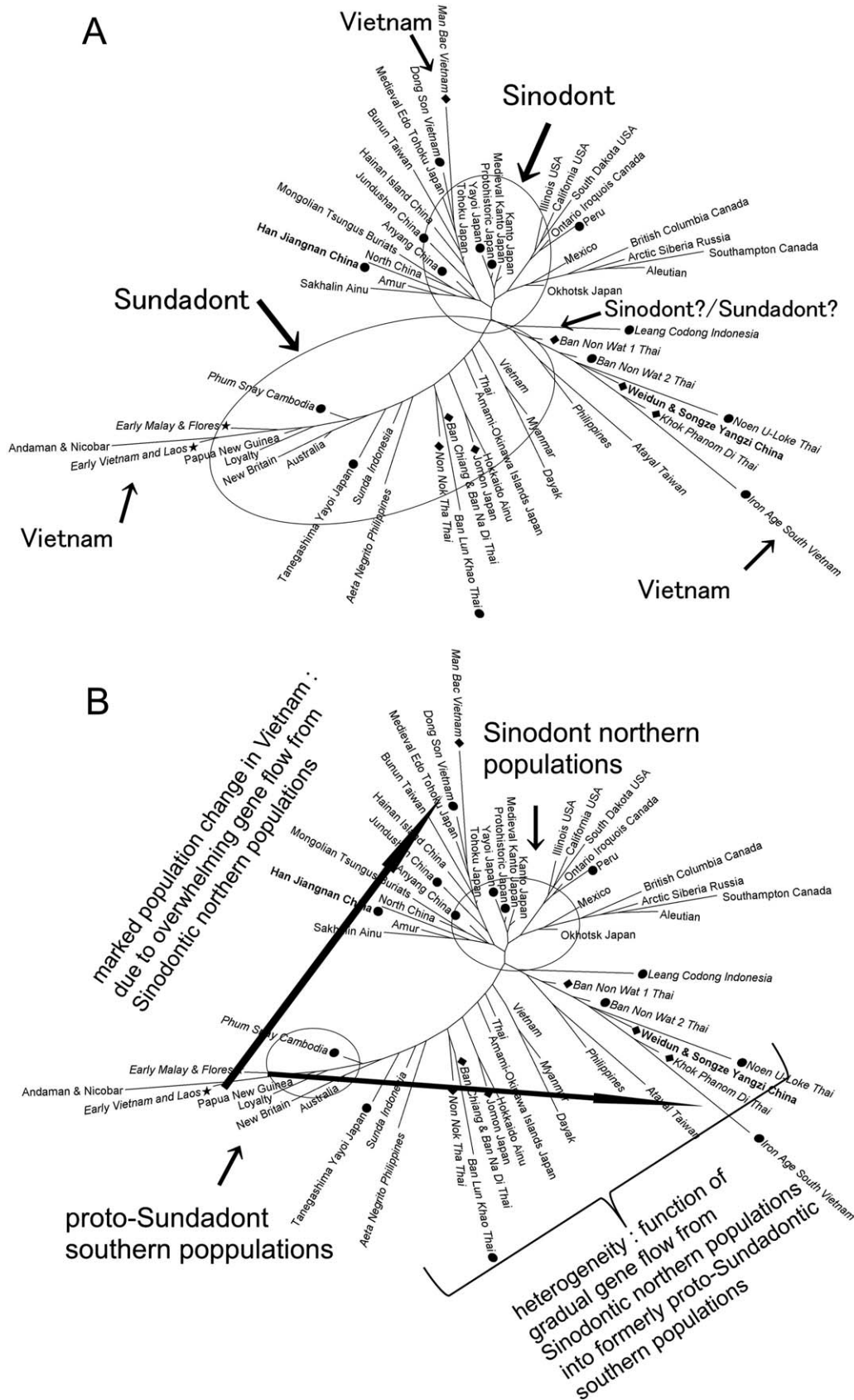
Fig. 4. Interpretations of population aggregations of NJ tree depicted in Figure 2. **A**: Regional continuity model. **B**: Two layer model.

In terms of land routes, the very strong affinities between both Neolithic (e.g., Man Bac) and Bronze/Iron Age (e.g., Dong Son) populations in northern Vietnam to Northeast Asian series attests to the immediate effects of agriculturally driven demic diffusion in this region (see Oxenham and Matsumura, 2011). By contrast, Iron Age sites, such as Phum Snay further to the south in Cambodia and Tanegashima Yayoi in southern Japan, represent areas located on the periphery of the major avenues of population movement during the Neolithic and subsequent Metal Ages, thereby explaining their much closer affinities to the original Australo-Melanesian colonists of the region.

The two-layer model

Proponents of the "two-layer" model advocate large-scale agriculturally driven demographic expansion coupled with subsequent admixture with local indigenous populations in Southeast Asia. By contrast, proponents of the "regional continuity" model argue that modern Southeast Asian populations are the product of long-standing continuity withoutany significant gene flow from outside. As mentioned previously, Turner's (1987, 1990) Sundadont/Sinodont hypothesis uses dental nonmetric traits to support the "regional continuity" model. Given the overlap in dental traits and samples used by both Turner and this study, it is fair to question the very different conclusions drawn from these data. There are two fundamental issues to consider here: (1) the distribution of samples with respect to relative Sundadonty and Sinodonty, and what this means and (2) the timing and speed of dental change seen in the region.

With respect to the first issue, our interpretation of the pattern of dental nonmetric trait frequencies is based on the manner in which these samples aggregate (see Fig. 4). An initial impression of sample aggregations depicted in Figure 4A tends to support Turner's original Sinodont/Sundadont dichotomy. However, a closer examination reveals that most modern Southeast Asian samples actually occupy an intermediate position between East Asians, found at the top of the figure, and early Southeast Asians and Australo-Melanesians who occupy positions at the bottom. Indeed, it is difficult to draw a definitive boundary between clearly Sinodontic and Sundadontic samples. For instance, an ambiguous subcluster, at least in terms of Sinodonty/Sundadonty, is formed by several prehistoric samples (Ban Non Wat, Noen U-Loke, Iron Age Southern Vietnam, Weidun and Songze Chinese) and, with such a simplistic scenario, Vietnamese samples occupy a disquieting trio of markedly divergent positions within the array of samples. However, an alternative interpretation of these aggregates is shown in Figure 4B. In this instance, arrays of nonmetric dental traits observed in early Southeast Asians and Australo-Melanesians can be interpreted as a "proto-Sundadont" dental complex, identified to the bottom left of the figure, while the array of dental traits found for modern Southeast Asians, so far referred to as "Sundadont" populations, can be seen as the result of differential admixture between the proto-Sundadont and Sinodont complexes.

Proponents of the regional continuity model interpret the considerable genetic variability characterizing Southeast Asian populations as a product of a deep genetic history that facilitated regional divergence and microevolutionary change. This brings us to the second issue: timing and speed of change. Differential levels of phenetic, and by proxy genetic, heterogeneity in a range of prehistoric Southeast Asian samples has been dealt with previously, with a combination of differential levels of contact somewhat moderated by topography suggested as an explanatory model. Moreover, the situation seen at both Neolithic Man Bac in northern Vietnam and Neolithic Khok Phanom Di in coastal Thailand, can only be interpreted within the context of the two-layer model. There is a fundamental and rapid change in population makeup between the early Vietnamese samples and Neolithic (Man Bac) and later (e.g., Dong Son) samples in northern Vietnam. Prior to Man Bac there is no evidence in Vietnam, or Southeast Asia for that matter, of either Sinodont or Sinodont-Sundadont hybrid populations. The change seen at Man Bac is so rapid as to reasonably exclude the possibility of a significant role for the regional continuity model. Contemporary with Man Bac, Neolithic Khok Phanom Di is placed quite close to the Sinodont array (Fig. 4B), but still clearly demonstrates a mixture of Sundadonty and Sinodonty. As with Man Bac, there is no evidence in Thailand for any pre-Neolithic Sinodont populations. The only reasonable conclusion is that the dental makeup of Khok Phanom Di was significantly influenced by genetic input from Northeast Asian populations, with no evidence for continued long-standing regional continuity.

It is clear that Southeast Asian genetic heterogeneity can more parsimoniously be seen as a result of differential genetic input from East/Northeast Asian population flows into the region on the back of agriculturally driven demic expansion. Moreover, this study clearly shows a great deal of shared genetic heritage, assessed by way of nonmetric dental traits, between East Asian and Southeast Asian populations. The differential contribution, often clinal in nature, of East Asian genes into Southeast Asia is readily explained by the speed and direction of demic diffusion, which in turn appears contingent on the nature of the geographic barriers and the distance separating local Southeast Asian populations from the dispersing East/Northeast Asian source populations. Such an observed pattern is not, and cannot be, accounted for by the regional continuity model.

A range of genetic studies provide further support for the two-layer model. For instance mtDNA sequences suggest Taiwan aborigines have temporally deep roots, likely in central or south China (Melton et al., 1998) while other mtDNA, single nucleotide polymorphism and classic genetic marker research (e.g., Ballinger et al., 1992; Cavalli-Sforza et al., 1994; Ding et al., 2000; Tan, 2001; Cox, 2013) demonstrate very close biological relationships between Chinese and Southeast Asian samples, findings which also suggest significant gene flow from north to south across the region. Cox et al. (2010, 2013) have also found a significant genetic cline across Island Southeast Asia and the Pacific, traced back to incoming populations from mainland Asia. They go on to conclude that the phenotypic gradient likely reflects mixing of two long-separated ancestral source populations; one descended from the initial Melanesian-like inhabitants of the region, and the other related to Asian groups that immigrated during the Neolithic. Unfortunately, our dental study lacks data on Neolithic samples from insular Southeast Asia, although phenotypic variation observed among the present-day Islander samples accords with the aforementioned model.

Somewhat analogous to the case of Southeast Asia is the demic expansion of East Asian agriculturalists into

the Japanese archipelago, where a number of studies have demonstrated a rapid population transition and associated large-scale genetic exchange with pre-existing hunter-gatherer populations (Jomon) (Hanihara, 1991). In the Japanese archipelago, by far the most gene flow occurred with the Yayoi migrations from the East Asian continent, associated with a spread of rice cultivation from about 850 BCE onward.

CONCLUSIONS

The chief objective of this study was to explore the nonmetric dental trait evidence for the population history of East and Southeast Asia and, more specifically, to test the two-layer hypothesis for the peopling of Southeast Asia. The use of NJ trees to visually depict the complex nonmetric dental trait, and by implication genetic, affinities of 7,247 individuals from 58 samples, including representative East and Southeast Asian populations spanning the late Pleistocene through to modern period, has been shown to have great value. Indeed, this tree shows a significant dichotomization of the dataset into an early Southeast Asian sample with close affinities to modern Australian and Melanesian populations on the one hand, and a very separate and distinct grouping of ancient and modern Northeast Asians on the other.

Beginning in the Neolithic, samples are distributed in a clinal fashion between the chief two morphological arrays. Assuming these clines are ultimately a function of agriculturally driven demic expansion and diffusion into Mainland and Island Southeast Asia, for which there is a wealth of supportive archaeological and linguistic evidence, the observed patterns are readily explained. For instance, very close affinities beginning in the Neolithic and extending into the Metal Ages between northern Vietnamese and Northeast Asian samples are a function of the immediate and direct effects of this demic diffusion originating from what is now southern China. The much lower rate of genetic diffusion seen in mountainously circumscribed early Thai samples on the Khorat plateau, followed by increasing levels of affinity with Northeast Asian series in the Iron Age in the same area, indicates initial partial isolation during the Neolithic and subsequent increased contact with migrating populations in the Metal Ages.

There is also a clinal pattern with respect to coastal populations. One of the earliest Neolithic samples in Thailand, Khok Phanom Di on the Gulf of Siam, shows considerable Northeast Asian genetic input from the outset. The presence of a South China Sea interaction sphere from at least as early as 500 BCE, but likely extending back to the Neolithic, facilitated the movement of genes as well as other traded goods, thus explaining the elevated level of Northeast Asian genes into these communities.

This research not only demonstrates clinally patterned variation in the distribution of nonmetric dental traits in North and Southeast Asia, it also provides archaeologically, linguistically and genetically attested models of human movement from the Neolithic through to the Metal Ages in the region explaining these patterns. Local or regional models of evolutionary continuity fail to address the complexity of the clinal variation seen in Island and Mainland Southeast Asia. The archaeological, linguistic and now dental data is clear, the origins of modern Southeast Asian populations are to be found in a complex interplay between local indigenous populations with extremely deep historical roots and multiple and multidirectional movements of new migrants, ultimately originating from amongst the first agricultural populations of what is now central China.

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