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FUNCTIONAL UNITS AND THEIR EVOLUTION

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INTRODUCTION

According to the neo-Darwinian ideal, organisms can be decomposed into atomistic traits or characters which, by definition, represent units of phenotypic evolution. Implicit in this view is the assumption that any given character can evolve independent of all other characters. As such, it is free to respond to

selection according to its own, unique relationship with the environment, unfettered by association with its fellows. While such a characterization of the neo-Darwinian position could justifiably be regarded as overstated and few, if any, modern biologists would profess it absolutely, it is at the same time the unstated credo of practicing systematists who, as a matter of pragmatic routine, must atomize their organisms into characters with little or no regard as to how they might be associated genetically, developmentally, or functionally.

This paradox is at the heart of our ignorance of how phenotypes evolve and it manifests a growing philosophical schism in the field. At one extreme we have the traditional, atomistic approach as noted—organisms viewed as little more than "bags of characters," each character available for individual honing by environmental selection to create adapted phenotypes (Rieppel, 1986). Accordingly, the phenotype is held to be highly responsive to the exigencies of an ever-changing environment, virtually protean through evolutionary time, with diversity the inevitable outcome. Change, though inevitable, occurs incrementally, character by character. Phenotypic stasis is seen as exceptional and explicable only by reference to unusually persistent environmental conditions (Simpson, 1953). In short, the organism can be understood as the sum of its parts in relation to the environment.

Yet this view of the phenotype is transparently false. Characters are not diffused through space, but are grouped and bounded within organisms where they exist in ordered relations with one another to form tissues, organs, and systems (Whyte, 1965). These character associations are further related temporally through development and growth, and dynamically through functional interaction. As historical entities, organisms transmit not only their morphological features from one generation to the next, but their unique set of organizational properties, as well—the patterns of interaction among their characters. Thus, by virtue of being *organismal* attributes, characters *must* evince associations with other characters. Organisms thus manifest complexly nested webs of character interaction and integration, such that a phenotypic change in one character will almost certainly have an impact on others.

This inescapable conclusion, virtually a truism, has led to an extreme, structuralist conception of the phenotype in opposition to atomistic doctrine (e.g., Whyte, 1965; Allen, 1980; Wake *et al.*, 1983; Webster and Goodwin, 1996). In this view, rather than the character-environment relationship, it is character integration that is held to be paramount in phenotypic evolution. This integration is necessary to maintain adaptive phenotypes in the face of environmental changes that would tend to disrupt them. As such, organisms are viewed as self-maintaining, self-stabilized, "autopoietic" systems:

The range of ontogenetic and phylogenetic change of one element is, therefore, determined by the structural and functional properties of all other elements. Each ontogenetic or phylogenetic change of the system must remain within the functional

limits of the process of circular production and maintenance of the elements, or the system itself will decompose (Wake *et al.*, 1983, p. 218).

Thus, successful phenotypes "gel," i.e., they become increasingly self-stabilized and resistant to phenotypic change due to the internal dynamics of their character associations. Long-term phenotypic stasis is expected and evident in *Baupläne* within which diversity is limited to "variations on a theme." Significant phenotypic change is seen as rare and the result of unusual processes or circumstances that perturb intrinsic stability. Implicit is that such perturbations will cause a rapid phenotypic reorganization followed by return to an integrated steady state (Arthur, 1997). Character integration is an emergent property of whole organisms, hence in this view the organism is more than the sum of its parts—it is, moreover, a set of organizational and coordinative conditions (Whyte, 1965).

In this dialectical view of the organism we are confronted, on the one hand, by evolutionarily malleable phenotypes that evolve in lock-step with the environment, and on the other, by evolutionarily static phenotypes that are intrinsically resistant to evolutionary change. In the former view an adaptive state is maintained dynamically by matching individual characters to the environment, while in the latter an adaptive state is maintained by matching suites of characters to the internal demands of coordination and integration, irrespective of the environment. In the first, phenotypic change is the null model of evolution, diversity its outcome, and stasis exceptional; in the second, stasis is the null model, disparity its outcome, and phenotypic change exceptional.

Although, as noted, the atomistic view cannot be wholly correct because organisms are integrated wholes, neither can the structuralist view be accepted entirely. It is clear that traits sometimes do behave atomistically, that organisms do maintain adaptive phenotype-environment matching and that *Baupläne* are remarkably diverse. Thus, while characters might not be truly atomistic, in many cases they are at least "quasi-independent" entities able to respond adaptively to environmental selection pressures (Lewontin, 1984; Wagner, 1996). Furthermore, there is no denying the efficacy and power of atomistic approaches, imperfect as they are, in evolutionary analysis; the success of cladistic methods in morphological systematics is proof enough of this. Clearly there exists a middle ground for phenotypic evolution.

To a large extent the philosophical differences just outlined reflect different emphases. The atomistic approach focuses on characters and adaptive evolution, whereas the structuralist approach focuses on *Baupläne* and nonadaptive forces in evolution, such as constraint. These foci follow logically from the fact that characters and body plans are most apparent as stable historical entities, i.e., phenotypic "units." However, there is a third level of organization that also manifests elements of stability, namely the character complex (Wagner and Schwenk, 2000). Evolutionary attributes of character complexes have received comparatively little attention. As Wagner and Schwenk (2000) pointed out, the

emergent stability evident at each level (character, character complex, *Bauplan*) is believed to reflect different causal mechanisms, hence each requires a different empirical and conceptual characterization. The object of this essay is to explore the middle ground of phenotypic evolution reflected in character complexes. Specifically, I consider the notion of "functional units," or character complexes identified by shared functional interactions. Examples are drawn from vertebrate zoology because this is where my expertise lies, but the concepts should be no less applicable to other animal systems and, with some modification, to plants as well.

WORKING CHARACTER CONCEPT

Although the character concept is by no means resolved (the subject of this book), neither is it of central concern here. It is enough to know that there are such things as characters and that these represent individuated units of phenotypic evolution (Wagner, 1999). As such, they are "quasi-independent" (Lewontin, 1984) and "quasi-autonomous" (Wagner, 1995, 1996, 1999) parts of the phenotype, meaning, in the first place, that they are capable of evolutionary change somewhat independent of change in other "characters," a property largely contingent upon the fact that they are, in the second place, developmentally autonomous units individuated from other such units. In short, my use of "character" in this paper follows the biological homology concept (e.g., Roth, 1984, 1986; Wagner, 1986, 1989a,b, 1999; see also Bock, 1963): characters are units of phenotypic evolution that are individuated by a unique set of developmental constraints. Homology among characters can be recognized at the phenotypic level at which these constraints are shared, i.e., homologues share the same set of constraints and variational properties (Wagner, 1999).

THE FUNCTIONAL UNIT CONCEPT

Gans (1969) attributed the concept of the "functional unit" to van der Klaauw (1945) and in a modern, formalistic sense this is true. However, that organisms comprise groups of interrelated parts was recognized as early as Aristotle (Russell, 1916). Etienne Geoffroy Saint-Hillaire saw the relationship among parts as the basis for "unity of plan" among diverse species: "Now it is evident that the sole general principle one can apply is given by the position, the relations, and the dependencies of the parts, that is to say, by what I name and include under the term of *connections*" (Geoffroy, 1818; in Russell, 1916, p. 53). However, Geoffroy's "principle of connections" was nonfunctional in the sense that the "relations" and "dependencies" to which he referred were purely

morphological. These morphological connections imposed on organs a particular function, rather than the converse.

In contrast, Georges Cuvier elaborated the view that it is the functional interrelationships among parts that are the primary determinants of form. As such, form followed from function. Thus the notion of functional integration is most clearly identified with Cuvier and his "principle of the conditions of existence": "It is on this mutual dependence of the functions and the assistance which they lend one to another that are founded the laws that determine the relations of their organs; these laws are as inevitable as the laws of metaphysics and mathematics, for it is evident that a proper harmony between organs that act one upon another is a necessary condition of the existence of the being to which they belong" (Cuvier, 1800; in Russell, 1916, p. 34). This principle is the basis for Cuvier's better known "principle of correlation" with which he asserted that one could (in most cases) reliably reconstruct the whole organism from one of its parts: "This must necessarily be so: for all the organs of an animal form a single system, the parts of which hang together, and act and re-act upon one another; and no modifications can appear in one part without bringing about corresponding modifications in all the rest" (Cuvier, 1826; in Russell, 1916, p. 35). Owen (1837) suggested that Cuvier's ideas were actually a refinement of much earlier 18th century ideas, but this is not wholly justified; in any case, the source of Cuvier's "functionalism" lies ultimately with Aristotle.

It is apparent from the quote that Cuvier's principal concern was the whole organism, which he viewed as a composite of interrelated parts. Most relevant here, however, is that Cuvier also applied his principle of correlation to lower hierarchical levels such as among parts within a single organ or organ system (Russell, 1916). Furthermore, although Cuvier believed that organisms were "adapted" to their environments, his "conditions of existence" related not to the Darwinian notion of the external environment ("the struggle for existence"), but to *intraorganismal* function. As summarized by Russell (1916, p. 34), "The very condition of existence of a living thing, and part of the essential definition of it, is that its parts work together for the good of the whole." Thus Cuvier perceived organisms as hierarchically organized into systems and "characters" whose phenotypes were ultimately determined by the internal dynamics of functional interaction. Although Cuvier was not an evolutionist, his work foreshadowed not only the functional unit concept, but systems-level approaches to the phenotype (e.g., Dullemeijer, 1974; Riedl, 1977; Wagner, 1986) and the structuralist notion of "internal selection" (Whyte, 1965; Wake *et al.*, 1983; Arthur, 1997; Wagner and Schwenk, 2000), i.e., the idea that the internal dynamics, or temporal and functional relationships among parts, create selection pressures on character phenotypes independent of the external environment (see later).

Other workers such as Owen (1837, 1866) embraced Cuvier's principles, but most 19th century morphologists continued to focus on anatomy and embryology while functional analysis was relegated to the separate tradition of physiology. Functional morphology as a discipline did not emerge until mid-20th

Olson and Miller (1958) wrote an ambitious book that developed a quantitative, statistical approach to the concept of morphological integration within organisms. They posit at the outset what is, in effect, Cuvier's "principle of the conditions of existence," little modified: "Each component of the organism must be formed so that the part it plays in the existence and function of the whole is carried out properly with respect to all other parts. It would seem logical that the degree of interdependency of any two or more morphological components in development and function would bear a direct relationship to the extent of their particular morphological integration" (p. v). They went on to show that certain groups of morphological characters within an organism were more tightly correlated, in a statistical sense, than other such sets of characters and that tightly correlated (integrated) character sets usually corresponded to functionally interrelated suites of characters, or "F-groups." F-groups therefore represent functional units which they found to have a coherence not evident in functionally unrelated characters. Their system of correlation and covariance emphasized the hierarchical organization of such relationships within organisms with centers of integration organized around functional complexes and the complexes, themselves, integrated within the whole organism.

Bock (1963) acknowledged that characters in a system compose a set of functionally interrelated parts whose mutual interactions tend to influence patterns of phenotypic evolution in the system (and the organism). Bock (1964) and Bock and von Wahlert (1965, p. 272) formalized this idea in their own concept of the "functional complex or functional unit" which they suggested is composed of "a group of smaller features which act together to carry out a common biological role." The essential point is that all participating characters in a functional unit subscribe to the same "biological role," i.e., the part played by the character complex in the natural life of the animal which determines a set of selection pressures to which it is exposed (for example, the function of horns in mountain sheep might be to absorb the energy of impact incurred during head-butting behavior, but their biological role is to establish dominance in a polygynous breeding hierarchy, the "source" of selection for the evolution of horns). Individual characters might participate in more than one functional unit, but a functional unit is uniquely characterized by a set of characters that all function together to perform a particular biological role. The application of "biological role" to functional units is similar to Wagner and Schwenk's (2000) use of "proper function" to characterize "evolutionarily stable configurations" (see later).

Importantly, Bock and von Wahlert (1965, p. 272) explored the relationship between part and whole in their conception of the functional unit. They noted that:

No real distinction exists between individual features and character complexes; forms, functions, and biological roles may be described for each. Usually, however, the biological roles of the individual features are the same as those of the character complex; this concurrence of biological roles results from the traditional division of the major functional units of the organism into smaller but still distinguishable morphological units.

They thus express the hierarchical organization of organismal phenotype into systems, or functional units, and these into individuated (morphological) characters. Moreover, by suggesting that all individual characters of the complex share the same set of biological roles as the functional unit, itself, they highlight the "comparatively separate" nature of functional units within the organism, i.e., not only the characters are individuated, but the functional units are, to some extent, as well.

Bock and von Wahlert (1965, p. 272) go on to acknowledge the difficulty inherent in accurately atomizing such systems into characters ("features"): "Should, for example, a muscle-bone unit be considered as a single feature or should this unit be considered as a character complex that can be divided into smaller units—the muscle and bones to which it attaches. Is the hind limb of a tetrapod, which everyone would agree is a character complex, a single feature or a series of smaller features?"

With the concept well-established and sophisticated functional analyses on the rise, functional units were increasingly invoked in the empirical literature (Gans, 1969). Gans (1969), however, complained that the concept was being misapplied by most workers. His objection seems partly to have stemmed from his erroneous conflation of "functional component" and "functional unit" concepts (see earlier discussion). In any case, he suggested that separate concepts were required to distinguish between essentially anatomical subdivisions and true, functional subdivisions. He proposed to call the former "mechanical units" which were to be recognized by relative degrees of movement: relatively little movement among component parts within a unit and relatively greater movement between and among units. "Functional unit" was to be reserved for cases in which a much greater knowledge of function in a biological context was available. Gans (1969) objected to the use of "functional unit" when an individual element might participate in different functions. However, overlap among functional units has been recognized and even emphasized by all workers noted earlier. Despite his concerns about overlap, Gans (1969, p. 366) recognized that "there is a basic coordination of parts that obviously circumscribes certain regions."

Finally, Wagner and Schwenk (2000) identified a type of functional unit they called "evolutionarily stable configurations" (ESCs). ESCs are character systems united in their performance of a particular "proper function" (Millikan,

1984), roughly, the purpose for which the complex evolved ["proper function" combines elements of both "function" and "biological role," *sensu* Bock and von Wahlert (1965)]. Wagner and Schwenk (2000) argued that the functional integration among characters constituting an ESC exerts intraorganismal selection pressures on individual characters. This selection derives from the need of characters to function in a coordinated way with the other characters of the system to produce the proper functional output. Too great a phenotypic deviation in one character would disrupt the functionality of the system, as a whole, and would therefore be selected against. This type of selection occurs with little regard to the particular external environment because it is imposed by an intrinsic, organismal attribute, hence it has been called "internal selection" to distinguish it from typically Darwinian, adaptive "external selection" (Whyte, 1965; Dullemeijer, 1980; Arthur, 1997; Wagner and Schwenk, 2000). ESCs are putatively self-stabilized phenotypic units that resist modification in a wide range of environments, thus promoting phenotypic stasis in the system through time and cladogenesis. This stability arises from an emergent property of the system which is evident as functional integration. Thus, ESCs are similar to Bock and von Wahlert's (1965) conception of a functional unit with the additional conditions of functional integration and self-stabilization. The ESC concept is developed further (see later).

FUNCTIONAL UNITS RECONSIDERED

While it is unlikely that there will be universal agreement on the nature of functional units, there appears to be little doubt about their reality. In this sense, functional units are no different from characters and other putative "unitary" entities which must be defined and characterized within a specific context and with reference to particular processes (e.g., Wagner, 1999, for characters; Wagner and Schwenk, 2000, for ESCs). Functional units are recognizable as such in two different contexts: within an individual organism in the context of function and within a population of organisms through evolutionary time, during which functional units manifest some level of phenotypic stability. Thus functional units are potentially definable with reference to particular functional and evolutionary processes. A characterization of these processes provides the grist for generating testable hypotheses about the nature of functional units, particularly in regard to the phenotypic and phylogenetic patterns we expect them to produce. In this portion of the essay I make a preliminary foray into this arena and identify three general "types" of functional unit (Table I). Each proposed type should be taken as an hypothesis, ideally to be dissected, tested, modified, refuted, or supported.

TABLE I Types of Functional Unit

Type	Components	Attributes	Putative examples
1. STRUCTURAL UNIT	a. morphogenetic units	a. morphological unity	a. rodent mandible
		b. intrinsic functional integration c. phylogenetic stability	b. snake maxilla c. some skull roof bones
2. MECHANICAL UNIT	a. characters	d. may exhibit phylogenetic fission a. morphological composite	a. mammal skulls
	b. structural units	b. intrinsic functional integration c. phylogenetic stability	b. primitive fish skulls (e.g. <i>Amia</i> , <i>Acipenser</i> , fossil Dipnoi) c. lizard skull/parietal foramen position d. turtle shell
3. EVOLUTIONARILY STABLE CONFIGURATIONS (ESC)	a. characters	d. solidity/little intrinsic movement	e. limb girdles
		e. strong selection on total form, weak selection on components	f. snake cranium
		f. total form canalized, components variable	a. mammalian masticatory system
		a. morphological composite	b. lizard lingual feeding
		b. intrinsic functional integration	c. kinetic skulls
		c. mechanical units d. other ESC's	d. cognitive systems (?) e. internal selection on components f. phenotypic stability of components within threshold limit g. phenotypic stability of total form h. buffered from environmental change

The conceptual and especially operational ambiguity of functional units reflects the complexity inherent in hierarchically organized systems that are not only integrated through function, but also temporally through development and historically through phylogenesis. Thus, to invoke function exclusively as a causal explanation for the coherence exhibited by certain sets of characters and the stability they evince through evolutionary time is to ignore, rather egregiously, several facts: (a) some characters are likely to be included within one or more additional functional units, i.e., the functional domains of such "units" overlap; (b) all characters identified as integrated through function are simultaneously nested within potentially noncongruent sets of developmentally correlated characters; (c) in the vast majority of cases we have no knowledge of the genetic architecture underlying the functional unit, nor of its heritability; nor do we know how the genetic variance-covariance structure of the characters might change in different environments (Schlichting and Pigliucci, 1998); (d) we rarely have information about the "variational properties" (*sensu* Wagner, 1999) of constituent characters since we lack developmental information for most characters, let alone suites of characters; in any case, we typically view the characters in a population after natural variation has been reduced by selection; (e) functional units comprise elements deriving from many tissue types and organ systems, e.g., bone, muscle, connective tissue, nerve, and blood vessel, but we rarely consider more than one or two of these at a time (Gans, 1969; Dullemeijer, 1974). In short, even a well-developed characterization of a functional unit is a one- or two-dimensional projection of a multidimensional entity.

Despite the cautionary pessimism just expressed, it is remarkable how much explanatory power functional units seem to have in evolutionary morphology, at least on a qualitative level. A clearer conceptualization of functional units and heightened recognition of their importance in evolutionary character analysis should facilitate the design of empirical studies that elaborate more fully their multidimensional nature. The three broad categories of functional unit identified here are based on the literature review and my own thoughts (Table I). These types are best considered modal patterns of functional unit organization that blend one into the other and are not intended to be mutually exclusive. It is likely that there are others. Although the three modal types have different attributes, they are united in that each represents a complex of actually or potentially separate (i.e., individuated) characters that are integrated by participation in a common function. Their reality as historical, evolutionary units is supported circumstantially by the stability they exhibit in comparative analysis (see later).

Type 1: Structural Units

The simplest form of functional unit is an apparently single morphological structure, unitary in its adult form, but arising through fusion of two or more developmental precursors. Such functional units are most clearly manifest in certain bones whose precursors take the form of mesenchymal condensations, sometimes evident as separate centers of ossification (Fig. 2). It could reasonably be argued that developmental fusion of multiple *Anlage* into single adult structures forms a separate class of developmentally integrated structures not related to functional units, *per se*. I suggest they are worth considering here for two reasons: first, because in many cases the fusions are causally related to functional demand, and second because structural units comprising more than one individuated, morphogenetic "unit" are likely to differ from truly unitary structures in their "variational properties" (*sensu* Wagner, 1999) and therefore in their evolutionary potential.

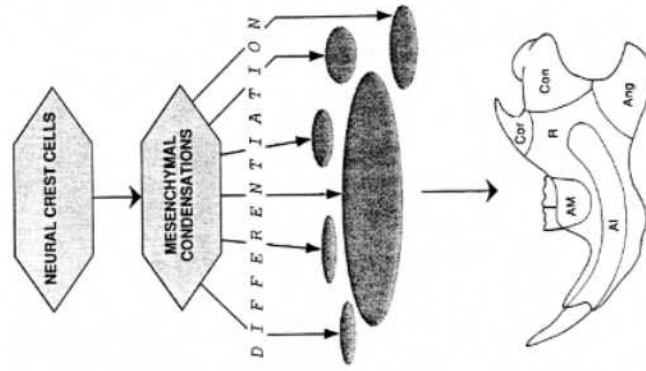


FIGURE 2 The mouse mandible as a structural unit (see text). Separate mesenchymal condensations coalesce into a single dentary bone, the solidity of which is presumed to reflect its functional role in the mammalian masticatory system. AI, alveolar-incisor; AM, alveolar-molar; Ang, angular process; con, condylar process; cor, coronoid process; R, ramus. After Atchley (1993).

The case of the mammalian (mouse) mandible is an especially well-developed example (summarized by Atchley and Hall, 1991; Atchley, 1993). The mammalian mandible consists of a single bone, the dentary. Indeed, a mandible comprising a single bone is a diagnostic character of the crown group Mammalia. The dentary bone, however, is a developmental composite of six, separate morphogenetic units that coalesce into a single adult structure (Fig. 2). These morphogenetic components arise as condensations of neural crest cells that contribute to the body (ramus) of the dentary, its two alveolar (tooth-bearing) portions, and its three processes (condylar, coronoid, and angular). Given the nature of the mammalian feeding system, particularly the function of mastication, there can be little doubt that the solidity of a single, fused dentary is functionally adaptive, hence one can argue that the composite dentary represents a functional unit. A consequence of maintaining separate morphogenetic units within a unitary structure, however, is enhanced evolutionary potential. Atchley and Hall (1991) proposed that interspecific differences in mandibular form among mammals result from modifications in individual morphogenetic units, and work summarized by Atchley (1993) supports this view.

The skull provides many cases of bones with multiple centers of ossification that correspond to ancestrally separate bones that have fused in a descendant taxon. In addition, there are examples of the reverse polarity, i.e., bones that are ancestrally single with multiple centers that in the derived condition are represented by separate bones. Whether such phylogenetic fusions and fissions have a functional basis is an open empirical question. However, their existence highlights the hierarchical complexity of character individuation. Of more relevance here is that they represent a cryptic source of evolutionary variation that can be exploited when novel functional demands arise. A good, if unusual, example is the case of the bolyeriid snake maxilla. Bolyeriids (Round Island boas) comprise only two known species, one recently extinct. They are unique among tetrapod vertebrates in having a maxilla (upper jaw bone) divided into two, articulated parts (Frazzetta, 1970; Cundall and Irish, 1989). This arrangement permits the anterior end of the upper jaws to be depressed beyond the rest position, an ability unique among snakes (Cundall and Irish, 1989). Dietary and other ecological data suggest that bolyeriids are skink specialists. Skinks are unusually hard, slippery lizards due to their smooth, chain mail-like integument. The unique bolyeriid jaw mechanism allows the upper jaws to bend around the lizard when it is held transversely in the mouth in order to retain it in the jaws' grasp (the lizard tending otherwise to slip out). Analogous adaptations are found in other snakes that specialize on skinks (Savitzky, 1983; Cundall and Irish, 1989). This feeding mechanism arguably constitutes a novel and specialized functional unit but how could it have evolved? A developmental study of an unrelated snake with a typical, unitary maxilla found that the bone formed from "two distinct and independent centers of ossification" (Haluska and Alberch, 1983, p. 54). The maxilla extends farther posterior in snakes than in lizards (representing the ancestral condition) and it was suggested that the

derived, elongated snake maxilla may have arisen by addition of a new, posterior center of ossification (S. B. McDowell, in Haluska and Alberch, 1983). A speculative scenario is that strong selection on the feeding apparatus for dietary specialization in bolyeriids, whose food options were limited to terrestrial skinks (Cundall and Irish, 1989), drove a paedomorphic shift in maxillary development, leading to a jointed, two-part bone, with each segment corresponding to an ancestral ossification center. In fact, heterochronies in late stage ossifications are strongly implicated in the evolution of snake skulls generally (Irish, 1989).

In the case of the mammalian mandible it was argued that the fusion of separate morphogenetic units into a unitary dentary is maintained by functional (as well as developmental) integration, thus the dentary represents a functional (structural) unit, but in the bolyeriid maxilla the opposite is true. In this case, an ancestrally fused structural unit became divided into two separate elements, revealing its ancestrally composite nature. The cryptic variation represented by separate centers of ossification in the snake maxilla may have permitted a repatterning of the feeding system into a novel form in bolyeriid ancestors. Thus, the patterning of morphogenetic units within a structural unit is likely to influence both its own direction of phenotypic evolution as well as that of the larger functional unit within which it is embedded as a constituent element. In effect, structural elements increase the evolutionary degrees of freedom inherent to the functional unit (see later).

Type 2: Mechanical Units

Mechanical units are complexes of individual elements which form a more-or-less solid or unitary structure. As such, I use mechanical unit in the sense of Gans (1969) to indicate that this type of functional unit is characterized by limited intrinsic movement (i.e., among component elements) as compared to the relatively greater movement possible between units. The best examples of mechanical units are found in the vertebrate skull, but there are others (discussed later). In developing the example of the skull I will concentrate on the bony elements, as have previous authors, but as noted above, this must be taken as a pragmatic simplification of the true complexity of any functional unit. Skulls are obviously associated with a variety of soft tissues that are integrated along with the bony elements in the performance of particular functions (e.g., Fig. 1).

The essential quality of mechanical units is that they are relatively solid structures despite the fact that they visibly comprise multiple constituent parts. The mammalian skull, in particular, exemplifies this condition in that it is composed of many separate bones, but these are joined in such a way that the skull, as a whole, forms a single, akinetic structure. That the skull functions as a mechanical unit cannot be doubted, but the skull obviously subserves multiple functions and biological roles. It was this factor which led van der Klaauw (1945) to recognize 36 separate, if overlapping, functional units within the skull, each unit corresponding to a principal function.

