ONTOGENETIC DEVELOPMENT OF ANTIARCH DERMAL OSSIFICATIONS

ALEXANDRE IVANOV, GENNADY CHEREPANOV & ERVINS LUSKEVICS

IVANOV A, CHEREPANOV G & G. LUSKEVICS 1995. Ontogenetic development of antiarchs dermal ossifications. [Développement ontogénétique des ossifications dermiques des antiarches]. GEOBIOS, **M.S. n° 19** : 97-102.

ABSTRACT

The histological structure of the dermal ossifications of juvenile and adult *Asterolepis* (Placodermi, Antiarchi) is described. Six development stages of the dermal ossifications are described in living soft-shelled turtle (*Trionyx*). An attempt of reconstruction of the dermal plates and scales development in *Asterolepis* is made using a complete cycle of the dermal bone development in *Trionyx*.

KEY-WORDS : PLACODERMS, ASTEROLEPIS, TURTLES, DERMAL OSSIFICATIONS, DEVELOPMENT.

RÉSUMÉ

La structure histologique des ossifications dermiques d'individus juvéniles et adultes d'*Asterolepis* (Placodermi, Antiarchi) est décrite. Six stades de développement de l'ossification dermique ont été décrits chez une tortue trionychidés (*Trionyx*). Un essai de reconstruction du développement des plaques et écailles dermiques d'*Asterolepis* est proposée sur la base du cycle de formation de l'ossification dermique de *Trionyx*.

MOTS-CLÉS : PLACODERMES, ASTEROLEPIS, TORTUES, OSSIFICATIONS DERMIQUES, DÉVELOPPEMENT.

INTRODUCTION

Complete specimens of extraordinary well-preserved juvenile and adult of *Asterolepis ornata* Eichwald were recorded from the Gauja Formation (Late Givetian) of Lode Quarry, Latvia (Upeniece & Upenieks 1992 ; Ivanov in press). *Asterolepis* material is represented by different stages of dermal bones development. Specimens of *Asterolepis* are housed in the Latvian Museum of Natural History, Riga (LDM). Complete development series (embryos and postembryos) of the living soft-shelled turtle (*Trionyx sinenesis* WEIGMANN) are used in reconstruction in a comparison purpose of the dermal ossification development. The embryos were fixed in 4% formalin, the histological sections were stained with hæmatoxylin and eosin. The development stages were defined after Yntema (1968). The collections of *Trionyx* are kept in the Department of Vertebrate Zoology, Biological Faculty, Saint Petersburg University.

The authors are greatly indebted to Mrs. Ieva Upeniece for the loan of the material of juvenile *Asterolepis* ; Mrs. R. Sorkina for her help in preparing this paper. This study was supported by the International Science Foundation (Soros Grant). This research is a contribution to IGCP 328.

EXOSKELETON OF *ASTEROLEPIS*

The exoskeleton of the head, trunk and squamation is preserved in both juvenile and adult individuals. The dermal plates of tiny juveniles with the dorsal trunk armour 13-14 mm long is made of a thin compact bony lamina (thickness : 0.0008-0.012 mm). Bony trabeculæ are located on the external surface of the lamina (Pl. 1, fig. 1) forming an irregular network. Scarce vascular canals are opened on the outer surface of the plate (Pl. 1, fig. 2). They are visible on the cross

sections of the plate, under trabeculæ (Pl. 1, fig. 1B). The squamation in these specimens consists of bony scales. The scales have a thin lamina at the base and one tubercle in the center of the dorsal surface, corresponding to a pit on the opposite face (Pl. 1, figs 4, 5). The lamina consists of a compact bony tissue similar to that of the trunk armour plates. The tubercle is composed of loose tissue with small canal openings. There are two different types of scales : fulcral with elongated dorsal part of the lamina and rounded flank scales (Pl. 1, figs 3, 4). Larger juveniles with the dorsal trunk armour longer than 30 mm and of 0.25-0.40 mm plates thickness have a fine-meshed reticular ornamentation. Sometimes the ornamentation bears tubercles at the crossing points of anastomosing ridges. The scales of these specimens have sometime trabeculæ on the external surface and a flat visceral surface (Pl. 1, fig. 6).

The dermal plates of adult *Asterolepis* are composed of three layers : basal, spongious and trabecular (Gross 1931). It is difficult to trace a clear boundary between spongious and trabecular layers, because there is a gradual change between them. The spongious layer has a concentric osteon system around the lumens ; the tubercular layer bears numerous vascular canals. The squamation of the adults includes two types of scales : fulcral and flank scales similar to those of the juveniles. Scales ornamentation, overlapping and histological structure depend on their position on the body, and change from the posterior margin of the trunk armour to the caudal fin. The squamous part of *Asterolepis* body is divided into five zones related with the scale position on the body : zone A, from the posterior margin of the trunk armour to the begining of dorsal fin ; zone B, under the dorsal fin ; zone C, from the end of the dorsal fin to the begining of the caudal fin ; zone D, caudal fin ; zone E, dorsal fin (Ivanov *at al.* in press). The scales from zone A just behind the trunk armour have an ornamentation consisting of longitudinal ridges and tubercles. Cross sections of these scales show clearly three layers : a compact laminar basal layer, spongious layer and a well-developed trabecular layer with vascular canals. Such a structure resembles that of the dermal plates. The ornamentation of the scales in the caudal direction becomes faveolate with tubercles, then it is pitted and smooth with rare pores at the end of the tail. The tubercular layer of the scales with faveolate-tubercular ornamentation is becoming thinner than the former scales. The scales with pits in their ornamentation have also a thinner spongious layer. The smooth scales with occasional pores have a relatively thick laminar basal layer, a thin spongious layer and a dense superficial layer with very rare vascular canals (Pl. 1, fig. 7). The tiny smooth scales of the caudal fin possess a very thin spongious layer consisting of several small cavities.

EXOSKELETON DEVELOPMENT OF *TRIONYX*

The recent material can help to reconstruct a possible process of the dermal ossification development of *Asterolepis*. The most suitable object for this purpose is a soft-shelled turtle *Trionyx* . The armour of *Trionyx* is made of dermal plates not covered by epidermal horny scutes. The ornamentation of trionychid plates strongly resembles that of asterolepid and bothriolepid antiarchs. Beside, the bone histological structure in the adult *Trionyx* evokes that of the adult *Asterolepis*. Six development stages of the dermal ossification within a stratified dermis were described on the basis of ontogeny in *Trionyx* armour.

Stage 1 (embryonic stages 16-17, Fig. 1A). The formation of the accumulations of mesenchymatous cells in the middle level of undifferentiated dermis.

Stage 2 (embryonic stages 17-18, Fig. 1B). The appearance of an ossification center inside the cell accumulation ; the formation of a primary bony lamina (source of the basal layer).

Stage 3 (embryonic stages 19, Fig. 1C-D). The growth of bony trabeculæ from the basal layer to the epidermis, the formation of the spongious layer. The basal layer is similar to trabeculæ of the spongious layer in its thickness and histological structure. The dermis is delaminated into the subdermis, hypodermis, fibrous and papillar strata. A denser collagen matrix is formed inside the fibrous stratum. It has a regular arrangement of collagen fibers, i.e. large collagen bundles are responsible for the orthogonal pattern of layers. The upper part of hypodermis and papillar stratum are strongly vascularized.

Stage 4 (juvenile, age approximately 1-2 years, Fig. 1E). The appearance and expansion of the upper compact layer, which histologically resembles the bony trabeculæ at the begining of this stage. The formation of a three-layered bone structure within hypodermis as a result of the process.

Stage 5 (subadult, age approximately 3-5 years, Fig. 1F-G). The appearance of a trabecular layer

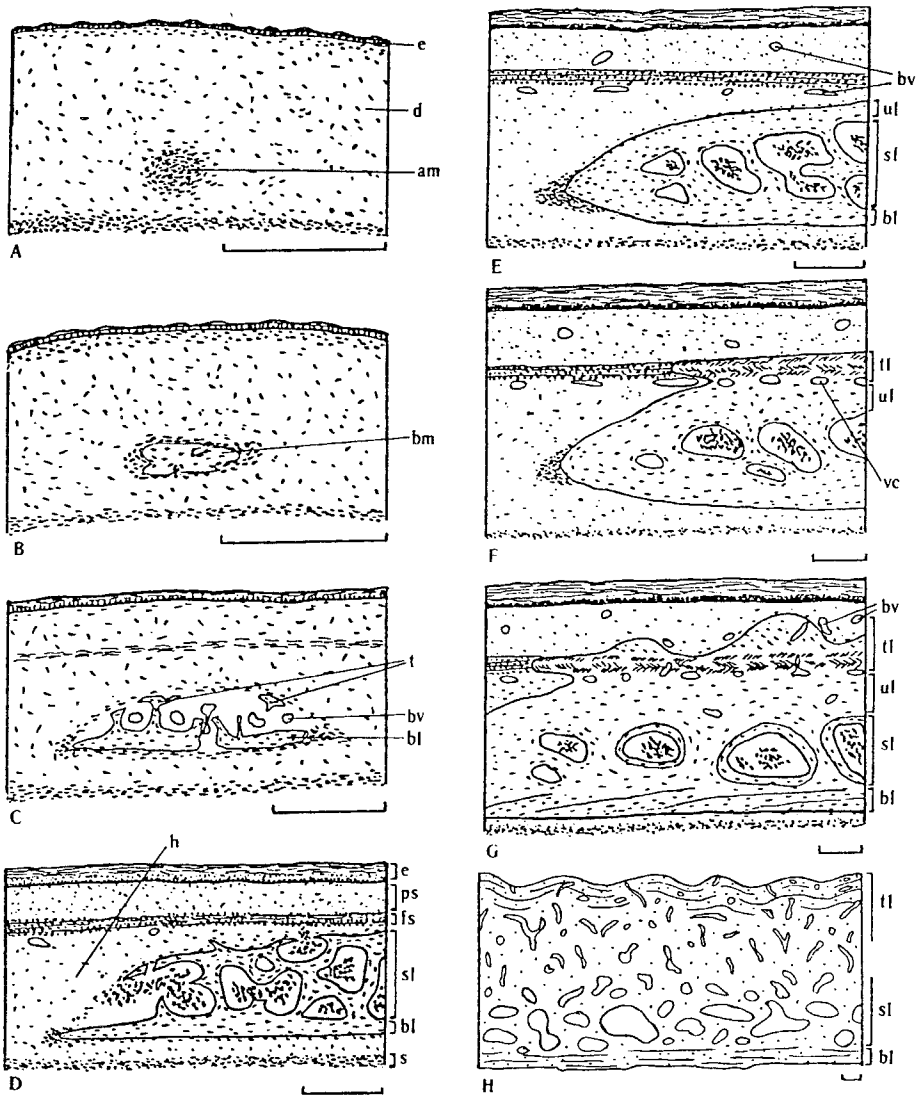


Figure 1 - Stages of the dermal ossification development in ***Trionyx sinensis*** Weigmann. **A**, stage 1 ; **B**, stage 2 ; **C-D**, stage 3 ; **E**, stage 4 ; **F-G**, stage 5 ; **H**, stage 6. Scale bar = 0.25 mm for all figures. am, accumulation of mesenchyme ; bl, basal layer ; bm, bony matrix ; bv, blood vessel d, dermis ; e, epidermis ; fs, fibrous stratum ; h, hypodermis; ps, papillar stratum ; s, subdermis ; sl, spongious layer; t, trabecula ; tl, tuberculated layer ; ul, upper compact layer vc, vascular canal. *Différents stades du développement de l'ossification dermique de* ***Trionyx sinensis*** *Weigmann.* ***A****, stade 1 ;* ***B****, stade 2 ;* ***C-D****, stade 3 ;* ***E****, stade 4 ;* ***F-G****, stade 5 ;* ***H****, stade 6. Échelle = 0,25 mm. am, accumulation de mésenchyme ; bl, couche basale ; bm, matrice osseuse ; bv, vaisseau sanguin ; d, derme ; e, épiderme ; fs, strate fibreuse h, hypoderme ; ps, strate papillaire ; s, sous derme ; sl, couche spongieuse ; t, trabécules ; tl, couche tuberculée ; ul, couche compacte supérieure ; vc, canal vasculaire.*

inside the fibrous stratum of the dermis as the upper compact layer grows. The expansion of tuberculate layer to papillar stratum. The formation of the superficial ornamentation consisiting of tubercles separated by subepidermal blood vessels. As a result, the plate structure consists of four layers : basal, spongious, upper compact and tubercular layer. The upper compact layer differs from the basal compact layer in the presence of vascular canals. The tubercular layer is composed of coarse-fibered bony tissue perforated by numerous meandering vascular canals. The latter are opened mainly around the ornamental tubercles. There are two levels, upper and lower, inside the tubercles layer. The lower one is formed in the fibrous stratum retaining the orthogonal structure of collagen complex, while the upper with vascular canals appears inside the papillar stratum of the dermis and has no regular arrangement of collagen fibers.

Stage 6 (adult, Fig. 1H). The formation of a simple three-layered structure of the dermal ossification as a result of on-going processes of resorption and reconstitution of the bony tissue. The upper compact layer disappears. The tuberculate layer becomes relatively homogeneous in structure. It consists of strongly vascularized compact tissue with upper lamellar part. There are no clear boundary between the tuberculate and spongious layers. superficial ornamentation of the dermal plate becomes faveoláte. Therefore the bony dermal plate of the final stage of development is as a rule subdivided into three layers : basal, middle and superficial (Moy-Thomas & Miles 1971 ; Stensiö 1934). The middle layer marks

the transition from a zone with large lumens and osteons to a zone having small vascular canals. Nevertheless, these zones differ in their origin. The lower zone primarily correlates with the spongious layer of the early stage. The upper zone is represented by the lower part of the tuberculate layer. The so-called superficial layer, corresponding to ornamentation amplitude, is an upper lamellar part of the tuberculate layer.

CONCLUSIONS

The above described stages form a complete cycle of the dermal bone development inside such stratified dermis. The formation of multilayered bone structure depends on the stratification of the dermis. The multiple superficial blood vessels inside the dermis define the number of vascular canals in the tuberculate layer and the character of the ornamentation pattern. If the dermis has no developed papillar and fibrous strata, the formation of bony structure is stopped at stage 4. For example, such processes take place in the dermal ossifications of *Emys orbicularis* and *Testudo græca* (Cherepanov 1992 ; Ivanov *et al.* 1992), that have only basal, spongious and upper compact layers.

Histological similarity of the dermal plates in adult *Trionyx* and *Asterolepis* is obviously due to their dermis structures. The dermal ossifications in *Asterolepis* could develop through the same stages in *Trionyx* armour. The dermal plates of the above described tiny juvenile *Asterolepis* individuals correspond to stage 3 of *Trionyx* ossification development. Stensiö (1934) has illustrated the cross sections of the plates of young and adult *Bothriolepis*. The upper compact layer is preserved between the spongious layer and friable vascularized part of the tuberculate layer in the dermal plate of young individuals (Stensiö 1934, fig. 9B). *Asterolepis* squamation, as an element of the exoskeleton develops slowly when compared with the armour plates. The scale structure in the juvenile individuals with a dorsal trunk armour length of more than 30 mm resembles that of the dermal plates in juvenile individuals having dorsal trunk armour of 13-14 mm long, or stage 3 of *Trionyx* ossification development. The scales of adult *Asterolepis* just behind the trunk armour exhibits a histological structure very similar to that of the dermal plates of adult *Asterolepis* and *Trionyx*. The histological structure of scales from zone C with pitted ornamentation resembles that of the plate in the late stage of *Trionyx* (Fig. 1G). The external part of smooth scales with rare pores from zone D have an upper compact layer. The structure of these scales is similar to that of stage 4 of *Trionyx*. Thus the scales of adult *Asterolepis* squamation depending on the position on the body correspond to different stages of the growth plate in the ontogeny. It can be attributed to the fact that the dermis is thinning in caudal direction and the papillar and fibrous strata could disappear in this region of the dermis.

REFERENCES

CHEREPANOV G. 1992 - New morphological data on the turtle shell : discussion on the origin of the horny and bony parts. *Studia Palæocheloniologica, Salamanca*, **3** (1) : 9-24.

GROSS W. 1931 - *Asterolepis ornata* Eichwald, und das Antiarchi-Problem. *Palæontographica A*, **75** : 1-62.

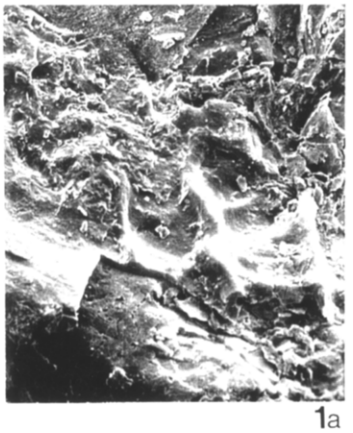
IVANOV A., PAVLOV D. & CHEREPANOV G. 1992 - Some aspects of biomineralization of vertebrate exoskeleton. *In* E. MARK-KURIK (ed.) : Fossil Fishes as Living Animals, *Academia,* Tallinn **1** : 159-164.

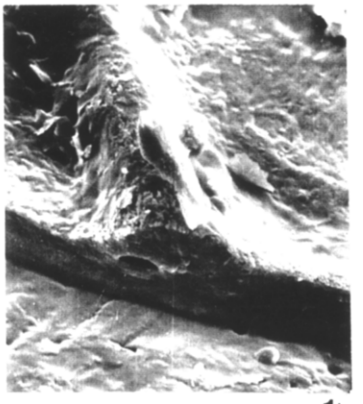
PLATE 1

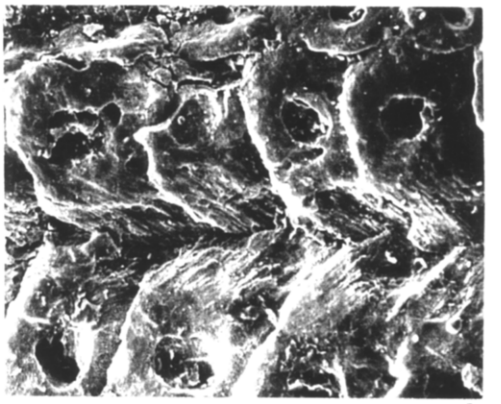
Figs 1-7 - ***Asterolepis ornata*** EICHWALD. **1-6** juveniles individuals. **1A**, **2A** details of the dermal plate LMD 260/80 ; **1B**, trabecula and vascular canal ; **2B**, vascular canal ; **3**, **4**, squamation in visceral view ; **3**, fulcral scales, LMD 260/236 ; **4**, flank scale, LMD 260/236 ; **5**, isolated flank scale in external view LMD 260/243 ; **6**, flank scale in external view, LMD 260/244 from specimen LMD 260/10 ; **7**, transversal cross section of adult ***Asterolepis*** scale from zone D, LP 15/1. ***1-6** individus juvéniles. **1A, 2 A** détails de plaque dermique, LMD 260/80 ; **1B**, trabécule et canal vasculaire ; **2B**, canal vasculaire ; **3, 4**, écailles en vue viscérale ; **3**, écaille fulcrale, LMD 260/236 ; **4**, écaille du flanc en vue externe, LMD 260/236 ; **5**, écaille isolée du flanc en vue externe, LMD 260/243 ; **6**, écaille du flanc en vue externe LMD 260/244 d'après le spécimen LMD 260/10 ; **7**, section d'une coupe transversale chez un adulte d'**Asterolepis**, écaille de la zone D, LP 15/1.*

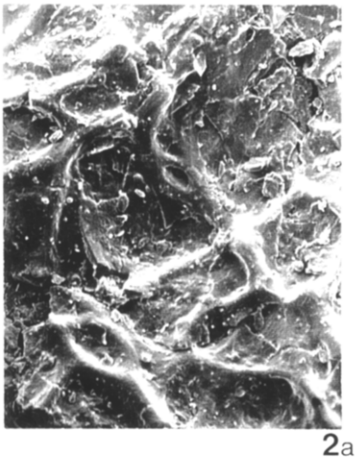
Figs 8-9 - ***Trionyx sinensis*** WEIGMANN. **8**, longitudinal section of a costal plate, subadult, VZ 2306A ; **9**, transversal section of xiphiplastron, subadult, VZ 2305. ***8**, coupe longitudinale d'une plaque costale d'un subadulte, VZ 2306A ; **9**, coupe transversal du xipohiplastron d'un subadulte, VZ 2305. Echelles : fig. **1A**, 0, 33 mm ; fig. **1B**, 0, 038 mm ; fig. **2A**, 0, 28 mm ; fig. **2B**, 0, 3 mm ; fig. **3**, 0, 3 mm ; fig. **4**, 0, 26 mm ; fig. **5**, 0, 13 mm ; fig. **6A**, 0, 38 mm ; fig. **6B**, 0, 13 mm ; fig. **7**, 1, 0 mm ; fig. **8**, 0, 4 mm ; fig. **9**, 0, 5 mm.*

Scale bars : fig. **1A**, 0.33 mm ; fig. **1B**, 0.038 mm ; fig. **2A**, 0.28 mm ; fig. **2B**, 0.3 mm ; fig. **3**, 0.3 mm ; fig. **4**, 0.26 mm ; fig. **5**, 0.13 mm ; fig. **6A**, 0.38 mm ; fig. **6B**, 0.13 mm ; fig. **7**, 1.0 mm ; fig. **8**, 0.4 mm ; fig. **9**, 0.5 mm.

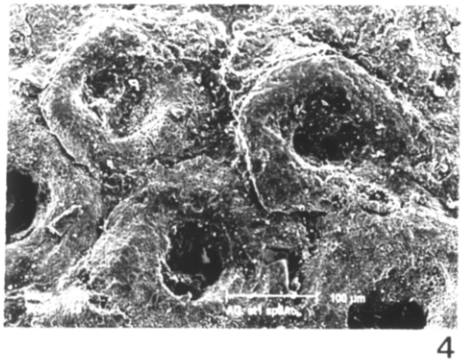

1a

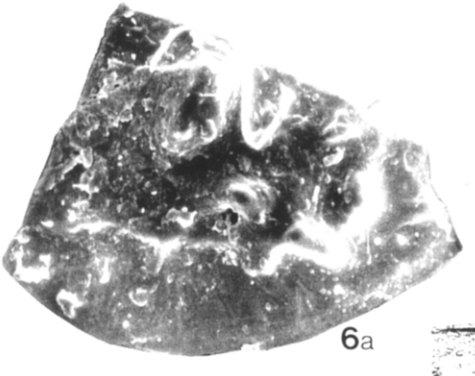

1b

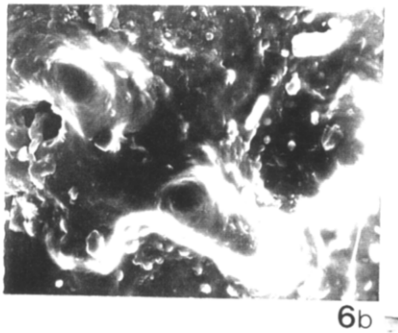

3

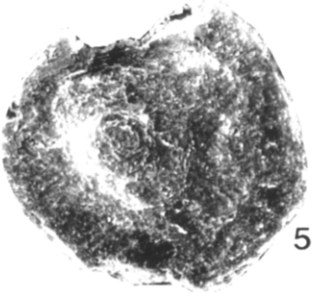

2a

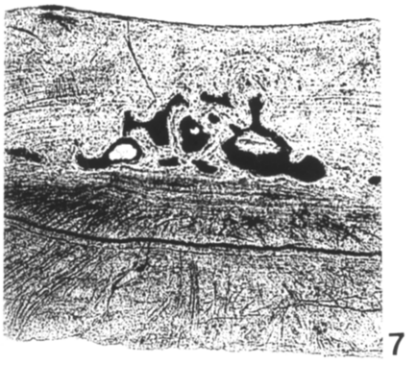

2b


4


6a


6b


5


7


8


9

IVANOV A., LUKSEVICS E. & UPIENICE I. (in press) - Squamous part of asterolepid body. *Modern Geology*.

MOY-THOMAS J.A. & MILES R.S. 1971 - Palaeozoic Fishes. Chapman & Hall, London : 259 p.

STENSIÖ E.A. 1934 - On the Placodermi of the Upper Devonian of East Greenland. Supplement to part 1. *Meddelelser om Grønland*, **97** (1) : 1-58.

UPENIECE I. & UPENIEKS J. 1992 - Young Upper Devonian antiarch (*Asterolepis*) individuals from the Lode Quarry, Latvia. *In* E. MARK-KURIK (ed.) : Fossil Fishes as Living Animals, *Academia,* Tallinn **1** : 167-176.

YNTEMA C.L. 1968 - A series of stages in the embryonic development of *Chelydra serpentina*. *Journal of Morphology,* **125** (2) : 219-251.

A. IVANOV
Institute of Earth crust
Saint Petersburg University
Saint Petersburg, Russia

G. CHEREPANOV
Biological Faculty
Saint Petersburg University
Saint Petersburg, Russia

E. LUSKEVICS
Latvian Museum of Natural Gistory Riga, Latvia