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SUR DEUX NOUVELLES ESPÈCES DE GRÉGARINES
PARASITES CHEZ L'AMPHIPODE *SYNURELLA AMBULANS*
(FR. MÜLLER) DE ROUMANIE

PAR
DOINA BĂLCESCU

The Amphipod genus *Synurella* Wrzeniowski is for the first time recorded as host for Gregarinida, namely *Cephaloidophora synurellae* n. sp. and *Cephaloidophora margaretae* n. sp. both founded in *Synurella ambulans* from the sources of the Romanian Plain.

The generic position of the Gregarinines parasites in Amphipods is discussed in relation with the study of different stages of their life cycle.

The necessity to revise the systematic state of crustaceans gregarines, especially based on a comparative knowledge of its spores is pointed out.

Depuis la seconde moitié du siècle dernier, on a fait connaître des grégariines parasites chez différents genres d'amphipodes d'eau douce et marins, tels *Gammarus*, *Orchestia*, *Talitrus*, *Caprella*, *Pontoporeia*, *Pallasea*, *Ampelisca* et autres.

Dans le présent travail, nous ajoutons pour les grégariines d'amphipodes, un nouveau genre hôte, *Synurella* Wrzeniowski, renfermant plusieurs espèces d'origine apparemment préglaciaire, réparties en Asie et en Europe, et dont *S. ambulans* ne dépasse pas l'Europe centrale et se signale par une forte inégalité de taille entre les deux sexes.

En examinant l'intestin de *Synurella ambulans* (Fr. Müller) provenant de sources de la Plaine Roumaine, nous y avons trouvé deux espèces nouvelles de grégariines, que nous décrivons ci-dessous.

Après dissection des hôtes en solution de Ringer, les grégariines dégagées de l'intestin ont été examinées sur le vivant, avec ou sans coloration vitale au rouge neutre ou au vert Janus, ensuite mesurées, dessinées à la chambre claire et photographiées en contraste de phase. Nous avons également utilisé des fixations extemporanées aux vapeurs osmiques.

1. *Cephaloidophora synurellae* n. sp.

Station de récolte : source à une végétation abondante dans le jardin de Cismigiu à Bucarest, d'où nous avons fait plusieurs prélèvements pendant les deux dernières années.

Sur 160 synurelles prospectées, le pourcentage général d'infestation a été de 80 % et, en le rapportant aux deux sexes, nous avons noté un pourcentage plus élevé, soit 84 % chez les mâles, malgré leur taille plus réduite, et seulement 75 % chez les femelles, qui sont toujours les plus grandes. Ce taux d'infection assez considérable ne semble pas varier avec la saison.

Les grégaries s'amassent dans l'intestin antérieur, moyen et postérieur, sans jamais se trouver dans les caecums latéraux, les kystes étant extrêmement rares relativement aux stades végétatifs.

Les plus jeunes stades observés sont des céphalins libres, qui se meuvent par de fréquentes oscillations, ayant une forme allongée, à l'extrême postérieure arrondie ; ils mesurent 18 μ de long sur 10 μ de largeur maximum (Pl. I, 1 - 3, Pl. III, A). Le protomérite étroit, latéralement arrondi, d'une largeur à peu près égale à celle du deutomérite, porte antérieurement un mucron hyalin de 2 - 3 μ , représentant l'épimérite. Le deutomérite ovalaire allongé renferme peu d'inclusions, entourant un noyau sphérique central d'un diamètre de 4 μ .

Chez des céphalins de 25 - 35 μ de longueur, qui sont les plus communs (Pl. III, B), après coloration vitale au rouge neutre, c'est dans le protomérite que s'agglomèrent des vacuoles rougeâtres plus apparentes que dans le deutomérite chargé d'inclusions de réserve.

Exceptionnellement, les céphalins isolés peuvent atteindre une taille de 65 - 70 μ , mais la plupart s'associent de bonne heure pour former des syzygies fronto-caudales, dont les partenaires sont généralement égaux (Pl. I, 4; Pl. III, C) mais il y a des cas où le satellite peut être beaucoup plus petit que le primitif (Pl. III, D) ou lorsque ce dernier porte deux jeunes satellites (Pl. I, 5).

Les syzygies sont plus fréquentes que tous les autres stades ; leur longueur varie de 55 - 140 μ , mais les plus nombreuses et d'une forme caractéristique globuleuse sont celles de 100 - 110 μ (Pl. I, 6; Pl. IV, E). Chaque gamonte présente un protomérite conformé en une calotte plus étroite que le deutomérite et offrant à son pôle libre un épimérite mucroniforme qui persiste assez longtemps. Le deutomérite volumineux, arrondi, séparé par un septum convexe de son côté, renferme un noyau sphérique plus ou moins central, de 12 - 13 μ de diamètre et pourvu d'un gros caryosome (5 μ).

Nous donnons ci-après les moyennes des dimensions des gamontes associés en syzygies, qui nous ont semblé caractéristiques pour notre espèce :

TL	LP	LD	LP : TL	WP	WD	WP : WD	N
55 μ	12,5 μ	38 μ	1 : 4,4	28 μ	38 μ	1 : 1,35	12,5 μ 6 μ

Les syzygies glissent par saccades, l'épimérite en avant, celui du satellite étant enfoncé dans le deutomérite du primitif. Chez les syzy-

gies agées (140 μ de longueur totale), l'épimérite s'efface et le deutomérite est tellement chargé d'enclaves que son noyau n'est plus visible (Pl. II, 1; Pl. IV, F). Dans les syzygies moyennes, le rouge neutre s'accumule surtout dans le protomérite et le vert Janus met en évidence les mitochondries granulaires, uniformément dispersées et plus fréquentes dans le deutomérite, où elles peuvent être disposées en un anneau autour du noyau.

Lorsque les syzygies se préparent à l'enkytisme, leurs partenaires se contractent, tournent l'un autour de l'autre, tendent à s'envelopper (Pl. I, 7) et finissent par se juxtaposer en se tassant sous la forme de deux calottes hémisphériques, à l'abri d'une paroi kystique épaisse de 3 - 4 μ . Les kystes sphériques mesurent 60 - 80 μ de diamètre ; les deux noyaux encore distincts atteignent un diamètre de 15 - 18 μ . (Pl. I, 8).

2. *Cephaloidophora margaretae* n. sp.

Station de récolte : source captée en bordure d'un ruisseau de plaine, Hotarele (département d'Ilov), novembre 1970.

Sur 8 exemplaires de *Synurella ambulans* d'assez petite taille, un mâle portait dans les caecums latéraux de son intestin des syzygies recourbées, formées, de partenaires à peu près égaux, allongés et striés transversalement (Pl. II, 2; Pl. IV, G - H). D'une longueur totale de 150 μ , ces syzygies ont des gamontes associés en direction fronto-caudale, ayant chacun un petit protomérite globuleux, surmonté d'un épimérite bombé, d'une hauteur de 4 μ . Le deutomérite beaucoup plus long vermiforme, d'un aspect annelidien à cause des nombreux plis qui le sillonnent transversalement, s'évase légèrement vers son extrémité postérieure arrondie. Le noyau assez grand, à un contour angulaire, d'un diamètre de 10 μ , se place très antérieurement en-dessous du septum dont la convexité est tournée vers l'arrière.

Les dimensions caractéristiques à ce stade sont les suivantes :

TL	LP	LD	LP : TL	WP	WD	WP : WD	N
76 μ	9 μ	67 μ	1 : 7,4	11 μ	20 μ	1 : 1,8	10 μ

Cette espèce, qui se distingue de la précédente par sa morphologie aussi bien que par sa localisation dans l'hôte, nous la dédions à la mémoire de Margareta Codoreanu, pour marquer ses mérites dans l'étude des grégaries.

CONSIDÉRATIONS SYSTÉMATIQUES

Tout en étant connues depuis plus de 140 ans (Siebold, 1839) et comptant actuellement près d'une vingtaine d'espèces, les grégaries parasites d'amphipodes soulèvent encore beaucoup d'incertitudes quant à leur appartenance générique.

Chez la plupart des gammarides prospectés, deux types de grégaries furent mis en évidence, l'un trapu et volumineux, l'autre très allongé, même filiforme, et cette distinction remonte clairement aux premières descriptions (Siebold, 1839, Kölliker, 1848).

Initialement rapportée au genre *Gregarina* (*G. gammari* Franzius, 1848), la forme trapue y est maintenue par différents auteurs (Diesing, 1859, Plate, 1886, Pfeiffer, 1895, Labbé, 1899, Minchin, 1903, Kamm, 1922), jusqu'à ce que Poisson (1921) la transfère dans le genre *Cephaloidophora* (*C. echinogammaris*) établi par Mavrodiadi (1908) pour une grégarine parasite de Cirripèdes. Ce genre fut le point de départ de la famille des *Cephaloidophoridae*, due à Watson-Kamm (1922), pour les grégaries des Crustacés.

En ce qui concerne les grégaries allongées de Gammarides, elles ont d'abord été situées également dans le genre *Gregarina* (*G. longissima* Siebold, 1839), mais, tandis qu'une série d'auteurs furent du même avis (Kölliker, 1848, Diesing, 1851, Lankester, 1863, Butschli, 1882, Plate, 1886, Pfeiffer, 1895, Wellmer, 1911), d'autres les font rentrer dans le genre *Didymophyes* (Franzius, 1848, Mingazzini, 1889, Labbé, 1899, Minchin, 1903, Leger et Duboscq, 1909). Poisson (1921) est le premier à les rapporter au genre *Uradiophora*, créé par Mercier (1912) pour une grégarine parasite des Cardines. Grassé (1953) sépare ce genre dans la famille nouvelle des *Uradiophoridae*, renfermant également des grégaries parasites de Crustacés.

Pixell-Goodrich (1949) ayant obtenu la maturation des kystes et la libération des spores chez les deux types de grégaries indiqués auparavant, crée deux nouveaux genres, *Rotundula*, pour les formes rassassées et *Heliospora*, pour les grégaries allongées, entre lesquels elle répartit les espèces connues chez les amphipodes.

Les spores n'étant toutefois observées que chez peu d'espèces, la discussion systématique, reste ouverte, car alors que certains auteurs ont adopté le genre *Rotundula* pour le type trapu (Kudo, 1966, Lipa, 1968, Geus, 1969), d'autres contestent sa validité au profit de l'ancien genre *Cephaloidophora* (Grassé, 1953, Tuzet et Ormières, 1956, Stein, 1960, Narasimhamurti, 1964, Théodoridès, 1967). Il en est de même quant à la forme allongée à propos de laquelle certains auteurs acceptent de remplacer le genre *Uradiophora* par *Heliospora* (Grassé, 1953, Stein, 1960, Kudo, 1966, Geus, 1969, Lipa, 1968) sans cependant avoir éclairci leurs caractères différentiels, ni la question de priorité.

Ils nous semble opportun de ranger provisoirement les deux espèces nouvelles trouvées chez *Synurella ambulans* dans le genre *Cephaloidophora*, qui demeure caractéristique pour les grégaries de Crustacés.

Nous partageons entièrement l'opinion de Théodoridès (1967) et Lipa (1968) sur la nécessité de reviser à fond le statut systématique des grégaries de Crustacés, et la connaissance comparée de la forme de spores nous semble la condition essentielle pour atteindre ce but.

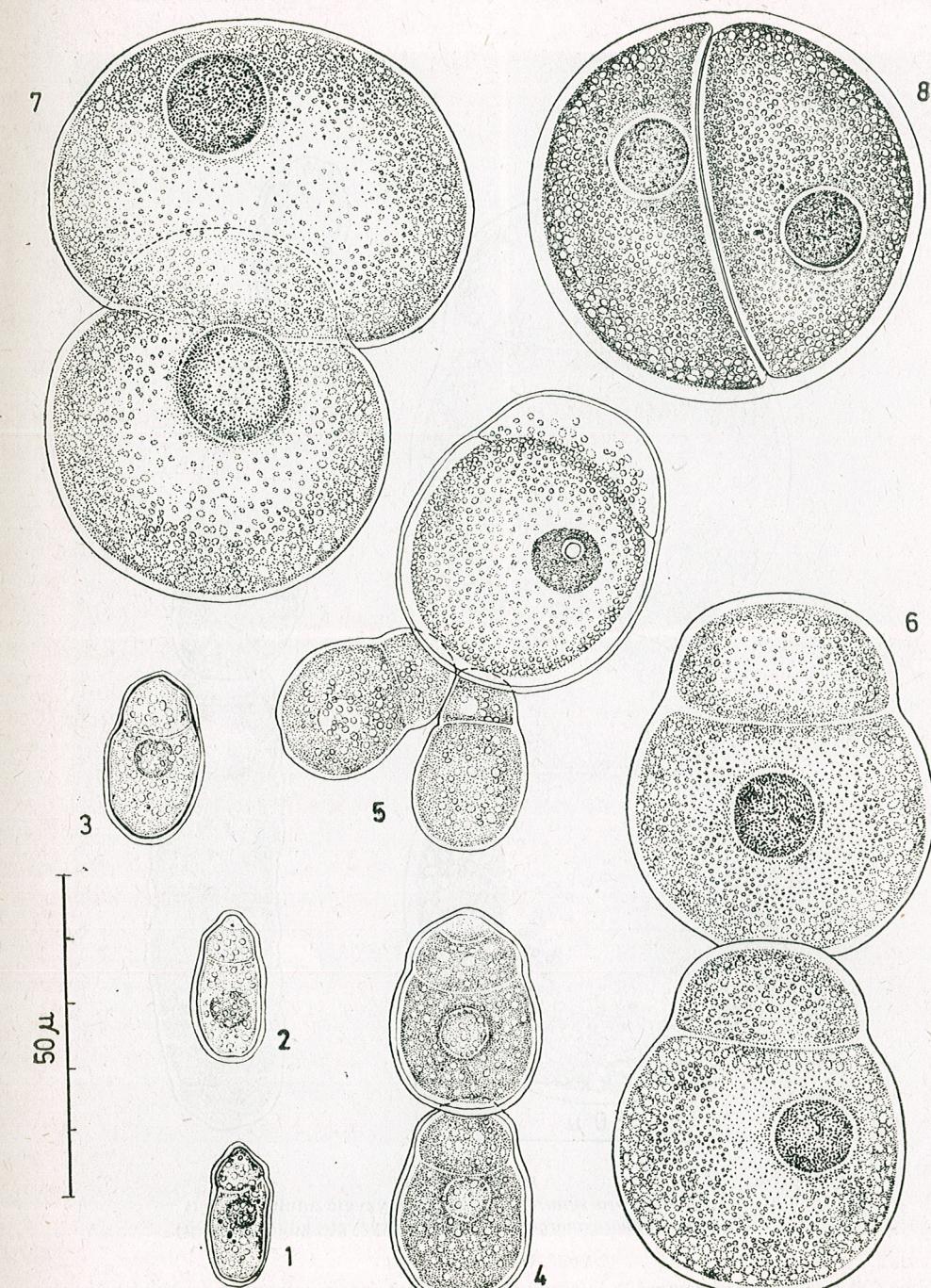


PLANCHE I
Cephaloidophora synurellae n. sp. 1 — 3 jeunes sporadins (15 — 20 μ) ; 4. jeune syzygie (40 μ) ; 5. syzygie multiple à deux satellites (80 μ) ; 6. syzygie de taille moyenne (110 μ) ; 7. syzygie en voie d'enkystement (95 μ) ; 8. gamontokyste (70 μ).

PLANCHE II
 1. *Cephaloidophora synurellae* n. sp. — syzygie adulte (140μ);
 2. *Cephaloidophora margaretae* n. sp. — syzygie adulte (150μ).

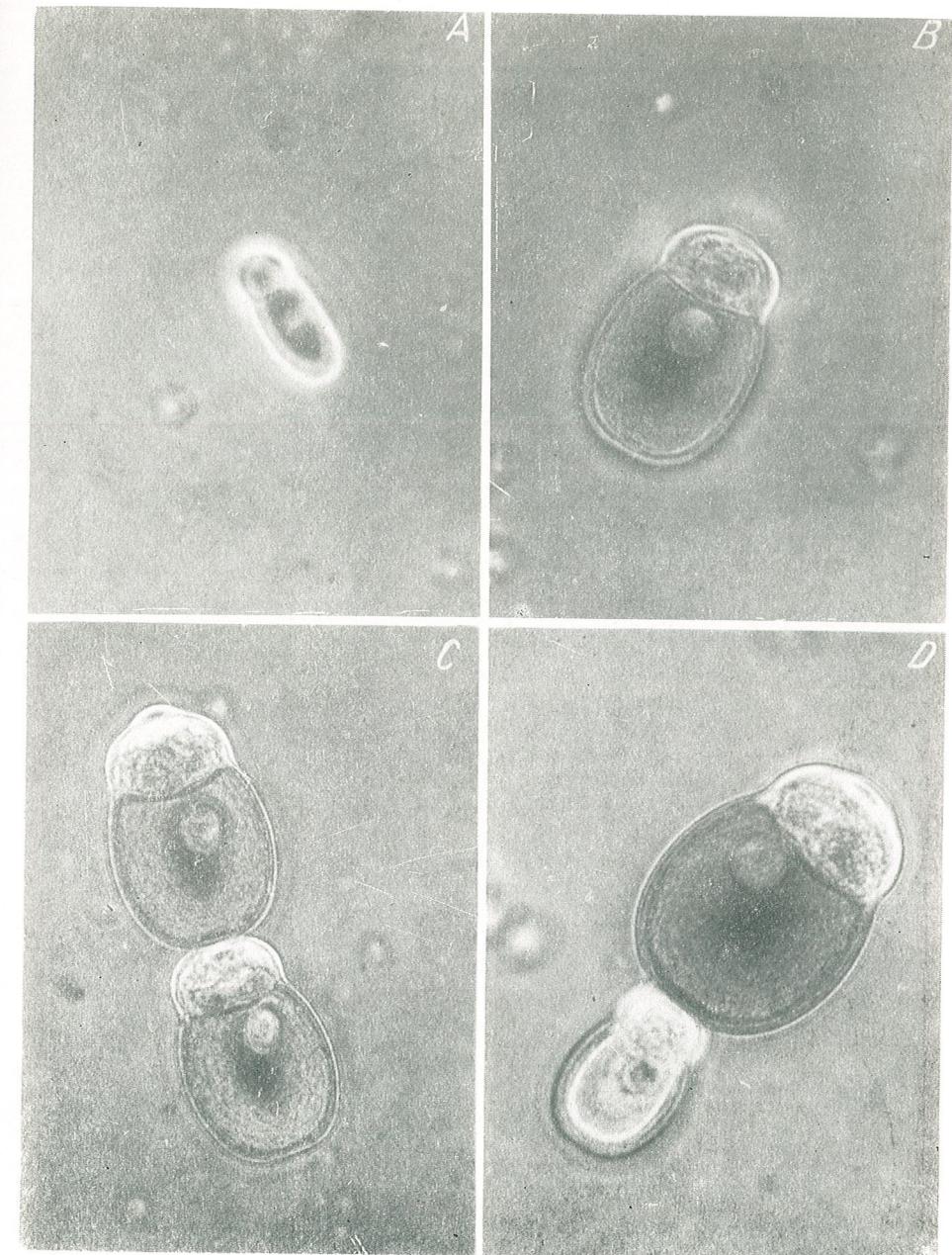
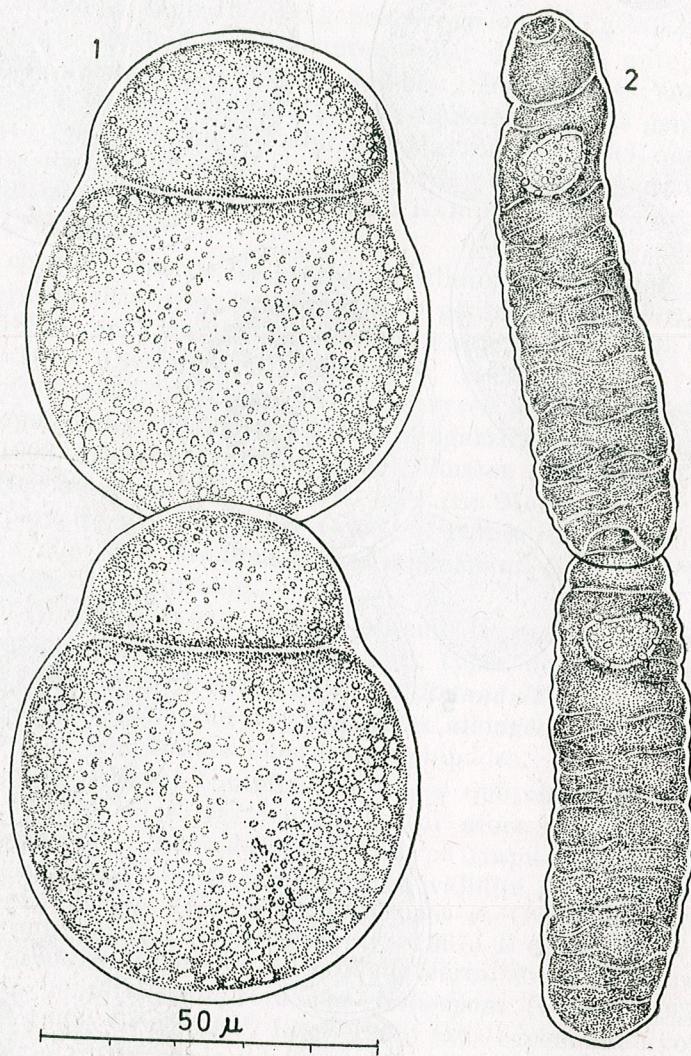


PLANCHE III
Cephaloidophora synurellae n. sp. (contraste de phase). A. jeune sporadin (20μ) ; B, sporadin de taille moyenne (40μ) ; C, jeune syzygie (70μ) ; D, syzygie à partenaires inégaux (95μ).

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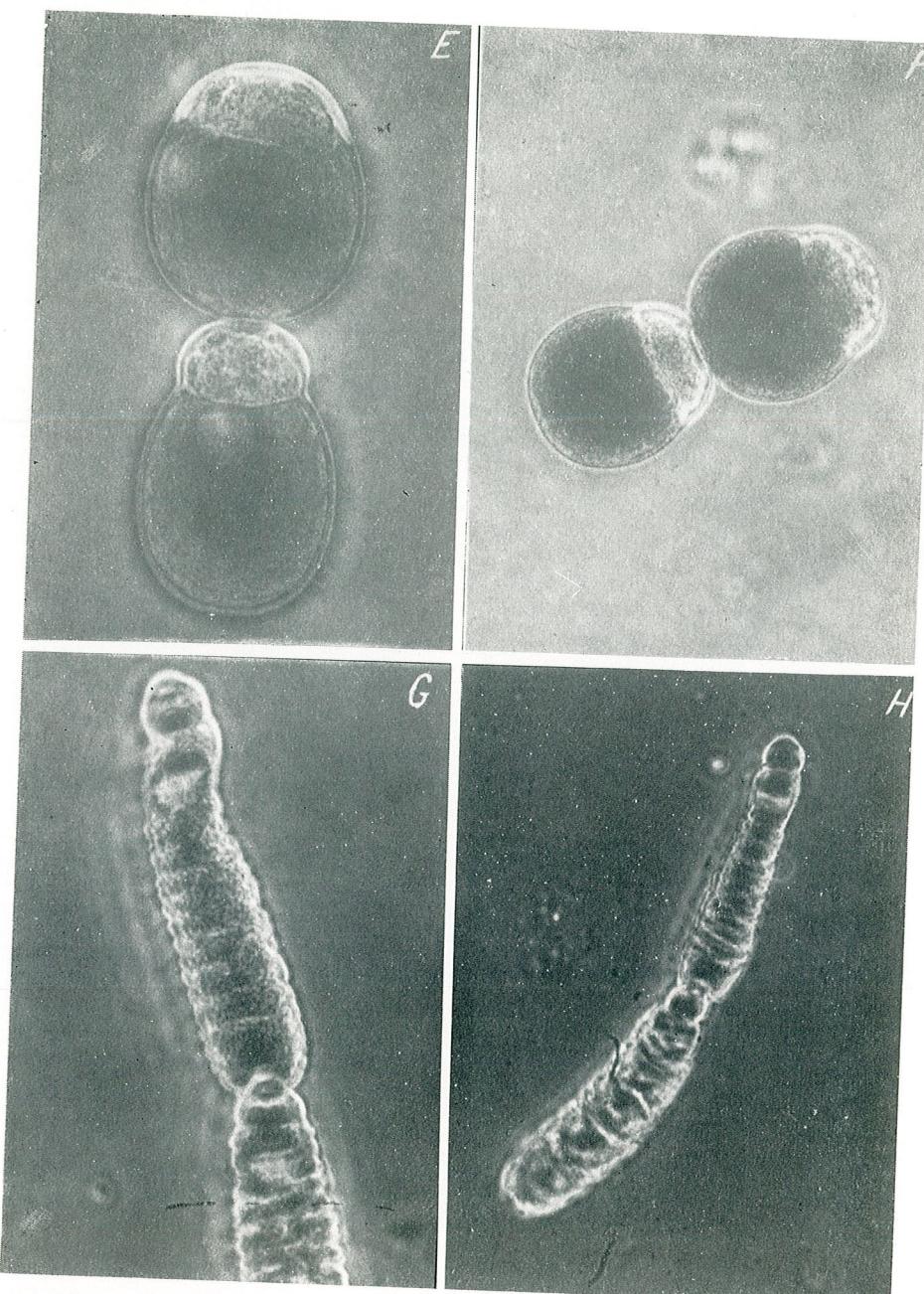


PLANCHE IV
E—F, *Cephaloidophora synurellae* n. sp. (contraste de phase) syzygies adultes (110μ ; 140μ);
G—H, *Cephaloidophora margaretae* n. sp. (contraste de phase) syzygies adultes (150μ).

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PHYLOGENETIC AND SYSTEMATIC CONSIDERATIONS
UPON THE MONOKONOPHORA (CRUSTACEA-TANAIDA-
CEA) WITH THE SUGGESTION OF A NEW FAMILY AND
SEVERAL NEW SUBFAMILIES

BY

MODEST GUTU

Starting from the idea that the establishing of a correlation between the morphological features and the taxonomic unity determining them would be necessary, the author suggests the fusion of the family Leiopidae Lang 1970 with the family Apseudidae G. O. Sars 1882 and, afterwards, its subdivision into three subfamilies : Apseudinae nov., Leiopinae nov. and Whiteleggiinae nov. At the same time, he suggests the subdivision of the family Kalliapseudidae Lang 1956 into the subfamilies Kalliapseudinae nov. and Hemikalliapseudinae nov. and of the family Metapseudidae Lang 1970 into the subfamilies Metapseudinae nov. and Synapseudinae nov., as these subfamilies better mark some evolutive steps.

For the genus *Apseudella* Lang 1968, the family Apseudellidae nov. is proposed. In the second part of the paper the n.nom. is given to the species *Leptognathia australis* (Vanhöffen 1914) which, owing to the synonymy of the genus *Strongylurella* Hansen 1913 with the genus *Leptognathia* G.O. Sars 1882, occurs twice, having to be named *Leptognathia vanhoffeni*.

As a result of his thorough researches of the morphological characters in monokonophores, Karl Lang published, in 1970, a more minute study ([6], p. 595 — 605) attempting to introduce some order into the systematics of Tanaidacea. By creating three new families (Pagurapseudidae, Metapseudidae and Leiopidae) along with the two existing ones (Apseudidae and Kalliapseudidae) the author tries to establish five main evolution lines in monokonophores.

Yet a thorough comparison between the diagnoses of the families Apseudidae and Leiopidae, as well as some personal observations upon them, have led us to the conclusion that they do not constitute two dif-

ferent taxonomic groups large enough to represent a family, because the feature by which Lang differentiates them (aspect of the inner caudo-distal hair of the maxilliped endite) is not sufficiently conclusive.

As fairly known, the genus *Leiopus* has been described by Beddard in 1886, on the basis of a single specimen collected by the "Challenger" expedition (lat. $37^{\circ}26' N$ -long. $25^{\circ}13' W$), the species being named *leptodactylus* ([2], p. 115 — 118). According to the diagnosis of the genus, given by the author, one of the characters which distinguishes it from the closest genus — *Apseudes* — is the slenderness of the chelae: "...the latter character connects *Leiopus* more closely with *Apseudes*, but the extreme slenderness of the chelae is peculiar to the genus" ([2], p. 116). Since that date, the literature has no more mentioned the genus *Leiopus* till 1949, when Lang made some assessments concerning the systematics and the synonymies of some species of Tanaididae ([4], p. 4). On this occasion the author advanced the opinion that the genus *Leiopus*, including only the species *leptodactylus* and differing from the genus *Apseudes* only by its more slender chelae, could not be considered a good genus: "On the other hand, I cannot accept Beddard's (1886, p. 116) genus *Leiopus*, for this genus, which only comprises the species *leptodactylus*, differs from *Apseudes* only in that it has slenderer chelipeds. Within *Apseudes* there are all transitions from robust (e.g. *A. spinosus*) to slender, and even very slender, chelipeds (e. g. *A. gracilis* and *A. gracillimus*)" ([4], p. 4).

As a consequence, T. Wolff, agreeing with Lang's opinion, describes a new species of *Apseudes* (*A. galathea*) which actually belongs to the genus *Leiopus* ([8], p. 191 — 200), also mentioning *A. leptodactylus* ([8], p. 200, 235, 236).

Later on, again K. Lang, studying a more abundant material, collected by the "Galathea" expedition from very deep waters, reappraised the genus *Leiopus*, considering it as good ([5], p. 87 — 120) because he discovered a character of its own which distinguishes it from the genus *Apseudes* (we refer to the inner caudo-distal hair of the maxilliped endite, as well as to the sexual dimorphism of the mandible), also describing five new species (*L. aberrans*, *L. conspicuus*, *L. hansenii*, *L. shiinoi* and *L. wolffi*); at the same time he included in the same genus *Leiopus*, other six species (*A. galathea* Wolff 1956, *A. gracilis* Norman & Stebbing 1886, *A. gracillimus* Hansen, 1913, *A. sibogae* Nierstrasz 1913, *A. weberi* Nierstrasz 1913, *A. zenchevitchi* Kudinova-Pasternak 1966). In the same paper four species, of which one was also taken from the genus *Apseudes* (ex. *A. simplicirostris* Norman & Stebbing 1886), a genus characterized, in his opinion, by the carpus of peraeopod II, longer than the meros, and by the inner caudo-distal hair of the maxilliped endite, similar to that specific to the species of *Leiopus*. Lang included these two new genera in the family Apseudidae but, on the 1970 revision, he ordered them in a new family, Leiopidae, together with other two genera — *Pseudowhitteleggia* and *Whiteleggia* — with one species each ([6], p. 603, 605 — 626) of which *Whiteleggia* has the known genotype, *W. multicarinata* also deriving from the genus *Apseudes* (ex. *A. multicarinatus* Whitelegge 1901). As demonstrated by its author, this new family, Leiopidae, with its four genera (*Carpoapseudes*, *Leiopus*, *Pseudowhitteleggia* and *Whiteleggia*),

is characterized by the shape of the inner caudo-distal hair of the maxilliped endite: "Innere caudo-distale Borste des Enditen der Maxillipeden zu einem blattförmigen Dorn transformiert" ([6], p. 603).

The abundant material of *Apseudes* put at my disposal through the kindness of prof. Dr. Mihai Băcescu, director of the "Grigore Antipa" Museum of Natural History, as well as his most valuable advice — for which I warmly thank him —, together with the material of the genera *Leiopus* and *Carpoapseudes*, allowed a very minute comparative analysis of these three genera, which led us to conclusions differing from those of Karl Lang.

It is not difficult to find, especially in monokonophores, the great similarity in shape and external morphology of the body outline, in the species belonging to a small systematic group, of the genus type. We could even assert that the body shape in species belonging to a certain genus joins a "hypothetic stencil" or "pattern" differing from the "stencil" of another genus, and that, generally, there are few species with a body shape which do not perfectly join the "stencil" of one or another genus, their place being between the "stencils" of the two genera. It may also be found that there is a close relationship, a close unity between the body shape and other characters determining their taxonomy; that is, a certain body shape corresponds to some anatomo-morphological features and these are mutually determined, as a consequence of the adaptation reaching a certain stage of evolution. True enough, sometimes there appear anatomo-morphological changes unconnected to those of the body shape; in this instance, according to the body shape the species should be assigned to one systematic unit, while according to other morphological features, it should be assigned to another one. Such cases demonstrate the evolution and, at the same time, the unity, the close kinship between the species belonging to two genera, becoming a sort of "intermediate" species or "connection" species, as we also could call them; only by a very thorough analysis of the microstructures which differentiate them, we could accurately situate them in the systematic unit they belong to. Such close relationships also exist between the genera *Apseudes*, *Carpoapseudes* and *Leiopus*.

The species of the genus *Leiopus* are characterized (besides the inner caudo-distal hair of the maxilliped endite and the sexual dimorphism of the mandible) by slender chelae and a long body, in opposition to those belonging to the genus *Apseudes*, which, generally, are sturdier. Nevertheless, the genus *Apseudes* also includes species with a body very similar to that of the species belonging to *Leiopus* (also taken from very deep waters) and only the analysis of the two characters accurately defines the genus, as in the case of *A. lagenirostris* Lang 1968 ([5], p. 33—39), to mention only this single instance, to which the species initially determined as belonging to the genus *Apseudes* are also added. The same fact is also observed in the genus *Carpoapseudes*. Besides the essential feature which determines the genus (the carpus of peraeopod II longer than the meros), associated with that assigned by Lang to the family Leiopidae, there are also other (but not sufficient), features enabling us to recognize the species of this genus, such as: the shape and length of peraeonite VII, the approximately triangular shape of the cephalothorax, as well as

the particular length of the pleotelson. By analysing the species of the genus *Apseudes*, we find that in some of them the body aspect resembles quite well those of the genus *Carpoapseudes* but without presenting the carpus of the peraeopod II longer than the meros, while the inner caudo-distal hair of the maxilliped endite is specific to the genus *Apseudes*, as it occurs with *A. grossimanus* Norman & Stebbing 1886, checked up, as it seems, also in this sense, by K. Lang ([5], p. 28 — 33).

Moreover, all the other appendages have a similar enough morphological structure, indicating, in our opinion, a very close kinship between these genera, which determines their inclusion in the same family. As a matter of fact, in 1949, K. Lang followed the same reasoning — yet confined to the chelae level — when he denied the validity of the genus *Leiopus* ([4], p. 4) and then, by the finding of a poorly significant character, but also present in other genera, he classified them into a new family ([6], p. 603).

It is true that it might be demonstrated, even by using our arguments, the relationship existing on the level of the two families : Apseudidae and Leiopidae. We agree with the possibility of its existence and with the fact that under the same conditions of close unity, as between the genera *Apseudes*, *Carpoapseudes* and *Leiopus*, two different families may coexist, but in such a situation, we deem that the determining character must be very strong and conclusive. We do not deny that this character (we still refer to the inner caudo-distal hair of the maxilliped endite) represents a certain adaptation, but this is not enough in the defining of a large systematic group, such as the family type.

A further comparative analysis between the group of the genera *Leiopus-Carpoapseudes* and that of the genera *Pseudowhiteleggia-Whiteleggia*, included by Lang in the same family, reveals greater differences than those between *Apseudes* and the group of the genera *Leiopus-Carpoapseudes*. A legitimate question arises : have the antenna, the antennule, the mandible palp, the maxilliped, the distal extremity of the labium, the uropods, the chela, the presence or absence of the chela exopodites and of peraeopod II, to which the general body shape is added, no importance in the systematics of the Tanaidacea ? We deem they do have, and hence, the group of the genera *Leiopus-Carpoapseudes* represents an intermediate unit closely related both to the genus *Apseudes*, by the above-mentioned characters, and to the group of the genera *Pseudowhiteleggia-Whiteleggia*, by the identical shape of the inner caudo-distal hair of the maxilliped endite. That is why, in order to settle from the systematics viewpoint this evolutive manner of passing from one group to another, we deem necessary to join the two families, Apseudidae and Leiopidae, into one taxonomic unit represented by the family Apseudidae which should be subdivided into three subfamilies : Apseudinae, Leiopinae and Whiteleggiinae*. Thus, we think that the evolution steps within a family would be better marked and at the same time these intermediate units would be taxonomically defined. We do not promote the crumbing prin-

* By the finding of new species belonging to the subfamily Whiteleggiinae which would be able to establish more accurately its characters, we think it would be possible to consider it as an independent family, the Leiopinae remaining then the linking ring with the Apseudidae.

ciple, the systematization for the systematics sake, but when it is necessary, it should be done.

Another problem we bring forward is the systematic position of the genus *Apseudella* Lang 1968 ([5], p. 120 — 126), included by its author, according to the last 1970 revision as well ([6], p. 603), into the family Apseudidae.

In the diagnosis of the family Apseudidae given by Lang ([6], p. 602 — 603), two striking exceptions are found as belonging to a single genus : *Apseudella*. As mentioned by the author, it differs from all other Apseudidae by the typical shape of the epignathus, as well as by the absence of the maxillula palp : "Palpus der Maxillulae entweder vorhanden oder ganz rückgebildet (*Apseudella*). Epignath der Maxillipeden entweder breit und schalenförmig oder schlank, zylindrisch, in Seitenansicht sensiformig (*Apseudella*)" ([6], p. 602 — 603). But the genus *Apseudella* is an exception not only within the family Apseudidae but also within the whole group of monokonophores, because there is no other genus without a maxillula palp and with the same type of epignathus. Yet a similar situation is encountered in the family Neotanaidae belonging to dikonophores, which shows that the genus *Apseudella* is not an accident within the whole order of Tanaidacea, a fact determining its admission among the genera of the family Apseudidae, on the basis of the presence of other similar features, without taking into consideration the lack of the maxillula palp and the shape of the epignathus. In our opinion the lack of this palp shows an independent evolution line within the monokonophores, similar to that in dikonophores, thus being situated at an adaptation level entirely different from the other genera and families.

Likewise if we compare the genus character assigned to the species of *Apseudella* with the family characters assigned by Lang to the Leiopidae, we find a discrepancy between the significance of the character and the rank of the systematic group it defines. In our opinion, the fact that the absence of a palp of considerable size and with a well-defined role, together with the distinctly different shape of the epignathus are considered as not very important characters, since they define a genus, while a simple modified hair, of a few microns, characterizes a family, is groundless.

On the basis of these reasons we deem that the genus *Apseudella* represents a systematic unit apart, superior to a genus as well as to a possible subfamily (even if at the time being only one species is known) and marking a distinct evolution line within the monokonophores — with a palpless maxillula —, an evolution line also found in dikonophores. As a solution, we suggest to take the genus *Apseudella* out of the family Apseudidae and to place it in the framework of a new family, to be named Apseudellidae.

Thus, by fusing the two families, Apseudidae and Leiopidae, into one single family and by dividing this one into three subfamilies, as well as by creating the family Apseudellidae, we think to have succeeded in establishing a balance between the importance of a character and the systematic group determined by it.

By further following up the same idea of marking the evolutive steps, and by analysing the diagnoses of the other families of K. Lang ([6], p. 603) we find that both the family Kalliapseudidae and Metapseudidae

include genera which, from a certain point on, show different adaptation and evolution lines. We consider necessary to differentiate these evolutive stages also from the systematic standpoint. Thus, within the family Kalliapseudidae there are genera with a uniarticulate palp on the mandible (*Kalliapseudes* and *Psammokalliapseudes*) as well as with a 3-articulate palp (*Hemikalliapseudes*). In this case, it seems logical to differentiate the genera with a uniarticulate palp in a group superior to the genus, and therefore we suggest the creation of the subfamily Kalliapseudinae, independent of that defining the species with a 3-articulate palp on the mandible, the subfamily Hemikalliapseudinae.

The same thing is also observed in the case of the family Metapseudidae, including genera with a pleon presenting five pleonites (*Apseudomorpha*, *Cycloapseudes* and *Metapseudes*) as well as the genus *Synapseudes*, with a pleon composed only of three or two pleonites.

Just like in Kalliapseudidae we consider necessary to divide the Metapseudidae into two subfamilies : Metapseudinae, including the genera with a pleon composed of five pleonites, and the subfamily Synapseudinae, including the species with a reduced number of pleonites, i.e. three or two pleonites.

In consequence of the above-mentioned considerations, the systematic picture, together with the diagnosis and determination key of the families and subfamilies belonging to monokonophores, modified by Lang, would have, according to our classification, the following aspect :

Family A P S E U D I D A E G. O. Sars 1882

Pleon with five pleonites. Palp of the mandible 3-articulate. Maxillula with palp. Epignathus of the maxilliped broad, cup-shaped. Inner caudo-distal hair of the maxilliped endite is or is not transformed into a leaf-shaped spine. Peraeopod II never uniform (not stalk-like), stronger than the others, adapted to digging. Dactylus without estetascae.
Subfamilies :

Apseudinae nov.* with the genera : *Apseudes* Leach, *Fageapseudes* Băcescu et Guțu 1971, *Parapseudes* G. O. Sars, *Sphyrapus* Norman & Stebbing, *Trichapseudes* K. H. Barnard, *Thyphlapseudes* Beddard.

Leiopinae nov. with the genera : *Carpoapseudes* Lang and *Leiopus* Lang.

Whiteleggiinae nov. with the genera : *Pseudowhiteleggia* Lang and *Whiteleggia* Lang.

Family K A L L I A P S E U D I D A E Lang 1956

Pleon with five pleonites. Uni-or 3-articulate palp of the mandible. Maxillula with palp. Epignathus of the maxilliped broad, cup-shaped. Inner caudo-distal hair of the maxilliped endite not transformed into a

* Since the diagnoses of the new subfamilies are given in the determination key and are minutely discussed within the paper, we no more insisted upon their characterization on this occasion.

leaf-shaped spine. Peraeopod II never uniform (not stalk-like), stronger than the other ones. Dactylus with estetascae.

Subfamilies :

Kalliapseudinae nov. with the genera : *Kalliapseudes* Stebbing and *Psammokalliapseudes* Lang.

Hemikalliapseudinae nov. with the genus *Hemikalliapseudes* Lang.

Family M E T A P S E U D I D A E Lang 1970

Pleon with five to two pleonites. Palp of the mandible 3-articulate. Maxillula with palp. Epignathus of the maxilliped broad, cup-shaped. Inner caudo-distal hair of the maxilliped endite not transformed into a leaf-shaped spine. Peraeopod II not uniform (not stalk-like) and not stronger than the other ones. Dactylus without estetascae.
Subfamilies :

Metapseudinae nov. with the genera : *Apseudomorpha* Miller, *Cyclopseudes* Menzies, *Metapseudes* Stephensen.

Synapseudinae nov. with the genus *Synapseudes* Miller.

Family P A G U R A P S E U D I D A E Lang 1970

Pleon with five pleonites. Mandible with a 3-articulate palp. Maxillula with palp. Epignathus of the maxilliped broad, cup-shaped. Inner caudo-distal hair of the maxilliped endite not transformed into a leaf-shaped spine. Peraeopod II uniform (stalk-like) and not stronger than the others. Dactylus without estetascae.

Genera : *Hodometrica* Miller, *Pagurapseudes* Whitelegge, *Pagurapseudopsis* Shiino.

Family A P S E U D E L L I D A E nov.

Pleon with five pleonites. Mandible with a 3-articulate palp. Maxillula without palp. Epignathus of the maxilliped elongated and cylindrical, in lateral view scythe-shaped. Inner caudo-distal hair of the maxilliped endite not transformed into a leaf-shaped spine. Peraeopod II not uniform (not stalk-like) and stronger than the others. Dactylus without estetascae.

Genera : *Apseudella* Lang.

DETERMINATION KEY FOR THE FAMILIES AND SUBFAMILIES IN MONOKONOPHORES

1. Dactylus of peraeopod II with estetascae *Kalliapseudidae* 5
Dactylus of peraeopod II without estetascae 2

2. Peraeopod II uniform (stalk-like) not stronger than the following ones **Pagurapseudidae** 3
 Peraeopod II not uniform (not stalk-like)
 3. Peraeopod II not stronger than the following ones, very similar to IV, developed as pushing limb. Flagellum of antennula very short, with a small number of segments **Metapseudidae** 6
 Peraeopod II stronger than the following ones, developed as digging limb
 4. Maxillula with palp **Apseudidae** 4
 Maxillula without palp
 5. Mandible with a uniarticulate palp **Apseudellidae** nov.
 Mandible with a 3-articulate palp **Kalliapseudinae** nov.
 6. Pleon with five pleonites **Metapseudinae** nov.
 Pleon with three pleonites at the most **Synapseudinae** nov.
 7. Inner caudo-distal hair of the maxilliped endite transformed into a leaf-shaped spine 8
 Inner caudo-distal hair of the maxilliped endite not transformed into a leaf-shaped spine
 8. Chelae and peraeopod II with exopodites. Propodite of the uropods without hook-shaped apophyses at the distal end **Leiopinae** nov.
 Chelae and peraeopods II without exopodites. Propodite of the uropods with hook-shaped apophyses at the distal end **Whiteleggiinae** nov.

★

We also wish to elucidate the situation of a species belonging to dikonophores, namely:

Leptognathia vanhoffeni n. nom.

syn. *Strongylurella australis* Vanhoffen 1914, p. 481, fig. 18.
Leptognathia australis (Vanhoffen 1914)

When describing new *Leptognathia* species, K. Lang ([5], p. 166 — 179) makes some remarks concerning the diagnoses of other genera, which led him to the conclusion of the necessity to synonymize some of them ([5], p. 157 — 161). Thus, within the genus *Leptognathia* G. O. Sars 1882 are also included the species of the genera *Haplocope* G. O. Sars 1882, *Tanaella* Norman & Stebbing 1886, *Leptognathiella* Hansen 1913 and *Strongylurella* Hansen 1913.

One year after the description of the genus *Strongylurella* made by Hansen in 1913, with one single species ([3], p. 120 — 121), in 1914 Vanhoffen also describes a species of this genus, which he named *australis* ([7], p. 481 — 482). Yet, within the genus *Leptognathia* there exists already a species *L. australis* described by Beddard in 1886 ([2], p. 127 — 129), while by the synonymy made by Lang two species of *Leptognathia* appear bearing the same name: *L. australis* Beddard 1886 and *L. australis* (Vanhoffen 1914), the latter being a synonym for *Strongylurella australis* Vanhoffen 1914.

Under these conditions, in order to avoid any error we compared the descriptions of the two species and we found that they differ, hence remaining as good species. It consequently becomes necessary to change the name of that deriving from the synonymized genus, i. e. the species *L. australis* (Vanhoffen 1914). We suggest, in this respect, that it should bear the name of the person who described it, that is it should be named *Leptognathia vanhoffeni*.

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LA CEINTURE PELVIENNE— IMPORTANT CARACTÈRE
DANS LA SYSTÉMATIQUE DE LA FAMILLE DES
COBITIDAE

PAR

LOTUS MEŞTER



The present paper is dealing with comparative description of the pelvic girdle of some members of the Cobitidae Family. It was pointed out the importance of this one as a useful criterium in separation of the genera and species. The genus *Noemacheilus*, with the species adapted at the mountain rivers conditions, has shown convergence with some Cyprinidae from torrents.

Les recherches morphologiques chez différentes espèces de poissons nous ont permis de trouver certains critères anatomiques importants, pouvant servir aussi en taxonomie, le degré de leur utilité étant une fonction de leur constance.

L'étude de la ceinture pelvienne chez les poissons a fait l'objet de nombreux travaux, mais seulement corrélée à l'étude des autres parties du squelette.

Ainsi, Murrich [4] étudie l'ostéologie chez *Amiurus catus*, Sarbahi [6] chez *Labeo rohita*, Dharmajan [2] chez *Otholitus ruber*, Nawar [5] chez *Clarias lazera*, Sinha [10] chez *Wallago attu*, Weitzman [11] chez *Brykon meeki*, etc. Des travaux consacrés tout particulièrement à l'analyse de la ceinture pelvienne sont ceux de Hora [3], Saxena [7], [8], Saxena et Chandy [9], Chang [1] — ces auteurs présentant les modifications subies par les os coxaux chez les Homaloptéridés, Cyprinidés et Sisoridés adaptés à la vie dans les torrents.

Le travail présent a pour but la description comparative des ceintures pelviennes chez certains poissons de la famille des Cobitidae, en corrélation avec leur écologie et taxonomie ; cette étude a eu comme premier résultat le fait que la ceinture pelvienne s'est avérée comme un précieux critérium dans la séparation des genres et des espèces.

MATÉRIEL ET MÉTHODE

Pour l'étude de l'anatomie de la ceinture pelvienne nous avons employé les suivantes espèces de poissons : *Misgurnus fossilis* L., *Noemacheilus barbatulus* L., *Cobitis taenia* L., *Cobitis elongata* Heck & Kner, *Sabanejewia aurata balcanica* Kar., *Sabanejewia romanica* Băc. et *Sabanejewia bulgarica* Dr. de Roumanie ; *Botia lohachata* Chaud. (Les Indes), *Oreonectes nikonnisi* Jordan & Fowler (Japon), *Niwaëlla delicata* Niwa (Japon), *Noemacheilus (Acanthocobitis) botia* Ham.-Buch., (Les Indes), *Cobitis calderoni* Băc. (Espagne).

Les ceintures pelviennes ont été mises en évidence par dissection, colorées par alizarine red S en solution de KOH 5% et ensuite dessinées à la chambre claire RA₄.

L'OSTÉOLOGIE DE LA CEINTURE PELVIENNE

Chez *Misgurnus fossilis* (fig. 1B) la ceinture pelvienne est faiblement développée par rapport à la taille du poisson, étant constituée d'os minces. Chaque os coxal présente une apophyse externe plus longue (a.c.), une apophyse médiane fragmentée en trois ou quatre prolongements osseux minces (a.m.) et une apophyse interne courte ± oblique et divergente (a.i.). La crête osseuse basale est puissante et l'encoche ventrale servant à l'insertion des muscles abducteurs (m.) est profonde, mais peu étendue. L'apophyse postérieure est pratiquement non exprimée (a.p.).

Chez *Noemacheilus barbatulus* (fig. 10) on remarque un élargissement accusé des os coxaux, qui sont soudés sur une large étendue, ce qui réduit presque totalement la fenêtre médiane. En conséquence, l'articulation des deux os coxaux devient évidente. Les deux apophyses antérieures des os coxaux sont distalement tronquées et presque égales, celle interne étant plus large. Dorsalement, vers la marge de l'apophyse externe, l'os coxal est pourvu d'une crête puissante qui délimite latéralement une dépression. Sur le côté ventral, l'os coxal ne présente pas d'arête osseuse, mais une fosse profonde qui se dresse vers la ligne médiane. L'apophyse postérieure est fort caractéristique, étant formée de quelques prolongements osseux (a.p., fig. 1C).

Chez *Botia lohachata* (fig. 1H) les deux os coxaux sont assez élargis, délimitant aussi une fenêtre médiane très réduite. Les deux apophyses antérieures sont extrêmement longues, presque filiformes, bordant chacune une fente latérale profonde (f.l.). La dépression ventrale accentuée est délimitée par une arête osseuse réduite. L'apophyse postérieure est longue et mince (a.p.).

Oreonectes (Lefua) nikonnisi (fig. 1F) avec les os coxaux larges, soudés presque sur toute leur étendue. Antérieurement, ils se terminent par deux apophyses courtes (celles internes, en quelque sorte plus longues). Les apophyses postérieures sont minces et très divergentes.

Niwaëlla delicata (fig. 1E) se distingue aussi par l'extrême délicatesse des os coxaux ; non ramifiés, avec une forme triangulaire, ils délimitent une large fente médiane. L'encoche ventrale, faiblement exprimée. L'apophyse postérieure, à peine esquissée (a.p.).

Noemacheilus (Acanthocobitis) botia (fig. 2D) avec les os coxaux larges et soudés sur une grande étendue, ainsi que chez *Noemacheilus l.s.* (l'élargissement, surtout vers la base) ; ils délimitent une fenêtre médiane fort réduite, triangulaire. Les deux apophyses antérieures sont minces (les internes plus longues), latéralement comprimées, délimitant des fentes allongées. Tout comme chez *Noemacheilus barbatulus* une arête osseuse ventrale manque, mais l'encoche servant à l'insertion des muscles abducteurs est profonde et étendue. Les apophyses postérieures sont massives, non pas dactyloïdes, marquées chacune par une légère dépression latérale.

Chez *Cobitis l.s.* la ceinture pelvienne présente un plan structural assez unitaire. Les os coxaux puissants, non soudés sur la ligne médiane ; très allongés chez *Cobitis elongata* (fig. 1A). Tout comme chez *Cobitis taenia* (fig. 2C) ils présentent deux apophyses antérieures, dont celle interne est plus longue, mais nettement différenciées comme forme, chez les deux espèces. La dépression ventrale, accentuée.

Cobitis calderoni (fig. 1D) a les os coxaux aplatis, foliacés, avec les apophyses externes fines, deux fois plus longues que les apophyses internes et avec une encoche ventrale peu évidente. Elles se rapprochent sur la ligne médiane au niveau des apophyses internes, en délimitant une fenêtre allongée, ovale.

Chez le genre *Sabanejewia* on rencontre des os coxaux massifs. Chez *Sabanejewia aurata balcanica* les os ont une seule apophyse antérieure et une encoche ventrale profonde (fig. 2B). Chez *Sabanejewia bulgarica* (fig. 2A) et *Sabanejewia romanica* (fig. 1 G) qui par la morphologie de la ceinture pelvienne sont plus rapprochées entre elles que de *S. balcanica*, les os coxaux ont trois apophyses antérieures ; chez la seconde espèce, on peut rencontrer des exemplaires à deux apophyses seulement. Ainsi que chez le genre *Cobitis*, l'apophyse postérieure est peu développée et légèrement proéminente.

DISCUSSIONS ET CONCLUSIONS

L'étude comparée des ceintures pelviennes nous a conduit vers l'observation de certaines différences nettes entre les genres, les modifications des os coxaux étant corrélées au degré où les nageoires ventrales sont utilisées par rapport au substrat.

Chez *Noemacheilus l.s.* (avec ses sous-genres) on remarque un puissant élargissement des os coxaux qui a conduit vers la réduction des dimensions de la fenêtre médiane. Ce fait a eu comme résultat la formation d'une aire articulatoire médiane longue — particularité qui favorise le maintien du poisson dans le courant de la rivière, ainsi que les fortes pressions des nageoires respectives durant la montée sur le gravier des rivières des montagnes. En même temps apparaissent des apophyses postérieures massives (fig. 2D) ou fragmentées (fig. 1C).

Chez *Botia* et *Lefua* on peut également observer une réduction de la fenêtre médiane réalisée par l'extension de l'articulation des os coxaux ; ces derniers sont moins élargis que chez *Noemacheilus*. Tout comme *Misgurnus fossilis*, *Niwaëlla* a une ceinture pelvienne faiblement développée.

Il est probable que pour la plongée, ces poissons utilisent dans une plus grande mesure les nageoires pectorales et les coups de queue et moins les nageoires abdominales, ce qui mène à un développement prioritaire de la ceinture scapulaire.

Les genres *Cobitis* et *Sabanejewia* présentent des ceintures pelviennes puissantes, avec des dépressions dorsales et ventrales accentuées, servant à l'insertion des muscles abducteurs et arrecteurs. On remarque *Sabanejewia aurata balcanica*, avec une ceinture massive avec un prolongement triangulaire unique, non fragmenté et *C. elongata*, la plus grande loche de rivière européenne, avec une ceinture pelvienne tout aussi bien développée.

Nous pouvons donc affirmer que la morphologie de la ceinture pelvienne présente des différences importantes en fonction des genres et espèces, subissant l'emprise directe des conditions écologiques et le degré dont le poisson se sert de sa nageoire abdominale pour plonger, s'appuyer ou coller au substrat. Le genre *Noemacheilus* dont les représentants sont adaptés à la vie libre dans les rivières des montagnes présente des convergences avec certains ciprinidés et sisoridés des torrents.

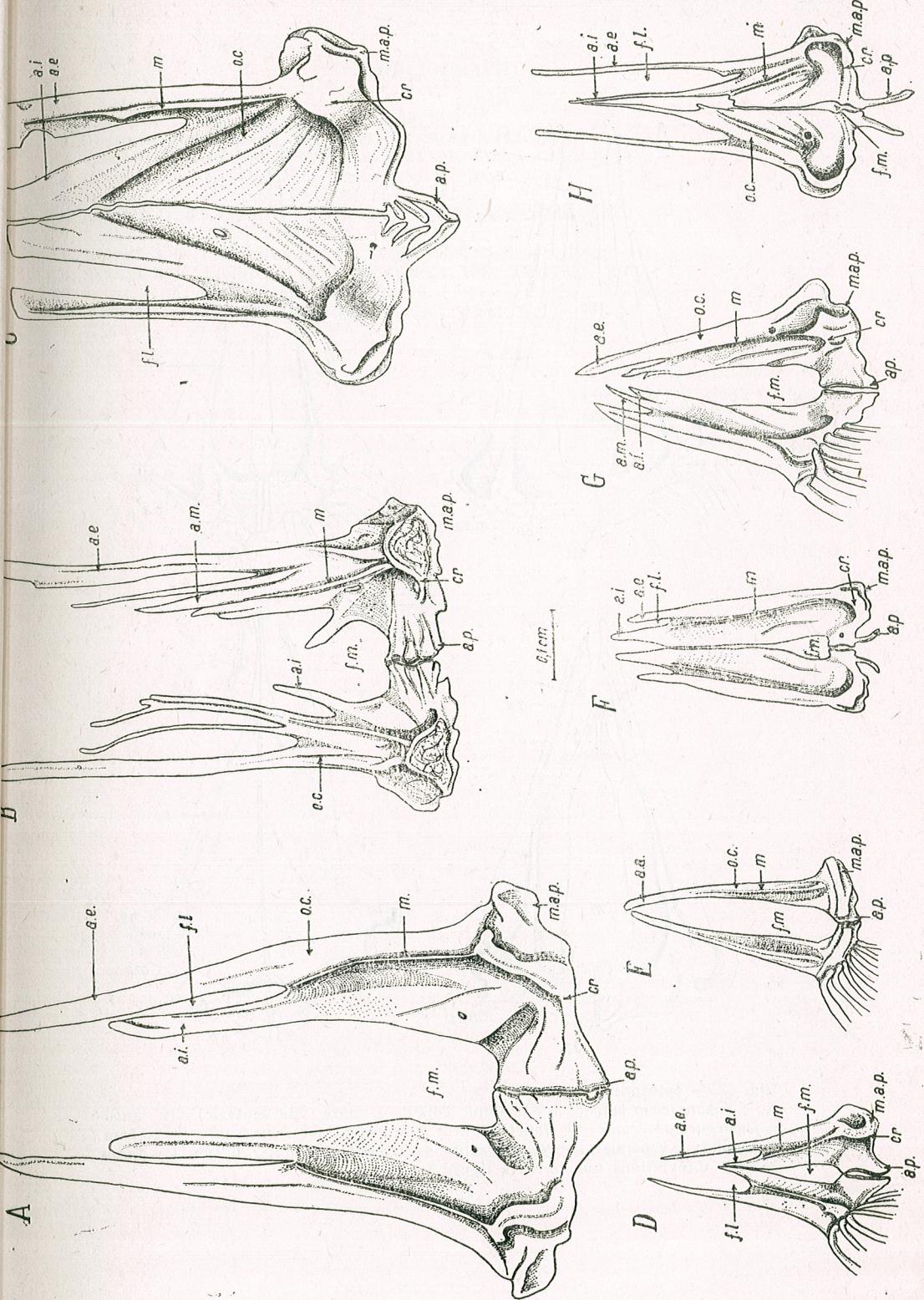


Fig. 1. — Ceintures pelviennes.
A — *Cobitis elongata* ♀, 18 cm, Nera (vue ventrale); B — *Misgurnus fossilis* ♀, 20,2 cm, Greci — Dolj (vue ventrale); C — *Noemacheilus barbatulus* ♀, 10 cm, Slătioara — Succeava (vue dorsale); D — *Cobitis calderoni* ♀, 7 cm, Espagne (vue ventrale); E — *Niwaella delicata* ♀, 9 cm, Japon (vue ventrale); F — *Oreonectes (Lefua) nikonis* ♀, 6,3 cm, Japan (vue ventrale); G — *Sabanejewia romanica* ♀, 6,9 cm, Olteț (vue ventrale); H — *Botia lohachata* ♂, 5,2 cm, Les Indes (vue ventrale) (orig.).

a.a. = apophyse antérieure; a.e. = apophyse externe;
a.i. = apophyse interne; a.m. = apophyse médiane;
a.p. = apophyse postérieure; cr. = crête médiane;
f.l. = fenêtre latérale; f.m. = fenêtre médiane;
m = arête osseuse; m.a.p. = marge articulaire postéro-latérale; o.c. = os coxal (orig.).

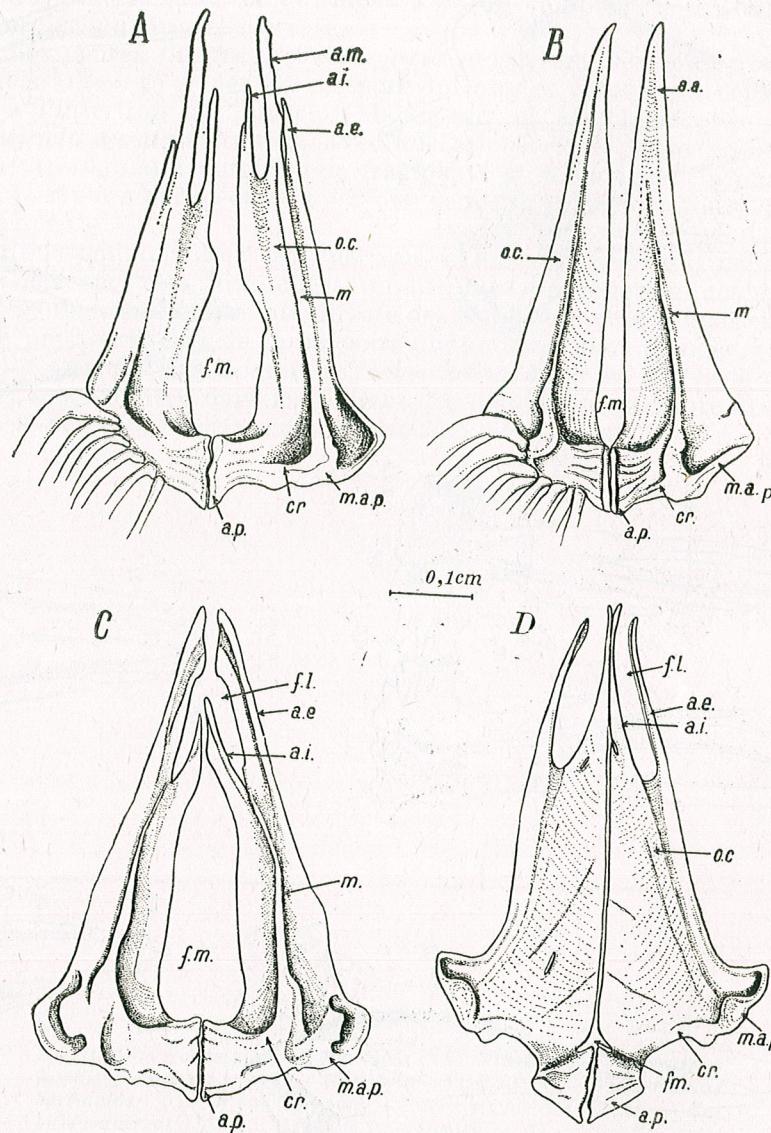


Fig. 2. — Ceintures pelviennes.
A — *Sabanejewia bulgarica*, ♀, 8 cm, Topalu, Dunăre (vue ventrale); B — *Sabanejewia aurata balcanica*, ♀, 7 cm Olteț (vue ventrale); C — *Cobitis taenia*, ♀, 10,5 cm, Frăsinet (vue ventrale); D — *Noemacheilus (Acanthocobitis) bolia*, ♀, 6,2 cm, Les Indes.
Mêmes abréviations que pour la figure 1.

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THE ZOOGEOGRAPHICAL POSITION OF THE EAST
ASIAN FRESH-WATER FISH FAUNA

BY
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The fresh-water fish fauna of East Asia is closer to the Oriental (South Asian) than to the Holarctic one. Yet it is not identical to the South Asian: one family and a few subfamilies occur only in East Asia, the common subfamilies are represented by distinct genera in both faunas. The watersheds between Amur and Lena and between Song Koi and Mekong represent sharp limits of the East Asian fish fauna, which includes also the Vietnam D.R. There are more basic groups of Cyprinidae in East than in South Asia. East Asia represents, since mesozoic times, an important dispersal centre for dominant and competitive fishes.

East Asia, e. g. the Amur drainage, Korean peninsula, Japan and most of the Pacific Ocean basin in China (including Taiwan and Hainan islands but excluding the upper reach of Hwang-ho and Yangtze) is inhabited by a very rich and still incompletely known fauna of fresh-water fishes. Most authors having dealt with the zoogeography of the East Asian fresh-water fishes adopted a regional point of view; their main purpose was to establish to which zoogeographical region (Holarctic or Oriental) belongs East Asia and where must one place the boundary between both regions. A. Günther [7] considered that the Yangtze river marks the boundary, without specifying to which region does the Yangtze drainage itself belong; L.S. Berg [4] [5] considered that most of China (except its High Asian areas and the upper Liao-ho-drainage) represents a distinct, Chinese subregion of the Sino-Indian (Oriental) region, while the Amur drainage, Sakhalin island, Japan, Korea and the upper Liao-ho represent a transitional area or region between the Holarctic and the Sino-Indian; he did not specify which is the boundary between the Chinese and the Indian or Indochinese subregions. T. Mori [10] considered on the contrary that most of China, south to Nan-shan mountain range, Korea and Japan belong to the Holarctic region (most of China, Korea and Japan, ex-

cept Hokkaido representing a distinct Chinese subregion, the Amur drainage, Sakhalin and Hokkaido islands belonging to the Siberian subregion, while southern China (Minkiang and Hsikiang drainage, Taiwan and Hainan islands) belong to the Indo-chinese subregion of the Oriental region. P. Bănărescu [1] ascribed whole East Asia, including the Amur drainage, to the Oriental or Sino-Indian region, considering that the Nan-shan mountain range marks the boundary between the East Asian and the Indo-Malayan subregion. Later on [2] he ascribed also South China and the Song-Koi drainage (Vietnam D.R.) to the East Asian subregion.

Sharp delimitation of regions and provinces is only a minor task of regional and historical zoogeography, whose main purpose is to establish the affinities and differences between faunas, the evolution centres and dispersal routes of higher taxa and of faunistic complexes, the areas in which competitive taxa dominate and those in which archaic, non-competitive taxa survive.

For establishing the zoogeographical position of the East Asian fish fauna, it is first necessary to give a general review of it.

PRIMARY FRESH WATER FISHES

The primary fresh-water fish fauna of East Asia is dominated by Cyprinoidei, especially by Cyprinidae. We consider that this family includes 9 subfamilies (the so-called Schizothoracinae being only a group, perhaps less than a tribe, within the Barbinae). All 9 subfamilies occur in East Asia.

The Danioninae or Bariliinae (including also the Rasborinae) are the most primitive subfamily and possibly an unnatural one. Until recently the subfamily was considered as occurring mainly in South and East Asia, then in Africa. Yet Ted Cavender (personal communication, June 1969) concluded, after a comprehensive osteological study of all North American and many European and East Asian genera of minnows, that the American ones (except *Notemigonus*), usually included within the Leuciscinae), as well as the Holarctic *Phoxinus* (=*Chrosomus*) actually are unrelated to the Euro-Siberian Leuciscinae, but close to some East Asian genera of Danioninae, such as *Zacco*. If he is right, and probably he is, the range of Danioninae includes also North America, Europe and Siberia.

The Holarctic *Phoxinus* is richly represented in the Amur drainage, Japan, Korean peninsula and North China, one species reaching to the Yangtze, but not to South China. Many genera of Danioninae are exclusively East Asian : *Zacco* (Japan and Korea to Vietnam D.R.), *Opsariichthys* (Amur to the Vietnam D.R.), *Elopichthys*, *Squaliobarbus* (same range), *Ochetobius* (Korea to Vietnam D.R.), *Luciobrama* (Yangtze to Vietnam D.R.), *Atrilinea*, *Fustis* (both : Yangtze and South China), *Yao-shanicus* (South China) and the closely related *Hemigrammocyparis* (Japan), *Aphyocypris* (=*Fusania*, *Caraspius*, *Pararasbora*, *Nicholsicypris* : Amur to South China) and *Tanichthys* (South China). The first five genera occur also in the Song Koi drainage, Vietnam D.R., but none of them in the Mekong or Menam drainage and none of the many South Asian genera

of Danioninae occurs in the Yangtze, Hsikiang or Song Koi drainages, although four of them reach in the Mekong drainage to Yunnan Province, China : *Barilius* (*B. buddhae* = *B. pellegrini*), *Danio*, *Brachydanio* and *Luciosoma*.

Leuciscinae : excluding most North American genera and *Phoxinus*, the main range of the subfamily includes Europe, Siberia and parts of West Asia. One genus (*Notemigonus*) is North American, five occur in East Asia : one Palaearctic, *Leuciscus* (in East Asia it ranges from the Amur to the Hwang-ho but not in Japan) and four endemic East Asian : *Pseudaspis* (endemic to the Amur, close to the European *Aspius* and to the Central Asian *Aspiolucius*), *Tribolodon* (the only salt-tolerant and partially migratory genus of minnows, ranging from the Amur to North China, Japan and Taiwan Island), *Ctenopharyngodon* and *Mylopharyngodon* (both : Amur to Hsikiang drainage).

Cultrinae : the subfamily occurs mainly in South and East Asia, one genus (*Pelecus*) being isolated in Europe. There are 12 East Asian genera : *Culter*, *Erythroculter*, *Hemiculter*, *Megalobrama* (Amur to Song Koi), *Parabramis* (Amur to South China and Hainan island), *Hemiculterella* (Hwang-ho, Yangtze and Chekiang), *Toxabramis* (Hwang-ho to Song Koi), *Pseudolaubuca* (Korea and North China to Hsikiang drainage), *Anchrythroculterus*, *Siniichthys* (both endemic to the upper Yangtze), *Ischikauia* (Japan, Taiwan and Hainan islands), *Rasborinus* (South China, Taiwan, Hainan islands and Song Koi drainage, Vietnam D.R.; introduced to Singapore). None of them reaches the Mekong or Menam drainages. Two South Asian genera (*Paralaubuca* and *Macrocheirichthys*) reach the Mekong drainage in Yunnan province, China, but not the Song Koi, Hsikiang or Yangtze drainages.

Xenocypridinae : a small, exclusively East Asian subfamily, not reaching the Mekong drainage. Three genera, the main one, *Xenocypris*, ranging from the Amur to Song Koi drainage, Vietnam D.R.

Acheilognathinae (=Rhodeinae) : almost exclusively East Asian, one subspecies (*amarus*) of the North-East Asian *Rhodeus sericeus* occurring in Europe (in preglacial times also in Siberia) and one species (*Acanthorhodeus deignani*) ranges both in the Song Koi and in the Mekong drainage; two further Chinese species reach the Song Koi drainage. The subfamily includes 6 genera, two of them being speciose : *Acanthorhodeus* (more abundant in the mainland) and *Acheilognathus* (more abundant in Japan).

Gobioninae : mainly East Asian, a single genus, *Gobio*, ranging also in Siberia, Europe, Anatolia and parts of Central Asia. The remaining 19 genera are confined to East Asia ; six genera have a quite restricted range in northern continental East Asia : *Coreoleuciscus*, *Pseudopungtungia*, *Ladislavia*, *Acanthogobio*, *Pungtungia*, *Mesogobio*; one genus is endemic to Japan (*Biwia*); the other 12 genera have a wider range, 5 of them occurring in Song Koi drainage, Vietnam D.R., but none in the Mekong or Menam drainage.

Barbinae : the most speciose subfamily of minnows, centering in South Asia. There are many genera in East Asia, most of them endemic : *Onychostoma* (Hwang-ho to Vietnam D.R. and central Vietnam), *Acrossocheilus* (Pai-ho to the Vietnam D.R.), *Spinibarbus* (Yangtze to Vietnam

D.R.), *Percocypris* (Yangtze and Vietnam D.R., but not Hsikiang drainage), *Semilabeo* (including *Pseudogyrinocheilus*: Yangtze and Hsikiang), *Ptychidio*, *Discogobio* (both endemic to Hsikiang), *Scaphiodontella* (Taiwan island), *Sinibarbus* (upper Yangtze), *Sinocyclocheilichthys* (Yunnan, upper Yangtze). There are in East Asia also representatives of mainly South Asian genera such as *Garra*, *Puntius*, *Osteochilus*, *Poropuntius*, *Lobocheilus* a. o., including species-groups within South Asian genera such as *Cirrhinus* and *Varicorhinus* (subgenus *Sinilabeo*). Some barbines from the upper Yangtze, usually included within the composite *Barbus*, seem actually to be related to the European and West Asian *Barbus* s. str. One peculiar group of Barbinae, the Schizothoracini, has a typical High Asian distribution; it includes also some species endemic to the upper Yangtze and Hwang-ho.

Cyprininae: a small subfamily, closer to the Barbinae and centering in East Asia, with one species also in Europe (*Cyprinus carpio*) and one Eurosiberian (*Carassius carassius*); one South Asian genus, *Puntioplites*, endemic to the Mekong and Menam drainages, seems to belong to this family. In Yunnan and in Hsikiang drainage live some endemic species of *Cyprinus* and of three small genera close to it. *Cyprinus carpio* and *Carassius auratus* were, since centuries, widely introduced through South Asia; in the Song Koi drainage (Vietnam D.R.) both seem to be autochthonous.

Hypophthalmichthyinae: endemic to East Asia (Amur to the Vietnam D.R., not in the islands); three species.

Catostomidae: a mainly North American family, but of apparent East Asian origin; a single recent East Asian genus, *Myxocyprinus*, in the Yangtze and Minkiang drainages.

Cobitidae: the second-largest family of Cyprinoidei, centering in South and East Asia. All three subfamilies occur in East Asia.

Botiinae: two genera — *Botia*, mainly South Asian, but ranging also in East Asia, North to the Yangtze, and *Leptobotia*, endemic to East Asia (Amur to South China).

Cobitinae: there are two Palearctic genera, *Cobitis* and *Misgurnus*, centering in East Asia and reaching also northern Thailand and Burma; two genera are endemic to East Asia: *Niwaella* (Japan and Korea) and *Paralepidocephalus* (Yunnan). None of the many South Asian genera (*Lepidocephalus*, *Acanthopsis*, *Acanthophthalmus*) occurs in East Asia (*Acanthopsis lachnostoma* belongs surely to another genus).

Noemacheilinae: the largest subfamily, whose taxonomy is still in a state of great confusion. Most species are at present ascribed to *Noemacheilus*; yet several generic groups may be recognized within it. Some of them are endemic to East Asia: *Yunnanilus* (Yunnan), *Homatula* (upper Yangtze, South China, Hainan island and the Vietnam D.R.; close to the speciose South Asian *Schistura*). Most Chinese species belong to the High Asian group, whose valid name is either *Triphophysa*, *Deuterophysa* or *Tauphysa*, but these species are confined to the upper Yangtze and Hwang-ho which belong rather to High- than to East Asia proper. *Orthrias* has one species in northern East Asia and Siberia (*toni*), one in Europe (*barbatula*), a few in West Asia. In East Asia occur also a few mainly

South Asian generic groups: *Oreonectes* (= *Lefua*), *Noemacheilus* s. str., perhaps also *Schistura*.

Homalopteridae: the family ranges in South and East Asia; a single one of the 7 South Asian genera includes one species occurring in the Vietnam D.R., but the specimens on which it is based may have been mislabelled [12]. Five genera are endemic to East Asia (Amur to South China, Hainan and Taiwan, one species in the Vietnam D.R., none in the Mekong drainage).

Gastromizonidae (including the so-called Crossostomidae): morphologically similar but apparently not very close to the former; 12 genera are restricted to Borneo, 9 to East Asia (upper Amur, southern continental China, Taiwan and Hainan islands), one, *Annamia*, to Kontum Lake, Tonkin Bay basin, Central Vietnam and one is isolated in the lower Mekong drainage, South Vietnam. Curiously enough, this genus is closer to the East Asian than to the Borneo ones [12].

The second group of the Ostariophysi, the Siluroidei, are represented in East Asia by much fewer genera and species than the Cyprinoidae; they belong to 4 families, three of which are better represented in South Asia.

Bagridae: there are three exclusively East Asian genera — *Leiocassis*, *Hemibagrus*, *Liobagrus* — ranging from the Yangtze to southern China, and one mainly Indochinese one, *Pseudobagrus*, distributed through East Asia, north to the Yangtze.

Siluridae: there is a single genus in East Asia, *Silurus* (= *Paramylloplus*), widely distributed also in South Asia and Europe. One species endemic to the Amur drainage, *S. soldatovi*, is closer to the European *S. glanis*.

The Cranioglanididae are a small family, restricted to Hsikiang (South China) and Song Koi (Vietnam D.R.) drainages, with two representative species or subspecies. It is the only family endemic to East Asia.

The Sisoriidae (Bagariidae) are mainly South and High Asian; three genera occur in East Asia: the widely ranging *Glyptothorax* and two endemic to the upper Yangtze: *Coraglanis* in Szechwan and *Glaridoglanis* in Yunnan; according to S. L. Hora & E. G. Silas [8], both last named genera belong to a mainly High Asian supergeneric group.

The Non Ostariophysi primary fresh-water fishes are very poorly represented; they include two Holarctic families, Esocidae (a single species, *Esox reicherti*, endemic to the Amur drainage and to Sakhalin island) and Polyodontidae (an archaic family with disjunct range, consisting of two genera, *Psephurus* in the Yangtze and the Hwang-ho, the second one in the Mississippi) and three mainly South Asian ones: Osphromenidae (the South Asian *Macropodus* reaches to the Pei-to), Mastacembellidae (one Yangtze species of the South Asian and African Mastacembellus) and Channidae or Ophiocephalidae (several East Asian species of *Channa* = *Ophiocephalus*, some endemic, some occurring also in South Asia).

SECONDARY FRESH-WATER FISHES

There are only two species of *Aplocheilus*, subgenus *Oryzias*, belonging to Cyprinodontidae (subfamily Rivulinae); the genus is rather salt-tolerant and has a wide range from India to Kalimantan and Japan.

VICARIOUS FRESH WATER FISHES

This category includes strictly fresh-water genera belonging to primary marine families. Several vicarious fresh-water genera from East Asia are Holarctic: *Eudontomyzon* (Korea, then East Europe), *Thymallus* (Holarctic, in East Asia only in the Amur), *Lota* (Holarctic; Amur and Sakhalin), *Cottus* (Holarctic; in East Asia south to Korea); two other genera are endemic but of Holarctic affinities: *Mesocottus* (Korea) and *Trachidermus* (Japan, Korea, north China). The closely related serranid (4 species, Korea and Japan to Vietnam D.R.) and *Coreoperca* genera in this area; according to S. Nishimura [11], they originated from a marine ancestor close to the recent genus *Stereolepis*. Some fresh-water genera of Gobiidae, too, may belong to the vicarious category, but the general systematics of this subfamily is too insufficiently known for enabling us to decide in this matter.

PERIPHERAL FRESH-WATER FISHES

Peripheral fresh-water fishes include migratory, euryhaline and well represented in East Asia. Some belong to northern (Holarctic) families: *Petromyzonidae* (Amur, Japan, Korea), *Acipenseridae* (south to the Yangtze), *Salmonidae* (*Oncorhynchus*, *Salvelinus*, *Salmo*, *Coregonus* only in the Amur, Japan, Korea; *Hucho* including also a resident freshwater species in the upper Yangtze), *Salangidae* (exclusively East Asian but cold-adapted; south to the Vietnam D.R.), *Gasterosteidae* (Amur and Japan to Pai-ho). Tropical (Indo-West Pacific) marine families occurring in the fresh waters of East Asia are: *Synbranchidae*, *Anguillidae*, *Heimirhamphidae*, *Ambassidae*, *Serranidae*, *Hemulidae*, *Tetraodontidae*, etc. and especially *Gobiidae*, which include genera apparently confined to fresh-waters and restricted to East Asia, taxonomically close to South Asian ones.



This review of the genera and higher taxa of fresh-water fishes occurring in the fauna of East Asia clearly demonstrate that this fauna is closer to the Oriental (South Asian) than to the Holarctic one. Typical and peripheral genera, most of which have a limited distribution in East Asia. From the very many endemic East Asian genera, only *Psephurus*, *Pseudaspius* (endemic to the Amur), *Ctenopharyngodon*, *Mylopharyngodon* to East Asia and to the Eurasian part of the Holarctic (Europe and Siberia) — *Rhodeus*, *Gobio*, *Cyprinus*, *Carassius*, *Misgurnus*, *Cobitis*, *Siluridae* — but these are fishes of undisputable East Asian origine having *Umbridae* and *Percidae* (which both occur in eastern Siberia) are totally

absent from East Asia. The bulk of the East Asian fish fauna is represented by the very numerous genera of Cyprinoidei, especially Cyprinidae, whose present distribution (and probably dispersal) centre is represented by both South and East Asia. Further higher taxa common to East and South Asia are the Siluroidei, Anabantidae, Mastacembellidae and Channidae.

Although zoogeographically close, the East Asian fish fauna is by far not identical to the South Asian one. As pointed out in this paper, the Gobioninae, Acheilognathinae, Xenocypridinae, Hypophthalmichthyinae, Cyprininae (except *Puntioplites*) and Cranioglanididae are higher taxa confined to East Asia or (Acheilognathinae) including also a few representatives which crossed quite recently the watershed to South Asia. The families and subfamilies common to East and South Asia are in general represented by distinct genera in both areas: Danioninae, Cultrinae, Cobitidae, Homalopteridae, Gastromyzonidae, even Barbinae, Bagridae and Sisoridae.

We think these facts enable us to consider that East Asia represents, for fresh-water fishes (and for fresh-water mussels, snails and crabs, too), a distinct zoogeographical subregion within the Oriental or Sino-Indian region.

The northern boundary of this subregion is very sharp: the watershed between the Amur and the Lena (e.g. the Jablonoi-Stanovoi mountain range). The Amur drainage fish fauna includes more Holarctic species or of Holarctic affinities than the other East Asian drainages and areas. Nevertheless there are much more East Asian species: 13 of Gobioninae, 8 of Cultrinae, 4 of Danioninae, 4 of Bagridae, etc. In the adjacent Lena drainage in East Siberia live u.o. two species of Percidae and 5 Eurosiberian Cyprinidae not occurring in East Asia.

Also the southern boundary of the subregion is very sharp: the watershed between the Song Koi drainage in North Vietnam and the small coastwise rivers flowing into Tonkin Bay on the one hand, the Mekong drainage on the other. The Song Koi drainage is inhabited by a typical East Asian and not a South Asian fish fauna. It was repeatedly pointed out in this paper that East Asian genera of Gobioninae, Danioninae, Cultrinae, Barbinae, etc. are present in this drainage but not in the adjacent Mekong drainage, whose fish fauna is typically South Asian. There are even some 11 species of minnows ranging from the Amur to the Song Koi. Evidently there occur in the Song Koi drainage also a few South Asian species (or endemic species of South Asian affinities) lacking in the Yangtze and even in South China (e. g. "*Tylognathus*" *delacouri* and *fowleri*, both actually belonging to *Lobocheilus*); but the number of East Asian genera and species is much higher. The Cranioglanididae are a family confined to the Song Koi and the Hsikiang drainage (South China).

Even the poor fish fauna of the small coastwise rivers flowing into the Tonkin Bay both in the southern part of the Vietnam D. R. and the northern part of South Vietnam (the former "Annam") is closer to the East than to the South Asian one. Here live one endemic species (*krempfi*) of a very typical East Asian genus (*Hemiculter*), then *Onychostoma macracantha*, a species occurring also in the Song Koi drainage.

As an argument for ascribing southern China (Minkiang and Hsi-kiang drainages) to the Indochinese subregion, T. Mori [10] invokes the occurrence of "southern" genera, such as *Yaoshanicus*, *Discogobio*, *Amplolabrius* (a synonym of *Semilabeo*), *Rectoris*, *Tanichthys*, *Procypris*. Actually these are endemic South Chinese genera, not occurring in the Mekong drainage, related to genera from Japan or North China (*Tanichthys* to *Aphyocypris* and *Hemmigrammocyparis*, *Procypris* to *Cyprinus*) or from the Yangtze (*Semilabeo* is close to *Pseudogyrinocheilus*).

No sharp limit can be traced between the East and the High Asian fish fauna, because there is no watershed between them. A gradual replacement of East Asian fishes by High Asian ones (Schizothoracini and noemacheiline loaches of the *Triptophysa*-*Deuterophysa* group) takes place in the upper Yangtze and Hwang-ho.

★

The Cyprinidae are the most competitive group of fresh-water fishes. There are somewhat more species in South than in East Asia, because of the abundance of the thermophilous Barbinae. But there are more basic groups in East Asia: 5 subfamilies are exclusively or almost exclusively East Asian (or Palaearctic centering in East Asia); from the only three subfamilies widely ranging also in South Asia, the Danioninae and Cultrinae include slightly more East Asian genera and only the Barbinae more South Asian ones. Yet some facts suggest that in tertiary (even in neogene) times the Barbinae were fairly more numerous than now in East Asia and occurred also in its northern part; a few of them (the ancestors of *Barbus* s. str. and of the West Asian „*Capoeta*“ sensu Karaman [9]) seem to have dispersed from East Asia through Siberia to Europe and West Asia.

East Asia seems thus to have been, until rather recent geologic times, the main dispersal centre of Cyprinidae, Catostomidae, even of Cobitidae, Homalopteridae and Gastromyzonidae.

The fauna of each area includes autochthonous taxa on the one hand, immigrants from adjacent areas on the other. The East Asian fish fauna includes mainly autochthonous genera and higher taxa. As older Holarctic immigrants one can consider the ancestors of *Pseudaspis*, *Otenopharyngodon*, etc.; more recent Holarctic intruders are *Leuciscus*, *Phoxinus*, *Esox*, *Lota*, etc. (some of which reached East Asia in pleistocene times). South Asian intruders are some Siluroidei, Anabantidae, etc. and the representatives of the barbinae genera occurring also in the Mekong drainage (*Osteochilus*, *Puntius*, *Lobocheilus*, etc.). Marine immigrants are *Siniperca*-*Coreoperca* and some other vicarious and peripheral fishes.

But all groups of immigrants together are far less numerous than the autochthonous fishes. The Cyprinoidei being the dominant and most competitive group of recent fresh-water fishes, East Asia (together with South Asia) was the main dispersal centre for continental fishes. The Ostariophysi from North America came from East Asia: a first wave included the Catostomidae and the ancestors of Ictaluridae, a second one the Cyprinidae. Siberia and Europe, too, were colonized from East Asia: first came the remote ancestors of Leuciscinae, then the recent genera

belonging to other subfamilies: *Rhodeus*, *Gobio*, *Cyprinus*, *Carassius*, *Noemacheilus* (*Orthrias*), *Misgurnus*, *Cobitis*, the ancestor of *Sabanejewia*. In a previous paper [1] we suggested that *Barbus* and "Varicorhinus" (*e.g. Capoeta*, sensu Karaman) represent offshoots of West Asian immigrants in the Europeo-Mediterranean fauna. But both genera are absent in the eastern parts of West Asia and have no close relatives in India; their closest relatives live in East Asia (some West Chinese „*Barbus*“ and *Onychostoma*). We therefore think, now, that the ancestors of both genera reached Europe and West Asia through Siberia, like *Gobio*, *Cyprinus*, etc.

East Asia seems to have been an important dispersal centre for fresh-water fishes also in mesozoic times: the Lycopteridae, considered by Greenwood [6] to be the oldest Osteoglossomorpha, lived in East Asia and parts of Siberia. The Osteoglossomorpha are now an archaic group which survives only in a few, rather peripheral areas (not in East Asia) but they were once the dominant group.

The Amur-Lena watershed represents now a very sharp boundary between two distinct fish faunas; yet in tertiary times it was repeatedly crossed by Ostariophysi which dispersed from East Asia to Siberia and from here both to Europe and to North America. The Song Koi-Mekong watershed seems on the contrary to have been also in tertiary times an important barrier, being only occasionally crossed by few fishes; the East Asian and the South Asian fish faunas evolved rather independently, although they have a remote common origin.

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TWO NEW SPECIES OF *MACHILIS* FROM THE SOUTHERN
CARPATHIANS (INSECTA THYSANURA)

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This note gives the description of two new species of *Machilis*: *Machilis dumitrescui*, belonging to the *tirolensis* group, and *Machilis capusei**.

The material which forms the object of the present paper has been submitted to us by Mr. I. Căpușe, to whom we wish to express our thanks for it.

***Machilis dumitrescui* n. sp.**

Material examined: 3 females and one male captured on May 22 1964 on the Domogled Mountain, 800 m., lapidicolous, Băile Herculane (The Cerna Mountains).

Description of both sexes. Maximum length of body=20 mm. Strong pigmentation of head (Plate I, E ♀ and pl. II, D ♂). In the middle of the frons a longitudinal stripe without pigment. Labrum either with little pigment or entirely without pigment. Black eyes (alcohol). Contact line/length of eye=0.66 (♀ and ♂); length /width=0.9 ♀, 1 ♂. Ocelli reddish. Length of antennae=22mm distal chains brown, the segments at the basis light-coloured. Maxillary palp stout, strongly pigmented on the outer surface.

Maxillary palp of ♀ (Pl. I, C). Segment 1 pigmented. Segment 2 almost entirely pigmented excepting an unpigmented basal spot and a distal ring. Segment 3 pigmented excepting a basal ring and a distal one. Segment 4 has a ring of pigment basally, then an unpigmented area, and the rest is entirely pigmented. Segment 5 has two wide pigmented

* We express our thanks to Dr. P. Wygodzinsky from the American Museum of Natural History, New York, who kindly confirmed the validity of the described species.

rings, one basally and another distally. Segment 6 with a wide pigmented ring basally, distally with diffuse pigment.

Maxillary palp of ♂ (Pl. II, C). Segment 1 with a big pigmented spot. Segments 2 and 3 similarly pigmented : a wide longitudinal pigmented stripe, distally an unpigmented ring. Segment 4 with a basal pigmented ring, followed by an unpigmented ring, then a large pigmented area. Segment 5 in the basal half with a wide pigmented ring, then distally a diffuse pigmented spot. Segment 6 with a basal pigmented spot. Length of last segment/penultimate = 0.6 ♀ and 0.5 ♂.

The labial palp pigmented at the base of segment 3 in both sexes (Pl. I, D, ♀ and Pl. II, E ♂).

Legs strongly pigmented (Pl. III, A—F). Coxa pigmented in the basal half. The femur of leg I (♀ and ♂) almost entirely pigmented. Femur of legs II and III (♀ and ♂) with a longitudinal pigmented stripe on the outer border and a distal pigmented spot, excepting the femur of leg III where the spot is absent. Tibia pigmented, excepting a wide distal ring in all three legs of both sexes. Tarsus with diffused pigment on segments 1—3. Tibia and tarsus with brown spines. Distribution of spines on tibia : ♀ I : 0, II : 6, III : 12. ♂ I : 0, II : 4, III : 5.

The abdominal sternites II—V with two pairs of coxal vesicles each.

Ratio stylet/coxite :	II—VII = ♂	♂ 0.75	♀ 0.5—0.6
VIII = ♂	0.83	♀ 1	
IX = ♂	1.4	♀ 1—1.1	

Brown ovipositor of secondary type, somewhat shorter than the stylets of coxite IX. Gonapophysis VIII with 36—38 segments (Pl. I, B). Brown fossorial spines, 1—3 for each segment, on the last 3—4 segments ; their distribution : 1—2, 2—2, 2—2, 3. Brown fossorial setae on segments 5—15, one on each segment. Brown long bristles on all segments excepting the basal ones. The apical setae have the length of the last two segments. 5—6 groups with 10 sensory spinulets each. Gonapophysis IX with 36—40 segments (Pl. I, A). Brown fossorial spines, 1—3 on the last 3—4 segments. Their distribution : 1—2, 3—2, 2—2, 2—2. Brown fossorial setae on segments 5—15. Apical setae having the length of the last 2 segments. The anterior parameres (Pl. II, A) have 1+5 segments, the posterior parameres (Pl. II, B) have 1+6 segments. The penis slightly surpasses the posterior parameres. The basal part of the penis is twice as long as the distal part.

Machilis dumitrescui belongs to the *tirolensis* group. Our species is clearly distinguished, however, from the other species of the group, by its greater size, by the total absence or little amount of pigment on the labrum, by the different distribution of pigment on segments 2, 4, 5, 6 of the maxillary palp, the different pigmentation of the femur of the anterior and posterior legs, the different form of fossorial spines (in our species they are shorter, thicker at the base, sharp and bent at the end), by the smaller number of sensory spinulets.

Machilis capusei n. sp.

Material examined : 3 females and one male, captured 27.VI.1964, Cireşu (Mehedinți Plateau), lapidicolous, P. Topolnița.

Description of both sexes. Maximum length of body = 16.5 mm. Strong head pigmentation (Pl. V, A ♀). Pigmentation of the male resembling that of the female. Frons having in its middle a light-coloured longitudinal stripe. Labrum with a little amount of diffuse pigment basally. Grey eyes with brown spots (alcohol). Contact line/length of eye = 0.56—0.66 ♀ and 0.65 ♂; length/width of eye = 1—1.15 ♀ and 1—1.25 ♂. The paired ocelli reddish. The antennae longer than the body = 23 mm. The distal chains uniformly brown, at the base of each chain some light-coloured segments. Maxillary palp stout, yellowish, with pigment on outer surface.

Maxillary palp of ♀ (Pl. V, B). Segment 1 with a wide pigmented spot at its centre. Segment 2 with a pigmented longitudinal stripe starting from the base and going as far as the distal part. Segments 3 and 4 have a small basal pigmented spot each. Segment 5 has in its middle a pigmented longitudinal stripe on the outer border, at the centre of the segment a small amount of diffuse pigment. Segment 6 has a large pigmented spot.

Maxillary palp of ♂ (Pl. IV, A). Segment 1 has a median pigmented spot distally. Segment 2 has an uninterrupted longitudinal pigmented stripe starting from the base of the segment and going as far as the distal part. The other segments without pigment. Segment 7 short and thick. Length of last segment/penultimate = 0.75 ♀ and 0.32 ♂.

The labial palp entirely without pigment in both sexes (Pl. IV, B ♂ and Pl. V, C ♀).

Pigmentation of legs (Pl. VI, A—F). Similar pigmentation in both sexes. Legs I and II have a similar pigmentation in male and female. Coxa having a pigmented spot at the base, somewhat smaller in the male. The femur with a distal pigmented spot. Tibia of all legs with a wide longitudinal pigmented stripe, unpigmented apically and distally. Tarsus with diffuse pigment on segments 1 and 3. Tibia and tarsus with brown spines. Legs III have a small pigmented spot on the coxa, on the tibia a wide longitudinal pigmented stripe in ♀, in ♂ a weak pigmented spot. Distribution of spines on the tibia : I : 0, II : 0, 3, 4, III : 7 ♀. I : 0, II : 2, 5, III : 5 ♂.

Abdominal sternites II—V with 2 pairs of coxal vesicles each. Ratio stylet/coxite :

II—VII = ♂	0.62—0.7	♀ 0.72
VIII = ♂	0.8	♀ 1
IX = ♂	1.6	♀ 1.63

Brown ovipositor of secondary type, does not reach the end of stylets of coxite IX. Gonapophysis VIII has 41 segments (Pl. V, D). Brown fossorial spines, 1—3 on the last 3—5 segments. Their distribution : 1—2, 2—2, 2—3, 2, 1. Brown fossorial setae on segments 6—13, one for each segment. Long bristles on all segments excepting the basal ones. Apical setae having the length of the last 3 segments. 7 groups of maximum 14 sensory spines each. Gonapophysis IX has 40 segments (Pl. V, E). Brown

fossorial spines, 1–4 for each segment, found on the last 3–4 segments. Their distribution: 2–2, 2–3, 2–4, 1–1. Brown fossorial setae on segments 5–14. The apical setae have the length of the last two segments.

The anterior and posterior parameres have 1+6 segments. The penis of the same length as the parameres (Pl. IV, C), having a basal part twice as long as the distal part.

Machilis capusei is related to the species *M. germanica* Janetschek 1953 and *M. mijerei* Wygodzinsky 1954 by the similar distribution of the pigment on the first two segments of the maxillary palp and by the pigmentation of the legs. It differs from these species by the following: labrum without pigment; segment 5 of the maxillary palp of the female with a longitudinal stripe distally, and diffuse pigment in the centre; segment 6 with a strong pigmented spot; labial palp entirely without pigment; *M. capusei* also has the same number of segments of the parameres for both pairs of parameres — 1+6. The size of the specimens belonging to our species is larger.

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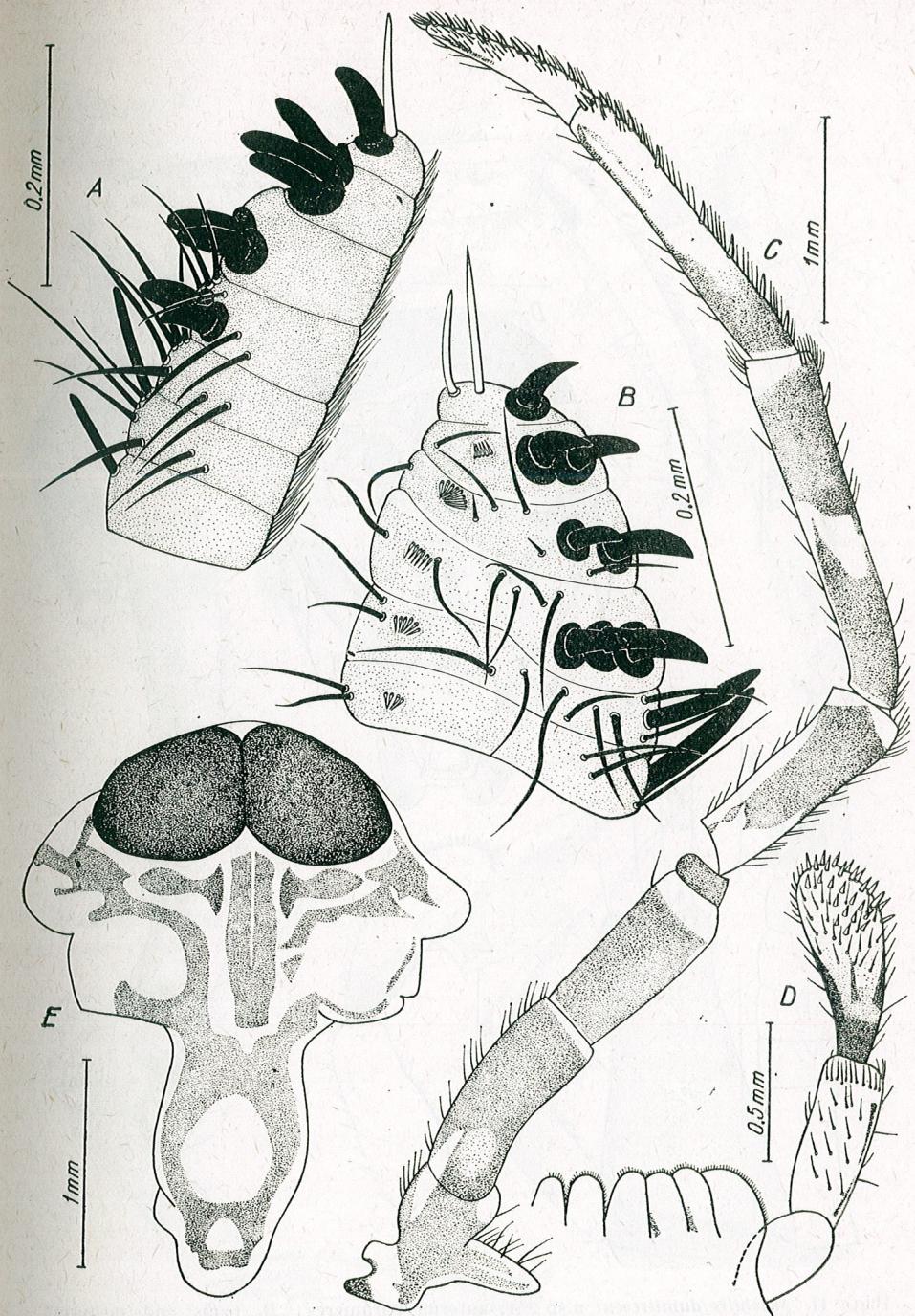


Plate I. *Machilis dumitrescui* n. sp.: A, apical segments of posterior gonapophyses; B, apical segments of anterior gonapophyses; C, maxillary palp of female, external surface; D, labial palp of female; E, pigmentation of head of female.

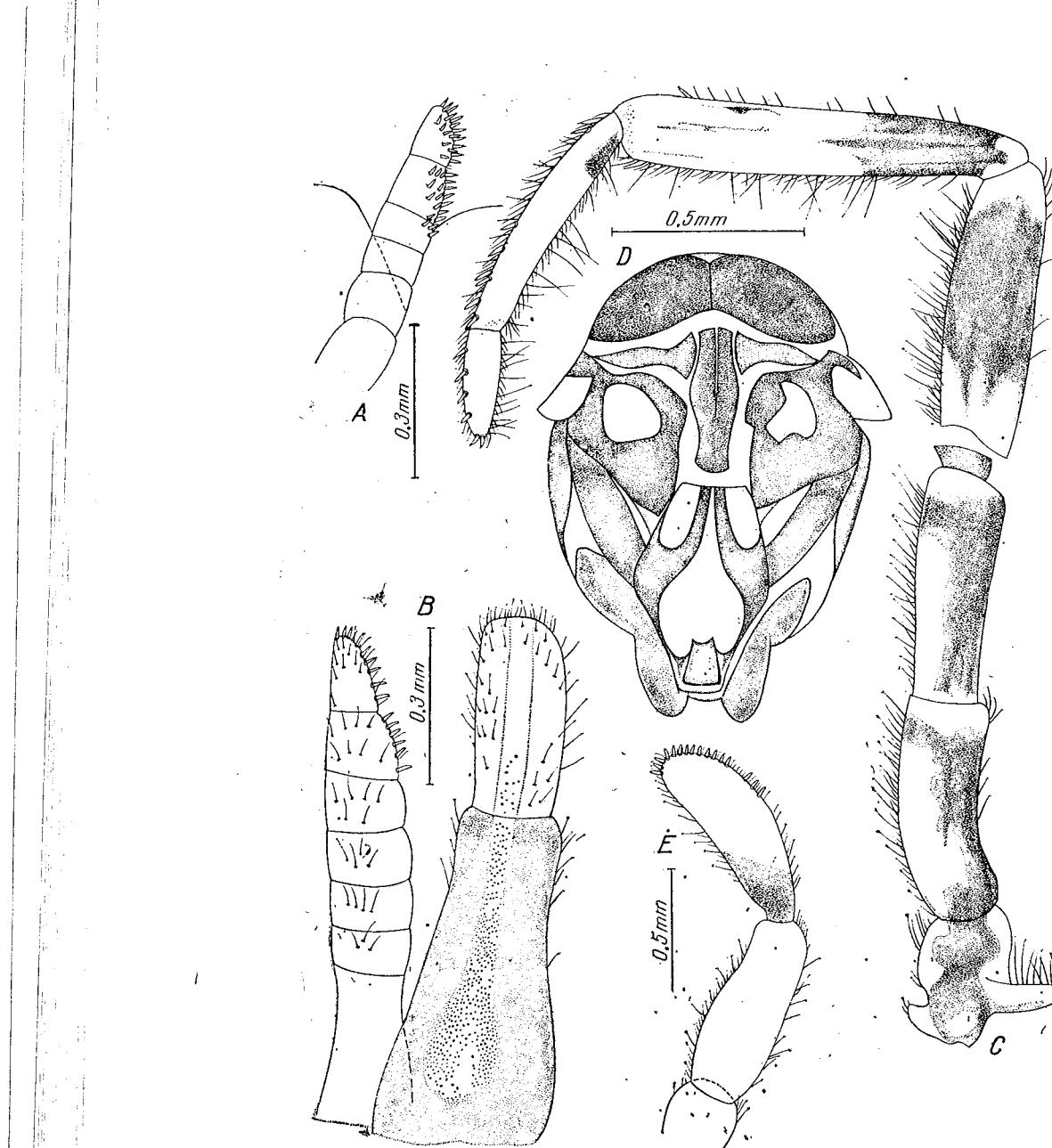


Plate II. *Machilis dumitrescui* n.sp.: A, anterior parameres; B, penis and posterior parameres; C, maxillary palp of male; D, pigmentation of head of male; E, labial palp of male.

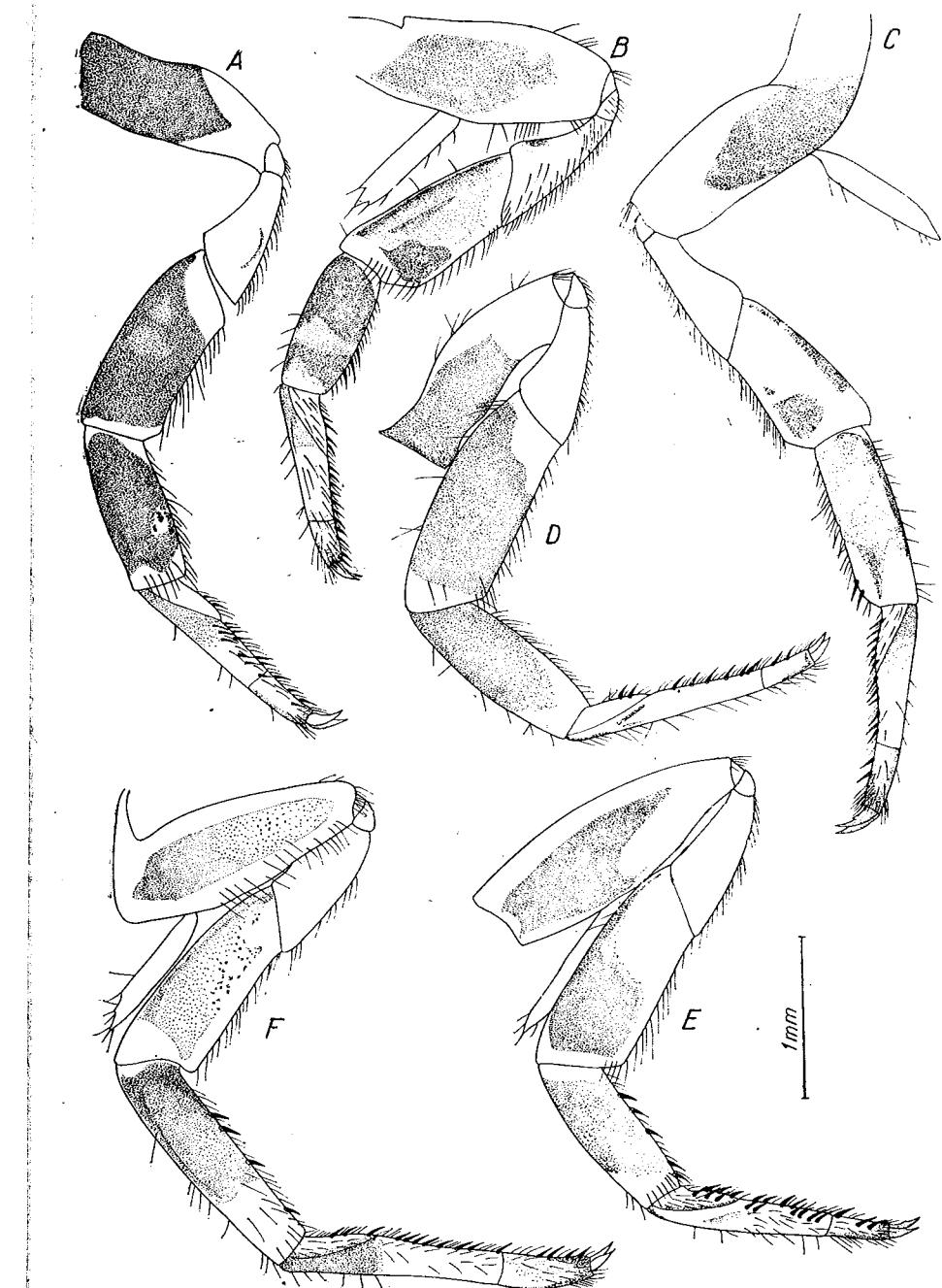


Plate III. *Machilis dumitrescui* n. sp. Pigmentation of legs, external surface: A, B, C, legs 1, 2, 3, female; D, E, F, legs 1, 2, 3, male.

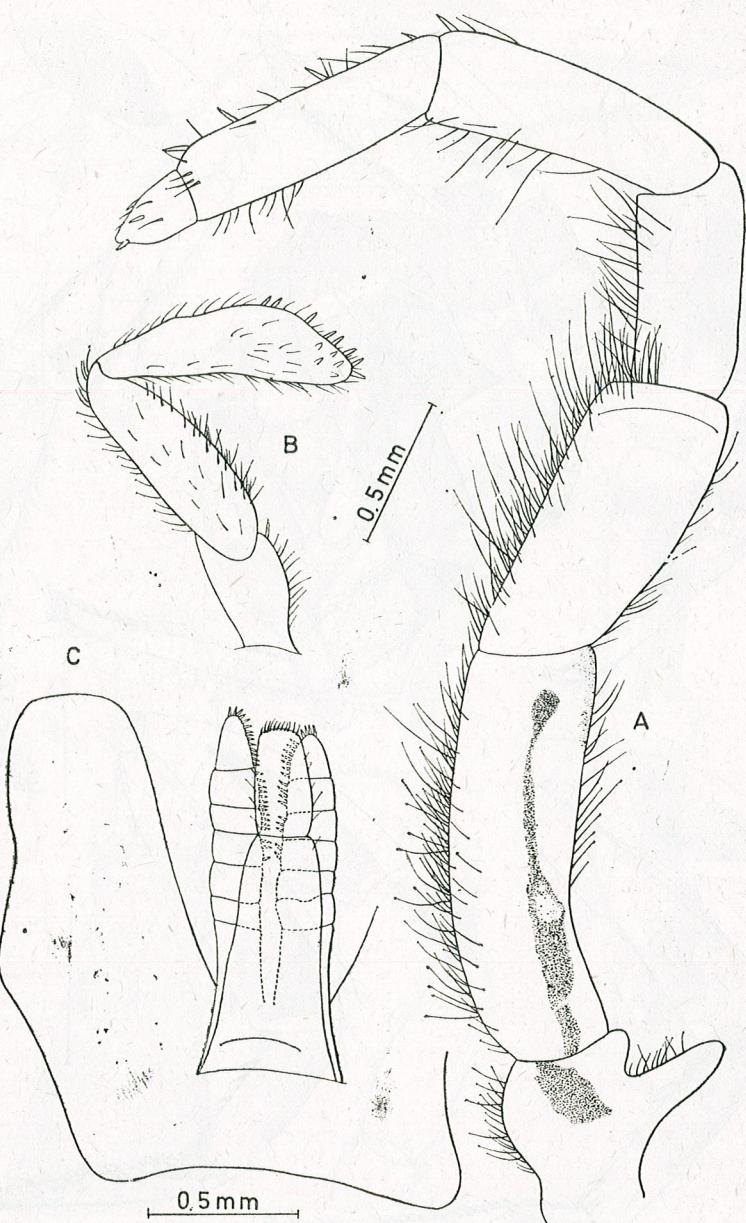


Plate IV. *Machilis capusei* n. sp.: A, maxillary palp of male, external surface; B, labial palp of male; C, penis and posterior parameres.

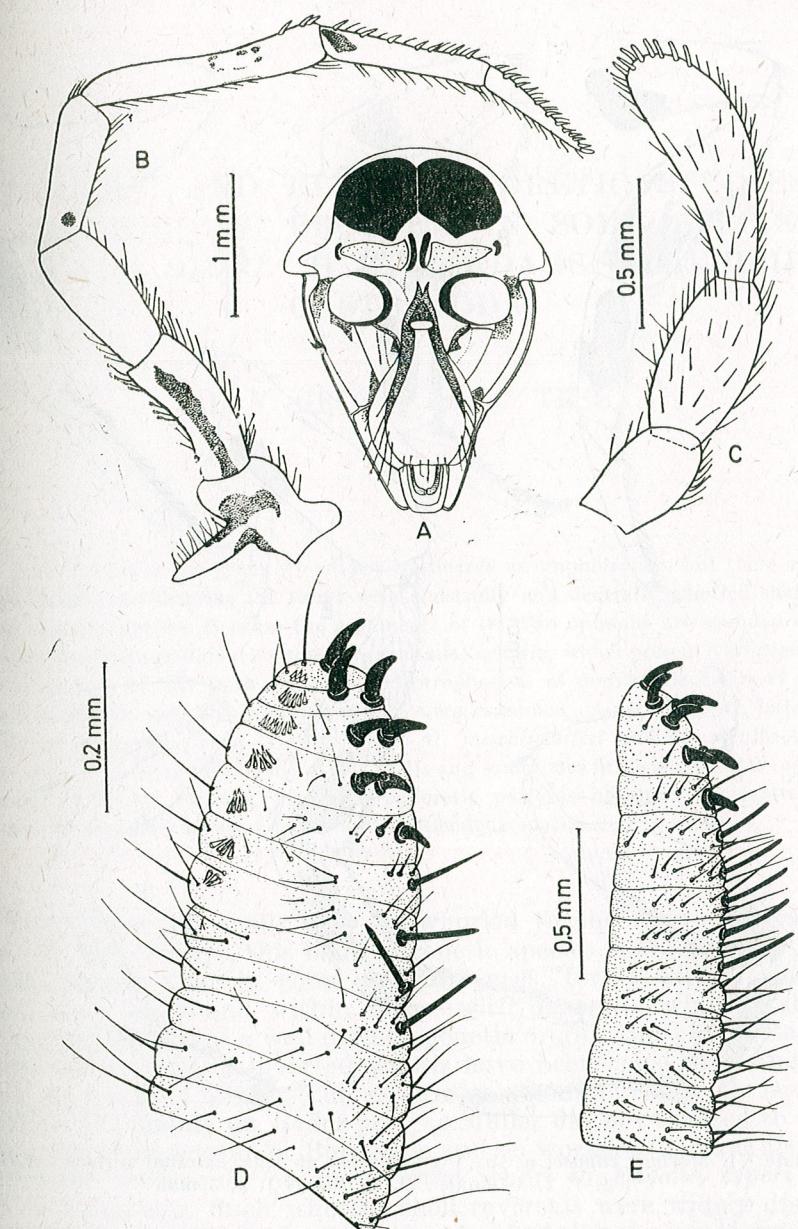


Plate V. *Machilis capusei* n. sp.: A, pigmentation of head of female; B, maxillary palp of female, external surface; C, labial palp of female; D, apical segments of anterior gonapophyses; E, apical segments of posterior gonapophyses.

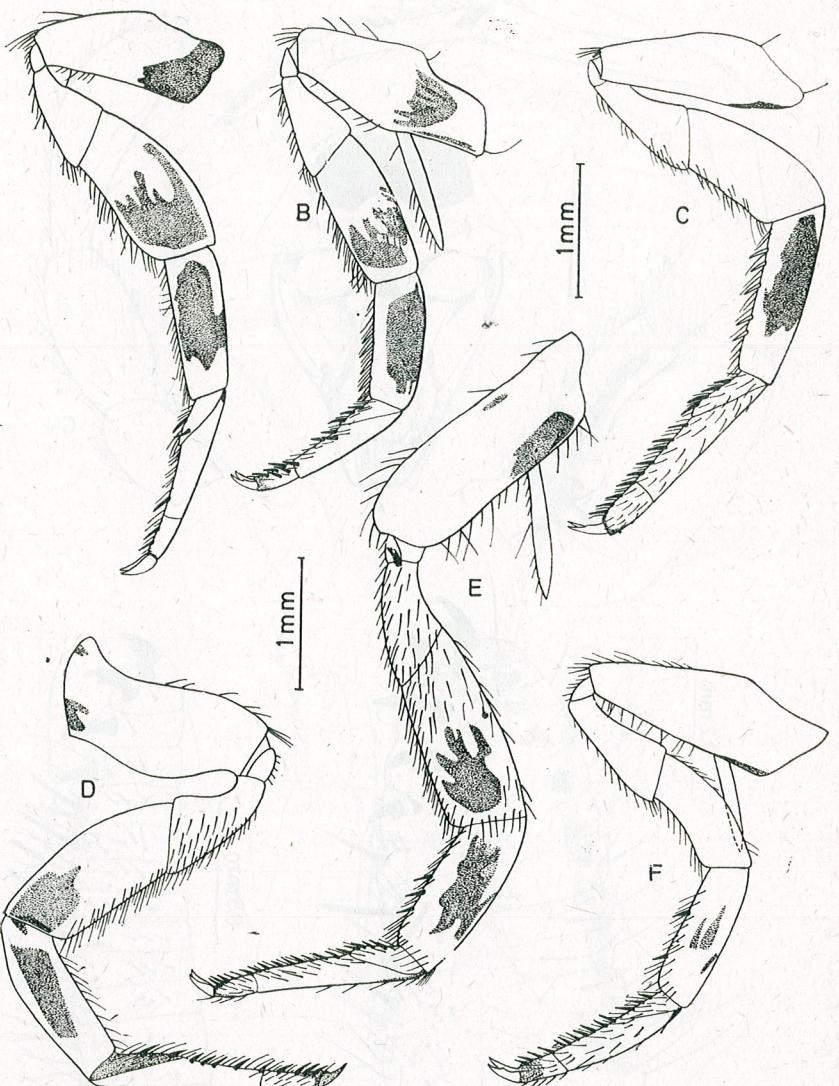


Plate VI. *Machilis capuset* n. sp. Pigmentation of legs, external surface : A, B, C, legs 1, 2, 3 female; D, E, F legs 1, 2, 3 male.

ANATOMICAL AND ELECTROPHORETIC STUDIES OF
THE AMPHIDROMIC PROBLEM IN SOME SPECIES OF
THE GENUS *ALOPIA* H. ET A. ADAMS (CLAUSILIIDAE,
GASTROPODA)

BY

AL. V. GROSSU and C. TESIO

Some species of the genus *Aloia* are considered as amphidromic, but there are specialists who describe the forms with sinistrally and dextrally whorled shells as separate species. Because the arguments of the two opinions are founded on morphological (shell) and anatomical (genitalia) criteria, which present variations, the authors of this work apply the electrophoresis of nonspecific esterases in polyacrilamide gel. The following species were examined : *Aloia nixa*-*Al. lactea*, *Al. canescens*-*Al. livida*, *Al. intercedens*-*Al. meschendorferi* and *Al. occulta*-*Al. fortunata*. These species have in their shells and sometimes in their genitalia common or similar features. The electrophoretic patterns obtained demonstrate that dextral and sinistral forms are independent species.

The Gastropod shells may be whorled to the right (dextrally) or to the left (sinistrally), this being a genetic species characteristic. It may however happen that in some few instances, forms with a sinistrally whorled shell are found within forms with dextrally whorled shells in the same population of a well defined genetic origin, and vice versa. These sporadic occurrences of inverted whorls have been considered anomalous features or freaks of nature. The experiments conducted by G. Diver and co-workers [7] mainly on *Radix peregrina* Müller did not succeed to explain conclusively their origin. N. Botnariuc and co-workers [2] have also found the sporadic occurrence of an inverted whorl in *Fagotia esperi* Müller grown in aquarium. Such whorled shell reversals were widely discussed, and D. Geyer [8], H. Schlesch [14] and others listed a great number of species where this phenomenon was observed.

Crampton [4] was the first to admit in the Haitian genus *Partula* the occurrence of amphidromic species (having their shells whorled both sinistrally and dextrally within the same population), from which species with sinistrally or dextrally whorled shells could then proceed allopatrically. Also in Romania numerous species of the genus *Alopia* have been admitted as amphidromic.

E. A. Bielz [1], S. Clessin [3], A. J. Wagner [16] mentioned a great number of species having an amphidromic character, but many research workers such as E. A. Rossmässler, M. Kimakowicz [12], L. Soós [15], Al. Grossu [9] consider that the forms with sinistrally and dextrally whorled shells are actually different Alopinae species. Neither of these opinions, however, is supported by sufficiently convincing arguments, the more so as a great number of morphological convergences were recently noted.

Considering the great taxonomic interest in accepting one of these two opinions, since the species number and their names are very inconstant, we aimed to investigate in this study, by making use of new methods for a thorough analysis of the species with such characteristics, whether the genus *Alopia* comprises some amphidromic species or not. At the same time we took also into account their geographical distribution (sympatric and allopatric species), and their ecological conditions as well. We were also prompted to approach this problem because these species occur in various mountain tops or peaks, as isolated dextral or sinistral forms, or both together, having a rather similar shell. We may also find forms with a primitive shell structure living alone on the highest peaks, and more evolved species with an intricate opening armature in the lower areas, thus rising a question about their phylogeny. The occurrence of primitive amphidromic species which afterwards generated dextral and sinistral species can be investigated and demonstrated, all the more as the genus *Alopia* is living in the Carpathian mountains only

MATERIAL AND METHOD

Among the forty species of the genus *Alopia* occurring in Romania, we purposed to study four pairs, both dextral and sinistral forms, that is eight species selected from those having very similar shells and living on the same spot or apart at some distance from each other. Our material comprised thousands of specimens of every individual species and was arranged according to the locality and heights; the variation within the populations was carefully analysed. In order to facilitate the estimations we assumed that the dextral and sinistral forms belong to separate species, irrespective if they were found together or separated by more or less large intervals, the final decision concerning their amphidromic character being taken only after the researches were completed.

We performed morphological analyses of the shells, most of which are very similar, with very little differences (striation, ribbing, size), be they dextral or sinistral.

For the anatomical research, we focused our attention mainly on the genitalia. Aiming at the same object, Soós [15] studied also the

disposition of the nerve ganglia. The genitalia of the Alopinae are similar in very remote species and are likely to represent a rather generic characteristic. We found the same situation also in other species belonging to genera we have studied, e.g. *Limax*, *Campylaea*, *Helicigona* [10], [11]. The evidence resulting from the shell and the genitalia, however, is not sufficient for taxonomic purposes and a number of convergences are difficult to detect; we employed therefore a new research method on a biochemical basis, that is the analysis of the species proteic structure.

The species were separated by whole extract electrophoresis in order to bring out the esterases. The species patterns were obtained by the Davis-Lindsay method [5] [6] of polyacrylamide gel electrophoresis. The extract was obtained by homogenization of the animal (without shell) in Carriker saline liquid with saccharose added. The nonspecific esterases were made obvious by incubating in α -naphthil acetate medium and Fast Blue R.R. In order to test whether this method is safe and to compare and check the results obtained, we developed electrophoretic patterns from a great number of individuals of the same population, our apparatus being able to provide ten patterns simultaneously. After obtaining repeatedly the same constant patterns, we concluded that all these individuals belonged to the same species. Aiming at the most trustworthy evidence, our experiments were reiterated for populations widely separated geographically and we obtained identical patterns thereof. Such a biochemical method is commonly used nowadays by taxonomists and has been tested by ourselves for certain species which raised some rather difficult problems.

RESULTS AND DISCUSSION

We made a careful analysis of the shell morphological characteristics and those of the genitalia. Moreover we compared the electrophoretic patterns, thus employing simultaneously three taxonomic methods for the amphidromic determination of all representatives of the genus *Alopia*; in the present study, however, we shall discuss only those having a similar shell but with inverted whorls. Without exhausting our researches, we selected for investigation, for the time being, the following species, resembling each other but differing in the dextrally or sinistrally whorled shell: *Alopia nixa*-*Al. lactea*, *Al. canescens* — *Al. livida*, *Al. intercedens*-*Al. meschendorferi*, *Al. occulta* — *Al. fortunata*.

Alopia nixa Kimakowicz 1894 and *Al. lactea* Bielz 1856

These species are separately distributed on the highest peaks of the Bucegi mountains, at over 2300 m. altitude: Bucura Dumbravă, Meeteșul Turcesc, Omul, Obîrșia. The first named species has a sinistrally whorled shell, the second a dextrally whorled one. Some research workers describe *Al. lactea* as an amphidromic species, while Soós considers it as sinistral and occurring in the Ciucas mountains. We assume that the dextral forms in the alpine zone of the Bucegi belong to *Al. lactea*

species. We noticed that both species have a small (12 — 14 mm.) shell, with a whitish-violet, milky colour, a very primitive opening armature, being often represented simply by the very short and poorly developed parietal lamella. The striation upon the last whorl, which is taxonomically very important, is not substantially differentiated (Fig. 1). According to such characteristics one may readily admit that the species might be amphidromic.

The anatomy of genitalia, however, demonstrates that there are differences between the two species. *Al. lactea* has a simple, cylindrical, rather uniform penis, with a relatively short epiphallus, and the receptaculum seminis has two branches, one more elongate and narrower than the other. The penis of *Al. nixa* is more evolved, irregularly expanded and even with a short appendix, the epiphallus thicker, and the branches of the receptaculum seminis are equally thick and almost of the same length. By comparing the anatomy of several specimens, we found a similarity but not an identity of the genital organs (Fig. 2). These species are allopatric, although closely distributed geographically; we never found them together on the same rocks and we may assume that they are isolated from each other. According to the anatomy of their genitalia and their geographical isolation they are not amphidromic, but separate species.

By means of electrophoresis we obtained however different enzymatic patterns for both species. In *Al. nixa* the three bands with a low migration are evenly thick and spaced, but in *Al. lactea* all bands are of various thicknesses and irregularly spaced. The localization, the thickness and the intensity of the nine bands are completely different in the two patterns (Fig. 3), showing a conspicuous lack of identity; a comparative analysis proves that there are two different species, and not a single amphidromic species.

According to the results obtained by the above ways of investigating the structure of the genitalia and the electrophoretic patterns, we may conclude that the dextrally and sinistrally whorled forms are actually different species. Some anatomical and electrophoretic similarities, however, show a possible phylogenetic relationship between these recently separated species, now living allopatrically within a neighbouring but discrete area.

Alopia canescens Charpentier 1852 and *Al. livida* Menke 1830

These are two allopatric species, *Al. canescens* being widely distributed in the Ciucas mountains, with various sizes and forms, and *Al. livida* in the Bucegi. Some dextral specimens which were found in the Ciucas are assumed to be *Al. livida*; therefore these two species are living together in the mountains of Ciucas, but in different places.

Both species show a wide range of variation in the shell size and colour, the shells being smaller in higher places. Their apertural armature is of a primitive structure, comprising only the variously sized upper and lower folds (Fig. 4). By each species there are several different ways of variation, thus evolving several subspecies with definitely outlined geo-

graphical areas. The dextrally whorled shell of *Al. livida* is very similar to the sinistrally whorled shell of *Al. canescens striaticolis* Kim., raising the question whether these two species are possibly amphidromic.

Al. canescens has a thickened penis with a more or less expanded appendix, followed by a short epiphallus and the deferent duct; the receptaculum seminis is divided into two unequally developed branches. The genitalia of *Al. livida* are closely similar to those of *Al. canescens* (Fig. 5). We should however note that in the dextral forms from the Ciucas mountains the epiphallus is much more developed and the deferent duct much more elongate and obviously distinct from the epiphallus, an unfrequent condition in Alopinae. Assuming that these dextral forms with a shell alike to those of the Bucegi belong to *Al. livida*, there might be a possible amphidromic condition, since the anatomical characteristics are not sufficient for separating them.

It was therefore interesting to know whether there is a difference in the biochemical structure of the two species. The electrophoretic patterns clearly show that the dextral and sinistral forms are different. A comparative analysis of the two patterns (Fig. 6) demonstrated that the migration speed and the thickness, intensity and localization of the bands are different. Moreover, only seven bands can be observed in the dextral forms (*Al. livida*), instead of eight in the sinistral forms (*Al. canescens*). The band arrangement show that we are dealing with different species. Our electrophoretic patterns were obtained from alpine specimens of *Al. canescens* and lower place specimens of *Al. canescens striaticolis* collected on the Mount Tesla. The patterns of *Al. livida* were taken from specimens gathered in Babele, Brina Mare-Caraiman and a place of 1500 m. altitude in Sinaia. In both cases similar patterns were obtained. Thus the biochemical method demonstrates that we are not dealing with amphidromic, but with two distinct species.

Al. intercedens Rossmässler 1859 and *Al. meschendorferi* Bielz 1852

The shell of these species, although inversely whorled, are much more similar. They received various names according to the collecting places in very different areas. A clear classification and a right geographical localization were made by L. Soós (1928), and later Al. Grossu performed their identification (1955) from numerous collections. According to the present data, *Al. intercedens* (with sinistrally whorled shell) is collected from Măgura and the Riu Valley near Zărnești, and *Al. meschendorferi* (with a dextrally whorled shell) occurs on the Mount Codlea as far as the Perșani Mountains and on Piatra Craiului, in the Riu Valley, in the quarry near Zărnești, but so far on the left river bank only.

Both species occur as many geographical races on distant areas and are characterized by a more or less large shell. The distribution of these species may be discussed and supplemented, but the most interesting statement is that they are living together only on the left river bank at the valley's entrance, near Zărnești. In this place the two areas are crossing each other, and in the same place on the same rocks we found a great

number of very similar dextral and sinistral specimens, which could be easily considered as belonging to an amphidromic species.

The shell of the two forms has a very similar shape and height, with an intricated apertural armature comprising 4 to 5 palatal folds and a clausilium. Among the palatal folds in the two forms, the third and fourth folds are generally smaller and frequently joined together (when they are five). The number and shape of these folds are variable. The striations on the last whorl (particularly on the cerbix) are well developed and identical in the two forms. The shell shape does not show any difference excepting the inverted whorls and therefore there are good reasons for assuming amphidromic conditions (Fig. 7).

The genitalia are of the same structural pattern as nearly in all Alopinae, but with a little difference. In the sinistral forms admittedly belonging to *Al. intercedens*, the penis is thick and has a more or less evolved appendix, followed by an elongate epiphallus and rather long and wound deferent duct. Between the epiphallus and the deferent duct there is a sharp narrowing, marking the origin of the latter.

The two branches of the receptaculum seminis are of a different length, the longer being usually also the narrower. The genitalia of the dextral forms (assumed to be *Al. meschendorferi*) are very similar to those of the sinistral forms, but the epiphallus and the deferent duct are shorter (Fig. 8). By comparing the two genitalia of many individuals, both dextral and sinistral, it is rather difficult to admit that the two forms are different. It is therefore impossible to assume that there are no amphidromic conditions.

The electrophoretic proteic analysis, however, shows a distinct difference between the two forms which were collected in the same place. In the sinistral forms (*Al. intercedens*) the electrophoretic pattern has nine slow and medium migration bands, and in the dextral forms (*Al. meschendorferi*) the eight bands are also showing a slow and medium migration. In contrast, the thickness, the intensity and particularly the localization of these bands are very different, clearly showing that there are two different species (Fig. 9).

From the little differences in the genitalia and mainly from the two different electrophoretic patterns we may draw the conclusion that although the two shells are similar, the two forms are distinct species, such as they were originally described under the names of *Al. intercedens* and *Al. meschendorferi*, and therefore no amphidromic situation exists.

Al. occulta R. Kimakowicz 1931 and *Al. fortunata* R. Kimakowicz 1931

These two species were described by R. Kimakowicz [13]. They are separate but very closely distributed species. The first named (*Al. occulta*) has a sinistrally whorled shell and was collected in great number in the neighbourhood of the village of Petreni-Vilcea (Cheile Costești); the second species, with dextrally whorled shell, was taken from Cheile Bistriței-Vilcea. These two valleys are separated by a wooded mountain mass on a distance of 5–6 km. Concerning these two species it was no question of an amphidromic situation, since Kimakowicz was of the opinion that

the dextral and sinistral forms are always separate species; we thought, however, that their analysis should be useful, since their shells are very similar and they are distributed in very close, although separate, areas.

Apart from the shells being inversely whorled, their form, colour and size are the same. The apertural armature of both forms is very similarly elaborated, with 4 to 5 palatal folds. In the dextral forms, the individuals with 5 palatal folds are more frequent, while in the sinistral forms the 4-fold pattern is prevailing. If there are 5 folds on the whole, then in both forms the third fold is connected with the fourth, giving rise to a single thicker fold with a V shape. The clausilium is well developed and very similar (Fig. 10). Since there is no difference in the shells of these allopatric forms, it seems that from the morphological standpoint an amphidromic situation is not out of question.

The anatomical structure of the genitalia follows the common pattern of the genus *Alozia*, but with certain differences. *Al. occulta*, for example, has always a thicker penis with a distinct appendage, a short epiphallus and a receptaculum seminis having two equally thick and elongate branches. *Al. fortunata*, on the other hand, has a more elongate and slender penis, a less frequent or no appendix, and the two branches of the receptaculum seminis are unequally long and thick (Fig. 11). In a great number of individuals we noticed sometimes, in both forms, the presence of a short flagellum close to the opening of the deferent duct, this characteristic being a common feature in other Alopinae, too. We may therefore assume, by comparing a great many specimens, that the sinistral and dextral forms have genital organs of a different anatomical structure, but these differences are not conspicuous enough to support a clear differentiation of the two species.

The biochemical method, however, provides interesting results. By the whole extract electrophoresis we obtained different esterase patterns of the two forms. The pattern obtained from the senestrial *Al. occulta* has ten bands, all of them with slow and medium migration, nearly equally sized, with various intensities and without any intergrouping. Four narrower bands with a slow migration are conspicuous. In the dextral *Al. fortunata*, on the other hand, the pattern shows only nine bands, forming three groups with a slow and medium movement (Fig. 12). The grouping of the four bands with a slow movement, a nearly similar thickness but with differing intensities, seems to be a characteristic feature. A comparative analysis of these two patterns clearly demonstrates that the proteic substances are of various kinds in the two forms, having a very different localization, grouping and thickness of the bands. We may therefore conclude that the two species are clearly different and not at all amphidromic, in spite of the resemblance of their shells.

CONCLUSIONS

From our study of the four species groups with very similar, but dextral or sinistral shells, raising the question of an amphidromic situation, we may draw the following conclusions:

— The morphological and anatomical methods so far used for the species identification cannot give sufficient evidence for an actual solution of the problem whether amphidromic conditions do exist or not in some species of the genus *Alopia*. Only the proteic electrophoresis may provide esterase patterns for a very safe differentiation of the species within this genus.

— The dextral or sinistral forms studied are independent species, even though their shells and sometimes their genitalia have common or similar features. The occurrence of amphidromic forms in this group cannot be ruled out, but we were not able to find a single such case in spite of a careful analysis of the most representative species.

— Morphological similarities in Alopinae with inversely whorled shells, raising an amphidromic problem, are found both in primitive species, living in the alpine area, and more evolved species, supplied with a clausilium and an elaborate apertural armature and distributed in a lower mountain region.

— In most of the studied species, as in the other Alopinae, too, the dextral and sinistral forms are allopatric. This may demonstrate that they are proceeding from a possible common ancestor with amphidromic features and from which they have been separated in a very remote past.

— A primitive shell structure does not mean also a primitive structure of the genitalia. The shell simplification is not related to an anatomical simplification, since the genitalia of *Al. canescens* are very different from those of *Al. nixa*, *Al. lactea* and particularly of *Al. glauca*, all being dextral or sinistral species from the alpine zone. This differentiation proves, first, that not all alpine species have a common ancestor, and second, that their way of life provided these species with a certain convergent characteristic.

— Among the studied species, we should mention particularly *Al. canescens* and *Al. livida*, occurring in two close mountain regions (Ciucas and Bucegi), and in which we noticed, besides the inversely whorled shell, a great number of similar characters, a wide variability and numerous geographical races. It is therefore possible that these species have a common ancestor, despite their geographical separation.

— The occurrence of species having an inversely whorled shell was sporadically ascertained in many gastropod species, but taken as an anomalous feature. We have studied thousands of specimens within certain dextral and sinistral Alopinae species, but never found any case of inverted whorl. We may therefore state that we are dealing with genetically well outlined species, with invariable characteristics, and that there are no more special unknown grounds which could throw any doubt on their heredity.

Without exclude a possible occurrence in the genus *Alopia* of species having an inverted whorled shell, we found no evidence of amphidromic conditions and accordingly we consider as separate species all the forms with dextrally or sinistrally whorled shells, whether they have primitive or evolved shells.

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Fig. 1. — Shell of : A, *Alopia lactea*; B, *Al. nixa*.

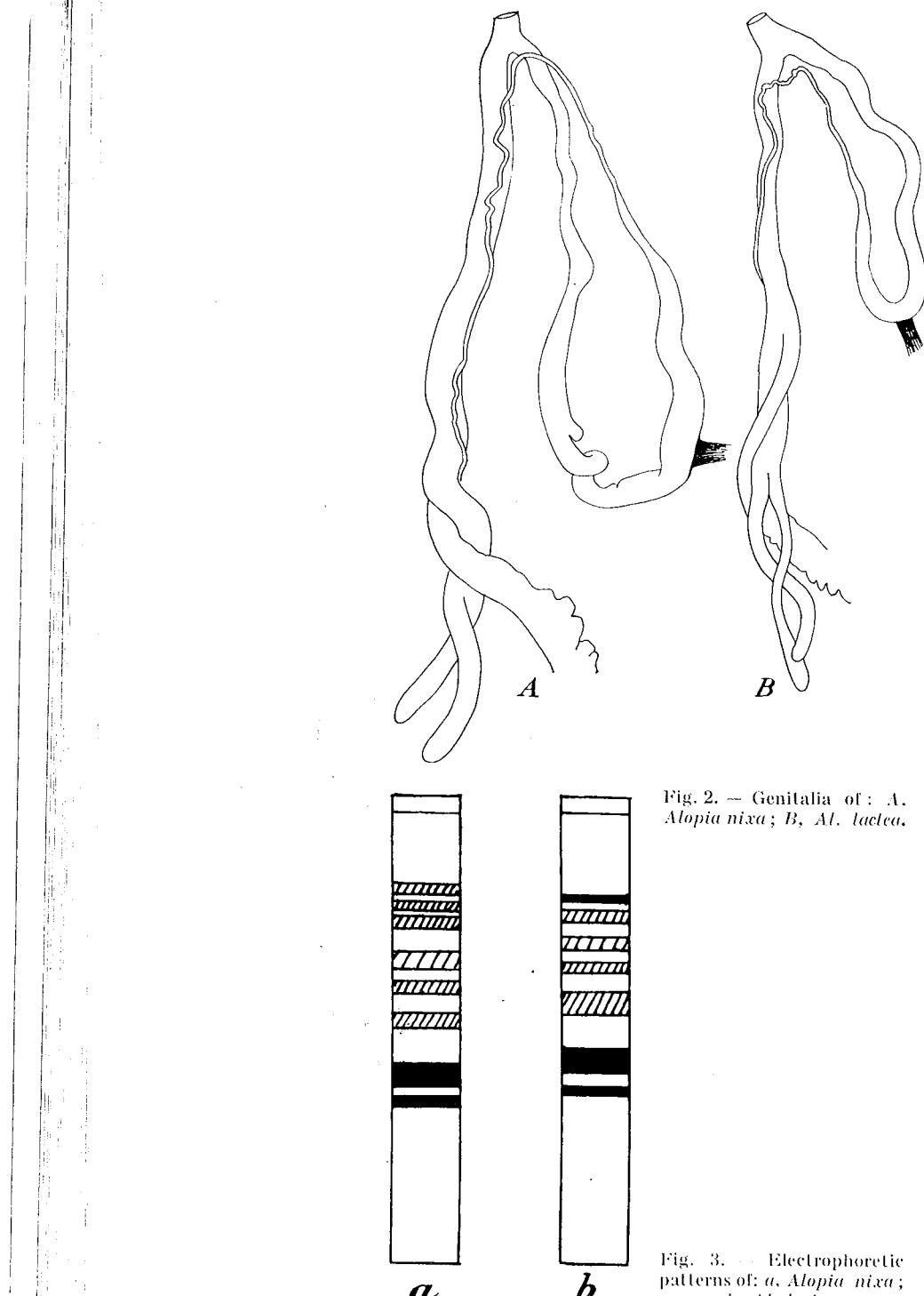


Fig. 2. — Genitalia of: A,
Alopia nixa; B, *Al. lactea*.

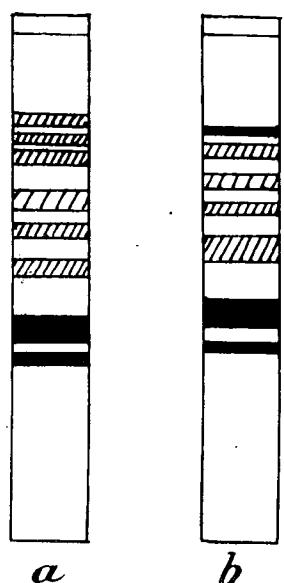


Fig. 3. — Electrophoretic
patterns of: a, *Alopia nixa*;
b, *Al. lactea*.

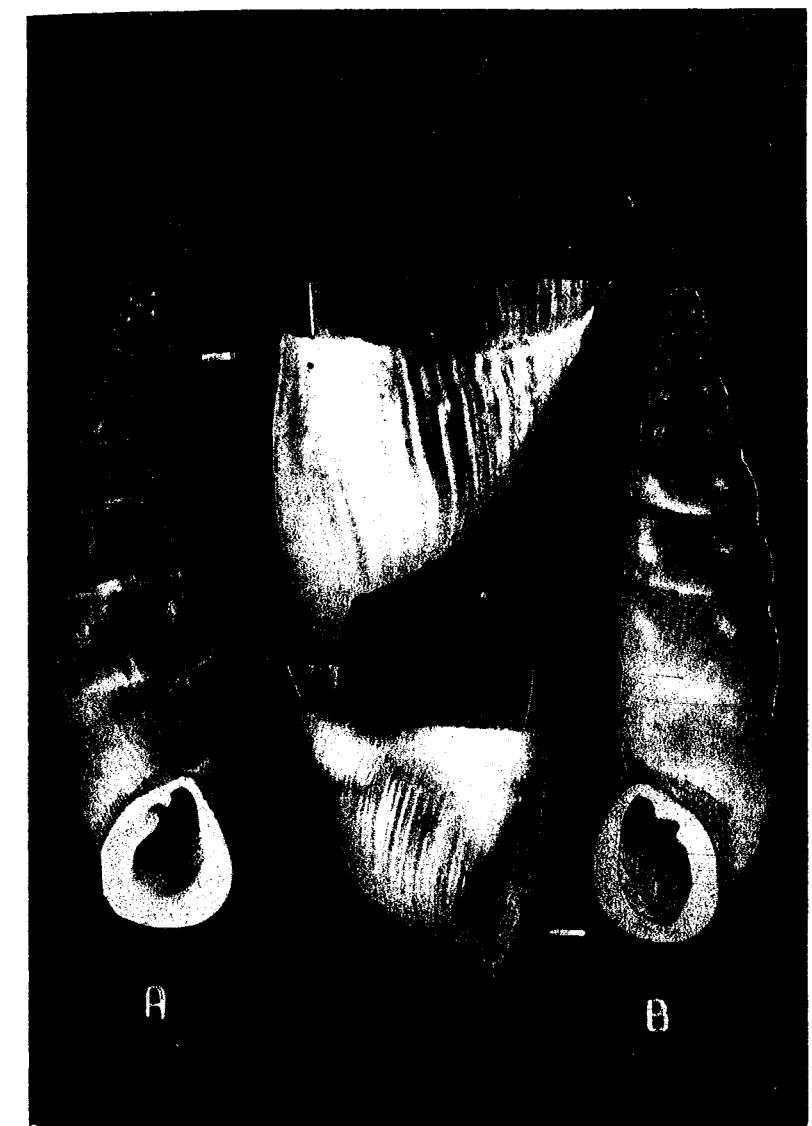


Fig. 4. — Shell of: A, *Alopia livida*; B, *Al. canescens*.

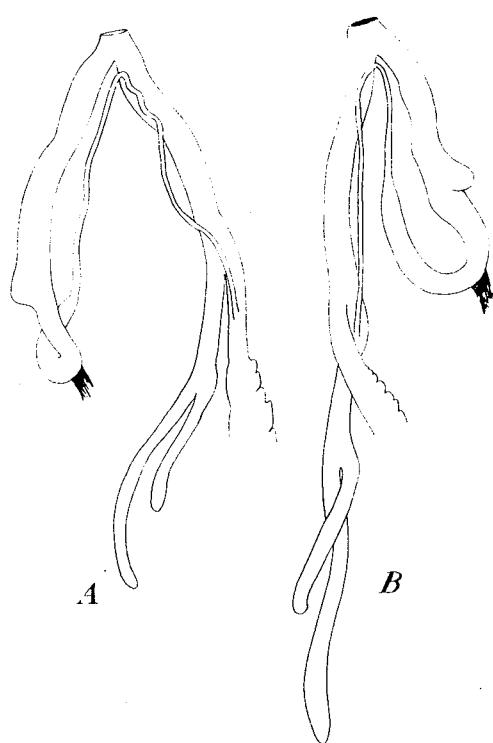


Fig. 5. — Genitalia of : A, *Alopia canescens*; B, *Al. livida*.

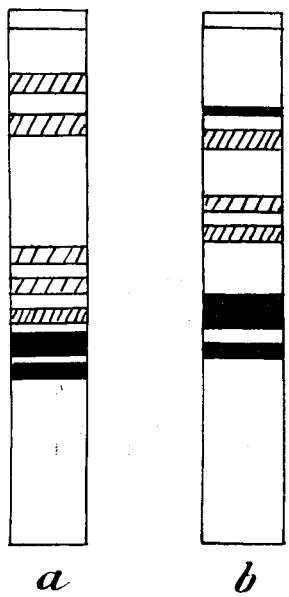


Fig. 6. — Electrophoretic patterns of : a, *Alopia canescens*; b, *Al. livida*.

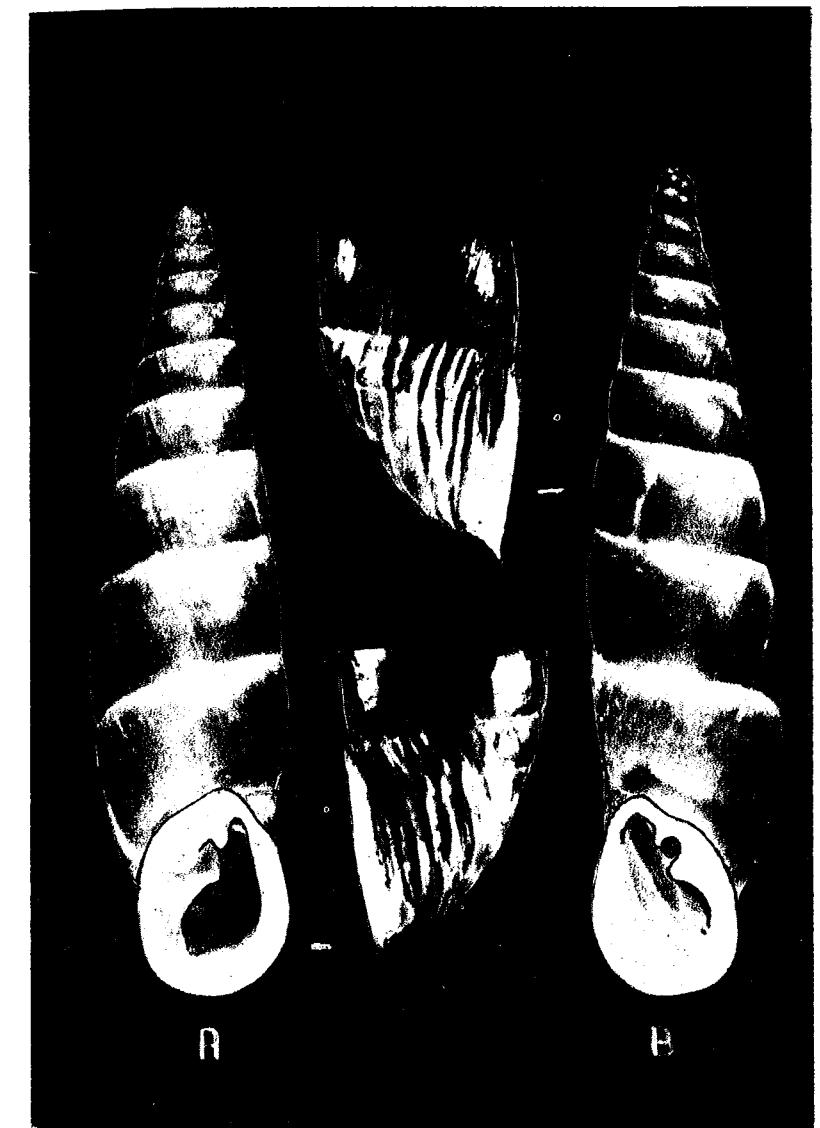


Fig. 7. — Shell of : A, *Alopia meschendorferi*; B, *Al. intercedens*.

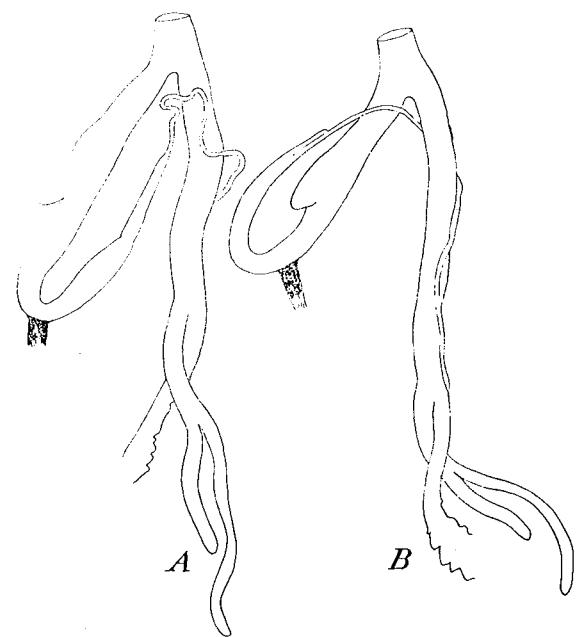


Fig. 8.—Genitalia of : A,
Alopia intercedens; B, *Al.
meschendorferi*.

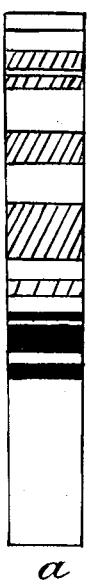


Fig. 9.—Electrophoretic
patterns of : a, *Alopia
intercedens*; b, *Al. meschen-
dorferi*.

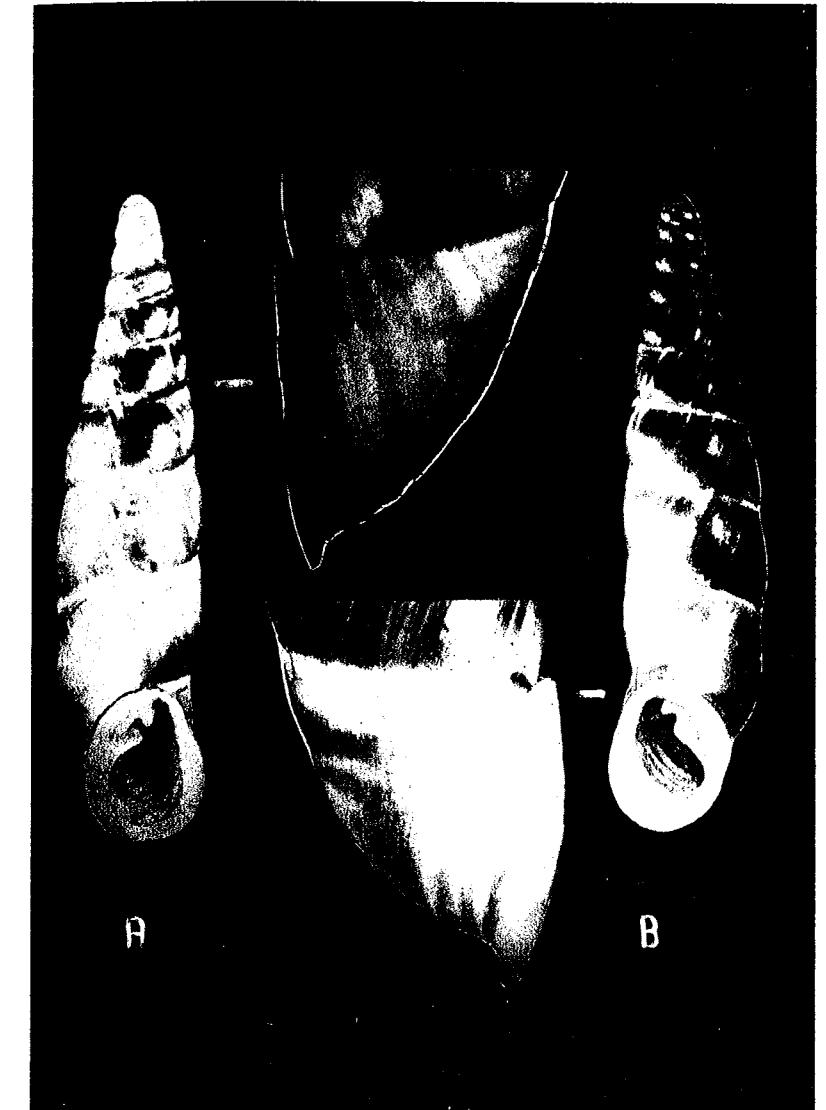


Fig. 10.—Shell of : A, *Alopia fortunata*; B, *Al. occulta*.

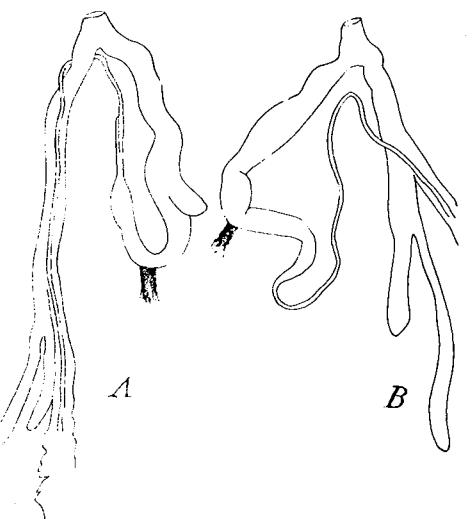


Fig. 11.— Genitalia of : A, *Aloia occulta*; B, *Al. fortunata*.

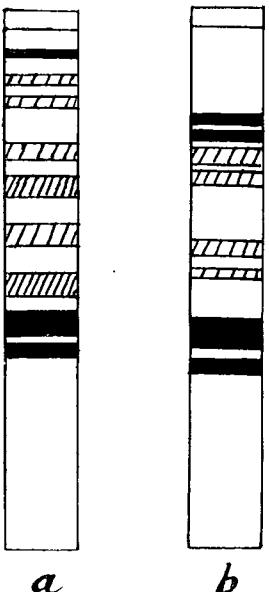


Fig. 12. — Electrophoretic patterns of : a, *Aloia occulta*; b, *Al. fortunata*.

STATIONARY AND TRANSIENT STATES OF AUTONOMOUS CARDIAC CENTRES

BY

C. PORTELLI

The work begins with an approach to the theory of automatic systems. Then the stationary and transient states of Remak's ganglion in the frog heart are studied, under the influence of a sinusoidal electric current of a 400 Hz frequency.

From the cybernetic point of view, the autonomous cardiac centres are self-adjustable systems and consequently the general theory of automatic systems may be applied to them.

The quality of an automatic system is assessed according to its stationary and transient states.

The stationary state is a functioning state in which, in the absence of external disturbing factors, the system is able to preserve its parameters constant. The quality of an automatic system increases with its ability to remain stable during a stationary functioning state. If, under the influence of disturbing factors, the automatic system deviates in a certain sense from its equilibrium point, its feed-back mechanisms intervene and make it evolve in an inverse sense till the equilibrium is restored.

While there exists only one equilibrium point for the simplest automatic systems, there are several ones in case of more complex systems. Some of these points have a stable equilibrium, while others, an unsteady one [1].

The present work was designed to study the stationary and transient states of Remak's ganglion in the frog heart submitted to the action of a sinusoidal electric current.

MATERIAL AND METHOD

A sinusoidal electric current of a 400 Hz frequency and adjustable amplitude was applied on the frog heart *in vivo*, by the agency of two electrodes placed on the sinus venosus near Remak's ganglion.

By means of two other electrodes placed on the ventricle, electrocardiograms were recorded (after the necessary amplifications).

RESULTS

The following were observed :

1. A sinusoidal electric current whose intensity was lower than 0.5 mA did not modify the cardiac frequency.
2. A sinusoidal electric current whose intensity was higher than 0.5 mA decreased the frequency of impulses emitted by Remak's ganglion (Fig. 1).

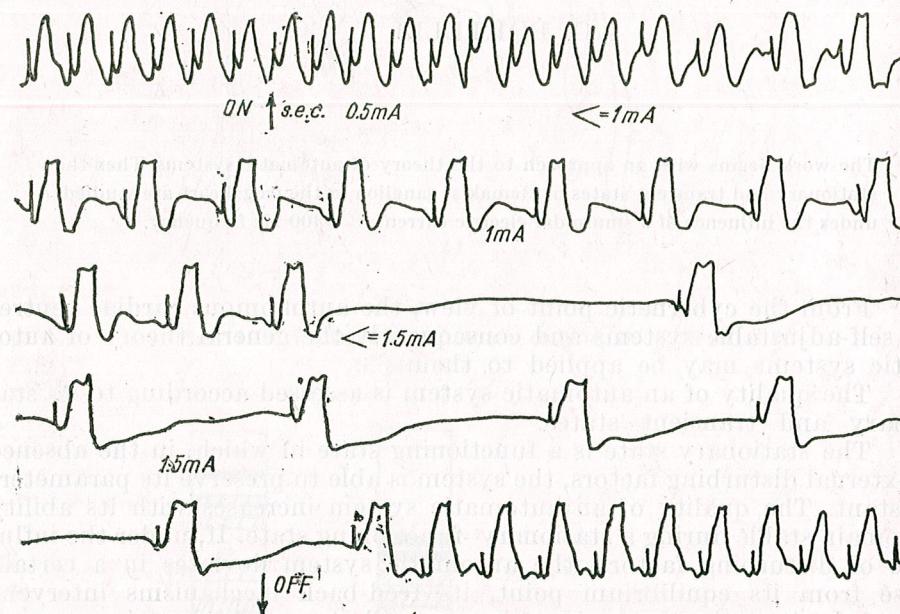


Fig. 1.—ECG of the frog heart *in vivo*. A sinusoidal electric current of 400 Hz frequency and 0.5 mA, 1 mA, 1.5 mA intensities was applied near Remak's ganglion.

3. The heart frequency (directed by Remak's ganglion) was inversely proportional to the intensity of the sinusoidal electric current applied.
4. If the intensities of the sinusoidal electric current were higher than 2.0 mA, Remak's ganglion was blocked.
5. When the sinusoidal electric current was switched off, Remak's ganglion gradually resumed its activity until it reached its initial rhythm.

DISCUSSION

The transient state of an automatic system represents the way in which, under the action of an external disturbing factor, it passes from a state of initial equilibrium to another state of equilibrium. The heart

passages, owing to a sinusoidal electric current, from one rhythm to another, with the stopping of certain cardiac generators of impulses and the starting of other generators (ganglia playing the role of pace-makers) are nothing but transient states between two quasi-stable states. A self-adjustable system is qualitatively the better, the faster and better damped is its transient state.

Here are 4 examples of transient states [2] :

- a. slow transient state
- b. little-damped transient state
- c. slow and little-damped transient state
- d. fast and well-damped transient state (Fig. 2).

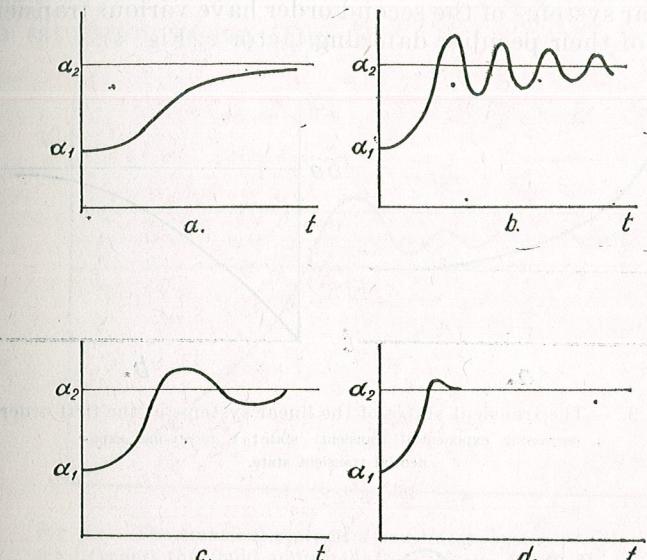


Fig. 2. — 4 types of transient responses from the α_1 state to the α_2 state :

a. slow transient response; b. little-damped transient response; c. slow and little-damped transient response; d. rapid and well-damped transient response.

The automatic systems with a slow transient state waste a long time in their passing from an equilibrium state to another and the little-damped systems begin to oscillate when they attain the new equilibrium level. The system with transient state point d. is qualitatively superior to the a., b., c. systems.

The type of transient state depends on the functional relationship between the input values and the output values. From this point of view, the self-adjustable systems may be linear and non-linear. In case of linear systems, the functional relationship is expressed by an equation in which the coefficients are constant and the unknown quantities and their derivatives are raised to the first power.

The linear systems have the following important characteristics :

— if two or more input values act simultaneously, an overall effect is obtained, equivalent to the sum of effects produced by each of the input values;

— if the input value increases or diminishes a certain number of times, the output value undergoes a similar transformation.

The linear systems may be in their turn of the first, second or higher orders, according as in the equations describing their functional relationship derivates of the first order (speeds), derivates of the second order (accelerations) or derivates of higher orders intervene.

The linear systems of the first order have a transient state of the increasing or decreasing exponential type without a latency time and oscillations. (Fig. 3).

The linear systems of the second order have various transient periods, as a function of their peculiar damping factor z (Fig. 4).

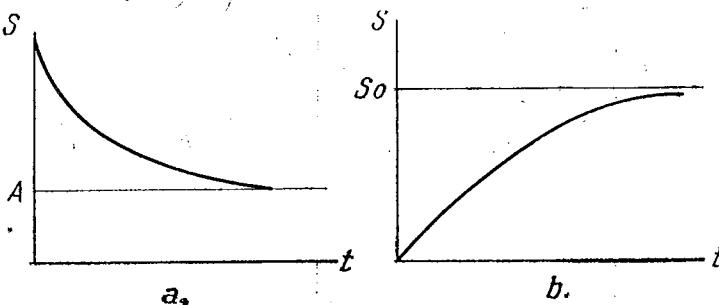


Fig. 3. — The transient states of the linear systems of the first order:
a, decreasing exponential transient state; b, increasing exponential transient state.

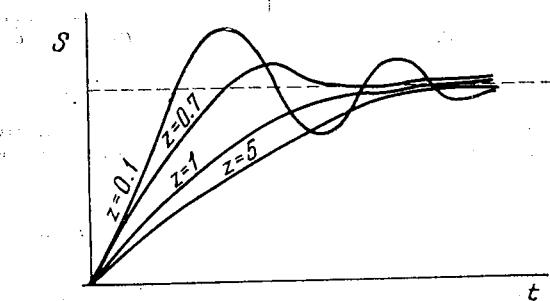


Fig. 4. — Transient states of linear systems of the second order. Systems with the damping factor $z = 0.1$; $z = 0.7$; $z = 1$ and $z = 5$.

If $z < 0.7$, an oscillatory transient state is obtained. If $z = 0.7$, oscillations may still be found, but they are of a negligible amplitude. If $z > 1$, an aperiodic transient state is reached. For a linear system of the second order, having $z=2$, a transient state similar to that proper to a linear system of the first order is obtained (except for the neighbourhood of

point $t = 0$, where the inertia obliges the systems of the second order to have a null speed). To conclude, linear systems of the second order have in addition, as compared to linear systems of the first order, oscillations and a latency time.

In non-linear systems, the functional relationship is expressed by an equation with variable coefficients, while the unknown quantities and their derivates are raised to powers different from 1. Such systems have no longer a linearity (proportionality) between the disturbing causes and their responses. Non-linear self-adjustable systems exhibit in their transient response :

1. an insensitiveness region ;
2. the possibility of producing oscillations when the new equilibrium is realized ;
3. a saturation region (Fig. 5).

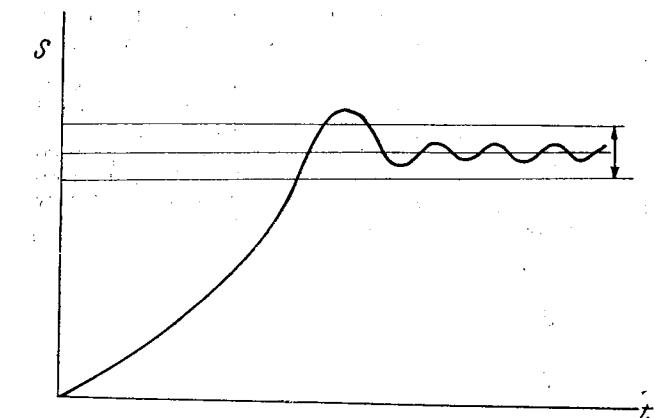


Fig. 5. — The transient state of a non-linear system having a sensitiveness threshold and oscillations at the limit of reaching a new equilibrium.

In the light of these data, a survey of the transient periods from one rhythm to another can be now performed for cardiac frequency generators, as they are influenced by a sinusoidal electric current.

1. If lower intensities of the sinusoidal electric current are applied, an insensitiveness range of cardiac generators may be observed, where their rhythm is not modified. This range corresponds to a non-linearity of the biological systems for values of stimuli under their sensitiveness threshold.

2. When the cardiac generator (the pace-maker) passes from one frequency to another, the RR interval existing between two successive QRS complexes is modified according to an increasing or decreasing exponential. This fact appears more obviously in case of a heart block caused by the applying of a sinusoidal electric current on Remak's ganglion when, after the current is switched off, a latency time follows and then the cardiac impulses gradually resume an ever higher frequency until they reach the initial rhythm (Fig. 6).

The RR interval displays in course of time a diminution of the exponential type until it reaches its former value (Fig. 7).

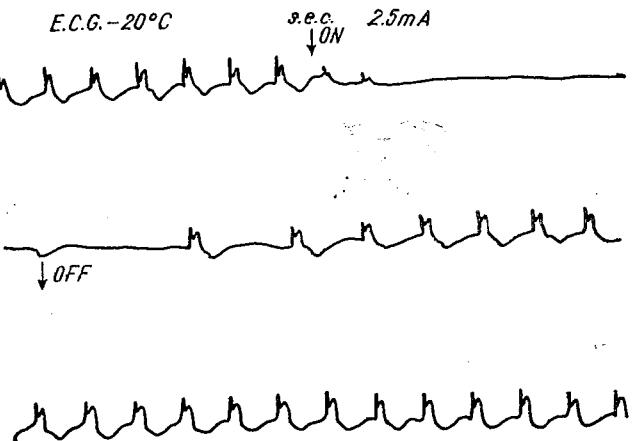


Fig. 6. — ECG of a frog heart *in vivo*, at the temperature of 20°C . A sinusoidal electric current of 400 Hz frequency and 2 mA intensity was applied on the sinus venosus, having as a result the blocking of Remak's ganglion. When the sinusoidal electric current was switched off, Remak's ganglion resumed, after a latency time, its activity, with a frequency increasing gradually till the initial value.

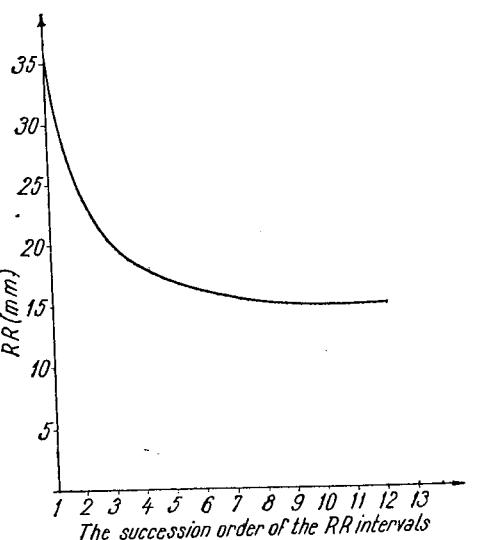


Fig. 7. — The transient state of Remak's ganglion when it resumes the activity after its blocking. On the abscissa: the succession order of the RR intervals when Remak's ganglion resumes its activity. On the ordinate: the RR interval (between 2 cardiac impulses) in mm. The graph was performed in accordance with the recording in figure 6.

These transition aspects of the exponential type are encountered in the linear systems of the first order. The linear systems of the second order also give transient responses of this type if their damping coefficient ζ is great enough ($\zeta > 0.7$).

CONCLUSIONS

Our experimental findings entitle us to consider the self-adjustable systems of cardiac pace-makers as having characteristics belonging to the linear systems of the first order (the passage from one state to another according to an exponential curve), to the linear systems of the second order (the latency time) and to the non-linear systems (the sensitiveness threshold).

The existence of these multiple characteristics has a justified biological functional utility, as the linear systems of the first order offer the advantage of a cause-effect proportionality, the systems of the second order have a great stability, while the non-linearity appears, at a given moment, as a necessity imposed by the external conditions, when the modification of certain functional constants is required in order to maintain the system in activity.

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A COMPARATIVE KARYOTYPE STUDY IN THREE
POPULATIONS OF PHEASANT (*PHASIANUS*
COLCHICUS) FROM ROMANIA

BY

MARGARETA MANOLACHE

Comparative karyotype in three populations of pheasant (*Phasianus colchicus*) from Romania, with different geographical locations: Chișineu-Criș, Ghimpăți and Cornești-Iași, was investigated.

The highest chromosome number was 82. 21 autosomal pairs in addition to the heterosomes according to size and shape were identified. Although the chromosomes in the pheasant karyotype showed a decreasing series, the biometric studies allowed to classify them in four groups.

Comparative biometric analyses of the karyotype (comparisons between idiograms and statistical treatment of the differences) did not reveal any significant difference at the chromosome level between the three populations.

Recent progress in cytological techniques (the use of colchicine for the accumulation of metaphase plates, the air-drying of preparations and the smear techniques) allowed a quite precise description of the avian chromosome set in somatic and germinal cells.

The first complete analysis of an avian karyotype was reported in 1965 only, in *Gallus domesticus*, by Owen [13], which revealed the possibility of analysing the morphology, as well as the size of chromosomes. Unlike the Mammals, cytogenetic studies in birds are rather unfrequent and were started in the last years only, due to the difficulty introduced by the great number of microchromosomes. Karyotype analyses in birds by means of modern techniques, such as hypotonic pretreatment and colchicine, were reported only for a few birds (approximately 60 species) [1] — [8] — [14] — [16].

The present paper reports a karyotype study in the Romanian pheasant, based upon the examination of the chromosome complement in three pheasant populations with different geographical locations, namely Chișineu-Criș, Ghimpăti and Cornești-Iași, seeking for any genomic difference between the above populations and between the karyotype of the Romanian pheasant and the karyotype of the species, as reported in the literature. It should be mentioned that the informations concerning the chromosomes of birds of hunting interest from the Romanian avifauna are rather sporadic [11].

MATERIAL AND METHODS

10 chicks (males and females) from each population were used for this study. In Romania, the ordinary pheasant (*Phasianus colchicus colchicus* L.) is no more available as pure breed, as by crossing with other subspecies the so-called hunting pheasant has been obtained.

The technique for cytogenetic study of bone marrow cells, already described in a previous paper [11], was used. The *in vivo* colchicinized material was treated by the air-dried method and stained with Giemsa. The preparations showing metaphase plates with chromosomes satisfactorily spread and allowing the recording of the big as well as of the small chromosomes were examined and photographed at the IOR MC₁ microscope, with the following magnification: photograph magnification = 4.375, microscope magnification = 1485, general magnification = 6497.

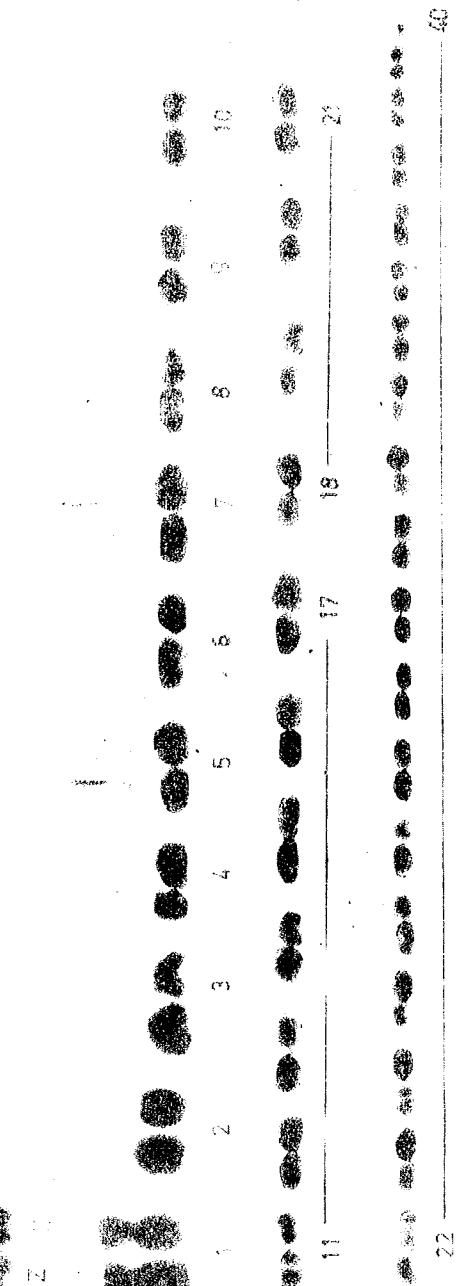
30 karyotypes were constructed for males and females; the autosomes were disposed according to their decreasing size, while the sex chromosomes were placed at the upper part of the karyotype.

To identify the individual chromosomes, measurements were performed on metaphase plates showing a certain uniformity of contraction and almost parallel chromatids. Each chromosome pair was individually measured, while, for every pair, both chromatids were measured and the mean was considered. The following parameters were investigated: 1. absolute length (μ), 2. relative length (the length of a given chromosome divided by the total length of the haploid male complement), 3. arm ratio, 4. centromere index.

RESULTS AND DISCUSSION

The first cytogenetic study in pheasant, performed by Suzuki [17] by using the classical method of testes sectioning, revealed a diploid chromosome number of 78 in male and 77 in female, with a sex determining mechanism of the ZO type, as due to the occurrence in the female complement of an unpaired chromosome (the 5th one, according to length).

Yamashina [19], using the same method in two subspecies of pheasant (*Ph. col. karpowi* and *Ph. col. versicolor*), found a diploid number of 82 in males and 81 in females for both subspecies with a ZZ/ZO sex determining mechanism. The diploid number was supported by the occurrence of 41 bivalents in the primary spermatocytes.

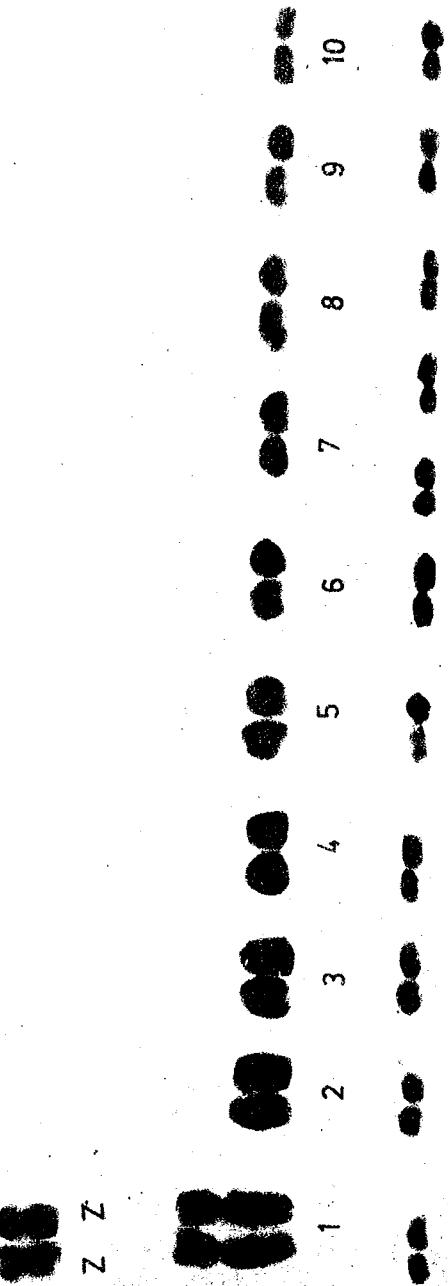


Phasianus colchicus ♂

PLATE I. -- Normal karyotype of *Phasianus colchicus* (Chișineu-Criș population): A, male; B, female.

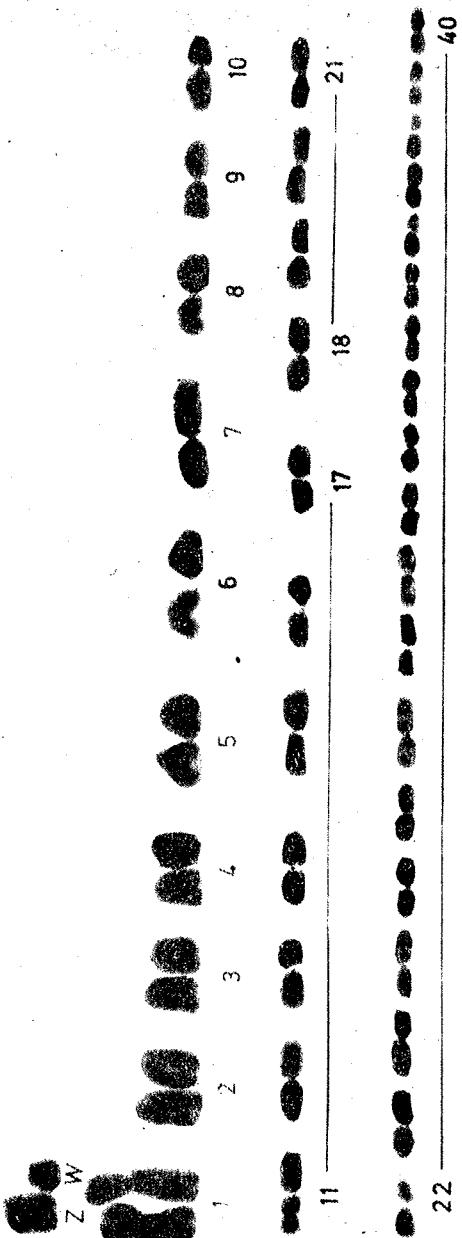
PLATE III. — Normal karyotype of *Phasianus colchicus* (Corneliști-Iași population) : A, male ; B, female.

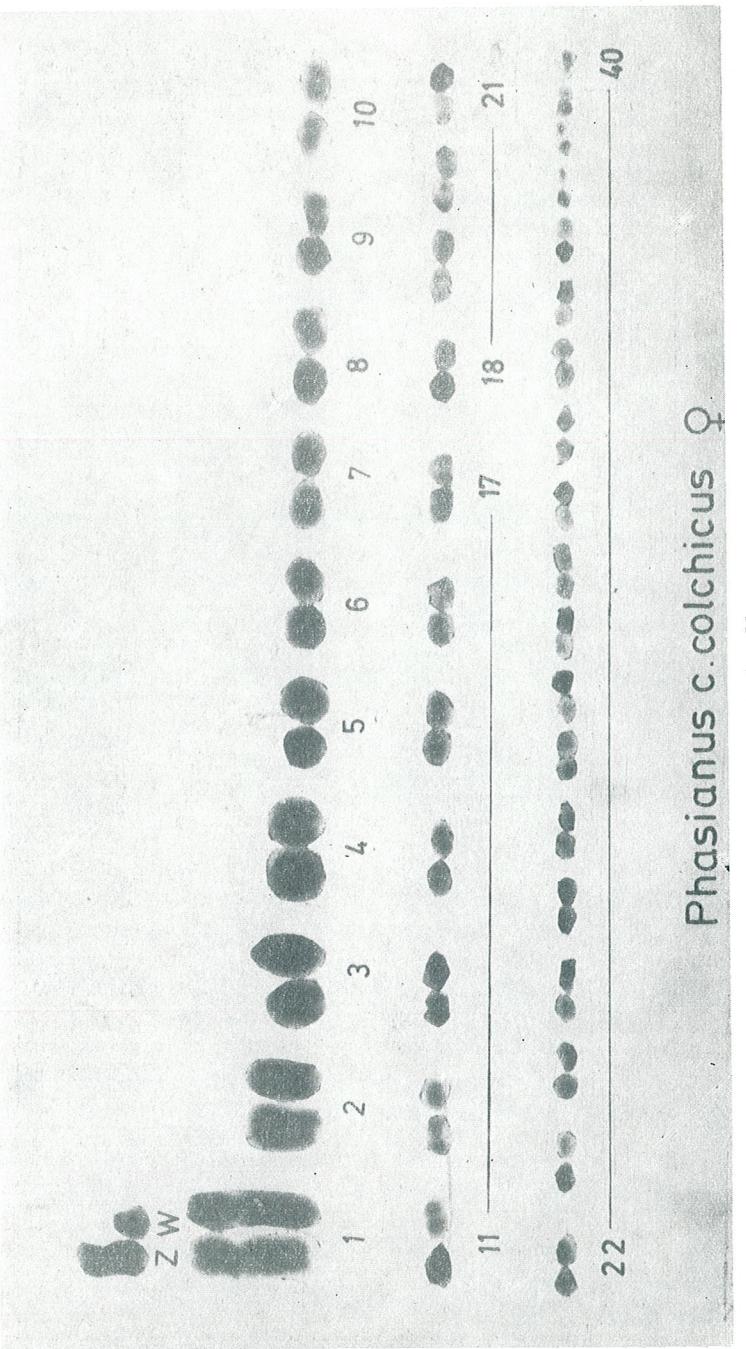
Phasianus c. colchicus ♂



Phasianus c. colchicus ♀

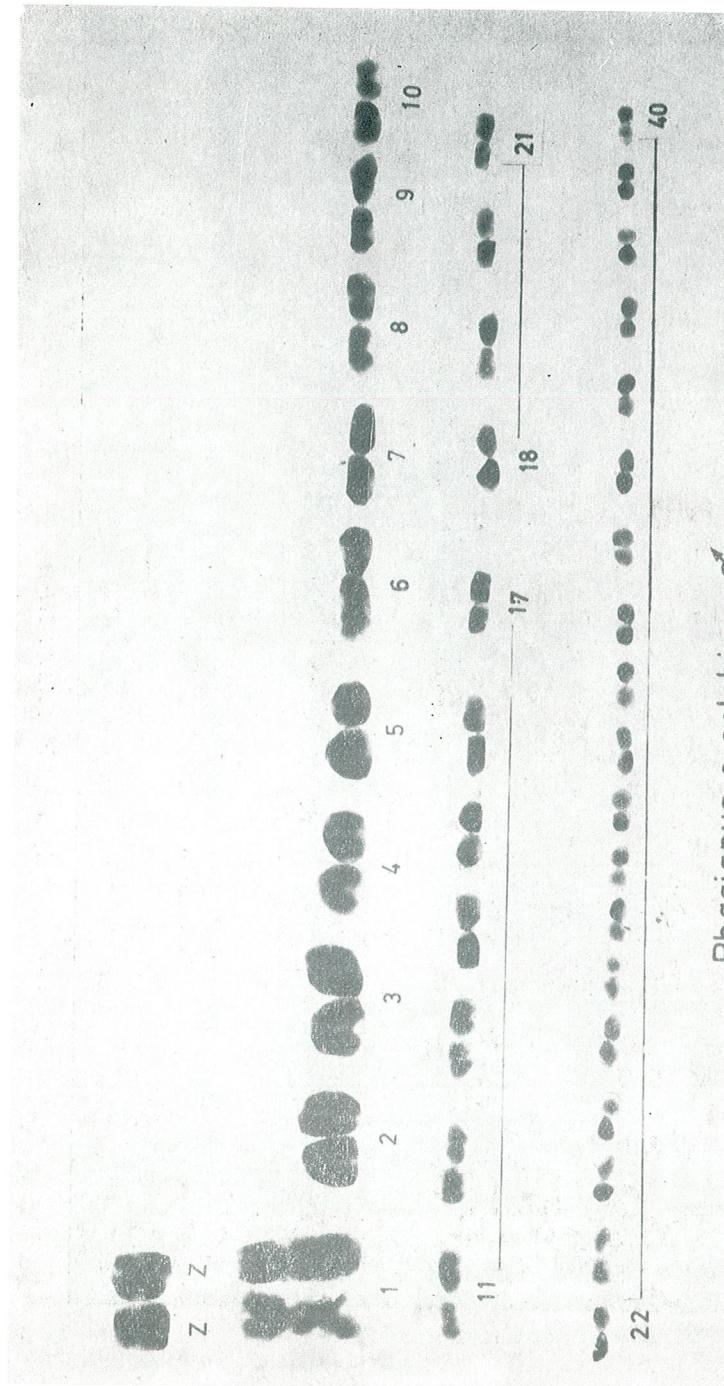
PLATE I B.





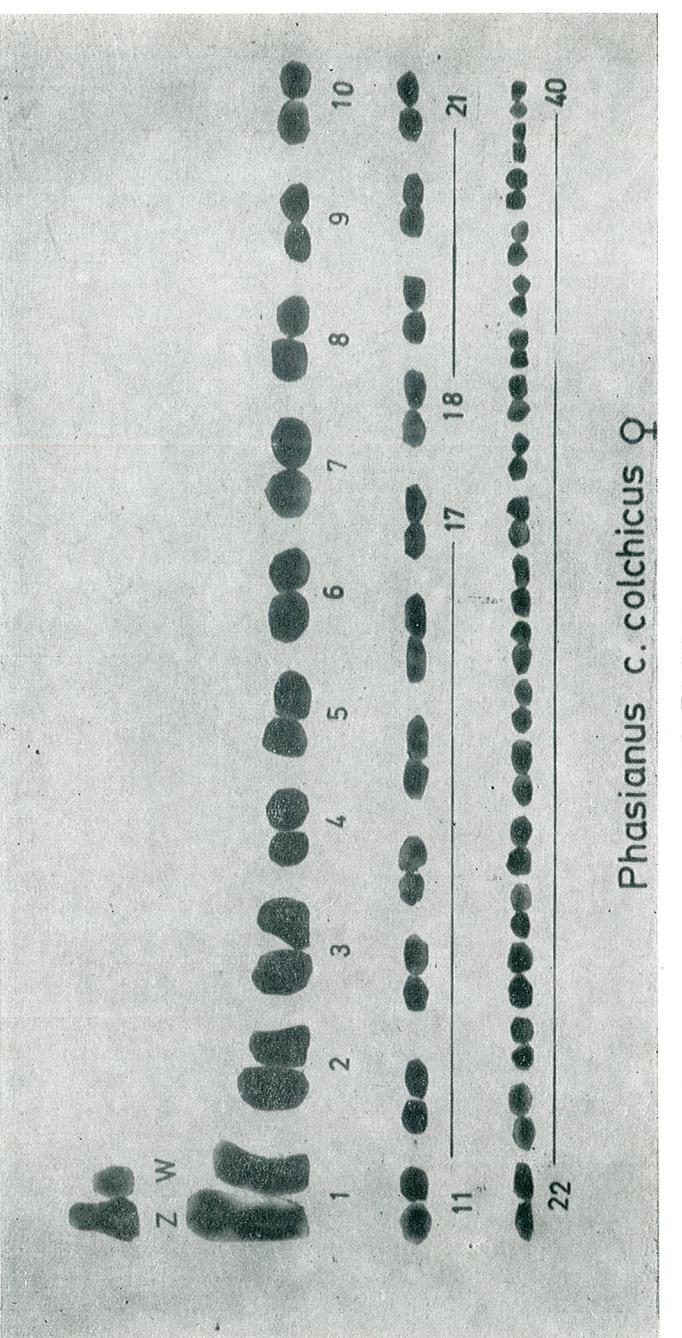
Phasianus c. colchicus ♀

PLATE III B



Phasianus c. colchicus ♂

PLATE IIII. — Normal karyotype of *Phasianus colchicus* (Ghimpati population) : A, male ; B, female.



Later, Stenius et al [16] investigated the somatic chromosomes in the subspecies *Ph. col. torquatus*, approximating a diploid number of 80, with a deviation of ± 10 . The morphology of the big chromosomes (the first 10 pairs) was in agreement with the description of Yamashina [19].

Takagi and Makino [18], working with tissue culture, found in *Ph. col. karpowi* a variation of the chromosome numbers ranging from 66 to 82, probably due to the difficulty of accurately scoring the smallest chromosomes. The morphology of 20 big chromosomes was also described.

The examination of metaphase plates with satisfactorily spread chromosomes in our preparations, allowed an approximation of the normal chromosome complement for the three pheasant populations of maximum 82, in both sexes, though most cells showed a chromosome number of 80, according to the recent results of Bloom [3], who indicated for the pheasant (*Ph. colchicus*) as a species, the diploid number $2n = 80 \pm$ (after [9]). The highest chromosome number of 82 was in agreement with the data of Takagi and Makino [18] obtained for the subspecies *karpowi*.

It is well known that a precise determination of the chromosome number in birds is almost impossible, because of the great number of microchromosomes, the small size of which leads to confusions between chromosomes and chromatids, to overlappings or to a faint staining, so that the photographic record of all the chromosomes is often impossible. In plates I, II and III, the male and female karyotypes with 82 chromosomes are given for the three populations.

From the chromosome complement, we succeeded in describing as to their morphology, the first 21 chromosome pairs in addition to the sex chromosomes, and the usual biometric treatment was applied. To identify morphologically the chromosomes, the nomenclature by Levan et al. [10] was used.

As a detailed description of the first 21 autosomal pairs and of the sex chromosomes was reported in a previous paper for the Romanian pheasant — Ștefănești population —, the present discussion will be restricted to a comparative examination of the three populations.

For the three populations, the first autosomal pair of the karyotype is of the metacentric type; the order 20 pairs are acrocentric, while the remaining 19 are small chromosomes. The sex chromosomes are of the metacentric type (Z) and of the submetacentric type (W).

An examination of each population indicated a progressive decrease in the absolute length of the 22 chromosome pairs, namely : for the Ghimpați population from 3.396μ to 0.331μ ($3.447 - 0.334 \mu$ for the male and $3.345 - 0.328 \mu$ for the female); for the Cornești-Iași population from 2.571μ to 0.325μ ($2.170 - 0.333 \mu$ for the male and $2.973 - 0.317 \mu$ for the female); for the Chișineu-Criș population from 2.911μ to 0.329μ ($3.043 - 0.315 \mu$ for the male and $2.779 - 0.343 \mu$ for the female).

Table 1 shows the absolute length of the first 21 autosomal pairs and of the sex chromosomes, for the three populations, comparatively.

Although the chromosomes in the pheasant karyotype show a decreasing series, the biometric studies allowed us to divide the 22 pairs examined into four groups :

— group I consists of the first autosomal pair, clearly distinct from the other chromosomes by its size ($> 2\mu$)

Table 1

Absolute length (μ) of the first 21 autosomal pairs and of sex chromosomes in three populations of *Phasianus colchicus*

Chromo-some	Group	GHIMPAȚI	CORNEȘTI-IAȘI	CHIȘINEU-CRIS
1.	I	3.396 \pm 1.431	2.571 \pm 0.978	2.911 \pm 1.027
2.	II	1.616 \pm 0.538	1.571 \pm 0.466	1.662 \pm 0.583
3.		1.368 \pm 0.353	1.311 \pm 0.470	1.321 \pm 0.566
4.		1.068 \pm 0.267	1.043 \pm 0.340	1.069 \pm 0.420
5.	III	0.967 \pm 0.306	0.856 \pm 0.307	0.926 \pm 0.297
6.		0.809 \pm 0.190	0.721 \pm 0.234	0.804 \pm 0.253
7.		0.689 \pm 0.225	0.625 \pm 0.063	0.700 \pm 0.154
8.		0.603 \pm 0.173	0.573 \pm 0.044	0.627 \pm 0.097
9.		0.547 \pm 0.158	0.529 \pm 0.085	0.586 \pm 0.100
10.		0.500 \pm 0.101	0.485 \pm 0.095	0.542 \pm 0.061
11.	IV	0.483 \pm 0.113	0.464 \pm 0.095	0.521 \pm 0.120
12.		0.468 \pm 0.120	0.442 \pm 0.099	0.503 \pm 0.102
13.		0.449 \pm 0.094	0.430 \pm 0.101	0.484 \pm 0.103
14.		0.438 \pm 0.107	0.413 \pm 0.098	0.466 \pm 0.102
15.		0.419 \pm 0.102	0.402 \pm 0.096	0.457 \pm 0.097
16.		0.411 \pm 0.100	0.383 \pm 0.074	0.444 \pm 0.106
17.		0.392 \pm 0.098	0.371 \pm 0.084	0.426 \pm 0.095
18.		0.380 \pm 0.098	0.362 \pm 0.084	0.415 \pm 0.102
19.		0.358 \pm 0.063	0.348 \pm 0.086	0.393 \pm 0.092
20.		0.345 \pm 0.063	0.332 \pm 0.094	0.383 \pm 0.115
21.		0.331 \pm 0.034	0.325 \pm 0.086	0.329 \pm 0.179
Z	II	1.591 \pm 0.181	1.438 \pm 0.394	1.409 \pm 0.258
W	III	0.786 \pm 0.146	0.748 \pm 0.227	0.795 \pm 0.020

— group II consists of the autosomal pairs 2, 3, 4 and the Z-chromosome ($1 - 2 \mu$)

— group III consists of the pairs 5, 6, 7, 8, 9, 10 and the W-chromosome ($0.5 - 1 \mu$)

— group IV consists of the remaining chromosomes, including the pair 11 ($< 0.5 \mu$).

To reveal any genome difference between the 3 populations, the idiogram of the first 21 autosomal pairs and of the sex chromosomes was constructed according to relative length for each population, as well as a comparative idiogram for the three populations (Figs 1, 2, 3, 4). No difference seems to exist between the three populations, according to idiogram analysis. Furthermore, the differences were tested using the F-test (Table 2), and no significant difference was found.

To investigate the evolutive changes in the avian karyotype, Ray-Chaudhuri et al. [14] performed comparisons between the chromosomes of different bird species, belonging to 5 orders. Among the Galliformes, 6 species were compared, including the pheasant, but the idiogram was confined to the first 11 chromosome pairs. Our studies provide further information concerning the karyotype of the pheasant.

The sex chromosomes (ZZ for the homogametic sex (δ) and ZW for the heterogametic sex (φ)) display the following features : the absolute length for the Z chromosome is of 1.628μ (Ghimpăti), 1.429μ (Cornești

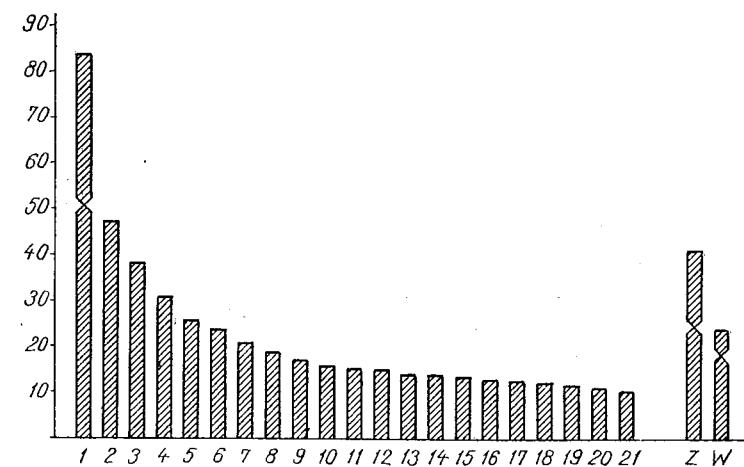


Fig. 1. — Idiogram of the first 21 autosomal pairs and of sex chromosomes in *Phasianus colchicus*, Chișineu-Criș population.

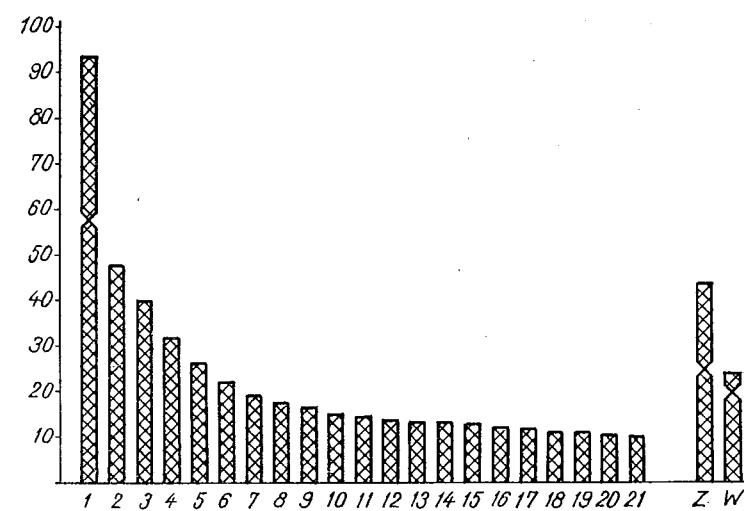


Fig. 2. — Idiogram of the first 21 autosomal pairs and of sex chromosomes in *Phasianus colchicus*, Cornești-Îași population.

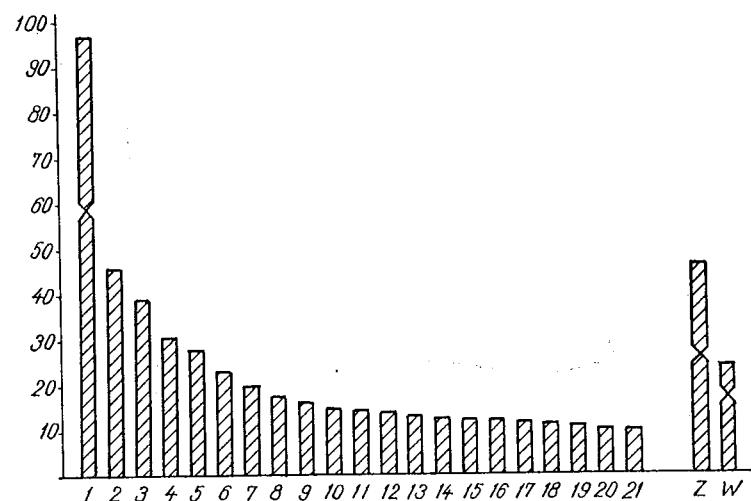


Fig. 3.— Idiogram of the first 21 autosomal pairs and of sex chromosomes in *Phasianus colchicus*, Ghimpăti population.

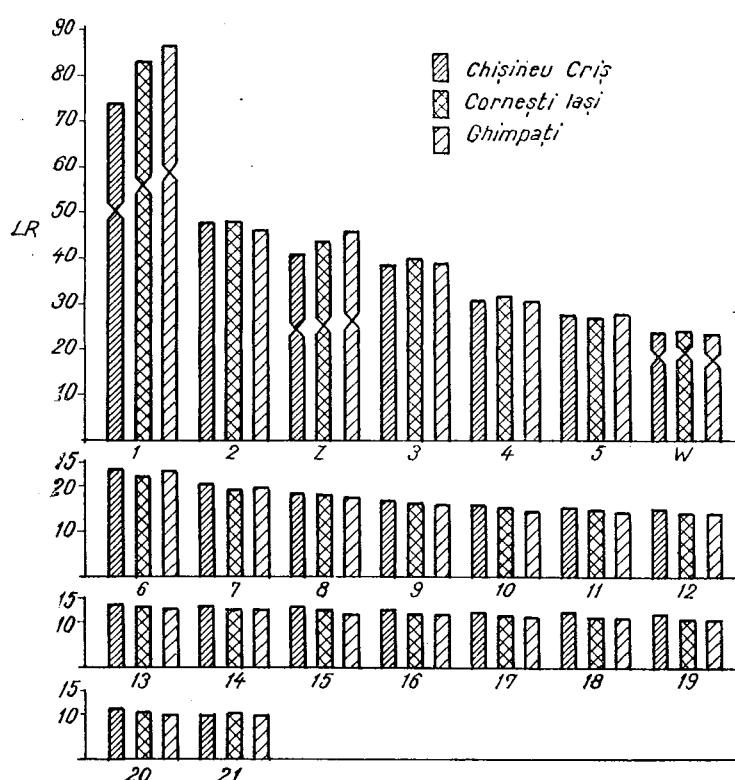


Fig. 4.— Comparative idiogram of the first 21 autosomal pairs and of sex chromosomes in *Phasianus colchicus* from the three populations.

Table 2

Comparative biometric studies on the first 21 autosomal pairs and on the sex chromosomes in pheasant (δ) from three populations

Chromosome	Absolute chromosome length (μ)			F*
	GHIMPĂTI	CORNEȘTI-IAȘI	CHIȘINEU-CRIȘ	
1.	3.447 \pm 1.468	3.170 \pm 0.960	3.043 \pm 1.911	0.387
2.	1.676 \pm 0.743	1.570 \pm 0.750	1.761 \pm 0.982	0.269
3.	1.454 \pm 0.681	1.327 \pm 0.433	1.336 \pm 0.885	0.209
4.	1.168 \pm 0.507	1.096 \pm 0.403	1.082 \pm 0.543	0.176
5.	1.091 \pm 0.591	0.916 \pm 0.284	0.899 \pm 0.395	1.166
6.	0.868 \pm 0.360	0.772 \pm 0.304	0.819 \pm 0.336	0.418
7.	0.755 \pm 0.357	0.659 \pm 0.014	0.728 \pm 0.157	0.963
8.	0.646 \pm 0.293	0.622 \pm 0.024	0.655 \pm 0.110	0.169
9.	0.562 \pm 0.273	0.582 \pm 0.104	0.602 \pm 0.130	0.237
10.	0.519 \pm 0.192	0.531 \pm 0.148	0.542 \pm 0.102	0.102
11.	0.501 \pm 0.198	0.493 \pm 0.141	0.534 \pm 0.101	0.419
12.	0.488 \pm 0.190	0.466 \pm 0.126	0.510 \pm 0.074	0.493
13.	0.468 \pm 0.129	0.449 \pm 0.130	0.495 \pm 0.076	0.793
14.	0.456 \pm 0.154	0.432 \pm 0.126	0.482 \pm 0.083	0.840
15.	0.429 \pm 0.110	0.422 \pm 0.109	0.467 \pm 0.073	1.152
16.	0.422 \pm 0.112	0.405 \pm 0.094	0.454 \pm 0.082	1.538
17.	0.399 \pm 0.112	0.386 \pm 0.104	0.436 \pm 0.086	1.308
18.	0.382 \pm 0.107	0.379 \pm 0.114	0.425 \pm 0.100	2.130
19.	0.366 \pm 0.076	0.366 \pm 0.109	0.411 \pm 0.164	1.326
20.	0.351 \pm 0.082	0.340 \pm 0.122	0.397 \pm 0.110	1.602
21.	0.334 \pm 0.059	0.333 \pm 0.109	0.315 \pm 0.338	0.702
Z	1.582 \pm 0.210	1.429 \pm 0.419	1.377 \pm 0.286	0.526

$$\begin{aligned} * \quad GL_1 &= 2 \\ GL_2 &= 12 \end{aligned}$$

$$F_{0.05} = 3.88$$

-Iași) and 1.377 μ (Chișineu-Criș). According to arm ratio and centromere index it is a metacentric chromosome. Due to its absolute and relative length, the Z chromosome ranges between the autosomal pairs 2 and 3, which is in agreement with recent observations by Ray-Chaudhuri *et al* [14] who indicated the Z-chromosome as the third one of the complement, showing almost the same size and morphology in 6 species of Galliformes. In addition, it is similar in size with the Z-chromosome of species belonging to other orders [12], which suggests that the Z-chromosome, originating in a common ancestor, was maintained as a whole in different bird species of today.

The W-chromosome of the female is a submetacentric, close to the limit of the acrocentric range, with an absolute length of 0.786 μ (Ghimpăti) 0.748 μ (Cornești-Iași) and 0.795 μ (Chișineu-Criș); it ranges between the autosomes 6 and 7 according to absolute length. The data in literature indicate the W-chromosome in *Ph. colchicus*, as a submetacentric chromosome, slightly bigger than pair 7 [9], or as an acrocentric chromosome, similar in size with 4 and 5 [18]. The W-chromosome was identified morphologically for several bird species, supporting the occurrence of a chromosome sex determining mechanism of the ZZ/ZW type in birds.

CONCLUSIONS

1. The maximal chromosome complement in the hunting pheasant from the three populations examined by us is of 82.
2. Our investigations allowed the identification of 21 autosomal pairs in addition to the heterosomes, according to size and shape, providing further information on the karyotype in pheasant, whereas previous studies failed to identify more than 11 chromosome pairs [9], [14] [16] [18].
3. The idiograms include more chromosome pairs than any previously reported ones.
4. The results allowed to ascribe the chromosomes to distinct groups, according to size, a procedure not yet applied to pheasant chromosomes, though very useful for cytogenetic studies in other species.
5. Comparative biometric analyses of the karyotype of the three pheasant populations so far examined (comparisons between idiograms and statistical treatment of the differences) did not reveal any significant difference at the chromosome level between the three populations.
6. Further informations are provided concerning the chromosomes of birds of hunting interest from the Romanian avifauna, a field not yet thoroughly approached, though very promising as a theoretical basis for breeding, selection and repopulation of these species in Romania.

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L'INFLUENCE DE LA TEMPÉRATURE SUR LE
COMPORTEMENT DU LÉZARD *LACERTA TAURICA*
TAURICA PALL., 1831

PAR

MIHAI CRUCE

This paper deals with the changes undergone by the body-temperature in the grass-lizard (*Lacerta taurica*), under the influence of the environmental factors, as well as the various behavior patterns allowing to this lizard the active selection of the temperature conditions.

Des travaux récents [1], [2], [7], [10] ont montré que les reptiles terrestres maintiennent leur « domaine thermoactif » dans les limites supérieures, grâce à leur propres activités de comportement, dans le but de développer dans des conditions optimales leurs activités sociales.

Nous nous sommes proposé d'étudier chez le lézard taurique les modifications subies par la température du corps, sous l'influence des facteurs du milieu, surtout sous l'action de la température de l'air et du sol, ainsi que les différents modèles de comportement qui lui permettent un choix actif des conditions de température.

MATÉRIEL ET MÉTHODES

Les observations portant sur un nombre de 200 individus, ont été faites dans la période mars-octobre 1968—1971, dans la zone des sables d'Obedeanu (2 km à l'ouest de Craiova).

J'ai utilisé les données météorologiques de la station d'Ishalnitza, à savoir : la température moyenne de l'air et du sol, l'humidité et la luminosité. Les variations quotidiennes de la température et de l'humidité ont été mesurées avec le psychromètre Asman et les thermomètres de sol ; pour la température du corps, on a utilisé un thermomètre à mercure. Au laboratoire, la température préférée a été mesurée à l'aide du thermogradient.

La densité des lézards a été estimée par la méthode des transects, tandis que la distance parcourue dans une heure par les lézards marqués [3] a été appréciée en notant sur l'esquisse cartographique du terrain (figurant une surface de 800 m² divisée en carrés de 2 × 2 m) la direction dans laquelle se meuvent les lézards.

RÉSULTATS ET DISCUSSIONS

A. La température du corps et le comportement

Les figures 1 et 2 montrent que la température du corps des lézards actifs suit en général la température du substratum, tout en y différant dans le détail. Ceci est prouvé par le fait qu'à des températures relativement basses du sol, de 20° à 32°C, les lézards ont dans la plupart des cas des températures du corps de 2° — 5°C plus élevées. Par contre, si la température du substratum est de 36° — 42°C, la température du corps est plus basse de 2° — 5°C. Toutes ces données confirment l'affirmation que parmi les différentes sources de températures, celle du substratum joue un rôle essentiel dans la thermorégulation des animaux poikilothermes.

Dans les limites des températures où l'activité est possible, les reptiles sont capables de modifier la température de leur corps, en la maintenant à un niveau relativement constant. H. Saint-Girons (1956) et T. A. Jenssen (1970) ont souligné l'importance majeure du comportement des reptiles dans le choix actif des conditions de température.

La température optimale du corps, chez le lézard taurique, est de 30 — 32°C un peu plus basse chez les jeunes et les individus âgés d'un an (fig. 1 et 2). D'habitude, cette température optimum se réalise à une température de l'air de 19 — 25°C, et du substratum de 30 — 36°C. Les lézards ayant réalisé cette température du corps ont un comportement plus tranquille, les mouvements sont tempérés, quoiqu'en cas de danger ou pour chasser une proie, ils sont capables de mouvements très rapides. Dans ces conditions, une activité vitale des plus intenses se déroule lorsque les lézards se rencontrent à la surface du sol en nombre maximum.

Quand la température du corps est inférieure à l'optimum, les animaux perdent leur mobilité, leurs mouvements deviennent plus lourds. A une température du corps de 18 — 20°, les lézards ne sont plus capables de se mouvoir à la surface du sol, mais peuvent rentrer dans leurs abris. J'ai observé plusieurs cas dans lesquels, par suite de la chute brusque de la température de l'air, le lézard perdait la capacité de mouvement et restait à la surface du sol. Ainsi, le 28 mars 1968, à 14 h, la température du sable ayant brusquement baissé de 26° à 18°C à cause du soleil couvert par les nuages amenés par un vent froid, j'ai trouvé un lézard qui se mouvait lourdement, la température du corps étant de 21°C. Le 24 avril 1970, j'ai rencontré sur le sol un lézard chez qui la température du corps avait baissé à 22,5°, ce qui l'a empêché de gagner son abri.

Quand la température du substratum et du corps dépasse 36°, les lézards commencent à s'agiter, se nourrissent moins, changent de place

Fig. 1. — Corrélation entre la température du corps chez le lézard *Lacerta taurica* et la température du substratum (les sables Obedeanu).

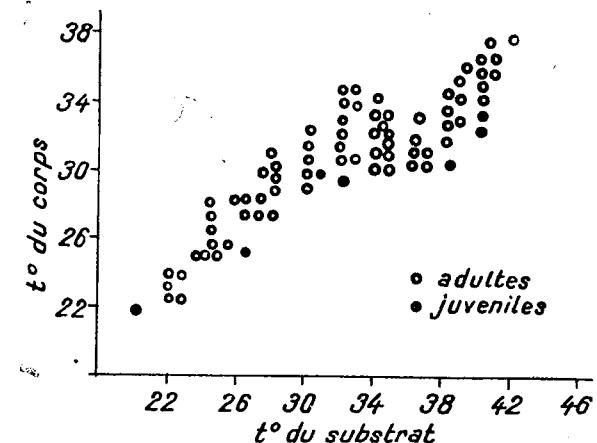
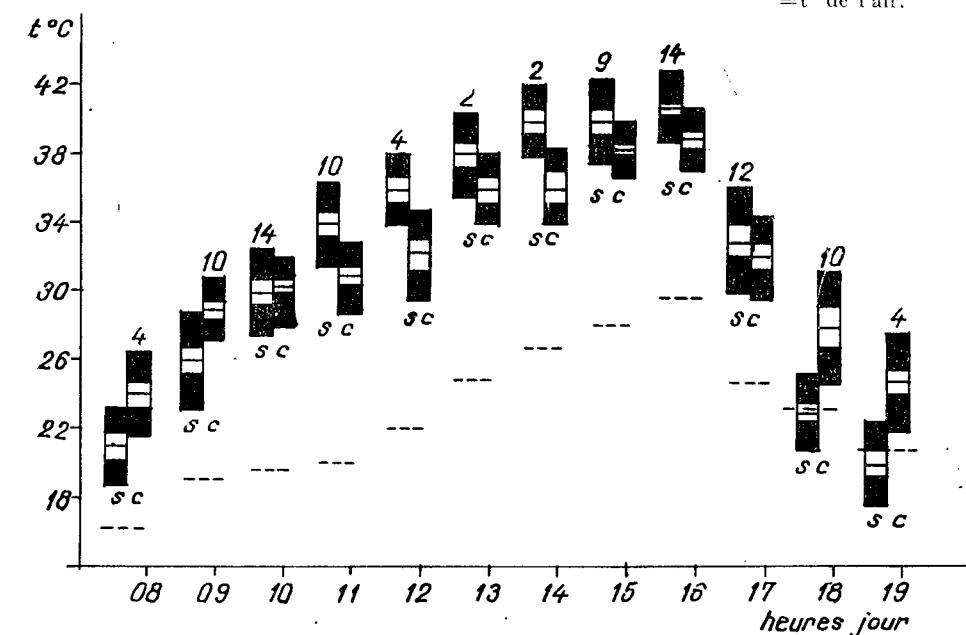


Fig. 2. — Corrélation entre la température du corps chez le lézard *Lacerta taurica* et les températures de l'air et du sol (les sables Obedeanu).

Ligne horizontale = moyenne arithmétique des températures; carrés blancs = erreur de la moyenne arithmétique; carrés noirs = déviation standard; chiffres au-dessus des colonnes = dimension de l'échantillon analysé; les lettres au-dessous des colonnes = c = t° du corps, s = t° du sol, les traits interrompus = t° de l'air.



fréquemment, leurs mouvements deviennent plus rapides et, parfois, ils soulèvent légèrement leur corps et la queue au-dessus du sol lors de leurs fréquentes stations.

A une température du sable supérieure à 44°C, on ne rencontre presque aucun lézard sur le sol, car ils sont cachés dans leurs abris où la température de l'air se maintient à 24 — 27°, même pendant les périodes les plus chaudes du jour, quand le substratum dépasse 52°. Les abris du lézard taurique ne sont pas très profonds — entre 10 — 20 cm dans les sables d'Obedeanu. En se terrant au fond de l'abri ou d'une galerie de rongeur, le lézard taurique obtient une rapide baisse de la température du corps, à 24 — 30°.

Sur un substratum fortement chauffé, la température du corps s'élève rapidement. Des expériences en laboratoire (à l'aide du thermogradient) ont montré que lorsque le substratum atteint 44°C, après 10 minutes la température du corps du lézard croît de 28° C, par l'effet du « choc thermique ». La même chose a été observée dans les conditions naturelles, notamment lorsque le lézard se trouve à la surface du sable dont la température marque 42 — 44° C. Après 5 — 7 minutes, la température du corps atteint jusqu'à 40° C. A un température plus basse du substratum, d'habitude au-dessous de 40° (entre 36 — 39°), les lézards dont la température initiale du corps était de 26 — 28°, atteignent après 10 minutes 40°, probablement sous l'action directe des rayons du soleil. Nos données concordent avec les observations des autres auteurs [4], [9] sur les stades du surchauffage. Toutefois, la température du corps à laquelle se manifeste le choc thermique a été plus basse chez le lézard taurique que chez les individus d'*Eremias arguta* étudiés par M.N.Okulova (1969). Il s'agit ici probablement de la variation géographique de la thermorégulation, signalée par L.G. Dinesman [5] chez les reptiles.

Lorsque la température du corps s'élève brusquement, le lézard se trouvant sur un substratum ayant une température de 42 — 44°C, on observe toutefois un ralentissement de l'accroissement de la température du corps entre 33 — 36° C. Ceci prouve l'existence chez le lézard taurique, comme par ailleurs chez tous les reptiles, de certains mécanismes de thermorégulation physiologique — au plus exactement du maintien de la température du corps dans les limites de l'optimum. Dans des conditions moins sévères, c.à.d. à une température du sable de 37 — 40°, ce phénomène ne se manifeste pas.

Dans les mêmes conditions, les jeunes et les individus âgés d'un an ont des températures du corps un peu plus basses que les individus mûrs sexuellement (fig. 1). La capacité d'être actifs à une température plus basse du corps permet probablement aux individus jeunes d'avoir en automne une période active plus grande. Parmi les individus mûrs sexuellement, les mâles sont plus résistants à l'action des températures basses ; après quelques jours pluvieux, ils remontent à la surface du sol avant les femelles.

Il faut mentionner le fait que si les températures sont élevées, les lézards tauriques, quoique occupant des biotopes ouverts (de steppe), se déplacent à la lisière des forêts ou, dans le cas des sables Obedeanu, sous les pins hauts de 1 — 2m. Les passages dans ces zones d'ombre ont une durée courte et correspondent aux périodes d'intensité maximum des

radiations solaires. Certes, ceci ne nous permet pas de considérer les *Lacerta taurica* comme un espèce non héliotherme, car les lézards ne restent pas au soleil un temps limité (comme les *Anolis* américains) mais recherchent les zones d'ombre pour un très court laps de temps, quand la température du sable atteint 50° C. En plus, dans ces conditions de température du sol, la majorité des lézards se trouvent dans leurs abris, tandis que les individus en activité supportent au soleil le choc thermique ou déplacent leur espace vital dans les zones ombragées ou contiguës. Les jeunes résistent aux températures élevées en se déplaçant par des mouvements ± longs à l'ombre des plantes herbacées. Les jeunes, et parfois aussi les adultes, grimpent sur certaines plantes : *Erigeron canadensis* et *Verbascum thapsus*, évitant ainsi à 40 — 80 cm les températures extrêmement élevées du substrat pendant les mois arides d'été.

Le tableau 1 présente la distribution diurne des lézards (mai-juillet 1970), en indiquant le pourcentage des individus exposés au soleil ou qui s'abritent à l'ombre ou dans le sol. On constate que les radiations

Tableau 1
Distribution horaire des lézards (*Lacerta taurica*) observés au soleil ou à l'ombre (mai-juillet 1971)

Heure	% des lézards à l'ombre	% des lézards au soleil	N (total) lézards observés
08	0	100	9
09	20	80	12
10	21,4	78,6	19
11	20	80	16
12	60	40	4
13	100	0	2
14	100	0	2
15	66,6	33,3	12
16	78,6	21,4	14
17	20	80	16
18	0	100	4

intenses vers midi réduisent le nombre des lézards ; même si à 15 heures les températures sont plus élevées en comparaison de celles à 13 heures, le déclin de l'intensité des radiations lumineuses détermine l'accroissement du nombre des lézards actifs. Aux premières heures du jour et avant le coucher du soleil, tous les lézards de la population s'exposent au soleil ; vers le milieu du jour, les lézards déplacent leur centre d'activité surtout à l'ombre. Vers midi, quand la température de l'air atteint 29° et celle du sol 45°, la luminosité dépassant 90 000 lx, un petit nombre de lézards se déplace à l'ombre, le reste gagnant leur abri.

Le changement de la position du corps est une modalité différente d'élection active des températures préférées par les lézards. Nos observations faites dans les places où les lézards s'exposent au soleil (pierres, sable), le matin au lever du soleil, l'après-midi avant le coucher du soleil, on même pendant le jour, lorsque les températures de l'air et du sol sont faibles, ont montré que les lézards orientent leur corps en angle droit par rapport à la direction des rayons de soleil, pour accumuler les radia-

tions de lumière en vue d'élever la température du corps. De cette manière, les lézards peuvent commencer leur activité diurne le matin, après 10 — 15 minutes d'exposition au soleil; de même, l'après-midi, ils continuent à rester sur les cailloux chauffés même après le coucher du soleil, ce qui leur permettra de regagner leur abri (à 10 — 20 cm de profondeur), ayant une température presque égale à celle de l'abri.

B. Influence des facteurs abiotiques sur l'activité diurne des lézards

Les conditions climatiques défavorables nous ont empêché de faire une statistique parfaite des fluctuations numériques diurnes des lézards, car le temps brusquement couvert ou l'intensification de la vitesse du vent déterminent des changements difficiles à différencier statistiquement. Toutefois, comme il résulte de la figure 3, nous pouvons faire les considé-

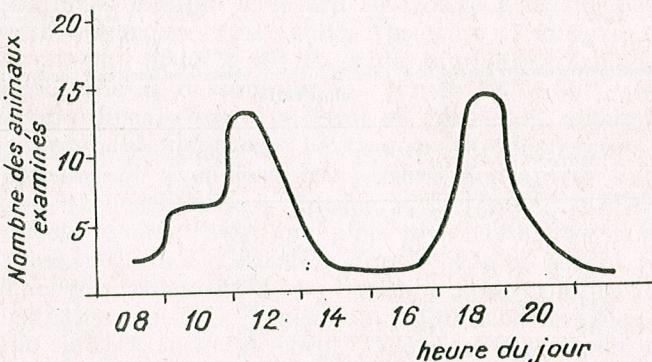


Fig. 3. — Nombre des lézards actifs aux différentes heures du jour, sables d'Obudeanu (le nombre est la moyenne de 14 jours d'observation dans une zone de 400 m² en mai 1971).

rations suivantes pour la période mai-juin 1971; le plus grand nombre des lézards tauriques se situe entre 10 — 11 heures, il baisse sensiblement entre 13 — 15 h, après quoi le nombre des lézards actifs croît de nouveau entre 16 — 18 h, en dépassant le niveau maximum de la première partie du jour; ensuite, après 18 h, le nombre baisse brusquement, les lézards disparaissent complètement 10 minutes après le coucher du soleil. Sur les pierres qui accumulent la chaleur de toute la journée, on observe parfois des exemplaires isolés de *Lacerta taurica*, qui y somnolent même après le coucher du soleil. Au début du printemps et en automne, dans des conditions assez similaires, le nombre maximum de lézards — 21 ex./800 m² — correspond à 11 — 13 h et respectivement à 12 — 14 h.

La densité des lézards à la surface du sol en avril-juin 1971, à des températures différentes de l'air, atteint son maximum à une température de l'air de 21 — 25° (1 individu par 10 m de transect). La densité est assez grande même pour les températures de l'air de 9 — 15° (1 individu par 35 m de transect); mais l'explication réside dans l'activité plus grande des mâles à la sortie de l'hibernation (c'est alors que les tempé-

ratures de l'air marquent 9 — 15°C). J'ai accordé une attention spéciale au cas de rencontre possible des lézards par mauvais temps ou, au contraire par un temps très chaud, après la pluie, le matin, le soir, en automne ou au printemps. Les températures du corps, mesurées dans des conditions de milieu différentes, ont présenté une amplitude comparativement faible.

Le rythme d'activité diurne a été apprécié aussi d'après le nombre des mâles ou des femelles, chez lesquels la température du corps indiquait des valeurs optimum (fig. 4). Parmi le 75 exemplaires examinés, 46,6 %

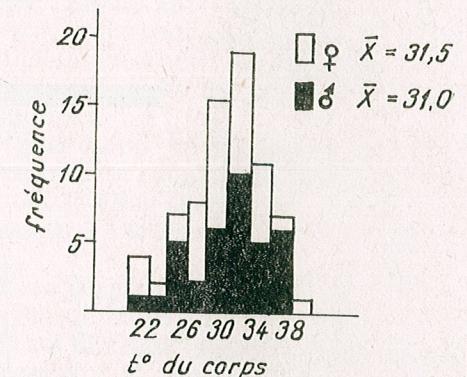


Fig. 4. — Fréquence des différentes températures du corps chez le lézard *Lacerta taurica*, en mai-juin 1971.

avaient la température du corps (optimum) entre 30 — 34°. La température moyenne du corps chez les mâles est de 31,5°, ne différant pas statistiquement de celle des femelles (31°).

Nous considérons avoir obtenu les résultats les plus éloquents pour l'appréciation de l'activité diurne du lézard taurique, lorsque nous avons utilisé pour modèle d'estimation du cycle nichéméral d'activité les distances parcourues dans une heure (m/h). La fig. 5 montre les distances moyenne parcourues par les lézards (en m/h) corrélées aux températures de l'air et du substratum, et naturellement, à l'heure (période mai-juillet 1971).

On observe que l'activité la plus réduite pour les deux sexes se situe entre 13 — 15 h, quand les radiations solaires sont au maximum (70 — 90 000 lx). Les lézards peu actifs effectuent des déplacements courts de 12 à 34 m. Les déplacements les plus importants ont lieu dans la première partie du jour (entre 9 — 11 h), de 68 à 180 m/h et l'après midi, entre 16 — 18 h, quand les valeurs approchent 42 — 172 m/h. L'activité intensifiée des individus des deux sexes dans la seconde partie de la journée s'explique par les radiations solaires moins intenses, quoique les températures de l'air et du sol gardent des valeurs similaires à celles de la première partie du jour. Ainsi, les mâles ont été deux fois plus actifs entre 17 — 18 h (172 m/h) à une température de l'air de 20,9° et du sol de 25,5°, en comparaison de l'activité à 12 h, quand les températures étaient ± similaires. En 82 heures d'observations, faites entre 13 — 15 h, j'ai vu 2 lézards qui regagnaient leur abri et un lézard qui se déplaçait à l'ombre des

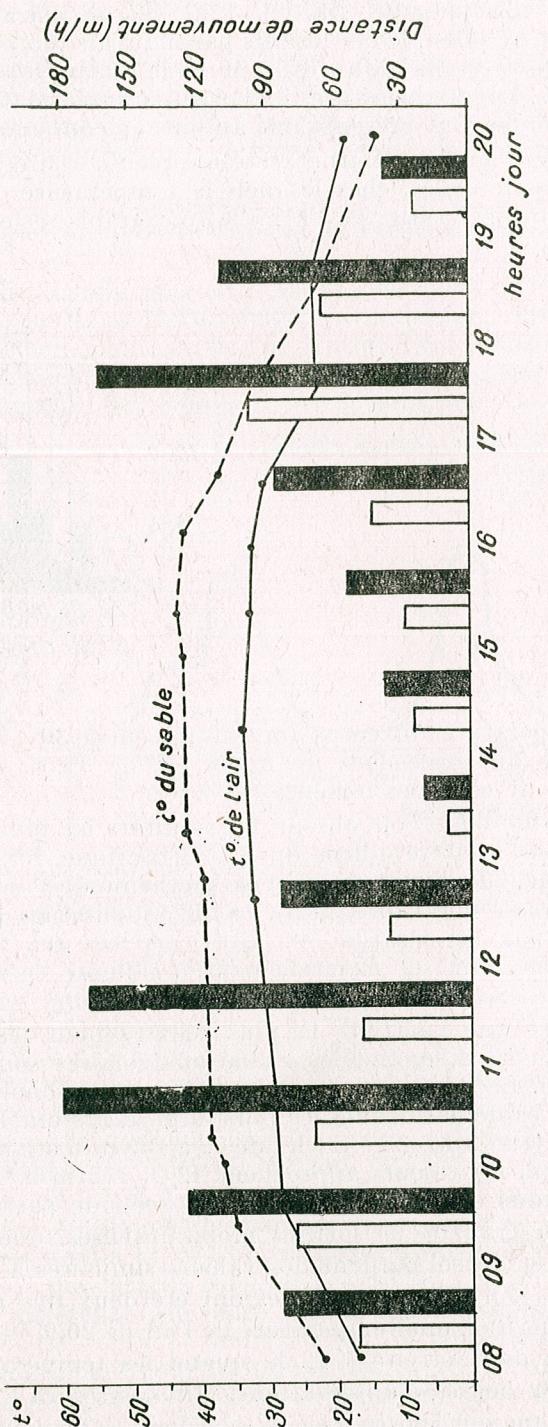


Fig. 5.—Estimation de l'activité des lézards d'après la longueur des déplacements (m/h) à différentes heures du jour (mai-juin 1971).

pins, où la température du substrat était de 15° plus basse. En se déplaçant dans ce microhabitat plus froid, ce lézard reste actif toute la journée.

Les mâles sont plus actifs que les femelles au cours de toutes les heures du jour (fig. 5) parce qu'ils ont aussi un espace vital beaucoup plus grand.

CONCLUSIONS

1. La température optimum du corps chez le lézard taurique est de 30 — 32°; elle se réalise à une t° de l'air de 19 — 25° et une t° du sol de 30 — 36°. Dans ces conditions, les lézards sont calmes, leurs mouvements tempérés et ils manifestent une intense activité biologique.

2. Au-dessous de la température optimum du corps, les lézards perdent leur mobilité et deviennent lourds.

3. À des températures élevées (plus de 36° t° du corps), les lézards deviennent agités, se nourrissent moins, se déplacent fréquemment; certains demeurent au soleil et subissent le choc thermique, d'autres évitent les températures élevées en passant à l'ombre ou en se mettant à l'abri dans leur terriers.

4. Le changement de la position du corps par rapport à la direction des rayons du soleil constitue un moyen de hausse active de la température du corps, quand la température du sol n'atteint pas les valeurs optima.

5. La preuve éloquente de la capacité d'autorégulation thermique chez le lézard *Lacerta taurica* est fournie par le fait que la température du corps est : de 2 — 5° plus élevée que la température du sol quand celle-ci a des valeurs de 20 — 32° ; et de 2 — 5° plus basse quand la température du sol est de 36 — 44°.

6. La densité des individus (par unité de surface ou le long d'un transect) et l'intensité de l'activité (estimée d'après l'ampleur des déplacements- m/h) déployée par les lézards pendant les mois d'été, atteignent le maximum le matin, entre 9 — 11h, et l'après-midi, entre 16 — 18h.

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