PERIODICUM BIOLOGORUM
VOL. 108, No 3, 365–371, 2006

UDC 57:61
CODEN PDBIAD
ISSN 0031-5362

Original scientific paper

A Multivariate Analysis of the Ontogeny of the Scapular Axillary Border

AMANDA M. BUSBY

Department of Anthropology
MSC 01-1040
University of New Mexico
Albuquerque, NM 87131
USA
E-mail: mbusby@unm.edu

Key words: Krapina, Neandertals, scapula, axillary border, sulcus

Received April 27, 2006.

Abstract

The axillary border of the scapula has long been a subject of interest to students of human evolution. The form of the axillary border varies in australopithecines, Homo erectus*, Neandertals, and early modern humans. These differences may be the result of genetic discontinuities or of biomechanical differences. The ontogeny of the axillary border was examined in order to determine the similarities and differences between Neandertals and recent humans at early ages. These groups exhibit similarities in development, but there are also differences from an early age. Because various patterns of axillary border morphology are present in different groups, this feature may not be useful as taxonomic tool, but further study may reveal additional patterns.*

INTRODUCTION

The presence of a dorsally placed sulcus on the axillary border of the scapula has typically been associated with Neandertal morphology, so much so that Stringer *et al.* *(1)* identified it as an autapomophic feature of these Late Pleistocene populations. However, the dorsal pattern of sulcus formation occurs in the Middle Paleolithic *(2)*, throughout the Upper Paleolithic and, in deceasing frequency, into Mesolithic and modern times *(3)*. The axillary border sulcus has typically been classified into three patterns, dorsal, ventral, and intermediate or bisulcate. Statistically, the dorsal pattern occurs most often in Neandertals, the ventral pattern occurs most often in more recent humans, and the bisulcate pattern occurs in both groups *(3–5)*. However, recent studies show that the dorsal pattern can occur in a high frequency in some modern human populations *(6, 7)*. As a result, the phylogenetic significance of this feature is ambiguous. Speculation has surrounded the issue of whether axillary border morphology is genetically controlled, influenced by biomechanical loading, or both *(8)*. The aim of this research was to determine the ontogenetic development of the axillary border and to examine similarities and differences in Neandertals and more recent humans.

BACKGROUND

A number of authors have focused on axillary border morphology, particularly the peculiarities of the Neandertal forms. Stewart's *(9)* review is still the most comprehensive synthesis of the literature on scapular studies. Marcellin Boule was the first to bring attention to the scapular axillary border morphology in Neandertals and described the remains of both the La Chapelle-aux-Saints and La Ferrassie I Neandertals. Gorjanović-Kramberger *(10)* followed with a detailed examination of twelve of the Krapina hominid scapulae, whose morphology he separated into three groups or patterns. Gorjanović-Kramberger *(11)* later added the remaining Krapina scapulae to his sample. McCown and Keith *(12)* contributed by describing the Mount Carmel remains, including Tabun I and Skuhl IV, V, and IX. Tabun I exhibits a dorsal sulcus; the Skuhl individuals show the bisulcate pattern.

In the last forty years, additional studies have expanded our understanding of axillary border form. The Shanidar Neandertals 1,2 and 4 possess the dorsal pattern, while Shandiar 3 exhibits the bisulcate pattern *(4)*. Smith *(13)* reviewed the upper limb remains from Krapina and concluded that while the axillary border morphology is difficult to determine in the Krapina juveniles, and is equally difficult to determine in modern human juveniles. A study of the Kebara 2 scapula by Odwak *(7)* suggested that the bisulcate pattern is actually more robust than the dorsal pattern. Odwak also suggested that because the dorsal pattern is only found in 59% of Neandertals and can be found in modern populations, axillary border morphology may be determined by individual upper limb activities rather than by genes. Dittner *(14, 15)* researched morphological changes on the axillary border and concluded that alterations in other regions of the shoulder (namely a flattening of the thorax and a laterally shifted humeral head), along with technological advances, may have produced changes in the morphology of the axillary border. Interestingly, Dittner *(14)* determined that the frequency of bisulcate borders in modern humans increased with age. More information has also become available for other Middle Paleolithic human remains from the Sima de los Huesos site. Carretero *et al. (2)* reported that all four of the scapulae from their site possess the dorsal sulcus morphology.

Of the literature reviewed, only Gorjanović-Kramberger *(10, 11)* and Smith *(13)* have discussed the axillary border morphology of juvenile individuals. This is primarily because their work focused on the Krapina Neandertal sample which includes six juvenile scapulae. The Krapina remains are the largest sample of Neandertal specimens from a single locality (Smith, *16*) and are thus an invaluable research tool. The number of juvenile remains from this site also aid in our understanding of Neandertal ontogeny.

MATERIALS & METHODS

Lieberman *(17)* suggested that ontogeny is crucial to interpreting morphology. Determining if a trait is in fact the product of several more discrete characters may be understood through studies of ontogeny. As a result, this study focused on several characters of the axillary border to determine if these could be discrete characters ultimately forming the axillary border. These traits include the infraglenoid tubercle, the axillary border crest, the axillary border buttress, the axillary border sulcus, and the degree of rugosity on the border itself. These traits are illustrated on an adult scapula in Figure 1.

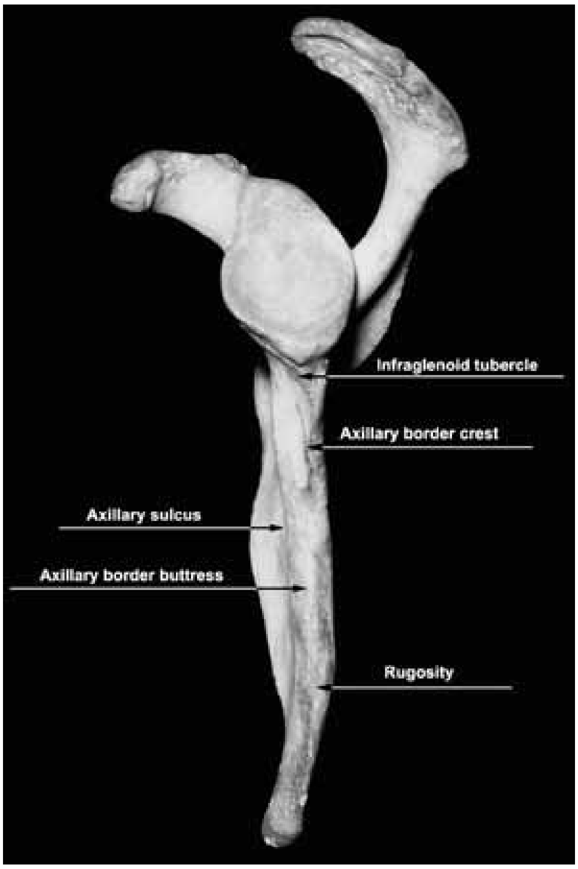

Figure 1. *The traits studied on the axillary border of the scapula.*

Notably, the scapula in general and the axillary border in particular are not strongly delineated features of the juvenile postcranial skeleton. Depending on age, the scapula is easily distinguished from other bones, but many of its morphological features are indistinct. In an effort to distinguish developmental stages in the axillary border in juveniles a scoring system was developed. The stages were determined as 0, not developed; 1, moderately developed; and 2, developed. These degrees of development are scored according to both visible and palpable assessment of the axillary border. Each of the five traits were treated independently and scored individually. A trait with no perceptible features is scored as 0, a trait with palpable features, but no visible features is scored as 1, and a trait with palpable and visible features is scored as 2. In the case of missing data, as many traits as possible were scored, missing values were not estimated. The samples included in this study are as follows, the Krapina Neandertal Collection, a pooled sample of white and black children from the Hamann-Todd Osteological Collection (Ohio), and a collection of Southeastern Mississippian-era Native Americans (Tennessee). The age of the Krapina Neandertals is unknown; recent human ages were assessed with standard methods from other portions of the skeleton and dentition *(18)*.

The presnt study investigates three mutually exclusive predictions about the patterns of development of the features of the axillary border. First, that the five features would develop at the same rate in modern humans and Neandertals. Second, that the five features would develop at different rates in modern humans and Neandertals. Third, that the five features would develop at different rates initially in the two groups, but have similar subsequent rates of development.

RESULTS

From the scores for each of the five traits, a total development score was created for each individual. These summed scores were plotted against age to assess how development varied across groups. Figure 2 shows a roughly linear positive correlation between the total development score and age. Several individuals fall below the average total development score for their age group, a likely result of individual variation in development in modern human children. Development stages can be difficult to assess because of the variability in childhood growth *(19)*. The majority of these individuals are from the Hamann-Todd Collection, however, and many of them died from diseases during childhood. Disease processes could certainly have had an impact on these individuals' growth and development *(20)*.

The variation of each age group can also be readily seen in Figure 2. The total development score for individuals within a certain age can be quite variable. For example, at age 3, individuals ranged from 0 to 3 for their total development score. At age 14, individuals ranged from 4 to 8 for total development. The Neandertals are placed on the same graph for comparative purposes only and are identified by their Krapina catalog numbers. The ages for these individuals are unknown, but an attempt to place these individuals within the same developmental framework as the modern human juveniles was attempted and will be discussed below. The three individuals in Figure 2 with a box surrounding their scores are individuals for whom one trait was not scored because of preservation. Each of these individuals is represented by three possible scores, which indicate the possibilty that their missing trait had a score of 0, 1, or 2.

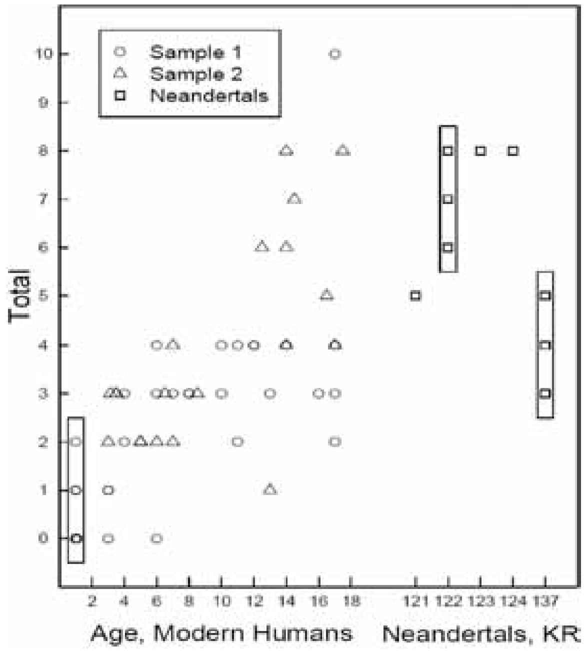

Figure 2. *Total development score for all five features versus age. The samples are: 1, Hamann-Todd; 2, Mississippian Native Americans; Neandertals are all Krapina specimens.*

A Spearman Correlation matrix (Table 1) was produced to examine relationships between these five discrete traits. From the correlation matrix, the following traits show interesting results. The axillary border buttress (x3) is relatively correlated with all other traits, while the level of rugosity on the border (x4) is not strongly correlated with any other trait. The axillary border buttress (x3) is particularly correlated with the infraglenoid tubercle (x1) and the axillary border sulcus (x5) is correlated to a lesser degree with both the axillary border crest (x2) and the axillary border buttress (x3). The axillary border crest and the axillary border buttress are often used to define the presence of the axillary border sulcus itself *(13)*. Thus, the correlation between the two is not surprising.

Logistic regressions were also calculated on the modern human samples to determine the likelihood of a trait

TABLE 1

Spearman Correlation Matrix for the five features of the axillary border.

Spearman (rank) Correlation Matrix for the five traits					
	x1	x2	x3	x4	x5
x1	1.0000000	0.4262931	0.6309301	0.2605091	0.5005893
x2	0.4262931	1.0000000	0.4359021	0.2943639	0.5922664
x3	0.6309301	0.4359021	1.0000000	0.5040576	0.5578880
x4	0.2605091	0.2943639	0.5040576	1.0000000	0.2436286
x5	0.5005893	0.5922664	0.5578880	0.2436286	1.0000000

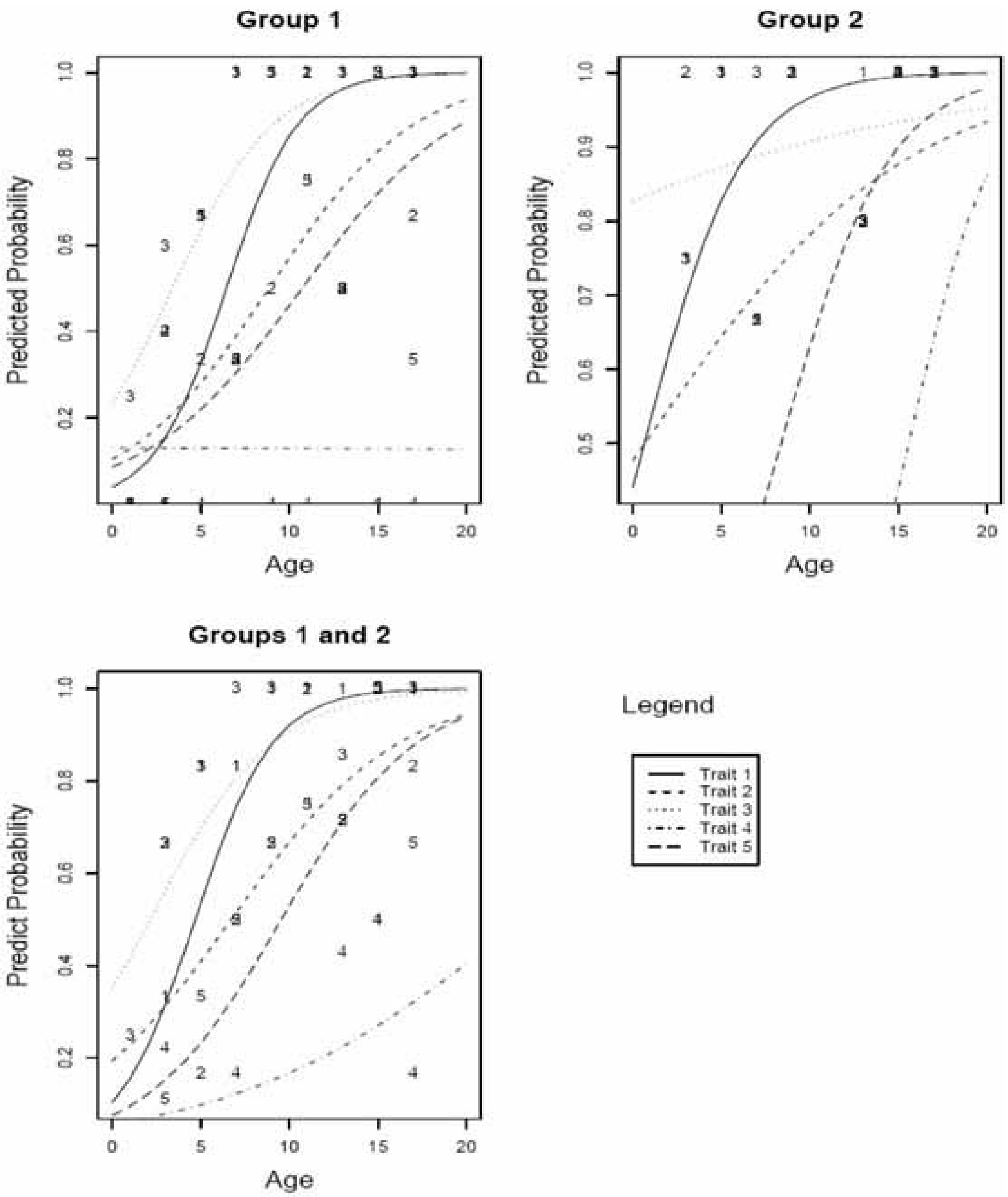

Figure 3. *Logistic regression of presence of axillary border features versus age. Trait 1 = infraglenoid tubercle; Trait 2 = axillary border crest; Trait 3, axillary border buttress; Trait 4 = degree of rugosity; Trait 5 = axillary border sulcus.*

being developed as a function of age. Figure 3 illustrates that these features develop at different rates.

Regardless of age, the axillary border buttress had the highest probability of being developed. The infraglenoid tubercle, the axillary border crest and the axillary border sulcus develop next and roughly in tandem with one another. The rugosity of the border had the lowest probability of being present regardless of age. In both groups of recent humans, the order of development is similar. In the Krapina Neandertals, which cannot be included in the logistic regressions because of their unknown age, a similar development pattern emerged.

The five features of the axillary border develop in a stepwise fashion in modern humans. From this, one can create a framework of developmental stages for the axillary border. The skeletal changes on the axillary border occur discreetly and vary greatly. The developmental framework, therefore, serves as a general guide to the skeletal changes on the axillary border and describes the typical age range when these changes occur. With the modern human framework in place, an effort was made to match the Krapina Neandertal juveniles with a developmental stage developed for the modern humans. While this does not suggest an exact age for any of the Krapina Neandertal juveniles, it does allow a general pattern for

TABLE 2.

Developmental Stages of the Axillary Border.

Developmental Stage	Age Range	Skeletal Changes
Early Childhood	3 to 4 years	• Early development of the axillary border buttress. • Early rugosity present.
Middle Childhood	6 to 8 years	• Axillary border buttress is consistently palpably present. • Early development of the axillary border crest. • Infraglenoid tubercle beginning to develop. • Early development of the axillary border sulcus.
Late Childhood to Juvenile	8 to 10 years	• Infraglenoid tubercle is visibly present. • Rugosity increasing along border. • Sulcus development continuing, but varies greatly.
Juvenile to Early Adolescence	10 to 14 years	• Axillary border buttress is consistently visibly present. • Axillary border sulcus is consistently visibly present.
Adolescence to Maturity	14 to 17 years	• Infraglenoid tubercle is approaching adult morphology. • Axillary border sulcus consistent with adult morphology.

these individuals to emerge. In Table 2, the stages of developmental follow Bogin's *(21)* general guide to childhood development, the age at which those stages generally occur, and the specific skeletal changes that occur on the axillary border of the scapula. Each of the Krapina Neandertal juveniles is then placed, as far as possible, into to a specific odevelopmental stage.

Krapina 121 is a right scapula with the glenoid and coracoid epiphyses not fused. The axillary border of the scapula is well rounded, with axillary border buttressing developed on the dorsal surface and moderately developed on the ventral surface. Similar development is seen in modern subadults during the Middle Childhood stage. The axillary border crest is not developed in this individual. The infraglenoid tubercle is beginning to develop and is palpably present as well as somewhat visibly present, consistent with the Middle Childhood stage of development. The axillary border sulcus is palpable on the dorsal surface of the border and is typical of the pseudosulcus that Gorjanović-Kramberger *(10)* described. If a modern human pattern of development holds for Neandertals, this individual would be placed in the Middle Childhood stage at six to eight years of age.

Krapina 122 is a right scapula with the glenoid and coracoid epiphyses not fused. The axillary border buttress is only moderately developed on the dorsal surface of the scapula. No buttressing is present on the ventral surface. The axillary border crest is clearly visible and developed along the midline of the border. The development of the axillary border crest is variable, and though it typically develops after buttressing is clearly present, this was not always the case it the modern children samples. The area around the infraglenoid tubercle is broken on this individual and was not scored. The axillary border sulcus was palpable and somewhat visibly developed on the dorsal surface and is consistent with the development of other features. This individual exhibits most of the developmental stages associated with the Middle Childhood stage of development, but could possibly be older, depending on the form of the broken infraglenoid tubercle.

Krapina 123 is a right scapula with all of its coracoid and acromion missing. The axillary border buttress is developed on the dorsal side of the scapula, with moderate development occurring on the ventral side. The axillary crest is developed and begins on the ventral portion of the border, runs medially and then merges into the lower third of the border. The infraglenoid tubercle is palpably present, but cannot be easily discerned visibly. This degree of development is consistent with stages of Late Childhood to the Juvenile stage. The sulcus is developed and clearly visible on the dorsal surface of the border. The Juvenile to Early Adolescence stage in modern human subadults is when the sulcus typically reaches the degree of development observable on Krapina 123. This individual was quite variable in the stages of development and was ultimately classified within the Juvenile to Early Adolescence stage based on the degree of development of the axillary border buttress, the degree of sulcus development, the cresting pattern and the overall size of the scapula.

Krapina 124 is a left scapula preserving only the axillary border. The glenoid, acromion, and coracoid areas are all missing. A moderately developed axillary border buttress is present on the ventral portion of the border, while the dorsal axillary border buttress is developed and clearly visible. The axillary border crest is very clearly developed on the upper third of the border. It begins on the dorsal surface and moves medially as it runs caudally. The infraglenoid tubercle shows only moderate development and can be palpated, but is not clearly visible. The sulcus on this individual may represent the beginning of a bisulcate pattern. The dorsal side of the border possesses a clearly developed sulcus under the crest, while a moderately developed sulcus is palpable on the ventral portion towards the midline. Comparable development is seen in the Juvenile to Early Adolescence stage in modern human subadults. The degree of development in other features however, places Krapina 124 within the Late Childhood to Juvenile stage of development. As has been noted by other authors *(7, 14, 22, 23),* the bisulcate pattern may be more often observed in older individuals exhibiting particular usage patterns of the upper limb. It may be a pattern that develops in response to mechanical forces and is perhaps a pattern unlikely to be found in young individuals.

Krapina 137 is a short (43mm) midsection of axillary border. Suprisingly, the only feature that could not be assessed on this individual was the infraglenoid tubercle. This individual exhibits moderate development of both the dorsal and ventral buttresses. There is a palpable axillary border crest running along the midline of the border. A palpable sulcus is present on the ventral portion of the border. The sulcus is developing quite close to the midline of the border however, and may have developed into a bisulcate pattern. The degree of development assessed on this individual was made with caution, due to the missing portions of bone. Conservatively, Krapina 137 may be placed within the Middle Childhood stage of development on the basis of the crest and the degree of development seen in the buttresses.

DISCUSSION

Based on quantitative observation, total development scores, and the logistic regressions, it appears that the axillary border buttresses are the first features to develop on the scapular axillary border. Next, the infraglenoid tubercle, axillary border crest, and axillary border sulcus develop roughly in tandem. When present, any rugosity on the border is the last of the five features to develop and is highly variable. Rugosity along the border typically occurs only with increased age, as evidenced by several of the individuals in the recent human sample with very large scapula, well developed features along the border and the presence of rugose bone.

The position of the axillary border sulcus is still a topic of discussion. This research did not attempt to determine why there is such variability in the placement of the axillary border sulcus. Nevertheless, this research does support earlier claims that the bisulcate pattern of sulcus development typically occurs in older individuals. Younger subadults rarely displayed the bisulcate pattern and those that do typically display advanced development of their other features of the scapular border. It is likely that this pattern represents a stronger, more robust form of the morphology and that the dorsal and ventral positioned sulci are less remarkable presentations of the morphology.

CONCLUSIONS

The pattern of development seen in the five features of the axillary border is similar in both of the recent human samples and in the Krapina Neandertal juveniles. The axillary border develops throughout ontogeny as the result of discrete changes in four areas, the axillary border buttressess, the infraglenoid tubercle, the axillary border crest and the axillary border sulcus. The age at which Neandertals exhibit these changes is not testable with the Krapina Neandertal juveniles. However, research on more completely preserved Neandertal juveniles would allow for additional testing.

Of the predictions put forth in this study only the second can be falsified. The first, that the five features develop at the same rate in recent humans and Neandertals, would seem to be confirmed by this research. The third, that the five features develop at different rates initially and different rates subsequently, cannot be falsified until these features can be evaluated in Neandertal juveniles whose age can be estimated more reliably.

Acknowledgements: *I am very grateful to David Frayer, Alan Mann, Janet Monge and Jakov Radovčić for the invitation to participate in this volume in honor of the 100th anniversary of the publication of Gorjanović-Kramberger's (1906) monograph on the Krapina Neandertals. I would also like to thank Dr. Osbjorn Pearson for his assistance in preparing this manuscript. Dr. James Degnan was also very helpful with the preparation of the multivariate analyses. I am very grateful to Dr. Fred Smith for his continued support and advice. Portions of this research were funded by Northern Illinois University. I would also like to thank the curators of the fossil and recent skeletons featured in the analyses reported here: Jakov Radovčić, Lyman Jellema, and Lynne Sullivan.*

REFERENCES

1. STRINGER C B, HUBLIN J-J, VANDERMEERSCH B 1984 The origin of anatomically modern humans in Western Europe. *In:* Smith F H, Spencer F *(eds)* The Origins of Modern Humans: A World Survey of the Fossil Evidence. Alan R. Liss, New York, p 51–135
2. CARRETERO J-M, ARSUAGA J–L, LORENZO C 1997 Clavicles, scapulae and humeri from the Sima de Los Huesos site (Sierra de Atapuerca, Spain). *J Hum Evol 33:* 357–408
3. FRAYER D W 1992a The persistence of Neanderthal features in post-Neanderthal Europeans. *In:* Bräuer G, Smith F H *(eds)* Continuity or Replacement: Controversies in *Homo sapiens* Evolution. Balkema, Rotterdam, p 179–188
4. TRINKAUS E 1983 The Shanidar Neandertals. Academic Press, New York.
5. FRAYER D W 1992b Evolution at the European edge: Neanderthal and Upper Paleolithic relationships. *Préhistorie Européenne 2:* 9–69
6. MORAN A J, CHAMBERLAIN A T 1997 The incidence of dorsal sulci of the scapula in a modern human population from Ensay, Scotland. *J Hum Evol 33:* 521–524
7. ODWAK H 1995 A Study of Neandertal Scapular Shape With Special Reference to Kebara Mousterian Hominid 2. M.A. Thesis, Simon Fraser University.
8. TRINKAUS E 1977 A functional interpretation of the axillary border of the Neandertal scapula. *J Hum Evol 6:* 231–234
9. STEWART T D 1962 Neanderthal scapulae with special attention to the Shandiar Neanderthals from Iraq. *Anthropos 57:* 779–800

10. GORJANOVIĆ-KRAMBERGER K 1914 Der Axillarand des Schulterblatts des Menschen von Krapina. *Glasn hrv prirodosl dr 16:* 231–257

11. GORJANOVIĆ-KRAMBERGER K 1926 Das Schulterblatt des diluvialen Menschen von Krapina. *Bull Inst geol Zagreb 1:* 67–122

12. MCCOWN T D, KEITH A 1939 The Stone Age of Mount Carmel II: The fossil remains from the Levalloiso-Mousterian. Clarendon Press, Oxford.

13. SMITH F H 1976 The Neandertal Remains from Krapina: A Descriptive and Comparative Study. Dept. Anthropol., Univ. Tenn. *Rep Invest 15:* 1–349

14. DITTNER C B 1976 The Morphology of the Axillary Border of the Scapula with Special Reference to the Neandertal Problem. M.A. Thesis, University of Tennessee.

15. DITTNER C B 1981 Morphological Changes on the Axillary Border of the Scapula with Special Reference to the Neandertal Problem. Ph.D. Dissertation, University of Tennessee.

16. SMITH F H 1982 Upper Pleistocene hominid evolution in South-Central Europe: a review of the evidence and analysis of trends. *Curr Anthropol 23:* 667–686

17. LIEBERMAN D E 1995 Testing hypotheses about recent human evolution from skulls. *Curr Anthropol 36:* 159–197

18. BUIKSTRA J E, UBELAKER D 1994 Standards for Data Collection from Human Skeletal Remains: Proceedings of a Seminar at the Field Museum of Natural History. Arkansas Archaeological Survey Press, Fayetteville, AR.

19. SCHEUER L, BLACK S 2000 Developmental Juvenile Osteology. Academic Press, San Diego.

20. JONES-KERN K, LATIMER B 1996 Skeletons out of the closet. Explorer, The Cleveland Museum of Natural History, 75th anniversary issue, p 26–28

21. BOGIN B 1988 Patterns of Human Growth. Cambridge University Press, Cambridge.

22. FRANCISCUS R G, SCHOENEBAUM C R 2000 Cross-sectional metric analysis of scapular axillary border morphology in recent humans and the Krapina Neandertals. *Am J Pys Anthropol (Suppl) 30:* 152

23. BUSBY A M 2000 The Ontogeny of the Axillary Border of the Scapula of Neandertal and Modern Human Juveniles. M.A. Thesis, Northern Illinois University.