Belg. J. Zool. — Volume 121 (1991) — issue 1 — pp. 111-124 — Brussels 1991

(Manuscript received on 23 September 1989)

SOME PECULARITIES OF LIZARD DENTAL SYSTEMS

by

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SUMMARY

On the basis of complex data (studies of morphology and teeth replacement *in vivo*, dissections of stomachs, observations of feeding behavior with recordings on cine-film) particularities of the dental systems are established for 65 lizard species from 9 families. The obtained data allows us to apply a universal approach to this system in connection with taxonomy, problems concerning variability of teeth, feeding mechanisms and ecology of lizards. Among the components of the jaw apparatus the dental system of these animals demonstrates the highest degree of plasticity and diversity. Its features display interrelations of compensatory nature, and adaptations to similar kinds of food can be achieved on the basis of different specializations of teeth. Pecularities of taxonomic significance are outlined for some of the species.

Key-words : Lizards, dental system, teeth.

INTRODUCTION

Numerous contributions on the dental system of lizards fail to produce a complete impression and are often incompatible. This is true even of the most voluminous account by EDMUND (1969). Currently this information is steadily being enriched, mostly by morphological and histological descriptions of teeth in separate species.

The latest classification of squamata elaborated by RIEPPEL (1988) almost entirely lacks information on dental morphology. At the same time such problems of dental morphology as growth and development of teeth, correlations with types of feeding, and interrelations with other parts of the jaw apparatus remain unsolved.

We attempted a comparative morpho-functional analysis of the dental system in different lizard species, with the goal of unification of previous and newly acquired data and further application of these to morphological, ecological, taxonomical and phylogenetical interpretations.

Six morphotypes were defined (VOROBYEVA and KRASNOV, 1979) in the dental system from the study of 33 lizard species, representing 20 genera and 8 families. Their evolutionary history involved adaptations of feeding mechanisms and adaptations to certain food items. Later these investigations were developed (VOROBYEVA and CHUGUNOVA, 1986a) through introduction of new species and new methods (filming, dissections of stomachs, staining of teeth in the process of their replacement). This confirmed the definition of six morphotypes and considerably added to their descriptions. We were also able to separate the more stable features from variable ones in dental morphology and replacement. The compensatory and correlative trends were traced. The age and sex-dependencies of dental differentiation and their relations to wearing and replacement of teeth were studied in greater detail. In our research we employed a view, presuming that the dental system always remains a part of the jaw apparatus as a whole (in the sense of an intricate morpho-functional adaptive complex).

MATERIAL AND METHODS

More than 400 lizards specimens belonging to 65 species, 29 genera and 9 families (Gekkonidae, Scincidae, Lacertidae, Xantusiidae, Agamidae, Chamaeleontidae, Iguanidae, Anguidae, Varanidae) were studied, predominantly from the USSR fauna. Dental system structure was studied on macerated skulls totally devoid of soft tissues and on those with soft tissues partially removed from the dental area.

The analysis of teeth morphology included the following parameters : 1) shape of the teeth (in lingual, labial views, in transverse section and form of the dental apex) ; 2) number and differentiation of teeth ; 3) interdentary spaces ; 4) dental recline as related to the maxillary bone ; 5) type of teeth attachment to the jaw-bone and features of their resorption ; 6) dental differentiation along the jaw bones ; 7) teeth height above the jaw-bone ; 8) nature of dental wear, acquired defects ; 9) sexual dimorphism and age-associated changes ; 10) features of teeth replacement and intensity of this process.

An extensive observation on teeth replacement (3-5 months) was carried out for two lizard species : *Tenuidactylus caspius* (EICHWALD, 1831), and *Lacerta armeniaca* (MEH, 1909). A new method of *in vivo* staining was established for the study of this process. This method includes a single injection into the body cavity of a concentrated solution of alisarine red « C » (1, 5-4 ml). It was established that differentiation in the staining of teeth depends on their age : the junior teeth have a more red colour (Fig. 1).

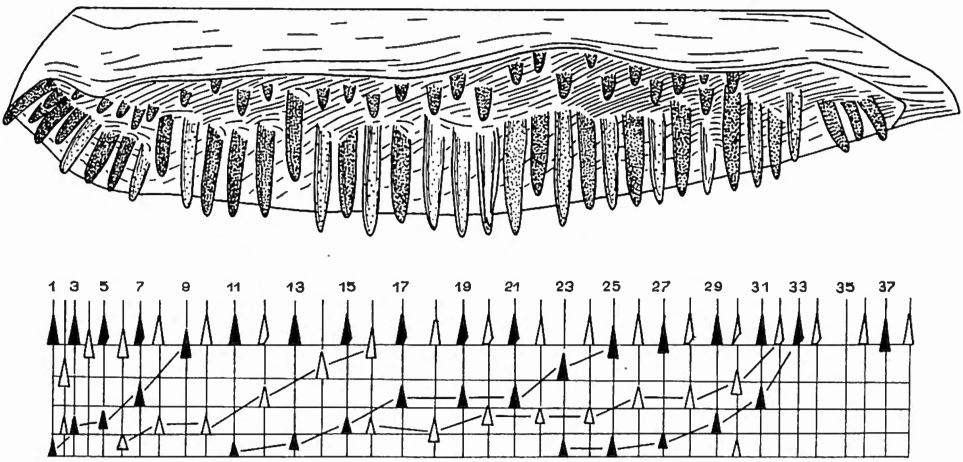

Fig. 1. — *Tenuidactylus caspius*. Right maxillary in lingual view.
A diagram of teeth replacement (after Edmund) is based on the results of alizarine red « C » injections. The youngest teeth feature the deepest staining.

A resection of stomachs was made in 54 specimens from 8 different families and diet components were studied. The nature of food treatment in the mouth cavity, the degree of its morcelment were defined according to teeth markings on the prey and to the different patterns of bitesk and breaks of the hard sclerotised parts of invertebrates. The use of various types of dentition in this process was thus defined (Fig. 2).

The feeding behavior of lizards, i.e. pecularities of capture, treatment of prey in the mouth cavity, transportation of the particles to the pharynx was observed in laboratory and in Zoo. In some species movements of the head and of the jaws were recorded on cine-film (Vorobyeva and Chugunova, 1986a). This material was used to describe the feeding mechanisms of some species : *Trapelus sanguinolentus* (Pallas, 1913), *Stellio lehmanni* (Nikolsky, 1896), *Phrynocephalus mystaceus* (Pallas, 1776), *Lacerta viridis* (Laurenti, 1768), *Eremias velox* (Pallas, 1771), *Pseudopus apodus* (Pallas, 1775), and *Varanus griseus* (Daudin, 1903). The film was shot by « Krasnogorsk-3 » 16 mm camera with the use of negative material A-2 and positive OCh 180. The speed was 32 frms/sec.

RESULTS

The completed comparative-anatomical analysis of the teeth system in lizards revealed that its diversity presents on the one hand a result of certain adaptive trends and on the other hand a result of initial morpho-phylogenetical features. And while in lizards the skeletal-muscular jaw apparatus is relatively uniform in structure and functions (Frazetta, 1962 ; De Vree and Gans, 1987 ; Iordansky, 1970), the dental system presents the most variable of its components, providing access to the wide spectrum of food items and opening possibilities of adaptive radiation.

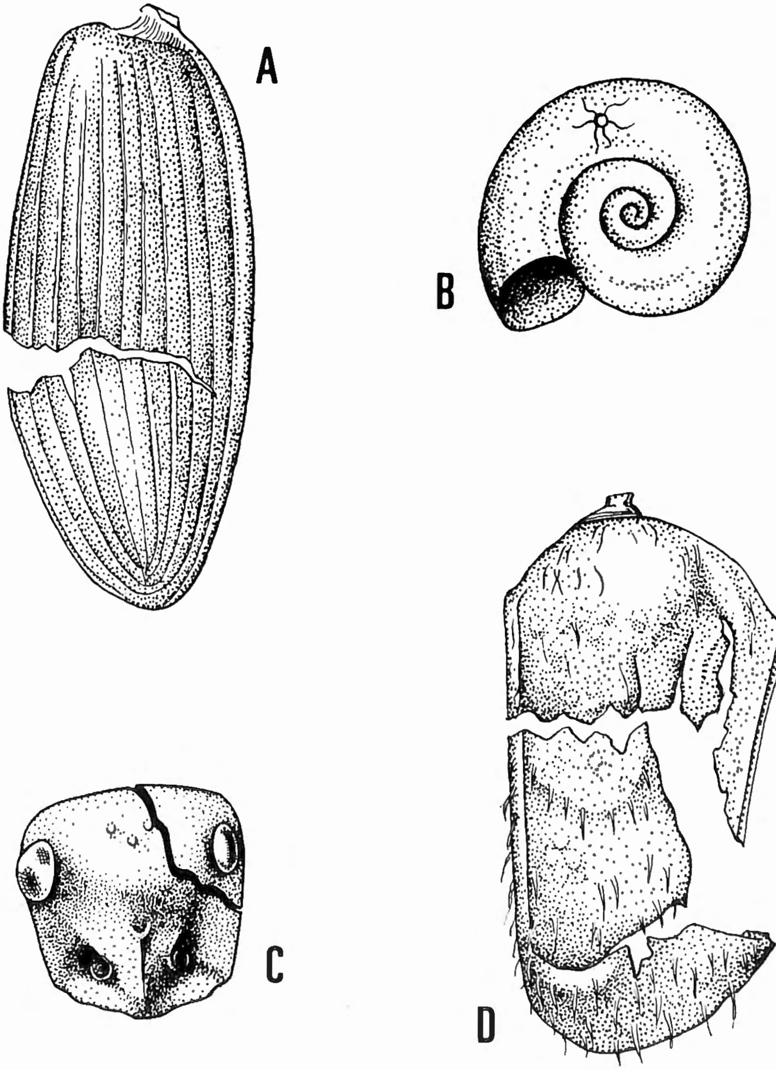

Fig. 2. — Traces of bites on the prey in different lizards : A : *Eremias velox* ; B : *Pseudopus apodus* ; C, D : *Phrynocephalus* sp.

Dental morphology.

The dental system in different taxonomic groups of lizards and in separate representatives differs by a number of morphological parameters : type of attachment, replacement, shape of the crown, number of teeth etc. All these parameters are subjected to individual, sexual and age variability and can be met in different combinations in different lizard groups. They often display difference in phylogenetically close groups and similarity in distant groups (convergences) (VOROBYEVA and KRASNOV, 1979 ; VOROBYEVA and CHUGUNOVA, 1986b). Thus a set of parameters must be used when a certain group is discussed.

From the positions of compensatority and correlations we assumed that the subdivision of lizards into « acrodont » and « pleurodont » types is valid, if not only the type of dental attachment is taken into consideration (OSBORN, 1984), but also other features related to this. So, pleurodont teeth system correlates with such features as occurrence of dental replacement, high teeth crown, extensive number of teeth and their weak differentiation. Acrodont teeth system features irreplaceability, teeth few in number and well differentiated. The most constant feature for relation of the lizards to one of the two these groups is the presence or absence of tooth replacement.

Our study revealed that in lizards with the iguanid pattern of teeth replacement variations of this process may occur. In *Corucia zebrata* (GRAY, 1855), *Eremias grammica* (LICHENSTEIN, 1823), *E. arguta* (PALLAS, 1773) and *Lacerta viridis* the successive tooth in the posterior part of the row arises somewhat posteriorly from its predecessor. In *Trachydosaurus rugosus* (GRAY, 1845) the successive tooth arises behind the predecessor : thus in forms of larger size, feeding on larger and harder prey (among *Eremias, Lacerta*) or in durophagous forms (*Trachydosaurus rugosus, Pseudopus apodus*) the successive tooth does not arise exactly underlying the functional tooth, but a little to one side. Probably, such a shift of the tooth bud occurred in connection with the growing pressure applied to the functional tooth.

In all pleurodont lizards the anterior teeth are similar in form and fulfil similar functions. Further posteriorly the teeth somewhat differ — to a different extent in different families. The most posterior teeth display generic tendency — widening of crowns and complication of their form. The more massive posterior teeth in part are due to different mechanical influence in the anterior and posterior part of jaw. In the majority of geckos the difference between anterior and posterior teeth is minor. In skinks it is more strongly expressed. In some lizards (iguanids, ophisaurids and varanids) the difference can be rather significant. Diversity of crown form in posterior teeth permits the definition of several stages with regard to their increasing complexity : sharp elongated crown with round basis in geckos, somewhat transversely widened in skinks, with an additional cusp before the main cusp in racerunners, and tricuspid crown in lizards and some iguanids (Fig. 3). Complexation of crown shape, and the enlargement of tooth surface through formation of additional cusps undoubtedly simplifies and improves treatment of food in the mouth cavity. Thus this increase in complexity must be regarded as progressive in the evolution of the lizard dental system.

In acrodont lizards all the particularities of attachment, shape and number of teeth are probably connected with a certain mechanism of jaw interaction, which

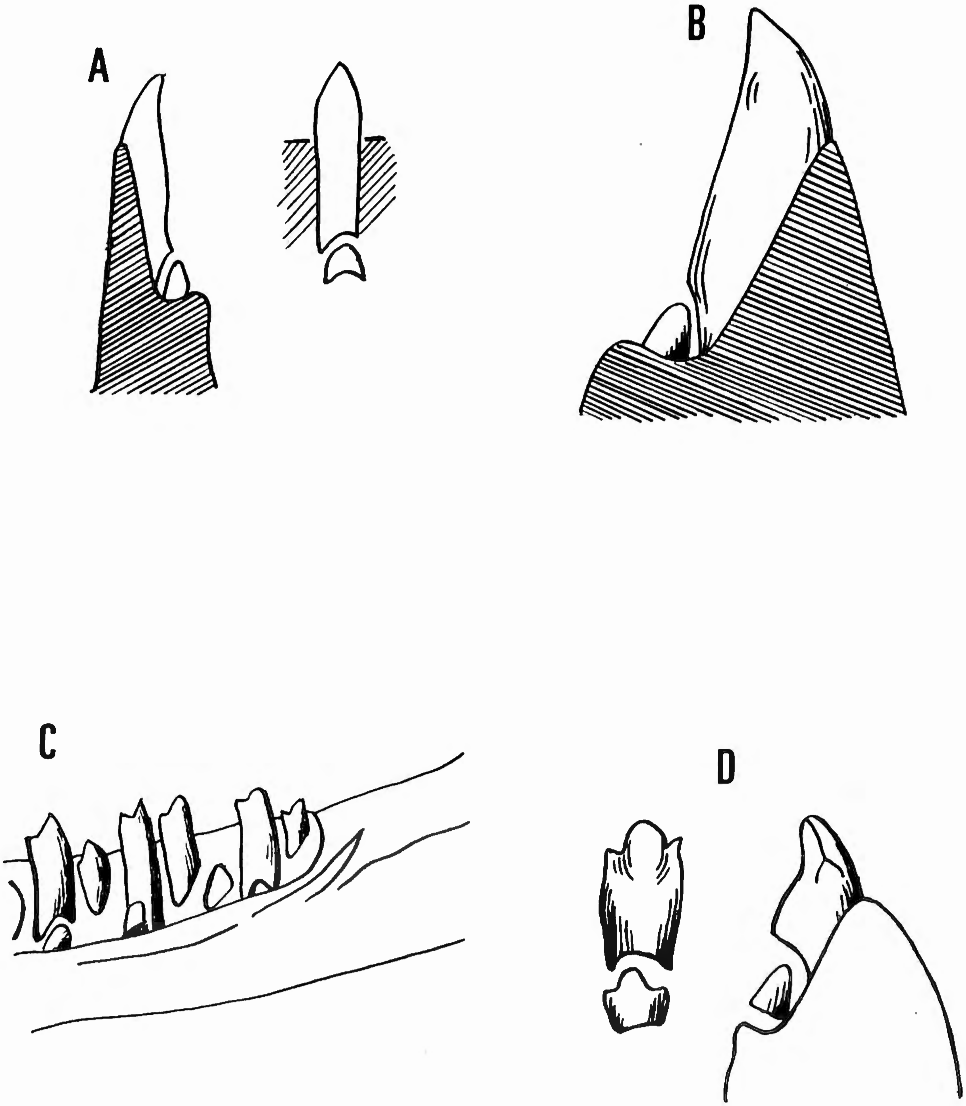

Fig. 3. — Crown form in posterior teeth. Side and lingual views : Geckos (A), skinks (B), racerunners (C), lizards (D).

differs from that in pleurodont lizards. The acrodont dental system was primarily adapted to « precision — shear bite » as in *Uromastyx* (Robinson, 1976) and other agamids ; when the teeth of the upper jaw covering the teeth of the lower jaw, on closing of the mouth, establish a close contact.

Teeth of the upper jaw leave traces on dental bone. With the growth of the animal there appear new acrodont « molars » in the posterior part of the tooth row and each of them is larger than it's predecessor. The difference in « premolars » and « molars » is well defined in *Agama* and *Phrynocephalus*. According to acrodont teeth differentiation 11 species of *Phrynocephalus* were classified into four groups (Table 1). In these groups some correlation between degree of teeth differentiation and size of the lizards was achieved. The larger species feature the stronger differentiation of dental system (CHUGUNOVA *et al.*, 1987).

DISCUSSION

Feeding mechanism.

The feeding mechanism is treated as a certain cycle of actions with a number of successive phases : (1) prey capture, (2) treatment of prey in the mouth cavity, (3) transportation into the pharynx, (4) cleaning (THROCKMORTON, 1976, 1980 ; SMITH, 1982 ; BRAMBLE and WAKE, 1985).

Treatment of prey and the « chewing » phase (TROCKMORTON, 1980) presents a series of repeated openings and closures of mouth, accompanied by movements of tongue and head. We ascribe a species specific meaning to this phase and in our studies of some species dedicate special attention to the nature of head and jaw movements, tongue activity, also to the role of tongue in prey capture and to the time of treatment in the mouth cavity.

The filming of the feeding mechanisms enabled us to describe this phase in detail for seven species of lizards (see above).

In geckos the prey almost escapes dental treatment in the mouth cavity. This is confirmed also by dissections of stomachs. In smaller species of geckos (*Hemidactylus frenatus* DUMERIL and BIBRON, 1836 ; *Tenuidactylus caspius, T. russowi* STRAUCH, 1887 ; *Crossobamon eversmanni* WIEGMANN, 1834) the number of cycles in the « chewing » phase during consumption of the flour worm amounts to 3-4. In these lizards during the 1 and 2 phases sudden head movements and secondary prey captures might be observed.

The observations on the feeding of *Eumeces schneideri* (DANDIN, 1862), *Lacerta viridis,* and *Eremias velox* revealed that the phase of prey treatment of the flour worm persists from 5-6 up to 12 (in *Eremias velox*) cycles. One cycle of the « chewing » phase in *Eremias velox* takes about 0,25 seconds. During capture and treatment of prey in lizards the sudden head movements and tongue movements are employed. The recapturing of prey by the jaws occurs with the active participation of the tongue. The principle disintegration of food in these forms is achieved with the use of teeth from the middle area of the dental series. Most apical damage was recorded in this area.

The filming of feeding mechanism in *Eremias velox* enabled us to observe the propalinaric move-ability of the lower jaw is rarely used by the lizard and serves usually for orientation of prey in the mouth.

The tongue actively participates in prey treatment in the feeding mechanism of *Pseudopus apodus.* Thus the lizard employs it's tongue to dispose of broken particles of snail shell. During swallowing of a large prey the lizard places its tongue under the prey, and then, simultaneously with recapturing via the jaws, the tongue is pulled inside the mouth cavity with the prey.

In the varanids (monitors) the tongue is, on the contrary, excluded from the feeding process (CONDON, 1989). The food is transported to the pharynx with the help of inertial thrust (RIEPPEL, 1979) and with participation of cranial kinesis (FRAZETTA, 1962).

SMITH (1984) demonstrated that the difference in the activity of the specialized tongue during feeding of the northern tegu from that of the unspecialized hervivorous iguana *Ctenosaura similis* (GRAY, 1983) is slight. At the same time MAC LEAN (1974) noted the activity of the specialized tongue in feeding of the crocodile-tegu.

Possibly, specialization of the tongue in lizards (often combined with it's sensory functions) does not influence it's activity in feeding processes.

TABLE 1

Differentiation of acrodont teeth in Phrynocephalus *(evaluated in points from 1 to 4)*

Species	Degree of acrodont teeth differentiation (upper/lower jaw)
1. Phrynocephalus mystaceus (PALLAS, 1776)	4/4
2. Ph. versicolor STRAUCH, 1876	3/3
Ph. melanurus EICHWALD, 1831	3/3
Ph. maculatus ANDERSON, 1872	3/3
3. Ph. raddei BOETTGER, 1890	3/2
Ph. rossikowi NIKOSKY, 1899	3/2
Ph. reticulatus EICHWALD, 1831	2/2
Ph. helioscopus (PALLAS, 1771)	2/1
Ph. guttatus GMELIN, 1787	
Ph. moltschanovi NIKOLSKY, 1913	2/1
4. Ph. interscapularis LICHTENSTEIN, 1856	1/1
Ph. sogdianus ČERNOV, 1959	1/1

Our observations revealed that all of the studied species of agamas and most toad agamas (Table 1) capture minute prey with the aid of their tongue. The relatively large prey is captured by jaws. The phase of flour worm treatment in agamas includes 7-20 cycles. One cycle of the « chewing » phase takes about 0,27 seconds. The treatment of a solid large object, for instance, of a bug, takes 20-30 cycles and is carried out mainly by the hindmost teeth. The jaws are opened to about 50 ° for this. For comparison, the maximal opening of the jaws in *Eremias* *velox* gives about 30,5 °. An inconsiderable forward displacement of the lower jaw during mouth opening was registered in *Trapelus sanguinolentus.*

Thus, the time of one cycle of the « chewing » phase is similar in agamas, *Lacerta viridis, Eremias velox* and as in *Amphibolurus barbatus* (CUVIER, 1929) (THROCKMORTON, 1980) amounts to 0,25-0,30 seconds. However, the number of cycles is different, and that depends upon the carnivore-prey size relations and upon the hardness of the prey. Apart from that, the intensity of prey treatment increases in a hungry carnivore.

Thus the particularities of feeding mechanisms in different lizards are explained not only by the morphological features of dental apparatus, but also by variations in prey (size, hardness) and also by the state of the carnivore at the moment of feeding.

Pleurodont and acrodont teeth systems evidently provide different functions and both have a long history behind them. In comparison with acrodont teeth, the pleurodont ones display a wider spectrum of diversity of dental parameters, connected with adaptations to different types of prey.

Diet correlation.

The specialized forms feature the most vivid correlation between dental structure and diet (GREENE, 1982). The specialization of the teeth system in durophags, predators swallowing large prey in a single piece, phytophages and myrmecophags is expressed in a number of parameters. In durophags and predators most of the parameters are subjected to changes (attachement, crown shape, type of substitution) ; in phytophages only the shape of the crown apex is modified ; in myrmecophags the adaptation of the dental system followed different trends and no certain single type of specialization is observed (Table 2).

Specialization towards duraphagy can be observed in almost all of the families. Among geckos this happens in the case of *Teratoscincus,* among skinks — *Trachydosaurus rugosus ;* true lizards — *Lacerta viridis* and *L. agilis* (LINNÉ, 1758), iguanids — *Chamaeleolis chamaeleontides* (DUMERIL and BIBRON, 1837), anguids — *Pseudopus apodus.* In the diets of these animals insects with hard shells are common, together with large and hard objects. Adaptation to feeding on hard objects involves modification of posterior teeth crowns, however there is a suggestion that many lizards with molariform teeth may be functioning as everyphages rather than specializing in durophagy (ESTES and WILLIAMS, 1984).

In specialized predators, swallowing their prey in a single piece — *Varanus* and *Anguis* — we also find subpleurodont attachment of functional teeth and their low number. Still, the crown shape, number and distribution of teeth on the jaws and type of their replacement are rather specific : the teeth are high, sharp, posteriorly curved, widely spaced, and their number is low.

TABLE 2

Correlation of specialization with different changes (t) *of various parts of dental system*

Kind of adaptation / Some parameters of dentition	Tooth shape	Nature of thooth attachment	Type of tooth replacement	Number of teeth
durophagy	+ +)	+	+	+
predators, swallowing, large prey in a single piece	+	+	+	–
phytophagy	+	–	–	–
myrmecophagy	+/–	–	–	–

+) The parameter subjected to changes.

Adaptation towards plant eating involves mostly changes in the form of the crown apex. All of the other family — specific features remain unchanged.

The acrodont lizards feature a diet which is also quite diversified. However, they display fewer adaptative modifications of the dental system. Probably, the acrodont dental system is more universal. It is adapted to animal foods of different hardness and size, as well as to plant food. Still, among Agamidae, for example, there are also forms with food specializations. Thus *Moloch horridus* (Gray, 1841) is highly specialized towards myrmecophagy. *Phrynocephalus* and North American iguanids feature a diet based largely on ants, but including some other types of food as well.

The differences in dental morphology in different taxonomic groups of myrmecophagous lizards (blunt crowns in horned lizards, flattened and triangular in toad agamas; of more complicated form in moloch) reveal that myrmecophagous specialization is achieved by different means and does not provide a single morphological result.

Morphotypes.

Six morphotypes of lizards were defined in the course of unified morphofunctional evaluation of teeth systems and of their feeding mechanisms (Vorobyeva and Krasnov, 1979; Vorobyeva and Chugunova, 1986a). These morphotypes correlate partially with the taxonomical subdivision and in part unite the specialized forms from different families : I — geckos, II — skinks + true lizards, III — iguanids, IV — agamids + chameleons, V — durophags, VI — predators, swallowing their prey as a whole;

Each morphotype demonstrates certain interrelationship between morphological components of the dental system (skeletal-muscle jaw system, tongue, teeth) and compensatory phenomena in prey capture or its treatment and further transportation into the pharynx.

Taxonomical conclusions.

The use of dental morphology in taxonomy of many recent lizards is limited by wide distribution of convergencies, caused by specific adaptations, and by considerable variability of features. The complexes of such features provide a possibility for establishing the status of lizards at the family level and in some cases at the level of subfamilies and genera. In his family diagnoses CAMP used particularities of the dental system as early as in 1923. CAREVSKIJ (1929) tried to employ such features as teeth number and degree of dental differentiation in *Phrynocephalus* taxonomy. RIEPPEL (1978) distinguished Platynota and Anguinoidea on the basis of difference in tooth replacement (with resorbtion of the changed tooth base and without such resorbtion).

The literary data provide examples of dental number used for separation of a species or for distinguishing between two similar species. Thus, two species of venomous lizards possess a different number of teeth (6-7 or 8-9), apart from that one species lacks palatal teeth (BOGERT and CAMPO, 1956). Thus, the number of teeth was used by GEER (1970, 1974) in a subfamiliar classification of scincid lizards, and also by BICHOFF (1986) for the separation of *Podarcis filfolensis* (BEDRIAGA, 1876). EREMTCHENKO and TSCHERBAK (1986) use the number of premaxillary teeth in their classification of lidless skinks.

Fig. 4. — *Eremias grammica*. Diastema between maxillary and premaxillary teeth.

We defined some features useful for separation of genera and species. Thus, in racerunners, unlike that in some lizards, the « diastema » is always found between premaxillar and maxillar teeth in the upper jaw (Fig. 4). In *Prynocephalus* the crown features a simpler triangular form and is more strongly compressed laterally, than in *Agama* (Fig. 5). Such a feature as number of premaxillar teeth turned out to be rather constant and less liable to change in the majority of pleurodont forms. This feature is diagnostically valid for two allied species of geckos — *Teratoscincus scincus* SCHLEGEL, 1858 and *T. przjewalskii* STRAUCH, 1887 (the first one has 9, the second one possesses 11) (VOROBYEVA and CHUGUNOVA, 1989).

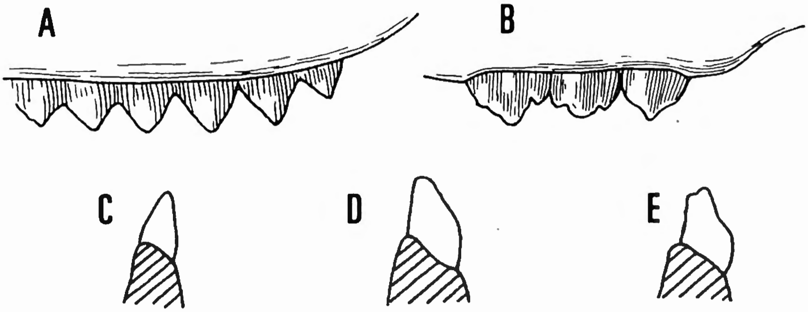

Fig. 5. — Acrodont teeth in *Phrynocephalus* (A), *Agama* (B) labial view. Transverse section through posterior tooth in *Phrynocephalus* sp. (C) and *Stellio caucasicus* (D, E).

On the whole, we come to a conclusion that the main components of jaw apparatus are closely connected by their participation in the feeding process. Often the compensatory phenomena occur when development of one adaptive particularity compensates the unadaptedness of the other.

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