

Modularity and integration in ontogeny of the middle facial skeleton in two West African monkey species: collared mangabey (*Cercocebus torquatus*) and olive colobus (*Procolobus verus*)

Andrej A. Evteev* & Olga G. Nanova

ABSTRACT. Could studying of a single bone's morphological variation and growth provide some additional information? For addressing this question a configuration of 13 landmarks from the middle part of the upper facial skeleton was digitized by Microscribe 3D digitizer on 25 skulls of *Cercocebus torquatus* and 16 skulls of *Procolobus verus* of different age and sex. Our results suggest that despite of strong ontogenetic integration in postnatal growth of the primate facial skeleton a study on a single bone's growth could provide a lot of biologically meaningful information. Elongation of the snout is far more pronounced in *C. torquatus* and related specifically to growth of the maxilla. This process can be described by a linear growth model and seems to be closely related to the general somatic growth rather than be by itself adaptive since an elongated snout could decrease bite force generation capacity at the incisors. Premaxillary growth is to a substantial degree independent from maxillary growth. The lower part of the bone attains its species-specific shape early in ontogeny what can be considered as a preparation to strong masticatory loadings which begin in this species during the first year of life. Later growth processes of the two bones are closely related and as a result shape of the premaxilla is substantially modified. Proximal and distal parts of the nasal bones seem to show differences: the former could be apparently different among individuals of the same species while shape and size of the later much more reflect elongation of the maxilla during postnatal period.

KEY WORDS: mid-facial ontogeny, Old World monkeys, geometric morphometrics.

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Модульность и интеграция в онтогенезе средней части лицевого скелета у двух видов западноафриканских обезьян: красноголового мангобея (*Cercocebus torquatus*) и зеленого колобуса (*Procolobus verus*)

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РЕЗЮМЕ: Может ли изучение морфологической вариации и ростовых процессов отдельно взятой кости дать какую-то дополнительную информацию? В поисках решения этого вопроса мы оцифровали с помощью трехмерного дигитайзера Microscribe конфигурацию из 13 точек, расположенных в средней части верхнего лицевого скелета на 25 черепах *Cercocebus torquatus* и 16 черепах *Procolobus verus* различного пола и возраста. Наши результаты свидетельствуют, что, несмотря на сильно выраженную онтогенетическую интеграцию в постнатальном росте лицевого скелета приматов, изучение роста отдельно взятых костей может дать немало ценной с биологической точки зрения информации. Удлинение морды заметно сильнее выражено у *C. torquatus* и связано оно именно с ростовыми процессами верхнечелюстной кости. Этот процесс может быть успешно описан с помощью модели линейного роста и, по всей видимости, тесно связан с общими соматическими ростовыми процессами. Он, видимо, не имеет непосредственного адаптивного значения, так как удлинение морды может привести к снижению силы укуса резцов. Рост предчелюстной кости в значительной мере независим от роста максиллы. Нижняя часть этой кости принимает свою видоспецифичную форму в раннем онтогенезе, что может рассматриваться как «подготовка» к сильным жевательным нагрузкам, которые начинаются у представителей этого вида уже на первом году жизни. В дальнейшем ростовые процессы двух костей тесно связаны и, как результат, форма премаксиллы существенно модифицируется. Проксимальная и дистальная части носовых костей отличаются: форма первой может явно различаться у представителей одного вида, тогда как форма и размер второй в большей степени отражают удлинение верхнечелюстной кости в постнатальном онтогенезе.

КЛЮЧЕВЫЕ СЛОВА: онтогенез лицевого скелета, обезьяны Старого Света, геометрическая морфометрия.

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Introduction

The concept of modularity is well established in evolutionary biology, particularly in evolutionary genetics, but distinguishing between different modules has always been a very challenging task when dealing with complex biological structures like mammalian skull (Cheverud, 1982; Altenberg & Wagner, 1996). The results of numerous studies on the primate skull integration and modularity are often controversial. While most researches agree that cranial modules exist, there are many ways of dividing the whole structure into *a priori* modules. Approaches to modularity greatly differ in terms of the number of modules, degree of comprehensiveness and theoretical basis. Each of the approaches has its own specificity (listed below) which strongly influences results of a study (Cheverud, 1982; Richtsmeier *et al.*, 1993; Hallgrímsson *et al.*, 2004; Cardini & Elton, 2008a):

1) *Mode of ossification: chondrocranium versus dermatocranium* (Sperber, 2001; Cardini & Elton, 2008a). The chondrocranial structures often serve as matrices for dermal bones and thus the shape of the later may depend on the shape of underlying elements of chondrocranium. A good example is relations between the nasal capsule and the nasal septum and dermal bones of the upper medial face in mammals (Latham, 1970; Mooney & Siegel, 1986; Depew *et al.*, 2005; Holton *et al.*, 2010, 2011) and dependence of growth of the avian beak structures on the shape of the prenasal cartilage (Abzhanov *et al.*, 2004; Wu *et al.*, 2004). Another problem with such an approach is that a mode of ossification is correlated neither with embryonic origins nor genetic regulation or functions of bones. For instance, a part of the facial dermal bones is first branchial arch derivatives while the nasalia and the premaxilla originate from the neural crest cell populations from the forebrain area so their growth and development are controlled to a large degree independently (Creuzet *et al.*, 2005; Depew *et al.*, 2005).

2) *"Big" modules: cranium versus the mandible, neurocranium versus viscerocranium, the upper face versus the middle face* (Richtsmeier *et al.*, 1993). Existence of these modules is obvious as well as the fact that this approach is too general since such modules are very heterogeneous inside themselves. On the other hand there is well established functional and genetic integration connecting these modules between each other (Cheverud, 1982; Lieberman *et al.*, 2000; Bastir *et al.*, 2006).

3) *Functional modules* selected according to main epigenetic effects of functional matrices - associated soft and hard tissues. This approach goes back to the classical works (Moss & Young, 1960; Cheverud, 1982) and the set of the modules is admitted unchangeably in most studies. Despite it there are some challenging questions about any of these modules. For example, the eyeball undoubtedly plays a great role in early morphogenesis of the face integrating surrounding structures

and stimulating its growth, but whether or not specific facial morphology of large-bodied animals depends on it, particularly taking into account relatively stable size of the eyeball in different species due to optical demands (Bunak, 1960; Enlow, 1975)? The results of several studies confirm that variation in size of the orbit is less than in surrounding structures (Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998) while measurements of the orbital module do not demonstrate a high level of integration (Cheverud, 1982). In the oral module its lower part, alveolar process, is undoubtedly affected by masticatory loadings but there are strong reasons to suppose an influence from the other functional matrix, nasal septum, onto its upper structures — the palate and the nasal spine area (Latham, 1970; Mooney & Siegel, 1986; Depew *et al.*, 2005; Holton *et al.*, 2010, 2011). The shape of the masticatory module depends not only on masticatory cyclic strain but also on the general somatic growth factors (Collard & O'Higgins, 2001; Hallgrímsson *et al.*, 2004; Bulygina *et al.*, 2006; Funatsu *et al.*, 2006) as well as on the shape of the cranial base (Bunak, 1960; Richtsmeier *et al.*, 1993; Lieberman *et al.*, 2000).

A relatively low level of integration in these functional modules was found in many studies (Cheverud, 1982; Cardini & Elton, 2008a; Adams *et al.*, 2011) and demonstrates that such an approach captures just a part (even though a very important part) of information about modularity of the facial skeleton and stimulates a search for new ways of separation of the whole structure into modules. Potentially a very promising way could be extracting modules according to the recent developmental genetics and experimental embryology data (Cardini & Elton, 2008a).

In the present study we describe morphological variation and growth dynamics of single bones of the facial skeleton. This approach goes back to very old times. For instance C. Pearson wrote that a single bone's measurements might suit for the aim of a special anatomical research better than more "general" measurements (cited by Cheverud, 1982).

While warning from the use of single bones as modules, Moss and Young (1960) clearly demonstrated how complex the internal structure of a single bone might be and how different parts of the bone could vary independently. Growth processes of different facial bones taken separately described in works of D. Enlow (1966, 1975).

Here we deal with growth and morphology of three bones which form the middle part of the upper facial skeleton: the maxilla, the premaxilla and the nasal bone. There are several features of these bones which worth a special attention.

First, while being placed very close and forming an integrated structure, these bones (the maxilla *versus* the premaxilla and the nasalia) have different embryological origins and further different profiles of regulatory genes expression (see above). It means that in the early prenatal period before forming of rigid sutures each

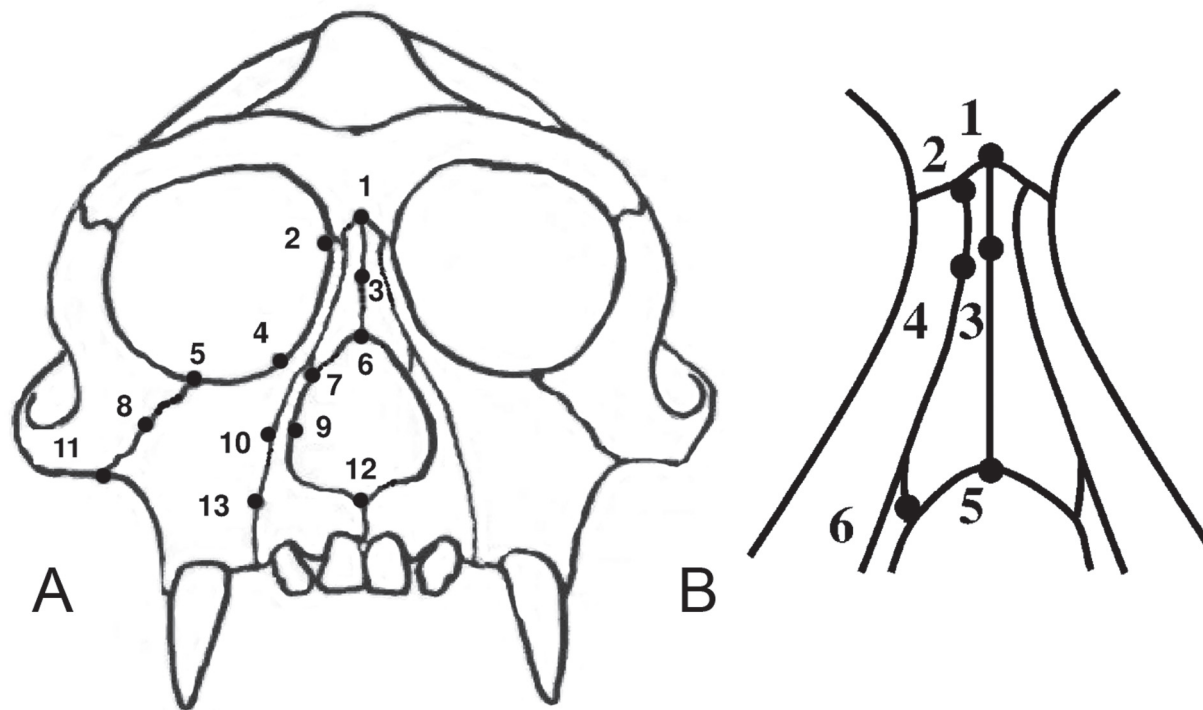


Figure 1. Facial landmarks used in the study: A — general configuration, 13 landmarks; B — the nasal bone configuration, 6 landmarks (for anatomical definition of the landmarks see Tab. 1).

bone attains a size according to its intrinsic growth rate and forms a bigger or a smaller part of the whole structure (Enlow, 1975; Depew *et al.*, 2008; Marimoto *et al.*, 2008; Rice, 2008). After a suture is formed bone deposition rates differ significantly at both sides of the suture thus the different bones continue to grow differently (Bjork, 1968; Rice, 2008).

Second, an intensive growth of these bones takes place at different stages of ontogeny. Both the premaxilla and the upper part of the nasal bones grow rapidly during the gestation so a morphological pattern of the midline facial structures is nearly developed by the end of the first year of life (Sysak, 1960; Schultz, 1963; Mooney & Siegel, 1986; Richtsmeier *et al.*, 1993; Francis, 1995). Human infant skulls from different populations can be classified nearly as correctly as the adults (Vidarsdóttir *et al.*, 2002), and an individual pattern of the facial skeleton is also determined by the age of 3 years (Bulygina *et al.*, 2006). Taking into account small size of the maxilla at this age the above-mentioned differences can be attributed predominantly to the premaxilla and the nasalia morphology.

Finally, due to asynchronous growth, the bones are involved in different ontogenetic events and influenced by different functional matrices. The nasalia, the premaxilla and only a small part of maxilla grow in close relation to the nervous system (eye) and the respiratory (the nasal cavity through the nasal capsule and the nasal septum) organs formation while the main growth of the maxilla occurs in correspondence with far later events —

molar and premolar emergence and pubertal growth spurt (Enlow, 1975; Richtsmeier *et al.*, 1993; Funatsua *et al.*, 2006; Bulygina *et al.*, 2006). We believe that considering single bones' growth processes may add some additional arguments for the long-standing discussion about a relative importance of early pre- and perinatal growth versus postnatal growth in the facial skeleton ontogeny (Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998; Collard & O'Higgins, 2001; Ponce de Leon & Zollikofer, 2001; Ackermann & Krovitz, 2002; O'Higgins & Collard, 2002).

Since choice of a set of landmarks for a study is a crucial point of any research design (Oxnard & O'Higgins, 2009) we followed some criteria while *constructing the configuration*:

1) Neurocranial landmarks were completely excluded from the configuration.

2) Points belonging to both the malar bone and the zygomatic arch, a "core" of conventional masticatory module (Cheverud, 1982; Richmond *et al.*, 2005; Curtis *et al.*, 2008), were also excluded. We have excluded points from the alveolar process as well since this structure is known to be particularly strongly influenced epigenetically (Enlow, 1975). Several studies have demonstrated that linear measurements with points lying on the alveolar process have very low narrow-sense heritability (Cheverud, 1982; Martinez Abadias, 2007).

3) We tried to describe the middle part of the upper facial skeleton more comprehensively than it's usually

done (O'Higgins & Jones, 1998; Ackermann & Krovitz, 2002; Hallgrímsson, 2004; Cardini & Elton, 2008a) by digitizing some additional landmarks (Fig. 1).

At the *stage of the analysis* we pursued the following aims:

1) Describe the morphological variation and growth dynamics of each of three bones separately, assess their interaction throughout ontogeny and evaluate a contribution of each bone to the general morphology of the middle facial skeleton ("muzzle"). For this purpose we divided the general landmark configuration into configurations of the single bones such that some landmarks were included both to "maxilla" and "premaxilla" configurations (see "Materials and methods"). Then the principal component and other statistical analyses were performed for each bone independently.

2) Visualize results of the analyses performed for the single bones.

Most authors place figures representing morphological changes of a landmark configuration of the whole facial skeleton and anterior neurocranium in their articles (Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998; Hallgrímsson, 2004; Cardini & Elton, 2008a). Such configurations include dozens of landmarks making their interpretation a challenging task. The most noticeable and strongly pronounced differences dominate while the smaller but not less important changes can be hardly noticed even with a careful examination of the graph. Publications of figures depicting single modules morphology are rare (Smith *et al.*, 2007; Cardini & Elton, 2008a). Another problem is that a visual output of a Geometric Morphometric Methods (GMM) analysis displays *relative* changes of adjacent structures and it's hard to distinguish growth of a certain bone from changes in its neighbours (O'Higgins *et al.*, 2001). So, in analyses of single bones' pictures we were trying to capture growth changes of each bone separately.

Crania of two West-African monkey species — *Cercocebus torquatus* (Kerr, 1792), fam. Cercopithecidae, subfam. Cercopithecinae and *Procolobus verus* (van Beneden, 1838), fam. Cercopithecidae, subfam. Colobinae — are an object of the study. The species have prominently distinct facial morphology. The face of the collared (white-collared, or sooty) mangabey (*C. torquatus*) is prognathous and fairly elongated and thus is to some extent similar to the shape of the face in the baboon. A characteristic trait of all mangabeys is large incisors that are used for crushing hard food items such as nuts. The facial skeleton of the olive colobus (*P. verus*) is shortened as in all Colobinae. Sexual dimorphism in facial morphology is far more pronounced in *C. torquatus* than in *P. verus*. These morphological differences can be explained by size differences, ecological and phylogenetic divergence (Davies & Oates, 1995). Male weight of *P. verus* is 3.3–5.7 kg, female weight is 3–4.5 kg; male weight of *C. torquatus* is 7–12.5 kg, female weight 5–8 kg. The diet differs strongly between the two species. The diet of *P. verus* includes a substantial amount of soft food (young leaves, flowers)

in contrast to the diet of the other Colobinae (Davies & Oates, 1995). The diet of *C. torquatus* contains a lot of hard food. For example, fruits of *Sacoglottis gabonensis* which constitute the bulk of mangabey's diet are comparable in hardness to a cherrystone. These fruits are eaten by both young and adult monkeys. There is no difference in the diet between adult and young *C. torquatus* (McGraw *et al.*, 2011).

Previous studies on these or similar species have clearly demonstrated differences in growth dynamics between the middle and the lateral parts of the monkey facial skeleton (O'Higgins & Jones, 1998; Collard & O'Higgins, 2001; O'Higgins & Collard, 2002) as well as between different facial bones (Enlow, 1966; Cheverud, 1982; Corner & Richtsmeier, 1991; Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998; Cobb & O'Higgins, 2004). In the present study we have tried to assess ontogeny of single bones comprising the middle part of the facial skeleton more comprehensively. We would like to emphasize that the study was aimed neither to a general description of cranial growth of these species (which can be found elsewhere) nor to resolving of systematic and phylogenetic questions.

Materials and methods

Twenty five skulls of collared (sooty) mangabeys *C. torquatus* and 16 skulls of olive colobuses *P. verus* from the University of York, Functional morphology and Evolution unit collection were digitized using Microscribe G2X 3D digitizer. Skulls of the animals of all growth stages from juvenile to adulthood were included in the analysis. Details of sex and age of the specimens are given in Tab. 2. Full information about each *C. torquatus* individual's dentition eruption and abrasion can be found in the article of O'Higgins and Jones (1998).

Thirteen landmarks were collected from the middle part of the upper face of each skull (Fig. 1A, Tab. 1). The landmark configuration for the maxilla includes 8 landmarks: 2, 4, 5, 7, 8, 10, 11, 13. The landmark configuration for the premaxilla includes 5 landmarks: 7, 9, 10, 12, 13. The nasal bones from 19 skulls (*P. verus* — 8, *C. torquatus* — 11) were digitized using a special set of landmarks for more comprehensive analysis of the nasal bone variation (Fig. 1B, Tab. 1). It must be pointed out that the results of this part of the study might be seriously biased due to uneven sampling: there are no fully adult females of *C. torquatus* and no juveniles of *P. verus* in the sample. Thus we did not apply ANOVA in this section but taking into account rarity of data on the nasal bones variation present the PCA and some other results.

Procrustes and Principal Component analyses were performed on the two species combined sample and for each species separately. For this purpose we used Morphologika 2.5 (O'Higgins & Jones, 1998). Morphologika was also used for visualization of the results. A regression analysis between PCs scores and centroid size was

Table 1. Anatomical definitions of landmarks.

Number	Name	Definition	“Module”
1	Nasion	The nasofrontal suture in the midline	
2	Maxillofrontale	The frontolacrimal suture at the medial orbital margin	Maxillae
3		A point at the internasal suture at the level of minimal width of the nasal bones	
4		A point of intersection of tangent to the lateral edge of lacrimal fossa and the inferior orbital edge	Maxillae
5	Zygoorbitale	The zygomatico-maxillary suture at the inferior orbital margin	Maxillae
6	Rhinion	Tip of the nasal bones in the midline	
7	Nasomaxillare	The most inferior point of the nasomaxillary suture (the point is very close to the superior point of the premaxillary frontal process)	Maxillae, premaxillae
8		The zygomaticomaxillary suture, a point of intersection with the line which connects landmark 10 and the most inferior point of the tempo-zygomatic suture (on the zygomatic arch)	Maxillae
9	Conchale	<i>Crista conchalis</i> at the nasal aperture margin	Premaxillae
10		The point of intersection between the maxillary-premaxillary suture and the line that connects landmarks 8 and 9	Maxillae, premaxillae
11	Zygomaxillare	The zygomatico-maxillary suture at the root of the zygomatic arch	Maxillae
12	Nasospinale	The premaxillary suture at the inferior margin of the nasal aperture in the midline	Premaxillae
13		Points of intersection between the premaxillo-maxillary suture and the line that connects landmarks 11 and 12	Maxillae, premaxillae
Additional nasal bone’s landmarks			
1a	Nasion	Intersection between the naso-frontal and the internasal sutures	Nasalia
2a	Infranasion	Intersection between the fronto-maxillary and the naso-maxillary sutures	Nasalia
3a		The midline of the nasal bones, the minimal width	Nasalia
4a		A point on the naso-maxillare suture at the minimal width of the nasal bones	Nasalia
5a	Rhinion	Tip of the nasal bones in the midline	Nasalia
6a	Nasomaxillare	The most inferior point of the naso-premaxillary suture	Nasalia

performed for estimation of allometric contribution to growth and variation of the face. In order to further assess allometry and covariation among different configurations we have also calculated Spearman rank correlations between centroid sizes and PC1-2 values of the general configuration, the maxilla, the premaxilla and the nasal bones configurations (Tab. 3; see also Tab. 2 for sampling details). RV-coefficient (Klingenberg, 2009) as a measure of covariation between the sets of variables was used for estimation of association between the single bones' variation. We tested modularity hypotheses for the maxillae, the premaxillae and the nasal bone using MorphoJ 1.02 (Klingenberg, 2009, 2011). Dispersion analysis (analysis of variance, General Linear Model) was used for estimation of contribution of factors “SEX”, “AGE” to variation of the PCs.

Results

Analysis of the general (whole face) configuration, 13 landmarks. PC1 from the analysis on the two species combined sample accounts for 71.8% of the total variation while PC2 explains just 6.0%. The two species are separated along PC1 without an overlap

(Fig. 2A). Both sexes and age stages are well differentiated in *C. torquatus*. In contrast, in *P. verus* sex and age variation is insignificant. Analysis of variation for each species separately has shown that variation in *C. torquatus* is more structured than variation in *P. verus*. PC1 explains 58.3% of variation in *C. torquatus*. PC2 and PC3 account for just a small portion of the total variation — 12.0% and 5.7% respectively. Factor loadings on the PCs in the two species are rather different. In the olive colobus PC1 accounts just for 26.6% of the total variation while PC2 takes only slightly less amount of variation, 21.9%.

Analysis of variance shows that the two species are different in terms of amount of variation in PC scores that can be attributed to contribution from SEX and AGE factors. In *C. torquatus* PC1 explains a large portion of sexual dimorphism (contribution of factor SEX to PC1 is significant, $p < 0.05$). At the same time PC2 corresponds to age variation ($p < 0.05$). So, contribution of factors SEX and AGE is clearly structured in *C. torquatus* being separated between different PCs.

In *P. verus* significant contribution of factor AGE is found for PC1–3 ($p < 0.05$), i.e. age variation in this species is distributed among the first three PCs.

Table 2. The sample of *C. torquatus* and *P. verus* used in the study.

Species	Catalogue no.	Sex	Age	Species	Catalogue no.	Sex	Age
<i>Cercocebus torquatus</i>	13.4	female	old adult	<i>Procolobus verus</i>	7.28	female	juvenile
	13.1	female	sub adult		c7.13	female	infant
	13.2	female	adult		c7.11	female	juvenile
	13.3	female	adult		c7.15	?	immature
	13.5a	?	adult?		c7.14	female	subadult
	13.8	female	immature		c7.12	female	juvenile
	13.7	?	juvenile		c7.16	female	adult
	13.6	?	juvenile		c7.17	female	adult
	13.9	female?	immature		c7.18	Male	adult
	13.18	male	adult		c7.19	Female	adult
	13.19	male?	adult		c7.20	male	adult
	13.23	male	adult		c7.21	male	adult
	13.22*	male	adult		c7.22	male	adult
	13.24	male	adult		c7.26	female	adult
	13.25	male	adult		c7.23	male	adult
	13.20	male	subadult		c7.24	male	adult
	13.21	male	adult				
	13.38	male	juvenile				
	13.41	?	juvenile				
	13.39	male	juvenile				
	13.36	female	immature				
	13.35	female	immature				
	13.34	female	immature				
	13.40	?	juvenile				
	13.37	male	juvenile				

* bold font indicates specimens that were used for an additional analysis of the nasal bones.

PC1 describes increase in the facial prognathism, i.e. progression of the distal part of the maxilla and the premaxillae (Fig. 2A, insets). This finding just repeats the results of previous studies (Corner & Richtsmeier, 1991; Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998; Collard & O'Higgins, 2001; O'Higgins & Collard, 2002; Cobb & O'Higgins, 2004). According to both previous and our results, the PC1 scores have a high and significant correlation with centroid size (Spearman $R = 0.93$; $p < 0.05$, Tab. 3) and hence corresponds to the main allometric trend ("linear growth model"; Fig. 3A). Exclusion of the neurocranial landmarks as well as the landmarks from the alveolar process and zygomatic region does not affect the results of the analysis: the largest part of variation is still accounted for the degree of prognathism which is far more prominent in *C. torquatus*.

Comparison of the analyses of configurations of the whole face and the maxilla. To describe the shape of the maxilla we used landmarks 2, 4, 5, 7, 8, 10, 11, 13 (Fig. 1A; Tab. 1). The variation trend in the maxilla is nearly identical to that of the general configuration. The analysis of data on the two species demonstrates that PC1 takes 71.0% of variation while PC2 accounts for 8.1%. The configuration of plot in PC1–PC2 space (Fig. 2B) is almost identical to that of general landmark configuration and even many specimens hold the same place on the plot (compare the insets, Figs. 2A and 2B). Maxillae PC1 scores are highly correlated with centroid size ($R = 0.93$; $p < 0.0001$; Tab. 3), i.e. PC1 explains the allometric variation (Fig. 3B).

Correlations between centroid sizes of the general configuration and the maxilla and PC1, PC2 scores (Tab. 3) are almost identical. It seems that the analysis

Figure 2. Principal components analysis of 13 (general) and 8 (the maxilla) landmark configuration. A — PC1 (horizontal axis) vs PC 2 (vertical axis) of the analysis of 13 landmarks configuration. Left inset — configuration representing PC1 = -0.18 and PC2 = 0, flat surface rendering; right inset — configuration representing PC1 = 0.18 and PC2 = 0, flat surface rendering. B — PC1 (horizontal axis) vs PC 2 (vertical axis) of the analysis of 8 landmarks configuration (the maxilla). Left inset — configuration representing PC1 = -0.18 and PC2 = 0, flat surface rendering; right inset — configuration representing PC1 = 0.18 and PC2 = 0, flat surface rendering. Symbols: 1 — adult and subadult males of *C. torquatus*; 2 — adult and subadult females of *C. torquatus*; 3 — infant and juvenile males of *C. torquatus*; 4 — infant and juvenile females of *C. torquatus*; 5 — infant and juvenile specimens of *C. torquatus*, sex is unknown; 6 — adult and subadult males of *P. verus*; 7 — adult and subadult females of *P. verus*; 8 — infant and juvenile females of *P. verus*; 9 — infant and juvenile specimens of *P. verus*, sex is unknown.

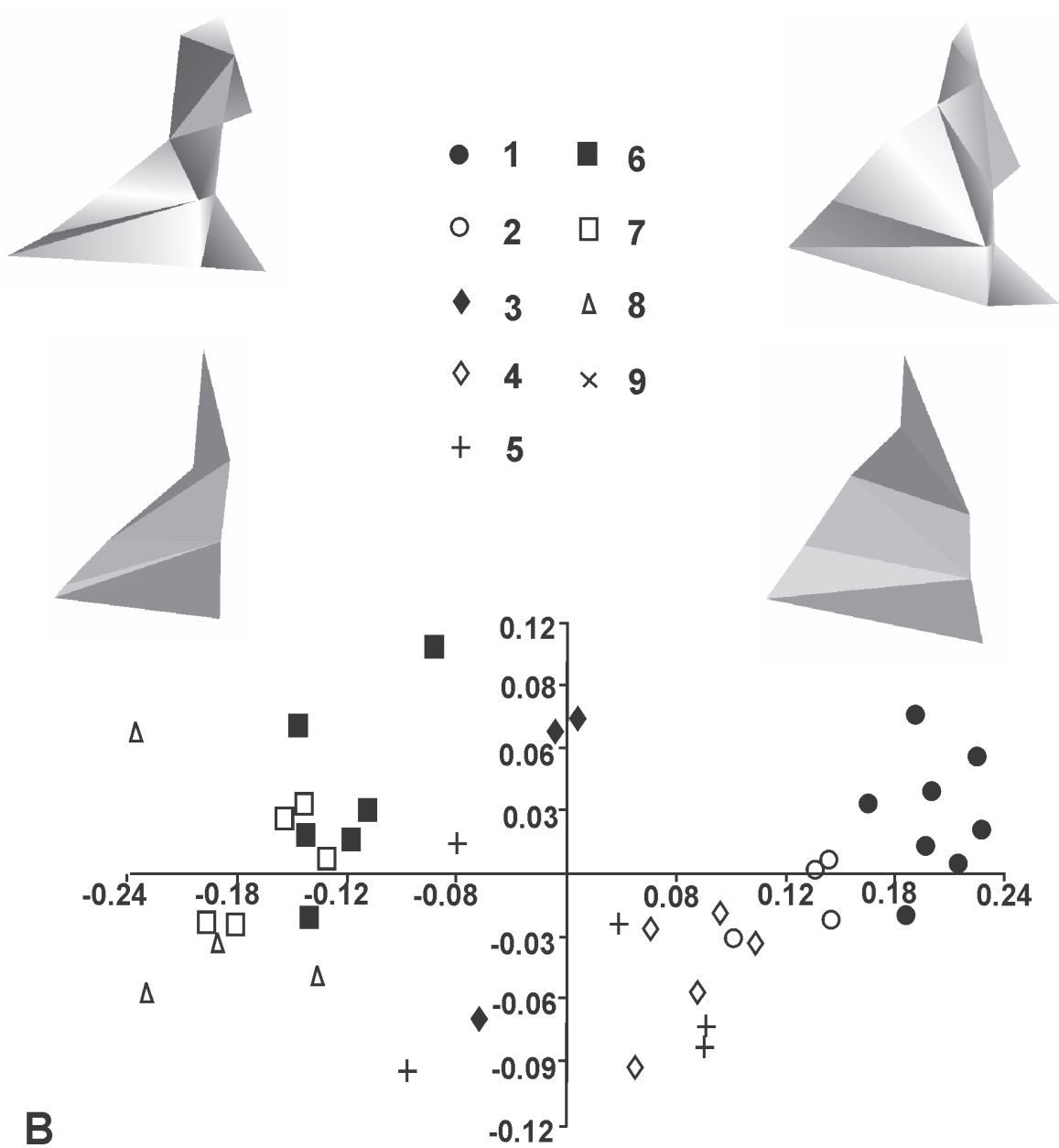
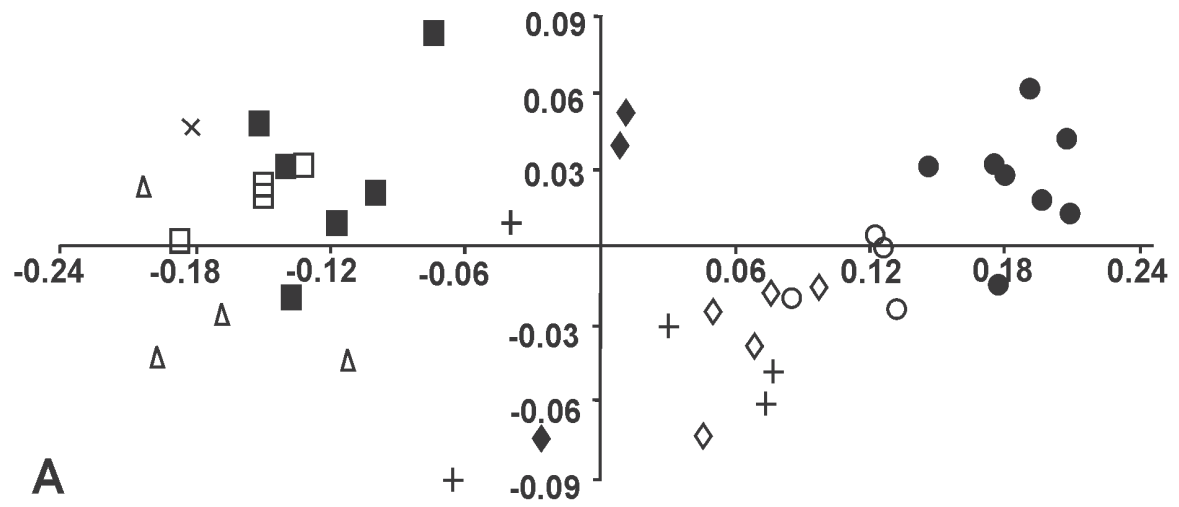


Table 3. Spearman's rank correlation coefficients between centroid size, PC1 and PC2 scores in the general configuration, and configurations of the maxilla, the premaxilla and the nasal bones (see Tab. 2 and "Materials and methods" section for sampling details).

	1	2	3	4	5	6	7	8	9	10**	11**	12**
1. Centroid size, general configuration												
2. PC1, general l configuration	0.93*											
3. PC2, general l configuration	0.14	0.02										
4. Centroid size, maxillae	0.99	0.92	0.10									
5. PC1, maxillae	0.94	0.99	0.04	0.93								
6. PC2, maxillae	0.11	0.01	0.96	0.09	0.03							
7. Centroid size, premaxillae	0.86	0.73	0.47	0.84	0.75	0.38						
8. PC1, premaxillae	0.37	0.44	-0.44	0.35	0.43	-0.49	0.08					
9. PC2, premaxillae	-0.17	-0.29	0.32	-0.19	-0.28	0.28	0.09	-0.02				
10. Centroid size, nasal bone**	0.93	0.96	-0.04	0.95	0.95	0.02	0.18	0.55	-0.17		0.89	-0.23
11. PC1, nasal bone**	0.88	0.93	0.10	0.86	0.91	0.09	0.25	0.44	-0.24	0.89		0.07
12. PC2, nasal bone**	-0.08	-0.17	0.54	-0.29	-0.19	0.34	0.45	-0.18	0.41	-0.23	0.07	

* significance level $p = 0.05$.

** different sample size, see Tab. 2.

of the general configuration of the facial skeleton is dominated by the maxilla variation whether it contains 31 (see O'Higgins, Jones, 1998 and Introduction) or 13 landmarks. Variation of the other facial bones is small comparing to variation of the maxilla. Reduction of landmarks configuration to 8 landmarks does not affect the result.

Analysis of maxillae modularity provides well interpretable results. The minimum covariation was detected between landmark sets comprising 2, 8, 10, 13 and 4, 5, 7, 11 (Fig. 6A). The second set might be associated with the eyeball growth (module "orbital", Cheverud, 1982). These landmarks almost do not change their relative position. Landmark 11 lies in the same plane with the orbital landmarks. Both landmark 5 and 11 belong to the zygomatic bone. Landmarks 8, 10 and 13 are located on the fast growing facial region. They are markedly displaced forward during the growth away from landmarks 4, 5, 7, but the distance among these landmarks itself remains unchanged. Landmark 2 moves up from landmarks 4, 5, 7 with growth in the frontomaxillary suture which takes place in the final stages of growth (O'Higgins & Jones, 1998).

Variation of the premaxilla in comparison to variation of the general configuration. A comparison of the covariance matrices of the two species done using

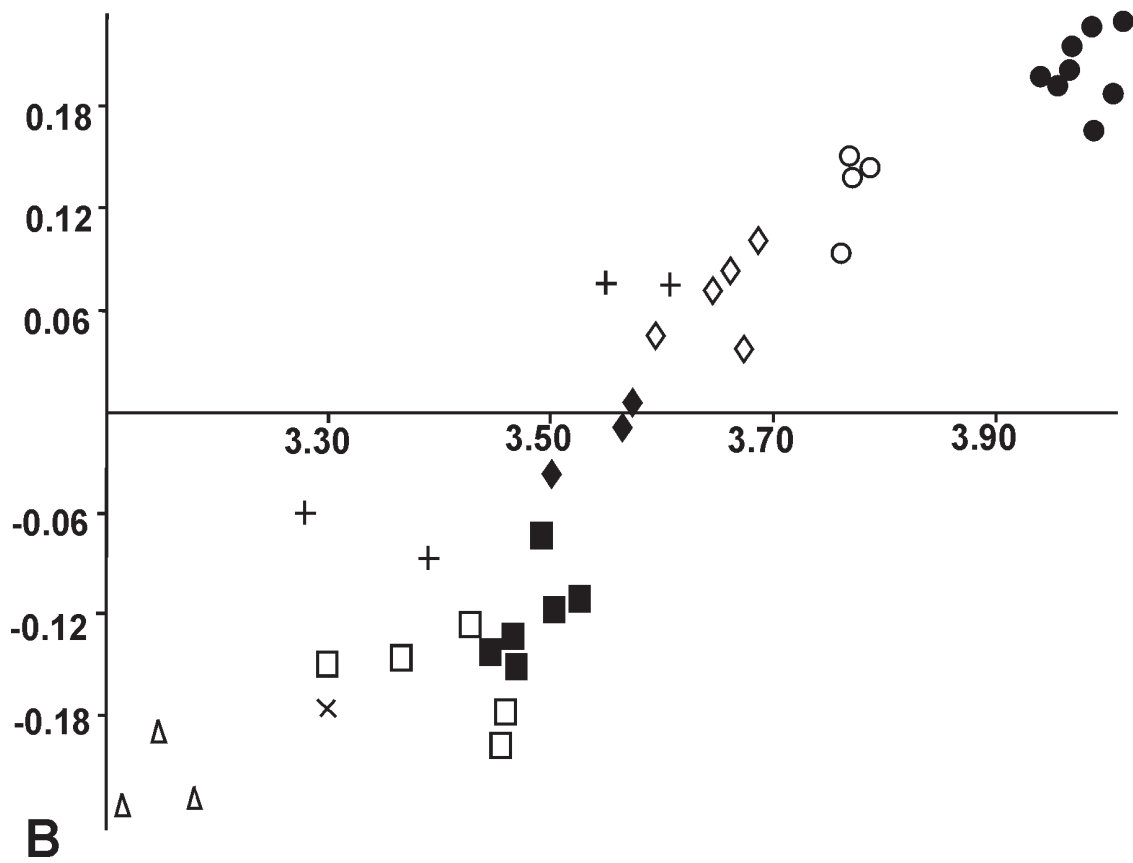
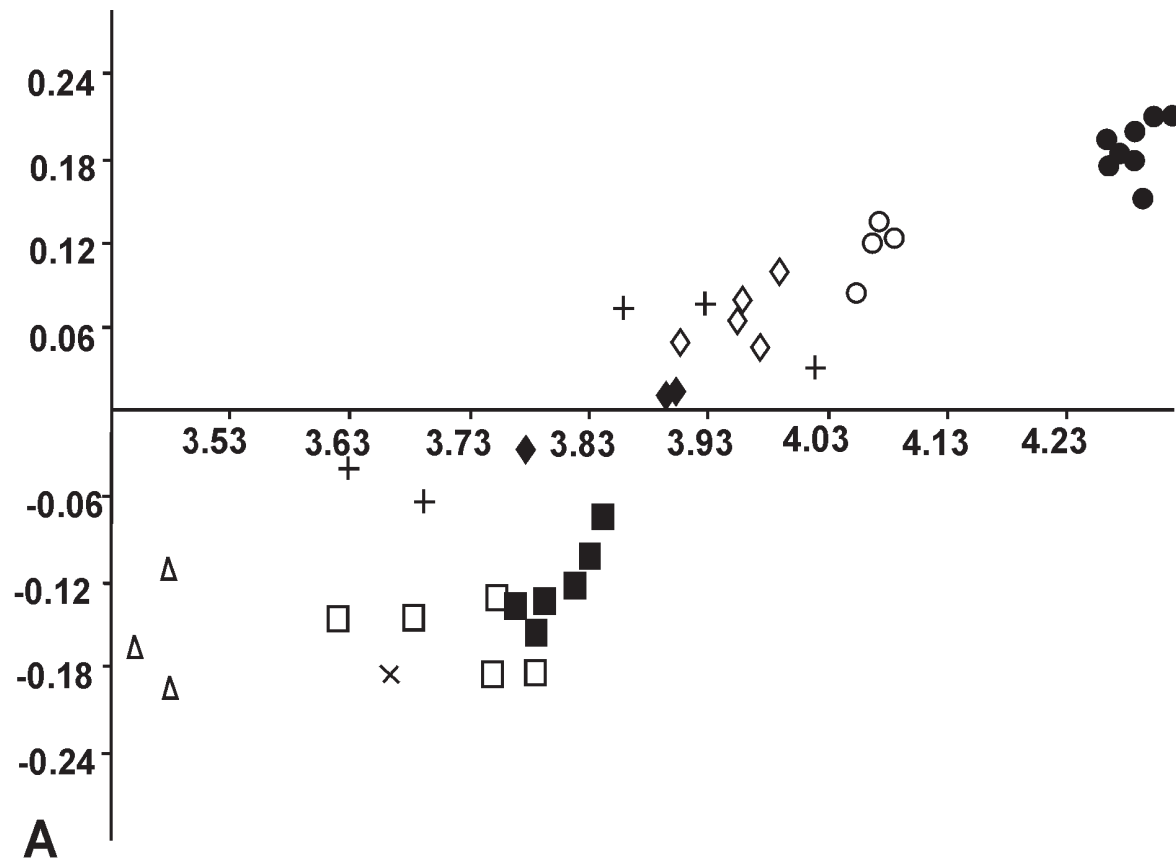
Mantel-test suggests that the overall patterns of the maxilla's variation in *C. torquatus* and *P. verus* are different ($R = 0.2$, $p = 0.8$). In contrast, variation of the premaxilla in *C. torquatus* is similar to that of *P. verus* ($R = 0.91$, $p < 0.01$). Variation of the premaxilla is less structured in comparison to the maxilla. In the analysis of data on the two species combined PC1 takes 53.3% of variation and PC2 accounts for 17.8% (Fig. 4A).

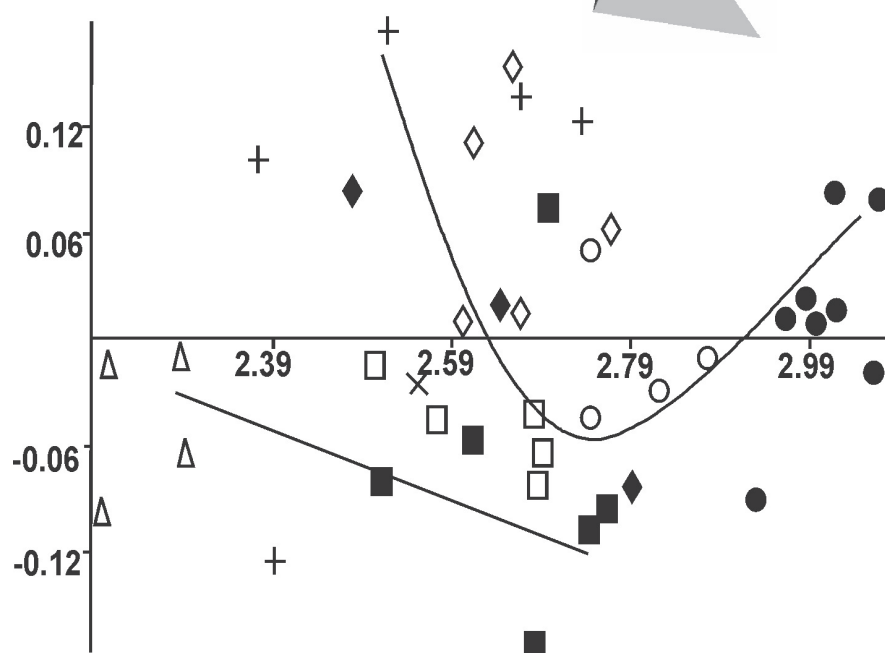
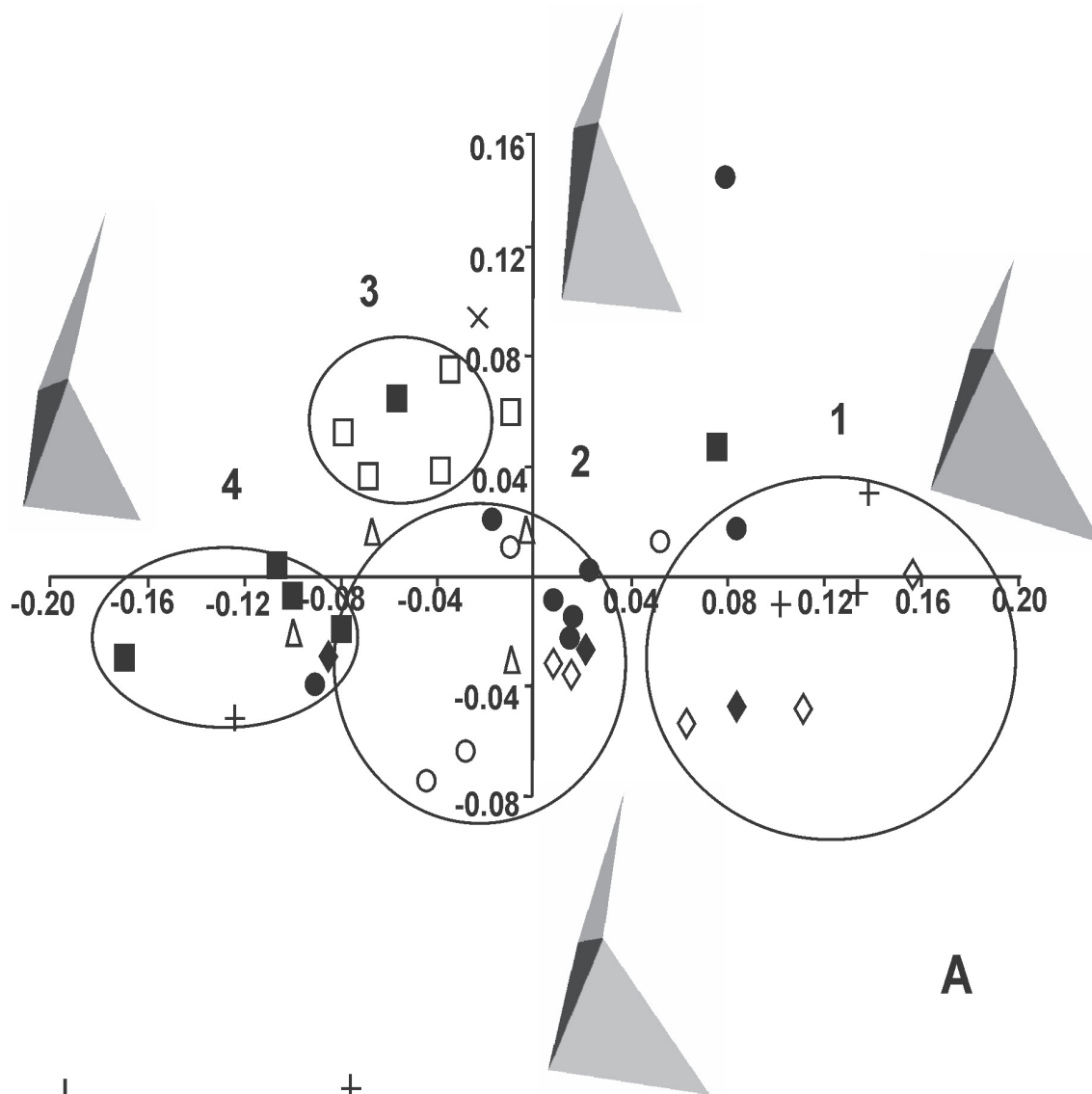
The two species overlap in the PC1/PC2 plot of the premaxilla shape (Fig. 4A). Specimens of juvenile and subadult mangabey's skulls lie within the range of the greatest values of PC1 (values > 0.08 , ellipse 1 on Fig. 4A). Adult mangabeys are dispersed in the range of the values of PC1 around zero (ellipse 2). Thus age axis of the mangabey has approximately the same direction as PC1. We can use PC1 as a proxy for the age vector for the premaxilla in *C. torquatus*. But note that PC1 scores are not correlated with centroid size (Spearman $R = 0.08$; $p = 0.62$, Fig. 4B).

Analysis of variance reveals that SEX and AGE factors do not contribute significantly to PC1–3 in *C. torquatus*, while factor AGE contributes significantly to PC2 in *P. verus*.

Scatterplot of the specimens in the space of PC1 and centroid size of the premaxilla (Fig. 4B) sharply differs from that of the maxilla. The premaxilla shape in imma-

Figure 3. Plot of the first principal component (vertical axis) from PCA vs ln centroid size (horizontal axis): A — analysis of 13 landmarks configuration; B — analysis of 8 landmarks configuration (the maxilla). Symbols — see legend to Fig. 2.





ture individuals strongly differs between the species despite their similarity in centroid size. At the same time the premaxilla of mature individuals of the two species converges in shape but not in size. Relationship between centroid size and PC1 for the premaxilla in *P. verus* looks like a linear relation. In contrast to that the relationship between centroid size and PC1 scores for the premaxilla in *C. torquatus* is obviously nonlinear (Fig. 4B).

As scores of PC1 of the premaxilla increase its lower part expands and extends (Fig. 4A, left and right insets). Greater values of PC2 scores of the premaxilla, which are characteristic for adult female (ellipse 3) but not male (ellipse 4) *P. verus* specimens, correspond to contraction of the frontal process and reduction in breadth and protrusion of the lower part of the premaxilla (Fig. 4A, top and bottom insets).

Significant correlation (Spearman $R = 0.86$, $p < 0.01$) between centroid sizes of the premaxilla and the general configuration is observed (Tab. 3). Variation of PC1 of the premaxilla is weakly correlated with variation of the total facial size (Spearman $R = 0.37$, $p = 0.018$).

RV-coefficient between variation of the shape of the maxilla and the premaxilla is as high as 0.29 ($p = 0.006$). Analysis of modularity of the premaxilla reveals minimal covariation between two sets of landmarks: two landmarks from the lower part of the bone versus three points from the frontal process (Fig. 6B).

Variation of the nasal bones. To describe the nasal bones shape variation we applied a smaller sample: 8 individuals of *P. verus* and 11 *C. torquatus* (Tab. 2). Due to uneven sampling (see Materials and methods) we don't present ANOVA results here and the specific of the sample used for this part of the study should be born in mind when interpreting the results. PC1 accounts for 48.7% of variation, PC2 — 26.0%. The two species are separated by the nasal bones shape along the PC1. The intraspecific differentiation along the PC2 is also observed (Fig. 5A). The nasal bones' shape is narrow and elongated within the range of positive values of PC1. This is particularly typical for the superior part of the nasal bones. The nasal bones are relatively broad and short within the range of negative PC1 values (Fig. 5A, right and left insets). Thus PC1 represents strong interspecific differences of the shape of the nasal bones. Variation along PC2 corresponds to variation of the proximal part of the nasalia from short and broad to narrow and elongated form (Fig. 5A, top and bottom insets).

Significant correlation (Spearman $R = 0.89$, $p < 0.0001$) between centroid size of the nasal bone and PC1 scores is observed, but this correlation is slightly lower than that of the maxilla (Tab. 3). Correlation

between PC2 scores and centroid size of the nasals bone fails to reach significance level. Variation of size of the nasal bone seems to be more pronounced in *C. torquatus* compared to variation in shape while the opposite is the truth in *P. verus* (Fig. 5B).

PC1 scores of the nasal bones are strongly correlated with variation of the total facial size (Spearman $R = 0.93$, $p < 0.05$; Tab. 3). The situation is different when the two species are analysed separately. The correlation coefficient is 0.96 ($p < 0.05$) in *C. torquatus* but only 0.62 ($p < 0.05$) in *P. verus*.

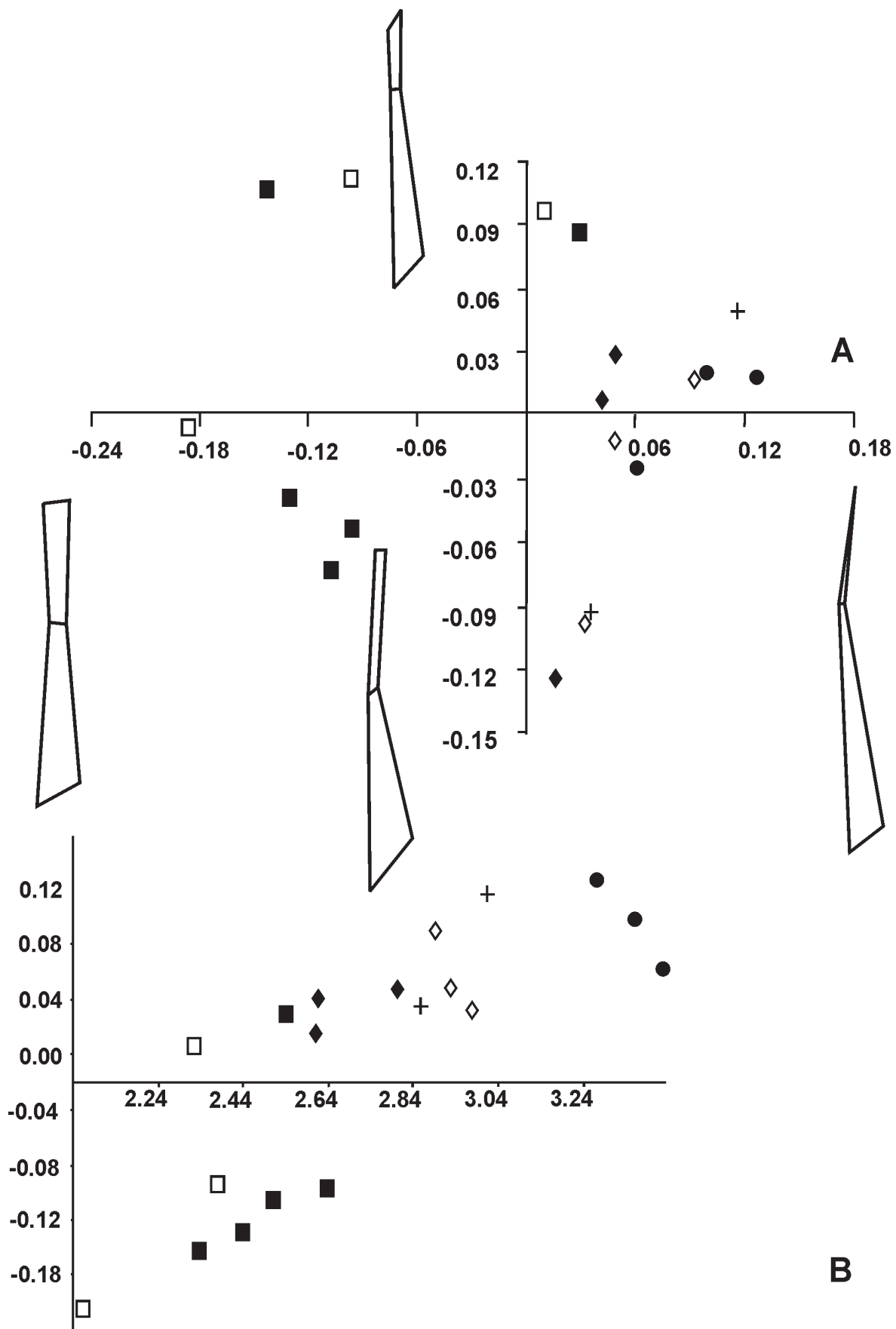
A modularity hypothesis for the nasal bones applied here is based on the concept of differences between the growth processes in the proximal and distal parts of the nasal bones (Fig. 6C). The proximal part grows pre- and perinatally (Sysak, 1960; Richtsmeier *et al.*, 1993; Sonek *et al.*, 2003; Marimoto *et al.*, 2008; Mogra *et al.*, 2010), but the distal part grows in the later ontogenetic stages accordingly to the general facial growth (Enlow, 1966; Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998; O'Higgins & Collard, 2002). Landmarks 1, 2, 3, and 4 were included into the first module and landmarks 5 and 6 into the second one. A test of modularity has confirmed the proposed hypothesis. We thus conclude that the upper and lower parts of the nasal bones vary to a substantial degree independently.

PLS analysis done in MorphoJ has shown that the nasal bone variation is not very strongly correlated with variation of both the maxilla (RV = 0.49, $p = 0.0294$) and the premaxilla (RV = 0.45, $p = 0.0523$, non significant).

Discussion

The results of embryological (Latham, 1970; Sonek *et al.*, 2003; Depew *et al.*, 2005; Marimoto *et al.*, 2008; Mogra *et al.*, 2010), functional anatomical and abundant morphometric (Bunak, 1960; Sysak, 1960; Enlow, 1966; Mooney & Siegel, 1986; Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998; O'Higgins & Collard, 2001; Holton *et al.*, 2010, 2011) studies clearly demonstrate a certain degree of independence of the growth processes of the main bones forming the middle part of the upper facial skeleton: the maxilla, the premaxilla and the nasalia. The results of present study are in very good agreement with those data and demonstrate that the analysis of single bones morphology and growth dynamics could potentially provide a lot of useful additional information that may be of interest from both functional anatomical and systematic points of view. Such an approach is more effective if structures experiencing direct and strong mechanical influence (the molars, the alveolar process, the zygomatic arch) are excluded from a landmark configuration. It is also note-

Figure 4. Principal components analysis of the premaxilla configuration: A — PC1 (horizontal axis) vs PC 2 (vertical axis). Left inset — configuration representing PC1 = -0.16 and PC2 = 0; right inset — configuration representing PC1 = 0.16 and PC2 = 0; bottom inset — configuration representing PC1 = 0 and PC2 = -0.06; top inset — configuration representing PC1 = 0 and PC2 = 0.12 (flat surface rendering); B — plot of PC1 (vertical axis) from PCA vs ln centroid size (horizontal axis). See text for details. Symbols — see legend to Fig. 2.



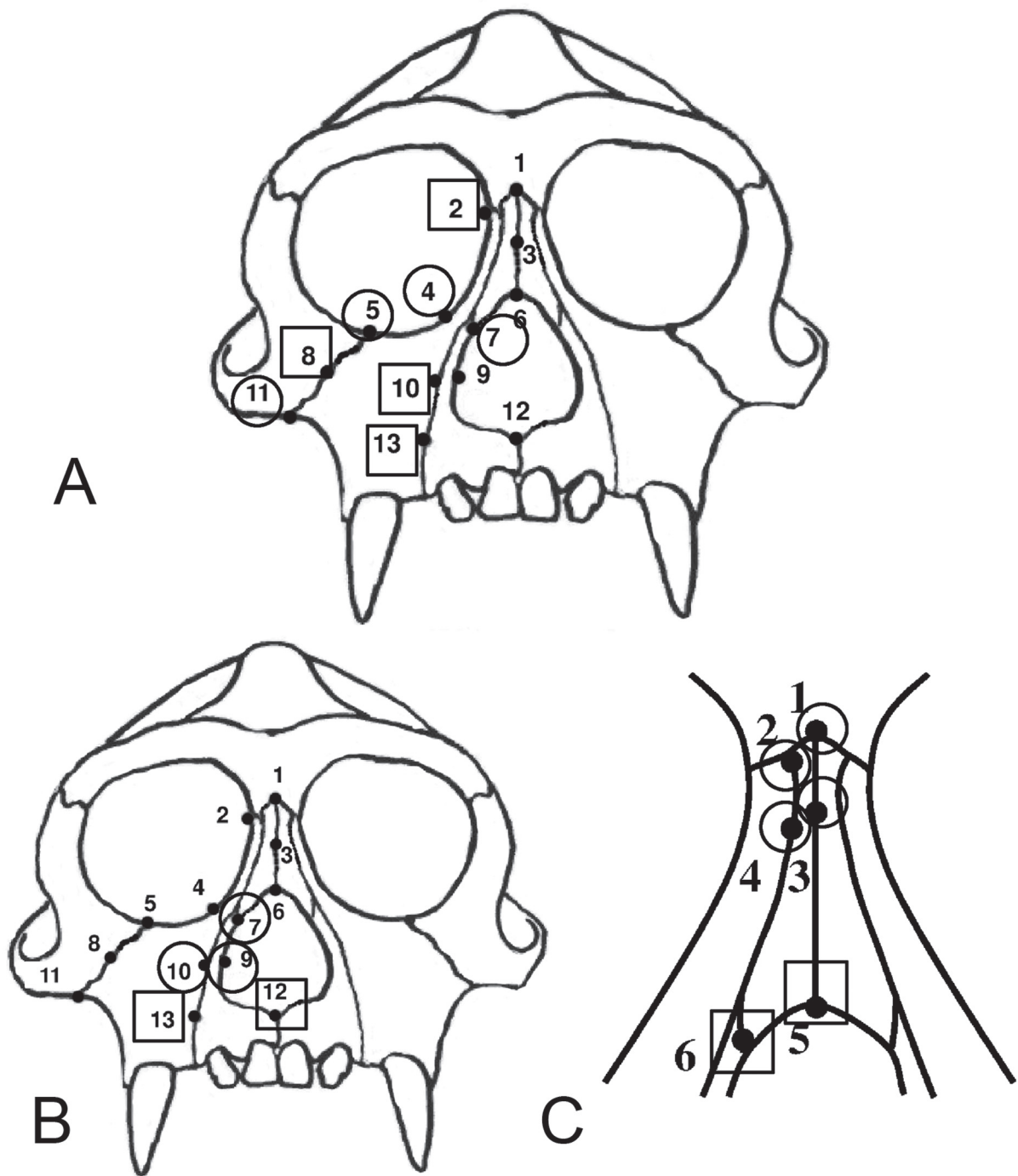


Figure 6. Modularity hypotheses testing: A — the maxilla. The minimal covariation was detected between landmark sets 2, 8, 10, 13 (squares) and 4, 5, 7, 11 (circles); B — the premaxilla. The minimal covariation was detected between landmark sets 12 and 13 (squares) and 7, 9, 10 (circles); C — the nasal bone. 2- and 4-landmarks sets which have minimal covariation. See text for details and Fig. 1 and Tab. 1 for definition of the landmarks.

Figure 5. Principal components analysis of the nasal bone configuration. A — PC1 (horizontal axis) vs PC 2 (vertical axis). Left inset — configuration representing PC1 = -0.14 and PC2 = 0; right inset — configuration representing PC1 = 0.11 and PC2 = 0; bottom inset — configuration representing PC1 = 0 and PC2 = -0.12; top inset — configuration representing PC1 = 0 and PC2 = 0.10 (flat surface rendering); B — plot of PC1 (vertical axis) from PCA vs ln centroid size (horizontal axis). Symbols — see legend to Fig. 2.

worthy that visualized configurations of single bones can be better understood by a reader and more easily interpreted since such configurations are far less complex comparing to a configuration of the whole face. When looking at the later observer's attention gets involuntary concentrated on the most noticeable morphological phenomena. Such as for example intensive growth of the maxilla in vertical and antero-posterior directions which is common for all the primates even for *Homo sapiens* and *Macaca* (Enlow, 1966). Dealing with single bone's morphology could provide information on its "localized" growth events (Enlow, 1966). Single bones cannot be considered as modules but each bone can comprise two or more distinctive functional or/and developmental units which wouldn't be identified without a closer look at the bone's morphology (Enlow, 1966; Klingenberg *et al.*, 2004).

It does not contradict to views on the facial skeleton as a tightly integrated structure. The integration is a result of general somatic growth factors' influence, biomechanical loadings and simple topographic correlations with other bones. One bony element can serve as a matrix for other being a source of quasi-static strain particularly if the two elements are connected with an interdigitated suture (Kopher & Mao, 2003; Herring, 2008). Remodelling maps of different species show that resorptive and depository fields do not coincide with bones' boundaries also argue against "independent" growth of single bones (Enlow, 1966; O'Higgins & Jones, 1998). High correlations of centroid sizes of the maxilla, the premaxilla and the nasal bones found in the present study again confirm a high level of integration in the facial skeleton.

But despite this integration the nasal bones and the premaxilla which do not share first branchial arch origin with the maxilla obviously retain in the adults some features of shape formed during the prenatal phase of growth. Thus careful examination of their morphology and growth could give us additional data on early growth events which is known to be in many cases crucial for emergence of between taxa differences in ontogeny (Franciscus, 1995; O'Higgins *et al.*, 2001). Such differences forms prior to beginning of intensive hormonal and mechanical stimuli activity and thus they are under a stricter genetic control so their morphological variation may be more suitable for phylogenetic researches (Cardini & Elton, 2008a). It can be also seen as an example of evolutionary modules that serve for different functions and are due to this controlled by different genes at different stages of ontogeny (Wagner & Altenberg, 1996). During postnatal growth the shape of each of these bones is substantially modified so research of ontogenetic samples is often more informative than just comparing adult morphology (O'Higgins & Collard, 2002).

An answer to the old question "natal morphology versus ontogenetic scaling" (O'Higgins *et al.*, 2001; Ackermann & Krovitz, 2002; Vidarsdóttir *et al.*, 2002; Cobb & O'Higgins, 2004) will be different depending on what part of the facial skeleton is discussed. Postna-

tal scaling which can be successfully described by the "linear growth model" (O'Higgins & Jones, 1998; O'Higgins *et al.*, 2001; O'Higgins & Collard, 2002) dominates in growth of the maxilla while most specific morphological features of the premaxilla forms prenatally. The proximal and distal parts of the nasal bones seem to behave like relatively independent units. The former attains its nearly adult shape and size very early in ontogeny, probably in the second trimester of gestation (Sonek *et al.*, 2003; Mogra *et al.*, 2010) and the later grows predominantly in the postnatal period in a strong dependence on growth of the maxilla (Richtsmeier *et al.*, 1993; O'Higgins & Jones, 1998).

This fairly complicated picture of interdependent growth processes also means that while a single bone's morphology is worth noting it should be only investigated in the context of the adjacent bones morphology otherwise some facts cannot be explained (Lang & Baumeister, 1982; Hwang *et al.*, 2005).

Since relative importance of different functions of the facial skeleton as well as a set of growth factors (FGF and BMP systems *versus* growth hormone and steroids) change dramatically between the gestation, infancy and adolescence it becomes difficult to outline some "constant" modules which hold its identity during the whole period of growth. Thus it might be a perspective approach to search for modules at each particular stage of ontogeny according to its biologically valid periodization. The premaxilla for instance can be considered as a module in the pre- and perinatal period but later it becomes a part of another module a "core" of which is actively growing maxilla ("muzzle"). Both this stages of the premaxilla's growth leave traces in the definitive morphology of this bone. Trends in the nasal bones are fairly similar: their growth seems to be autonomous during the gestation and probably has its own growth factors but later in ontogeny follows the maxilla growth. Finally, the maxilla (probably excepting frontal process) does not play a substantial role in determining the foetal and early infant primate facial skeleton architecture but becomes a "promoter" of postnatal growth of the face particularly in long-faced animals.

Comparison of the analyses of the whole face and the maxilla configurations. When comparing the whole face and the maxilla configurations (Figs. 2A, B) the most prominent morphological change attracting attention in the both cases is elongation of the muzzle. This phenomenon seems to be the major and the most dynamic event during postnatal growth but in the same time it can "eclipse" many subtle but not less important aspects of the facial skeleton variability. As a matter of fact the results are very similar in analyses of a comprehensive configuration of 31 landmarks including points from the anterior neurocranium and the zygomatic area (O'Higgins & Jones, 1998; O'Higgins *et al.*, 2001), 13 landmarks excluding the neurocranium and the zygomatic area and, finally, 8 landmarks which represent the anterior part of the maxilla only. In all these cases the first PCs accounts for enormous part of the total varia-

tion (not less than 70%) and describes essentially the same morphological features. This trend is particularly strong in the cases when specimens of a long-faced animal species are included in the analysis (Collard & O'Higgins, 2001; O'Higgins & Collard, 2002; Cobb & O'Higgins, 2004; Cardini & Elton, 2008a). According to Hallgrímsson (2004) a murine strain with elongated (i.e. normal) face demonstrated a craniofacial variation pattern which was closer to that in macaques (also long-faced animal) than to another murine strain with the facial skeleton shortened due to a mutation.

In the present study when the "general" configuration (13 landmarks) is analysed separately for the two species they show completely different results. In *Cercocebus* PC 1 again dominates while in *Procolobus* variation is far less "structured" or in the other words it's evenly distributed among the first three PCs. This observation completely confirms the results of the previous study where *C. torquatus* were compared with another orthognathic species, *C. apella* (O'Higgins *et al.*, 2001). The completely identical results of the whole face and maxilla configurations analyses found in our study (Figs. 2, 3; Tab. 3) suggest that rapid postnatal growth of the muzzle depends mostly on the maxilla's growth while the two other bones play a "subordinate" role. For interpretation of these results it may be useful to remember "branchial" origin of the maxilla which makes it ontogenetically closer to the postcranial skeletal elements. Though like in all cranial structures HOX genes are not active in the jaws, the latter have its own segmentation gene cluster, DLX. It is placed close to HOX cluster in the genome and works in the similar to HOX way (Depew *et al.*, 2005). High correlation of growth processes of both jaws with general somatic growth is very well known (Sperber, 2001; Bulygina *et al.*, 2006; Funatsu *et al.*, 2006) as well as the correlation of the length of the muzzle with body size in close Old World monkey species (Collard & O'Higgins, 2001).

In the same time it seems to be the case that elongation of the facial skeleton can lead to a decrease of bite force production capability, particularly at the anterior teeth (Koyabu & Endo, 2009; McGraw *et al.*, 2011). Thus elongation of the muzzle in *C. torquatus* which feed on very hard food can hardly be considered as an adaptive feature but rather as a result of a general body size increase.

Morphological variation of the premaxilla and its possible adaptive and ontogenetic explanation. Evidences for a specific growth pattern of the premaxilla comparing to the maxilla is clear in all the statistical analyses carried out in this study. Centroid sizes of the two bones are strongly correlated but neither PC1 nor PC2 of the premaxilla analysis is correlated with its own centroid size (Tab. 3). Regression analysis (GLM) has demonstrated that SEX and AGE factors do not contribute to PC1 in both species (even in long-faced *C. torquatus*) and it means that the most important morphological features of the bone described by these PCs form early in ontogeny *before* those factors start acting.

Probably the most interesting finding is the postnatal changes in the shape of the premaxilla in *C. torquatus* which demonstrate a kind of curvilinear correlation with centroid size of the bone (Fig. 4B). Modularity hypothesis testing seems to further support this finding showing that the inferior part of the premaxilla (excluding alveolar process) and its frontal process can be considered as relatively independent units (Fig. 6B). Speculatively it can be explained in the following way.

The inferior part of the premaxilla in infant and young mangabeys is expanded and anteriorly shifted while the frontal process is relatively short. It might be an adaptation for accommodation of large incisors (a characteristic trait of all mangabeys) and a way to increase of the whole bone "robustness" before beginning of the extreme masticatory loadings which start in this animals during the first year of life (McGraw, 2011). So in this case masticatory adaptation might express itself not as a result of direct stimulation of bone growth by cyclic strains (Kopher & Mao, 2003; Curtis *et al.*, 2008; Herring, 2008) but prior to this stimulation as a preparation for it. The masticatory muscles do not influence growth during prenatal and early postnatal periods but the nasal septum is very active at that time as a source of quasi-static stress to adjacent bones (Latham, 1970; Mooney & Siegel, 1986). Reaction of the bone to this stimulus may depend a lot on its intrinsic genetically determined capacity to growth. It fits very well with Cheverud's data (1982) according to which the lower breadth of the premaxilla is among very few facial dimensions with high narrow-sense heritability.

Then increase in the lower breadth of the premaxilla slows down while its frontal process begins stretching following the growing maxilla to which it is rigidly mounted by a suture. Thus the whole structure becomes more similar to the pattern of *P. verus* where disproportion of the two parts of the premaxilla is not so pronounced. Intensive antero-inferior growth of the muzzle in the adult male *Cercocebus* certainly involves the premaxilla — its lower part again increases in size. Thus *relative* length of the frontal process again decreases. Superficially such morphology reminds the juvenile pattern. The growth trajectory of the *C. torquatus* premaxilla can also serve as an example of sexual differences which are not directly related to size differences and occur in the final stages of growth (O'Higgins & Jones, 1998; O'Higgins *et al.*, 2001; O'Higgins & Collard, 2002).

Interestingly the premaxilla morphology is more similar in the adults of both species than in subadults due to great differences between the later. Such sharp interspecific differences in the earliest stages of postnatal growth were noticed by Richtsmeier *et al.* (1993). In humans a population-specific pattern of the nasal aperture and the anterior nasal spine also forms mostly prenatally (Latham, 1970; Mooney & Siegel, 1986; Franciscus, 1995) so even very young children from morphologically distinct populations can be correctly

statistically discriminated (Vidarsdóttir *et al.*, 2002). It may suggest that the “traction model” (Latham, 1970; Mooney & Siegel, 1986) that describes links between growth of the nasal septum and the premaxilla through the septo-premaxillary ligament is a universal ontogenetic mechanism in many primate species (see also Schultz, 1963). Thus formation of the adaptive features of the premaxilla morphology may be shifted to the earlier stages of growth to provide for a strict genetic control of growth with minimal biasing influence from common growth factors and biomechanical stimuli.

The nasal bones variation. Substantial inter- and intraspecific variation of the nasal bones in the primates is well established (Schultz, 1963). In *Homo sapiens* morphology of the nasalia is also extremely variable and plays an important role in the classification and comparing populations in both craniological and living people researches (Martin, 1928; Woo & Morant, 1934; Alexeev, 1969, 1974; Howells, 1989; Roseman & Weaver, 2004). Despite this there are very few studies devoted to comprehensive investigation of the nasal bones’ variation and growth, factors influencing its growth and interplay with the other bones’ growth (Enlow, 1966; Lang & Baumeister, 1982; Hwang *et al.*, 2005). Thus the results of the present study may be of some interest despite of using a small and biased sample (see Material and methods).

First of all, the results of all the statistical analyses (PCA, PLS, modularity hypothesis testing) have confirmed *a priori* hypothesis of relatively independent variation in the upper and lower parts of the bone. Like the premaxilla, the nasal bones grow rapidly prenatally when its proximal part almost attains adult size (Sysak, 1960; Sonek *et al.*, 2003; Mogra *et al.*, 2010). But in contrast to the premaxilla it does not seem to have a substantial adaptive value. Due to these facts the proximal part of the nasalia fits to “good module” criteria (Cardini & Elton, 2008a): it grows under strict genetic control while being free from strong functional influences. It is likely that a broader implementation of the nasal bone morphology in the primate craniometrical studies might provide some valuable additional information for phylogenetic reconstructions.

The nasal bone growth dynamic completely changes in postnatal ontogeny. Being rigidly attached to the maxilla by a suture it elongates accordingly to the maxilla elongation. This is more prominent in a long-faced species *C. torquatus* while the nasal bones of *P. verus* seem to be more “independent”. Similar tendencies have been described in many previous researches (Richtsmeier *et al.*, 1993; O’Higgins & Jones, 1998; Cardini & Elton, 2008b). But this “maxilla-dependent” growth is predominantly a feature of the distal part of the bone while the proximal part could keep its original size and shape relatively unchanged.

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