Extreme environmental change and evolution: stress-induced morphological variation is strongly concordant with patterns of evolutionary divergence in shrew mandibles

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Morphological structures often consist of simpler traits which can be viewed as either integrated (e.g. correlated due to functional interdependency) or non-integrated (e.g. functionally independent) traits. The combination of a long-term stabilizing selection on the entire structure with a short-term directional selection on an adaptively important subset of traits should result in long historical persistence of integrated functional complexes, with environmentally induced variation and macroevolutionary change confined mostly to non-integrated traits. We experimentally subjected populations of three closely related species of *Sorex* shrews to environmental stress. As predicted, we found that most of the variation in shrew mandibular shape was localized between rather than within the functional complexes; the patterns of integration did not change between the species. The stress-induced variation was confined to non-integrated traits and was highly concordant with the patterns of evolutionary change—species differed in the same set of non-integrated traits which were most sensitive to stress within each species. We suggest that low environmental and genetic canalization of non-integrated traits may have caused these traits to be most sensitive not only to the environmental but also to genetic perturbations associated with stress. The congruence of stress-induced and between-species patterns of variation in non-integrated traits suggests that stress-induced variation in these traits may play an important role in species divergence.

Keywords: environmental stress; canalization; functional integration; mosaic evolution; *Sorex*

1. INTRODUCTION

Understanding the evolution of complex morphological structures is a central question in evolutionary biology (e.g. Bonner 1988; Raff 1996). Complex structures often consist of simpler morphological traits which can be viewed as either integrated or non-integrated, e.g. functionally integrated traits are highly dependent on each other because they are involved in the same organismal function (such as attachment of a muscle). In contrast, non-integrated traits are functionally and developmentally independent of each other (reviewed in Cheverud 1996).

Quantitative genetics theory predicts that long-term stabilizing selection and correlated mutations will facilitate integrated traits evolving genetic correlations consistent with their functional or developmental relationships and, ultimately, evolving in a correlated manner compared to the more independent evolution of non-integrated traits (Lande 1979, 1980; Cheverud 1982, 1984). Indeed, many studies have documented strong influences of developmental and functional integration on the structure of phenotypic and genetic covariation (Cheverud (1996) and references therein).

However, it is unclear whether the correlated evolution of integrated traits constrains or facilitates adaptive modifications of morphological complexes (reviewed in Arnold 1992; Wagner *et al.* 1997). On one hand, morphological inte-

gration (and the associated environmental canalization) can strongly facilitate adaptive evolution by reducing the environmental variance in each of the integrated traits and, thus, minimizing environmental variance orthogonal to the adaptive direction of morphological change for the entire structure (Lande 1980, 1984; Wagner 1988). On the other hand, morphological integration could have been produced by historically invariant developmental patterns (e.g. Riedl 1978); the high genetic canalization of integrated traits can reduce the expression of genetic variation and slow or bias morphological responses to the present selection (Lande 1979; Stearns 1993; Wagner *et al.* 1997).

Attempts to resolve the constraining and facilitating roles of integration have led to the development of a concept of mosaic evolution (Simpson 1953; Wagner 1996). The theory of mosaic evolution assumes the existence of relatively independent morphological units (e.g. functional complexes) within a structure; such relatively invariant complexes are subject to a long-term stabilizing selection which preserves the basic level of integration necessary across environments. Directional selection exerted by changing environments can favour rearrangements of these complexes, thereby producing changes in the overall structure, while maintaining integration within each complex. Thus, the combination of a long-term stabilizing selection on the entire structure with strong short-term directional selection on a subset of units within a structure should result in higher variation between complexes of integrated traits, but lower variation within these complexes (Simpson 1953; Berg 1960; Cheverud 1984; Wagner 1996; Wagner & Alternberg 1996).

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371

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Here we test two predictions of the mosaic theory of evolution. First, persistent stabilizing selection on complexes of integrated traits favours low sensitivity of the integrated traits to environmental and genetic perturbations (i.e. environmental and genetic canalization; Schmalhausen 1949; Cheverud 1982; Wagner 1988; Wagner *et al.* 1997). High canalization of integrated complexes reduces the heritable phenotypic variation available to natural selection and, thus, can lead to low rates of evolutionary change within integrated complexes. Thus, we can predict a long historical persistence of complexes of integrated traits (Lande 1979; Björklund 1994) and high similarity of recently diverged species in integrated traits (Wagner 1988; Schluter 1996a). On the contrary, non-integrated traits which are relatively free of persistent stabilizing selection may be less environmentally and genetically canalized (Stearns & Kawecki 1994; Stearns *et al.* 1995). This should lead to greater variability in non-integrated traits in response to both environmental and genetic perturbations and to faster evolution in these traits (Wagner 1996; Wagner *et al.* 1997). Thus, we can predict that recently diverged species should be the most different in non-integrated traits. Second, if lower environmental canalization of non-integrated traits is associated with their lower genetic canalization (Gavrilets & Hastings 1994; Wagner *et al.* 1997), then the variation between recently diverged species should be similar to the environmentally induced variation within each species— species should differ the most in the same traits that are the most sensitive to environmental variation within species.

Three closely related species of *Sorex* shrews provide a good system in which to examine these predictions experimentally. First, existing work on the anatomy of the shrew mandible allowed us to assign mandibular areas *a priori* to integrated (i.e. participating in the attachment of the same muscle) and non-integrated units (e.g. Kindahl 1959; Dötsch 1982). Second, previous work on the sensitivity of the shrew mandible to environmental conditions (Badyaev *et al.* 2000) allowed us to design an appropriate experiment for the study of environment-induced variation. Finally, the morphological variation in the shrew mandible (particularly in the muscle attachments which determine bite force; Carraway & Verts 1994) is strongly associated with fitness and is under strong current selection (Badyaev *et al.* 2000). Under our predictions, (i) the shrew species should be most similar in their structure and position of integrated complexes (i.e. muscle attachment groups) and differ mostly in non-integrated traits (i.e. mandible tissues not associated with muscle attachments), and (ii) non-integrated traits should be more sensitive to the experimental increase in environmental variation than integrated traits and the patterns of environmentally induced variation, and the between-species variation should be similar in non-integrated traits.

2. MATERIAL AND METHODS

(a) *Data collection*

The study was carried out in June–July of 1994–1996 on eight experimental plots (*ca.* 17 ha each) located in four study sites within 32 km of one another in the Swan River Valley of western Montana, USA. Each study site contained control (untreated) plots and plots where the overstorey vegetation was removed. We designed our study within these plots to minimize the effects of immigration and emigration following treatments (see Badyaev *et al.* (2000) for details of the experimental design and trapping schedules). The vegetation removal treatment creates highly stressful conditions for shrews, as evidenced by large increases in the developmental instability of shrew embryos and by a decrease in the individual conditions of adults (Badyaev *et al.* 2000). We examined 560 two- to three-month-old individuals of three closely related *Sorex* species (Fumagalli *et al.* 1999; see Foresman (1999) for details of the species biology): *Sorex cinereus* (control, 46 males and 43 females, and vegetation removal, 74 males and 44 females), *Sorex monticolus* (control, 37 males and 37 females, and vegetation removal, 39 males and 38 females) and *Sorex vagrans* (control, 46 males and 52 females, and vegetation removal, 46 males and 58 females). All sex-related variation was removed from the data in general linear models and standardized residuals were used for all analyses.

Left and right shrew mandibles were positioned on a slide and then photographed under ×7.5 magnification using an Olympic SZH stereo photomicroscope and a video capture board. The resulting images were further magnified ×2 using Mocha Image Analysis software (Jandel Scientific). The data were the *x*- and *y*-coordinates of 17 homologous morphological landmarks (figure 1*a*). In studies such as ours, the variance resulting from the positioning of a mandible under a microscope is typically much higher than the variance from repeated measures of already scanned images. Thus, we used the repositioning error as a measurement error term in our analysis. Each mandible was repositioned and digitized three times. High magnification and three replicates for each measure allowed us to minimize and estimate the measurement error. Repeated measures were separated by several measurement sessions. Both mandible photography (by a laboratory technician) and mandible measurements by A.V.B. were conducted without prior knowledge of the treatment, sex or species of the measured animal. Thus, we assumed that the measurement error contributed equally to each treatment category.

To describe the functional integration in the shrew mandible, we selected landmarks associated with muscle attachment points and functionally related units of dentition (after Ärnbäck-Christie-Linde 1907; Kindahl 1959; Dötsch 1982; Dannelid 1998; Reumer 1998; shaded areas in figure 1*a*). We identified landmarks as being 'integrated' when they were associated with the attachment of the same muscle (e.g. integrated landmarks 6 and 7 are associated with attachment of the muscle musculi pterygoideus medialis). Functionally and developmentally independent tissues of the mandible were identified as non-integrated (figure 1). Patterns of integration between landmarks were evident in the strong covariation between landmarks (figure 1*b*; see § 2(*c*)); these patterns were highly congruent to those described *a priori* from the literature.

(b) *Data analysis*

Here we focused on the variation in mandible shape; thus, all variation in mandible size was eliminated before the analyses by scaling all specimens to unit centroid size. We applied a single Procrustes superimposition (generalized orthogonal least-squares fit; Rohlf & Slice 1990) to align the landmark configurations from all species, treatments, individuals, body sides and replicas simultaneously (after Klingenberg & McIntyre 1998). Before the superimposition, left mandibles were reflected to their mirror images by assigning a negative
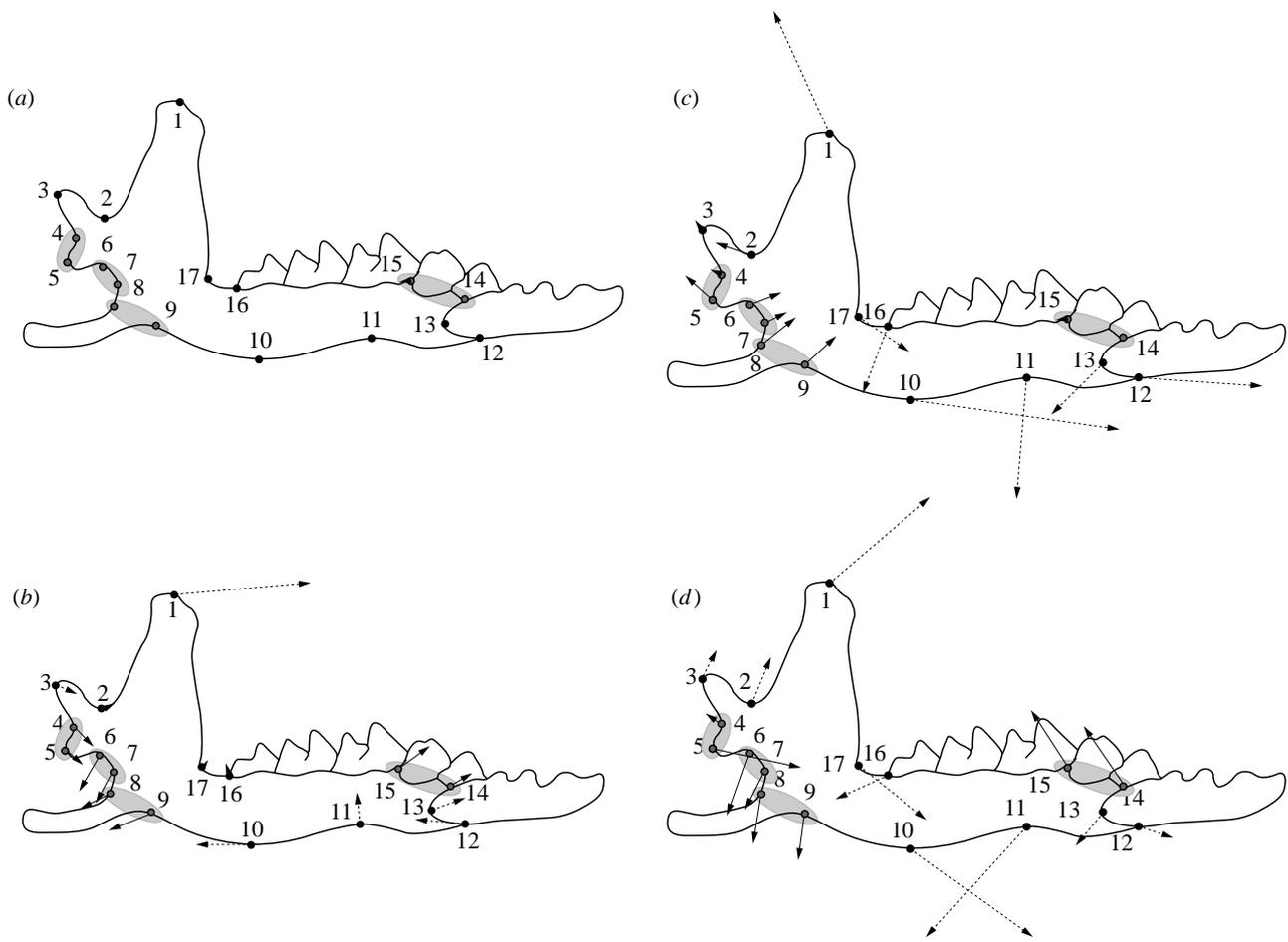
Figure 1. (*a*) Landmarks reflecting functional integration in the shrew mandible and principal components of the covariance patterns in landmark displacement due to variation (*b*) between individuals, (*c*) between treatments and (*d*) between species. Shaded areas indicate functionally integrated units and the numbers show homologous landmarks (integrated, solid lines and non-integrated, dashed lines; see §2). The PC coefficients are shown as a vector originating at the mean configuration of the landmark, and the length and direction of the PC coefficients. The PC1s for each effect and the accounted variation in the corresponding Procrustes mean squares are (*b*) 23.2%, (*c*) 73.2% and (*d*) 89.1%. The length of the vectors is proportionally magnified by a factor of ten for better visibility.

sign to their *x*-coordinates. We calculated the overall consensus of superimposed configurations with the SAS/IML (interactive matrix language) code provided by C. Klingenberg.

The variance in the set of optimally aligned landmark configurations (hereafter Procrustes coordinates) was then partitioned in ANOVA models (Goodall 1991). The variation in each set of Procrustes coordinates was assumed to be due to a combination of the effects of species, treatment, individual, body side and measurement replicate. In this ANOVA model, the individual and treatment were entered as random effects and body side as a fixed effect. The individual effects were nested within treatment groups. Degrees of freedom for the Procrustes ANOVA were calculated following Goodall (1991) and Klingenberg & McIntyre (1998).

(c) *Localization and visualization of effects*

To partition the effects of each landmark on the overall variation in mandible shape, we first summed the *x* and *y* mean squares of each landmark (Klingenberg & McIntyre 1998). We computed the variance components of these mean squares according to the expected mean squares for each of the effects (e.g. species, treatment and individual). This allowed us to localize influential landmarks for each effect separately (see

Klingenberg & McIntyre 1998). To examine the patterns of joint variation in the landmarks due to each effect, we analysed the covariance matrices of the Procrustes coordinates. Based on the expected mean squares, we computed separate matrices of the sums of squares and cross-products for the between-species, between-treatment, between-individual, between-sides and between-replicates variations (after Klingenberg & McIntyre 1998). To visualize the patterns of covariation in the landmarks due to each effect, we represented the principal components (PCs) of each of the matrices graphically as displacement of the landmarks from their consensus position. The vector associated with each landmark represents the direction and intensity of displacement of this landmark due to an effect.

To examine the similarity between the between-species, between-treatment and between-individual patterns of landmark covariation, we calculated the angles between corresponding PC1 vectors. For the PCs of two groups, the angle between them is the arc cosine of the inner product of the two vector elements. The statistical significance of the vector angles was assessed with resampling of the within-sample PC coefficients for each effect. We specifically compared the correlations and corresponding angles for the vectors of displacement of the integrated and non-integrated landmarks due to each effect.
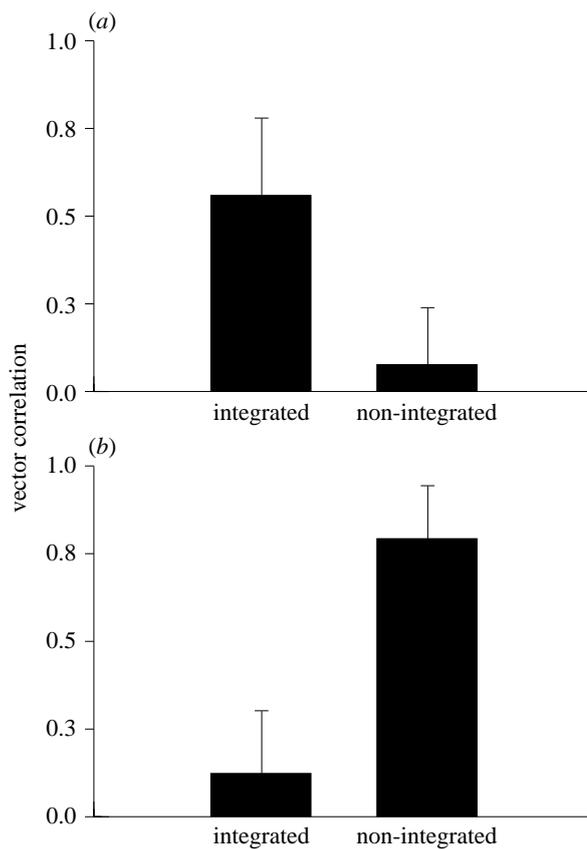
Figure 2. Vector correlations (mean and the bootstrapped standard errors of the estimates) of integrated and non-integrated landmark displacements for (*a*) between-species versus between-individual variation ($t = 4.73$ and $p < 0.001$) (species are more similar in patterns of displacement of integrated landmarks than in non-integrated landmarks), and (*b*) between-species versus between-treatment variation ($t = 2.49$ and $p = 0.01$) (species differ the most in the same set of non-integrated landmarks which are most strongly displaced by stress in each species).

3. RESULTS

The between-individual variation in landmarks revealed a strong pattern of coordinated displacements (figure 1*b*). The joint landmark displacement was highly concordant with the functional relationships in the shrew mandible (figure 1*a*), indicating that our *a priori* designation of landmark integration is biologically meaningful. Landmarks within the integrated units covaried with other landmarks within the same functional unit, but not with landmarks in different units or with non-integrated landmarks (figure 1*b*). Integrated landmarks 4–5, 6–7, 8–9 and 14–15 varied in highly coordinated patterns not only between individuals (figure 1*b*), but also between treatments (figure 1*c*) and between species (with the exception of landmarks 4 and 5, figure 1*d*). The historical persistence of functional integration is illustrated by the similarity of the between-individual and between-species variation in integrated landmarks (figure 2*a*). The effects of the between-individual variation were relatively evenly distributed among all landmarks (except for a large effect of landmark 1; table 1) (Procrustes ANOVA for the effect of individual, $MS = 0.54$, $F = 4.30$ and

$p < 0.0001$). PC1 accounted for only 23.2% of all variation and the first five PCs accounted for 62.7%.

Environmental stress had a large effect on mandible shape ($MS = 3.51$, $F = 6.43$ and $p = 0.0004$), but most of the stress-induced variation occurred in the non-integrated landmarks resulting in highly localized patterns of landmark displacement (table 1 and figure 1*c*). The PC1 for the effect of stress accounted for 73.2% of all the variation and most of the stress-induced variation occurred due to the displacement of non-integrated landmarks (landmarks 1, 10–13, 16 and 17; table 1 and figure 1*c*).

Mandible shape differed strongly between species ($MS = 233.96$, $F = 66.57$ and $p = 0.003$), but the between-species variation was limited to only a few landmarks and nearly all (89.1%) of the between-species variation in 17 landmarks was accounted for by PC1 (figure 1*d*). Similarly to the stress-induced variation within each species, the between-species variation was mostly due to variation in non-integrated landmarks 1, 10, 11, 16 and 17 (table 1 and figure 1*d*). Moreover, the direction and magnitude of the displacement of non-integrated landmarks was similar for the species and stress effects (figure 2*b*), i.e. species were most different in the same non-integrated landmarks that were most strongly displaced by stress in each species.

4. DISCUSSION

The constraining and facilitating roles of functional integration in the evolution of complex structures are addressed by the concept of mosaic evolution (e.g. Simpson 1953; Wagner 1996). This concept predicts that the combination of a long-term stabilizing selection on the entire structure with strong short-term directional selection on an adaptively important subset of traits (e.g. functional complexes) should result in parcellation—the evolution of relatively autonomous complexes of traits within complex structures. Such complexes may be capable of mutual rearrangements favoured by directional selection, while maintaining high integration within each complex (Berg 1960; Vermeji 1974; Wagner 1996; Wagner & Altenberg 1996).

Here we showed that macroevolutionary change in the shrew mandible is concordant with interspecific predictions of mosaic evolution. We found strong support for both of our predictions. First, we showed that shrew species were most similar in their relative placement of integrated landmarks (e.g. muscle attachments; figures 1*d* and 2*a*) and were most different in their placement of non-integrated landmarks (figures 1*c* and 2*b*). This result is expected if persistent stabilizing selection on integrated traits leads to higher environmental and genetic canalization of these traits (e.g. Gavrilets & Hastings 1994; Wagner *et al.* 1997); such canalization ultimately results in a long historical persistence of integrated functional complexes (e.g. Tucic & Avramov 1996; figures 1*d* and 2*b*). The absence of strong stabilizing selection on non-integrated traits results in their lower environmental canalization (Stearns 1993; Stearns *et al.* 1995) and, possibly, in lower genetic canalization (e.g. Wagner *et al.* 1997). Low environmental canalization may explain the high sensitivity of non-integrated traits to the effects of stress

Table 1. *Variance components (% variance) for each landmark for the effects in the Procrustes ANOVA of mandible shape for three* Sorex *species*

(All variances are multiplied by 10^6.)

landmark	species	treatment	individual	side	side × individual	error
1	3562 (35)	935 (9)	2432 (24)	427 (4)	2076 (20)	871 (9)
2	342 (29)	190 (16)	198 (17)	40 (3)	246 (20)	180 (15)
3	144 (9)	0 (0)	390 (24)	88 (5)	655 (40)	350 (22)
4	129 (11)	1 (0)	193 (17)	131 (11)	417 (36)	301 (26)
5	595 (26)	57 (3)	439 (19)	205 (9)	669 (29)	355 (15)
6	246 (20)	87 (7)	297 (25)	87 (7)	310 (26)	179 (15)
7	53 (7)	25 (3)	155 (20)	123 (16)	278 (36)	142 (18)
8	313 (26)	79 (6)	332 (27)	6 (1)	305 (25)	193 (16)
9	501 (20)	137 (6)	702 (29)	105 (4)	576 (24)	432 (18)
10	904 (17)	658 (13)	257 (5)	512 (10)	1883 (36)	1031 (20)
11	781 (19)	739 (18)	549 (13)	62 (2)	1144 (27)	910 (22)
12	52 (3)	213 (11)	405 (22)	4 (0)	761 (41)	431 (23)
13	51 (5)	139 (13)	152 (14)	0 (0)	530 (48)	226 (21)
14	174 (13)	8 (1)	261 (19)	50 (4)	575 (42)	317 (23)
15	356 (7)	52 (1)	609 (12)	17 (0)	3044 (62)	857 (17)
16	249 (11)	176 (8)	136 (6)	192 (9)	952 (43)	495 (23)
17	275 (21)	192 (15)	155 (12)	15 (1)	505 (38)	181 (14)

(figure 1*c*). Reduced genetic canalization of these traits may account for their stronger response to natural selection and genetic drift (Stearns 1993; Wagner *et al.* 1997); faster evolutionary change in non-integrated traits is evident in the strong divergence of related species in these traits (figures 1*d* and 2*b*).

The overall pattern of variation in the shrew mandible can be described by low phenotypic variation and low macroevolutionary change within functional complexes, but high variation and more frequent macroevolutionary change between functional complexes (table 1 and figures 1 and 2). This combination could provide a necessary balance between the requirements for the basic level of integration across environments (e.g. maintaining muscle attachment groups) and the need for an adaptive response to changing conditions (e.g. rearranging juxtaposition of muscle groups) (e.g. Simpson 1953; Berg 1960; Cheverud 1984; Wagner 1996; Wagner & Alternberg 1996). Similarly, Churchill (1996) found strong evidence for mosaic evolution of recent humans; a model combining the integration of some traits and parcellation of other traits most closely accounted for by the available fossil data.

Low environmental canalization of non-integrated traits may be associated (either directly or indirectly) with low genetic canalization of these traits (Gavrilets & Hastings 1994; Wagner *et al.* 1997). Thus, non-integrated traits may be highly sensitive not only to environmental but also to genetic pressures (such as selection and genetic drift). In this case, the patterns of stress-induced variation within a species should be similar to the between-species variation. We found that the shrew species differed from each other in the same set of traits (non-integrated landmarks) that were most sensitive to stress within each of the species (figure 2*b*).

Periods of intense stress can induce morphological change by disrupting normal development and thereby increasing morphological variation (reviewed in Hoffmann & Parsons 1997). Stress also can alter the population fitness landscape, thus creating an opportunity for new directions of adaptive divergence (Arnold 1992). In addition, stress is often associated with a strong decrease in population size and a corresponding increase in the effects of genetic drift (Hoffmann & Parsons (1997) and references therein). It is possible that less canalized, non-integrated traits are more sensitive to both the disruptive effects of stress during development and the effects of selection and genetic drift associated with stress (e.g. Bryant & Meffert 1988; Wagner *et al.* 1997), thus explaining the parallelism between stress-induced variation and evolutionary change in the shrew mandible (figures 1*d* and 2*b*).

We found that functional integration strongly influences the phenotypic variation in mandible shape in shrews; the between-individual and between-species variation (figure 1*b,d*) were highly concordant with *a priori* described patterns of functional relationships. For example, landmarks 8 and 9, which consistently covaried with each other (figure 1), are attachments of the musculi masseter muscle along the lateral aspect of the angular process (figure 1*a*; Dötsch 1982). Landmarks 14 and 15 also showed correlated variation among individuals and species and these are the attachment points of the musculi digastric muscle at the mandibular ramus (figure 1*a*; Dötsch 1982). Concurrently, landmarks which did not show correlated variation were not associated with functionally related tissues (e.g. landmarks 12 and 13 located around functionally and developmentally independent incisors; Kindahl 1959).

In shrews, periods of intense environmental stress are often associated with increased food competition caused by major habitat alterations (e.g. Badyaev *et al.* (2000) and references therein) or extreme population fluctuations (e.g. Zakharov *et al.* 1991). Stress-induced modifications of the shrew mandible traits may be beneficial if the resulting differences in bite force or chewing patterns allow consumption of new prey items (Carraway & Verts 1994). Small populations which are separated by

unsuitable habitats and increased competition for similar resources can favour rapid divergence and increase reproductive isolation among new forms produced by stress (Schluter 1996*b*). Interestingly, the traits in the shrew mandible that were most sensitive to stress (e.g. T-traits in Badyaev *et al.* 2000; landmarks 10–14, 16 and 17, this study) are also closely associated with chewing patterns and the diet (Carraway & Verts 1994; Dannelid 1998). Moreover, these traits commonly differ among closely related shrew species (Dannelid (1998) and references therein; figure 1*d*). For example, Sará (1996) found that two closely related species of the genus *Crocidura* were most different in their position of the lower mandibular branch (landmarks of 10 and 11; figure 1*a*), the area associated with differences in chewing patterns.

In summary, our analyses of the morphological variation in the shrew mandible have produced two principal results. First, the phenotypic variation and macroevolutionary change was mostly localized between rather than within the functional complexes, as predicted by the mosaic theory of morphological evolution. A long historical persistence of functional complexes was evident in the species similarities in their patterns of integration. Second, the stress-induced variation was highly concordant with the patterns of evolutionary change; the shrew species differed in the same sets of non-integrated traits which were most sensitive to stress in each species. We suggest that low environmental and genetic canalization of non-integrated traits may have caused these traits to be most sensitive not only to environmental pressures, but also to the changes in selection and genetic drift associated with stress.

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