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MIOCENE CIRRIPEDS DOMICILED IN CORALS

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*Abstract.* — Problems concerning the structure of shell and manner of its growth in the genus *Creusia* Leach, 1817, which have been examined on the example of a Miocene species, *Creusia sanctacrucensis* n.sp., constitute the subject of the present paper. All Miocene representatives of this genus, described so far, have been revised. It has been shown that *Creusia* Leach, 1817 and *Pyrgoma* Leach, 1817 are two different genera which, together with *Pyrgomina* Bałuk & Radwański, 1967, make up — within the family Balanidae Leach, 1817 — a separate subfamily, Creusiinae n. subfam. Furthermore, problems related to the ecology of the Creusiinae have been examined. It has been shown the growth of shells of these cirripeds is possible only within live and still growing anthozoans. The mutual relation of cirripeds and anthozoans should be determined as a commensalism. The stratigraphic distribution of the Creusiinae and problems of the phylogeny of this subfamily have subsequently been examined. On the basis of comparison of the shell structure in the genus *Creusia* Leach and particular ontogenetic stages in the genus *Balanus* da Costa, the conclusion has been drawn that the Creusiinae separated from the main stock of the Balanidae as a result of the neotenic development of a certain branch of this family which probably took place in the Oligocene.

INTRODUCTION

Aberrant cirripeds of the genus *Creusia* Leach, 1817 and related forms belong to enough rare fossils and, on the territory of Poland, have

not been known so far. The deviation of these cirripeds from an average structure type of the representatives of the family Balanidae Leach, 1817, to which they belong, is a result of their adaptation to the life solely within the coralla of the live anthozoans. Hence, they were most often found during the investigations of anthozoans.

Numerous, excellently preserved specimens of *Creusia*, found by the present writers in the anthozoans from the Korytnica clays (Miocene, Lower Tortonian, southern slopes of the Holy Cross Mts., Central Poland), allowed them for an analysis of the structure and ecology of these cirripeds which have never before been the subject of a more detailed palaeontological study. Since the Miocene forms known so far were very differently interpreted and the forms from Korytnica represented a new species, the necessity arose of the revision of most forms from the European Miocene. In view of divergent opinions as to the structure of shell and taxonomy of these cirripeds, the authors resolved to precede the description of the species from Korytnica with general information on the structure of shell and manner of its growth in the genus *Creusia*, as well as on the taxonomic position of this genus.

The data on the structure of shell in *Creusia* are mostly based on the material collected from the Korytnica clays since an only Recent species of this genus, *Creusia spinulosa* Leach, 1824, was never described in a modern manner. These data are in conformity with those, cited by other authors who studied fossil creusioid barnacles from the Miocene of Europe (Procházka, 1893), Pliocene of the U.S.A. (Brooks & Ross, 1960), and Pleistocene of the Barbados Island (Withers, 1926).

At the same time, the present writers' interest in other Miocene representatives of this genus, based on the examination of the Croatian material (Bałuk & Radwański, 1967a), as well as their studies on younger representatives of a related genus from the Pliocene of the Crete Island (Bałuk & Radwański, 1967b), allowed them for drawing new conclusions, concerning the taxonomy and phylogeny of the entire group of creusioid forms (Creusiinae).

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#### SHELL MORPHOLOGY IN THE GENUS *CREUSIA* LEACH, 1817

##### STRUCTURE

The shell of creusoid barnacles (*Creusia*) is cup-shaped. The lower part, in the form of an inverted cone, makes up a basis and the upper part, shaped like a low conical lid, a crown (Fig. 1). The entire shell is ornamented with more or less pronounced longitudinal ribs equal in number on basis and crown.

Both parts of the shell — basis and crown — may relatively easily be separated from each other, since the degree of their adherence is not great.

The crown of *Creusia* consists of four compartments which also may relatively easily be separated. The compartments are connected with each other by overlapping appendices, alae and radii, much the same as those in acorn barnacles (*Balanus*) although somewhat differently developed. On the basis of the situation of alae and radii, individual compartments of the crown may be recognized as the rostrum (R), carina (C) and two lateralia (2 L) — (see Figs. 1c-d; Pl. IV, Figs. 1, 3; Pl. V, Figs. 1, 3).

A compartment of the crown, determined here as rostrum, plays a similar role to that in *Balanus*. In relation to other Balanomorpha, thus understood rostrum of *Creusia* or *Balanus* actually represents two rostralateral compartments (RL) completely fused together as it obviously results (Runnström, 1925) from the ontogeny of *Balanus* and which is generally accepted (Broch, 1927; Withers, 1928, 1929; Krüger, 1940). Thus, unjustified are previous views (Darwin, 1854a; Pilsbry, 1916), repeated even recently (Davadie, 1963) that the rostrum in *Balanus*

represents an actual rostrum with two rostralateral compartments fused with it, as is the case of, for instance, the genus *Chelonibia* Leach. Thus, the rostrum in *Creusia* is analogous and homologous to that in *Balanus* (cf. Fig. 8 a-b), whereas in relation to several other Balanidae and Balanomorpha it is only analogous.

The crown of *Creusia* displays — as compared with that of *Balanus* — the lack of two carinolateral compartments (CL). In our opinion, this lack results from the fact that the carinolateral compartments are completely undeveloped as it has already been believed by Withers (1928) and Zullo (1961). These compartments did not vanish by fusion with some adjacent compartments (carina or lateralia). As a result, despite the presence of a smaller number of compartments in the crown of *Creusia*, all the four compartments are analogous and homologous to those in the crown of *Balanus*.

Opercular valves in *Creusia* are 2 terga and 2 scuta free (Pl. IV, Fig. 2; Pl. V, Fig. 2). In fossil specimens, they are usually situated on the bottom of the basis, although their position in the animal's life was of course different (Fig. 1f). All the four opercular valves of *Creusia* have their shape and morphology unusually similar to those of *Balanus* and, in relation to them, they do not display any structural transformation.

A cuplike extension of the basis in *Creusia* allows to hold in it almost entire body of the animal. Hence, the proportions in the structure of crown in *Creusia* are different than those in *Balanus* in which it is precisely the crown that the body is held in. In *Creusia*, the crown becomes a protective apparatus of the sheath within which opercular valves move. This is also the reason why the sheath occupies a considerable part of the crown and its lower edge descends more or less to the lower edge of the crown. At the same time, in *Creusia*, there disappears the inner lamina of the compartments of the crown, its role being taken over by the sheath. At middle of the carina, the sheath bends at an acute angle which, similarly as in *Balanus*, is a result of the adaptation to the shape of terga which move within the bent top part of the carina as in a bearings. The details of the inner structure of the shell of *Creusia* will be discussed together with the description of the material from Korytnica. As may be judged from literature, they are identical in all fossil representatives of *Creusia*.

In the shell of *Creusia*, like in *Balanus*, there are two openings differently developed and of a different origin. The first, a very small, almost punctual, opening in the very bottom of the basis, corresponds to the place of attachment of the first antennae of larva in the cypris stage settling on the substratum. This opening is, as a rule, very indistinct and seems to be secondarily filled with calcite. A principal opening (orifice), situated at the top of the crown, is, as compared to that in *Balanus*, small, almost ovate and occupies a relatively small space within the crown.

## MANNER OF GROWTH

In *Creusia*, like in *Balanus*, the crown grows uniformly with the basis, since the growth zone runs along a suture which occurs between the crown and basis. In this zone of *Creusia*, there appear ribs, all of them gradually continued on the basis and crown. Hence, the number of ribs on both parts of shell is identical (cf. Bałuk & Radwański, 1967a, where different data are discussed).

The fact alone of the development of ribs on basis indicates that the growth zone in *Creusia* does not adhere to the substratum. Quite different is the case of *Balanus* in which the growth zone does contact the substratum. This is the reason why in *Balanus* an own sculpture, which, at the same time, might correspond to the sculpture of the crown, is not developed on the outer side of the basis. Any exceptions from this rule are, in *Balanus* or in other Balanidae, very rare (Darwin, 1854a; Pilsbry, 1916; Krüger, 1940).

As a result of the course of the shell growth zone which is situated at a certain distance from the substratum, a pronounced constancy may be observed in a general shape of basis and a general aspect of its sculpture (manner of ribbing). Both these characters, together with the relation of the shell of *Creusia* to the corallum, surrounding it, which in the case of the forms from Korytnica under study, consists in pushing aside of the corallites, situated around the shell of *Creusia* (Figs. 4 a-b; Pls. II and III) and in embracing of the shells by corallites even deformed through the presence of *Creusia*, clearly indicate that the shell of *Creusia* is an element independent on the shape of corallum and that an anthozoan always adapted its shape to the shell of *Creusia*. The growth zone of the shell had to be always situated above the corallum and the body of an anthozoan. Consequently, the latter could not exert any influence on a general shape and manner of ribbing of the shell of *Creusia*. At the same time, *Creusia* defended itself against becoming overgrown by the increasing anthozoan and constantly grew above it so that its basis was constantly extended. *Creusias* lived, therefore, in the coralla of undoubtedly live and constantly growing anthozoans.

After the overgrowing of *Creusia* by corallites, the pattern of the latter still remained disturbed for a considerable period and, in many cases, this allows one to state the presence of *Creusia*, hidden within the coralla (cf. Pl. VI, Figs. 3a-3c).

TAXONOMIC POSITION OF THE GENUS *CREUSIA* LEACH, 1817

The genus *Creusia* Leach, 1817 was erected in 1817 by Leach for the cirripeds domiciled in coralla and having a crown built of four compartments (R+2L+C). This genus was erected as the next one after *Pyrgoma*

Leach, 1817 which included similar cirripeds domiciled in coralla, but having an indivisible crown which, in a way, consists of a single „compartment”. The distinction between these two genera, i.e. *Pyrgoma* Leach and *Creusia* Leach, was subsequently accepted by Sowerby (1823). On the other hand, Darwin (1854a) paid attention to a considerable similarity of both these genera and, consequently, expressed certain doubts as to their taxonomic individuality. Finally, he was inclined to believe that *Creusia* makes up only a subgenus of the genus *Pyrgoma*. Thus understood genus *Pyrgoma* was assigned by Darwin (1854a) to the subfamily Balaninae Darwin (First Section) of the family Balanidae. Subsequent authors shared Darwin's view on a considerable similarity of *Pyrgoma* to *Creusia*, but they mostly treated them as separate genera (Pilsbry, 1916; Nilsson-Cantell, 1921; Withers, 1926, 1928, 1929; Hiro, 1935, 1938; Krüger, 1940, Davadie, 1963, and others — cf. Brooks & Ross, 1960). Both genera were placed — in conformity with Darwin's view — within the subfamily Balaninae Darwin (cf. Pilsbry, 1916; Withers, 1928; Krüger, 1940, Davadie, 1963). Since Withers' (1926) times, many authors have been induced by a certain separateness of these genera from the remaining Balaninae to discuss *Pyrgoma* and *Creusia* together. Recently, a return has been noted to Darwin's view on the identity of both these genera (Brooks & Ross, 1960; Utinomi, 1962).

The analysis of the entire material of fossil „pyrgomas”, based on the available specimens and on the data, supplied by literature, allows the present writers to conclude that *Pyrgoma* Leach and *Creusia* Leach should be regarded as two different genera. In addition to a palaeontological argument that all Miocene forms correspond to the characteristics of the genus *Creusia* Leach and none to those of the genus *Pyrgoma* Leach which we shall examine in detail below, it should be stated that, among Recent forms, there are pyrgomas which differ from *Creusia* not only in the number of compartments. Far-reaching differences between these two genera are listed in Table 1.

*Pyrgoma grande* (Sowerby) should be cited as a characteristic species of pyrgomas, displaying all characters, listed above, which has been checked by the present writers in the Recent material from the Indian Ocean. A Miocene species *Creusia sanctacrucensis* n.sp. described below, may serve as a similar example in the case of *Creusia*.

With such a distinction between the genera *Pyrgoma* Leach and *Creusia* Leach, there still remain certain forms which display a different set of characters. Primarily, here belongs a species, known so far by the name of „*Pyrgoma anglicum* Sowerby” which — as known since Darwin's (1854b) times, as confirmed later by Withers (1926, 1929), Sakakura (1934), Hiro (1935) and as checked by the present writers in the Recent material from the coast of England — has a crown with 2 („carinal”) sutures only and, therefore, it is built in fact of 2 compart-

ments (Fig. 8c), as well as it has free terga and scuta of the *Balanus* type. Analogous characters are revealed by specimens, which represent another species, and have been found by Dr. G. J. Boekschoten in the Pliocene of the Crete Island. In the light of differences between the genera *Pyrgoma* and *Creusia*, cited above, these species — in our opinion — do

Table 1  
Differences between *Creusia* Leach and *Pyrgoma* Leach

No.	<i>Pyrgoma</i> Leach, 1817	<i>Creusia</i> Leach, 1817
1.	Crown's compartments completely fused together and forming a single "compartment" (Fig. 8d); in some species, indistinct sutures on the sheath (2 or 4). No bending of the sheath.	Crown consists of 4 compartments (Fig. 8b). The sheath sharply bent in the middle of carina.
2.	Sheath adheres to the inner side of the crown, septa almost completely reduced.	Sheath does not adhere to the inner side of the crown and is separated by distinctly developed septa.
3.	Sheath touches on the inner side of the basis and, therefore, descends below the edge of crown.	Sheath usually descends at most to the lower edge of the crown (in flat forms—lower), but the presence of septa prevents it from contacting the basis.
4.	Terga and scuta considerably depart from the <i>Balanus</i> type and, more than once, fused so that a tergum and a scutum fuse together to form a single tergoscutal valve.	Terga and scuta completely free, of the <i>Balanus</i> type.
5.	In several forms, the orifice is not covered by tergoscutal valves and a considerable free space is left (cf. Darwin, 1854a; Pl. 13, Fig. 1d); in addition, they seem to strongly adhere to the sheath, becoming almost immobile. These characters indicate the disappearance of such a functionality as that of opercular valves in the remaining balanids.	The functionality of opercular valves the same as that in the remaining balanids.

not represent either of these two genera, but a separate genus for which we have introduced recently (Bałuk & Radwański, 1967b) a new generic name *Pyrgomina* Bałuk & Radwański.

The three genera distinguished, i.e. *Pyrgoma* Leach, *Creusia* Leach and *Pyrgomina* Bałuk & Radwański, differ from each other primarily in the

structure of crown (number of compartments, Fig. 8) and morphology of opercular valves. These characters should be considered as principal generic differences. All the same, within thus understood genera, there exists a further differentiation that consists in less significant details of structure.

Within *Pyrgoma* Leach, which is a Recent genus only, there are distinguished three groups of species which have differently developed opercular valves, and this — in the light of the principles of all balanids — should be considered as diagnostic in their character. The present writers believe that these groups may be treated as subgenera (cf. p. 486). Their names have been adopted after former authors who — in pre-Darwinian times — considered them to be separate at the generic rank (cf. p. 487).

On the other hand, within the genus *Creusia* Leach, there are distinguished certain Quaternary (Pleistocene and Recent) forms in which sutures are indistinct and septa disappear, whereas terga and scuta seem to display a stronger junction than that in typical forms (cf. p. 485). Such forms have first been described by Withers (1926) from the Pleistocene of the Barbados Island. In our opinion, the characters referred to above enable the separation of such species and erection of a special subgenus (cf. p. 485).

The group of the three genera under study, i.e. *Creusia* Leach, *Pyrgoma* Leach and *Pyrgomina* Bałuk & Radwański, differs from other Balaninae to such an extent that, in the present writers' opinion, a new separate subfamily Creusiinae should be erected for them. *Creusia* Leach, as stratigraphically the oldest genus which persist until now, is a type genus of this new subfamily.

As indicated by the above mentioned facts, concerning the structure of shell in *Creusia*, this genus reveals — in the structure of its shell — a far reaching homology to the genus *Balanus* da Costa and, therefore, it is undoubtedly closely related to acorn barnacles (*Balanus*). The remaining two genera of the new subfamily, *Pyrgomina* Bałuk & Radwański and, in particular, *Pyrgoma* Leach, display many characters differing them from acorn barnacles but, on the other hand, also many characters in common with *Creusia* (for instance, structure of mouth parts, Nilsson-Cantell, 1921). Now in turn, in the ontogeny *Pyrgomina*, both in the nauplius and cypris stage (Moyses, 1961) and *Pyrgoma* in the settled stage (Utinomi, 1943)<sup>1</sup>, display a striking morphological similarity

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<sup>1</sup> Utinomi's (1943) data are the only ones, concerning the ontogeny of the settled stage of pyrgomas, in which a certain fusion of compartments is brought about in the crown, although this fusion — at least in the examined species *Pyrgoma indicum* Annandale (cf. p. 487) — is not ultimate. On the other hand, in the source literature, there are no other data on the fusion of 4 compartments into one during the ontogeny of pyrgomas. An information on such fusion comes probably from Abel's (1920) work and was several times repeated in the palaeontological literature (Abel, 1927, 1928; Termier & Termier, 1953; Müller, 1963).

and a development analogous to that in acorn barnacles. All these facts point out that the subfamily Creusiinae n. subfam. is related to acorn barnacles. Hence, the present writers place the subfamily Creusiinae n. subfam. within the family Balanidae Leach, treating it as a taxon of an equivalent rank as other subfamilies (Balaninae Darwin, 1854; Tetracitinae Gruvel, 1903; Chelonibiinae Pilsbry, 1916 and Coronulinae Gruvel, 1905 — cf. Krüger, 1940; Davadie, 1963<sup>2</sup>), distinguished so far within this family.

Domiciling only within coralla of live and constantly growing anthozoans is a very characteristic feature of the subfamily Creusiinae n. subfam. This feature cannot be, however, considered as a diagnostic character of only this subfamily since it also observed in some other balanids (Balanidae).

In our opinion, the genus *Pyrgopsis* Gruvel, 1907, which displays not only certain analogies to pyrgomas but also significant differences (Gruvel, 1907), should not be assigned to the subfamily Creusiinae n. subfam. Krüger (1940) pronounced himself in favour of a relationship of these two genera, and Sakakura (1934) even considered them to be identical. The dissimilarity in the structure of the body cover in which the main role is played by a soft, saclike basis which transforms itself into a peduncle and serves as an organ of attachment to the substratum, constitutes a set of characters so different from those in all Creusiinae that it seems to preclude any possibility of their relationship. This enigmatic genus is known only by 3 specimens (Gruvel, 1907) and it has not been recently studied. In the latest time, Zullo (1967) introduced a new generic name, *Pyrgopsella* Zullo, since the former one, *Pyrgopsis*, had been preoccupied by another animal (a loligopsid cephalopod).

#### SPECIFIC CHARACTERS WITHIN THE GENUS *CREUSIA* LEACH, 1817

In the zoological taxonomy, the genus *Creusia* Leach occupies quite an exceptional place since all its representatives are assigned (Darwin, 1854a) to the single species *Creusia spinulosa* Leach, 1824. According to Darwin (1854a), the differentiation within the genus under study is so great that it is impossible to distinguish particular species but only varieties of one species. As many as 11 varieties are distinguished within *Creusia spinulosa* by Darwin who considers this to be an only sound solution of the problem in face of taxonomic difficulties met with. His statement ... „If I do not thus throw much light on the subject, I shall at least not burden it with error. I believe that the species will be definitely made out only by persons resident in the coral-bearing zones” (*op. cit.*, p. 376) — may here be repeated word for word, although more than 100 years have

<sup>2</sup> The family Balanidae Leach also should probably include the subfamily Emersoninae Ross, 1967, recently erected for certain specific Balanomorphs from the Eocene of Florida (Ross & Newman, 1967).

elapsed since he expressed this opinion. In all these years, nobody advanced the knowledge of the species examined and the hope, expressed by Darwin, remains still topical.

Although no revision of the species *Creusia spinulosa* has been undertaken since Darwinian times, different authors described successive new varieties whose number increased to some 20 and simultaneously some of them have begun — after Broch — to be called „formae” (references in Hiro (Utinomi) 1935, 1938, 1962).

The authors who described fossil Creusiinae under the generic name of *Creusia* were aware that their specimens were different from any varieties or formae of the Recent *Creusia spinulosa* and erected new species (Procházka, 1893; Withers, 1926). Another method was adopted by Kolosváry (1949, 1962) who probably not knowing the works of the authors, referred to above (which is testified to by the fact that he described as new taxons those which have already been figured by Procházka), determined new taxons as formae, contained within limits of the species *Creusia spinulosa*. Kolosváry's method is erroneous not so much on account of his being weak in the literature, referred to above, but primarily on account of his misunderstanding of the above cited opinion of Darwin who by no means considered that all the taxons within the genus *Creusia* should be assigned to an infraspecific category of the species *Creusia spinulosa*.

In our opinion, all fossil forms described so far, belonging to the genus *Creusia* and different from the varieties of Recent *Creusia spinulosa*, should be assigned to separate species. Determining features characteristic of individual fossil species encounters other difficulties, resulting from by far insufficient knowledge of many of them, especially those from the Miocene of Europe from which they were many times recorded. The collected specimens were mostly worked out very carelessly and with an unusually small measure of criticism concerning both their morphology and taxonomy. Many authors described as new species ones that were already previously well-known or erected new species on the basis of a material which was unfit for any closer diagnosis and, in fact, several of these forms were not even figured. Consequently, an exceptionally tangled and intricate synonymy of forms from the European Miocene was brought about and now, these forms require a complete revision. Such a revision is presented in a further part of the present paper. It was necessary for both the justification of a new species from the Miocene of Poland and the solution of the problem of the occurrence of individual genera of Creusiinae in the Miocene. In the light of this revision, it is clear that out of the entire bibliography concerning fossil Creusiinae, only the works by Seguenza (1876), Procházka (1893), Withers (1926, 1929) and Brooks & Ross (1960) display a required degree of reliability and, until now, represent a real

scientific value. At the same time, these works allow to form an opinion on the taxonomic suitability of several characters of fossil *Creusiinae*.

On the basis of the works, referred to above and the material collected at Korytnica, it is clear that only a general shape and the outer sculpture of the shell, as well as the morphology and sculpture of opercular valves, are important from the viewpoint of the taxonomy of fossil representatives of *Creusia* Leach. For the reasons, examined below, the value of some of these characters is not, however, identical.

A general shape determining a more distinct elongation of the shell is only an approximate character, since — within a given population — it may considerably vary, much the same as between different populations. This problem has been presented by the writers when they worked out the species *Creusia miocaenica* Procházka from the Miocene of Croatia (Bałuk & Radwański, 1967a). Such a variability is also visible in the material from Korytnica (Fig. 2). This character may be of a taxonomic significance only in the case of reaching extreme values.

The sculpture of the outer side of the shell is of a great taxonomic importance since the growth zone of the shell never contacts the substratum at the moment of the shell growth. Hence the lack of any influence that might be exerted by the substratum on the sculpture, as is the case of acorn barnacles in which both the basis and crown may be subject to various modifications even within particular populations of the same species (cf. Darwin, 1854a; Pilsbry, 1916; Bieda, 1931; Krüger, 1940; Davadie, 1963 and others, as well as the problem of "mimicry", discussed below). In *Creusia*, due to this lack of contact between the growth zone and substratum, the sculpture of the shell is, as mentioned above, identical on both the basis and crown. For the taxonomic purposes, of importance is also the character of ribbing represented by the prominence of ribs, their shape, outline and their ratio to the rib interspaces. On the other hand, the number of ribs which displays a distinct variability and, in addition, depends on the size and age of an individual, is devoid of any taxonomic significance. A different degree of the manifestation of this group of characters is clearly visible in the material from Korytnica and other localities of the European Miocene. Their taxonomic suitability has already been discussed before (Bałuk & Radwański, 1967a).

A frequently occurring development of radii outside the crown is considered in *Creusia* an important taxonomic character. Some authors (e.g. de Alessandri, 1910; Abel, 1928) treated it even as a character determining the number of compartments in the crown and, therefore, decisive as to the assignment of a specimen either to *Creusia*, or to *Pyrgoma*. It is, however, beyond any doubt that the number of compartments may be only determined by the presence of sutures in the sheath since the degree of development of radii outside the crown is

considerably variable within a given population of a definite species of *Creusia*. Radii occur only in the cases when there arose a necessity to increase the orifice or to change the inclination of compartments during the growth of an individual. The reasons why this phenomenon occurs only in some individuals of a given single-species population, as well as its functional significance are not quite clear. The phenomenon itself is clearly visible in the species *Creusia miocaenica* Procházka from Croatia, referred to above (Bałuk & Radwański, 1967a). In our opinion, it is only the tendency itself to a more distinct development of external radii in some species of *Creusia* than in others that may be of a certain significance for the taxonomic purposes.

The morphology and sculpture of opercular valves in *Creusia* should be a greatest significance to the taxons of a specific rank since these valves are, during the growth of the animal, completely independent of the surroundings. Sometimes, it is, however, very difficult to obtain these valves from the palaeontological material and, hence, in two out of the seven Miocene species, accepted by the writers in the present paper, the valves are unknown so far. Thus, the separateness of these species cannot be now definitely solved, although the sum of the remaining characters seems to differ them sufficiently from the remaining species.

In *Creusia*, a certain taxonomic significance may probably be also ascribed to some characters of the internal side of the shell, such as the arrangement of the sheath or the manner of development of septa but, in the light of the data available so far, they cannot be properly characterized. The same applies to the internal structure of the compartments which has recently been considered a diagnostic character in acorn barnacles (Davadie, 1963), but which has not so far been examined in fossil *Creusia* and which cannot be appropriately observed in the material available.

The remaining characters of the structure or morphology of shells seem to be without any significance to the characteristics of taxons of the specific rank in the genus *Creusia*.

#### DESCRIPTION OF A NEW SPECIES FROM KORYTNICA

Family **Balanidae** Leach, 1817

(non Gray, 1825 — cf. comments by Ross, 1966; Ross & Newman, 1967)

Subfamily **Creusiinae** n. subfam.

Genus *Creusia* Leach, 1817

*Creusia sanctacrucensis* n. sp.

(Pls. I—VI)

*Holotypus*: Specimen in Pl. IV, Fig. 2; Pl. V, Fig. 2, in the authors' collection.

*Paratypes*: Remaining specimens in Pls. I—VI, in the authors' collection.

*Stratum typicum*: Lower Tortonian.

*Locus typicus*: Korytnica, 24 km SSW of Kielce, Central Poland.

*Derivatio nominis*: *sanctacrucensis*—after the Holy Cross Mountains region.

*Diagnosis*.—Shell moderately extended vertically, covered with not very prominent ribs which are folds in character. Crown low, conical, almost flat. Ribs mostly do not reach the top which is covered only with fine, round warts. Radii slightly marked on the outside of the crown. Terga relatively narrow, with a short carinal margin and a wide, but slightly marked and short spur. Scuta with a strongly elongated and convex basal margin.

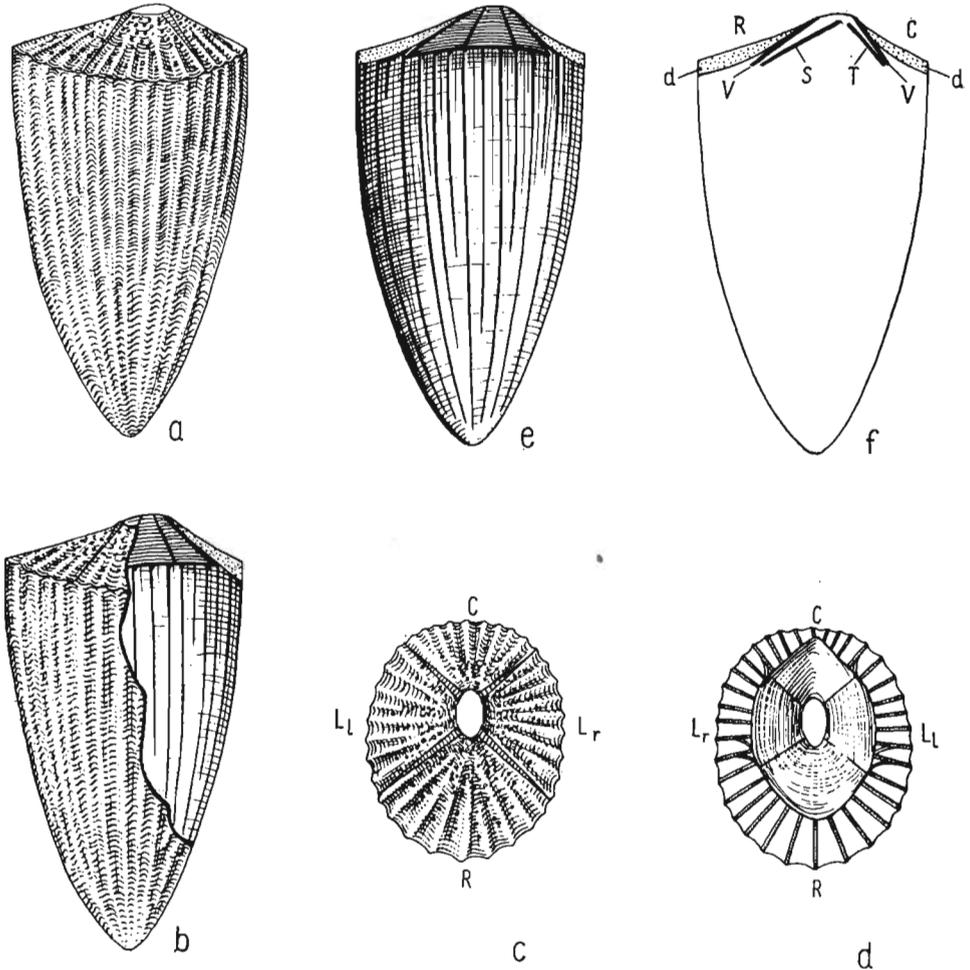


Fig. 1.—A schematic reconstruction of the shell of *Creusia sanctacrucensis* n. sp.,  $\times 5$ ; a entire shell from the outside, b interior partly uncovered, c crown from the outside (compartments: C carina,  $L_l$  left lateral,  $L_r$  right lateral, R rostrum), d crown from the interior (compartments signed as above), e interior of the shell, visible after cutting along the rostro-carinal plane (opercular valves not shown), f diagrammatic section along the rostro-carinal plane and situation of the opercular valves during the animal's life (V sheath, d septa, C carina, R rostrum, T tergum, S scutum).

*Material.*— The entire material worked out comes from the coralla of *Tarbellastraea reussiana* (Milne-Edwards & Haime). A total of about 60 specimens have been found and prepared to a varying extent. Due to the fragility of shells not a single specimen could be taken out in an undamaged state. Holotype (Pl. IV, Fig. 2; Pl. V, Fig. 2) has been established on the basis of the set of opercular valves. The remaining elements of shells, coming from different individuals, treated as paratypes, are presented in successive photographs (Pls. I—VI), whereas a general aspect of the entire shell, obtained on this basis, is depicted by a drawing (Fig. 1).

Dimensions (in mm):

	Average specimens (within limits of:)	Largest specimen
Shell height . . . . .	7.0 — 12.5	15.0
Crown height . . . . .	1.0 — 2.0	1.0
Crown length . . . . .	4.5 — 7.0	10.0
Crown width . . . . .	4.0 — 6.5	8.0

*Description.*— Shell short, cuplike in shape which was caused by a downward extension of basis. Crown very low, in some specimens almost flat, shaped like a wide cone with a uniformly inclined or slightly concave surface. The degree of elongation of basis in relation to its maximum diameter, corresponding to a maximum diameter of the crown, is variable and independent of the crown height. Consequently, the differentiation of shape between particular individuals is considerable (cf. Fig. 2) and the dimensions of shell — strongly varying (cf. a tabular list, above).

Basis varies from a V-shaped, broad, cuplike to an almost cylindrical slightly extended upwardly (Fig. 2). Sometimes, there occur small changes in particular individuals.

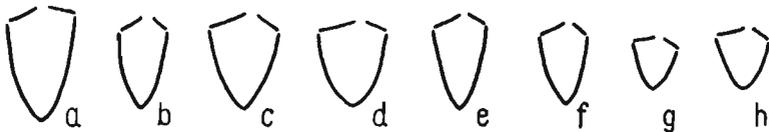


Fig. 2. — Individual variability of the shell morphology in *Creusia sanctacrucensis* n.sp.; longitudinal sections along the rostro-carinal plane (a—h), carina situated to the right; nat. size.

Crown slightly ovate, mostly elongated carino-rostrally (Pl. IV, Fig. 1) and, less frequently, almost round (Pl. V, Fig. 1). In some individuals, the outline of crown is here and there less regular (Pl. VI, Fig. 3c). At the same time, analogous irregularities occur in such individuals also in the basis and are visible in cross section.

Shell is covered with not very prominent, widely spaced ribs of a character of folds (Pl. IV, Figs. 1 and 3; Pl. VI, Fig. 1). Ribs are most prominent on the contact line of the basis and crown, marking the growth zone of the shell. The number of ribs on both parts of shell is identical, mostly amounting to about 30, in average specimens, and varying within limits of 27—35 and, less frequently, reaching about 40 which depends on the size of a specimen. Most ribs gradually vanish towards the lower part of the basis and towards the top of the crown. In addition, the entire crown is covered with fine warts which in the apical part, in the case of the disappearance of ribs, become the only morphological feature.

Of all the compartments, rostrum (R) is the widest and least sloping, whereas carina (C) is the steepest one (cf. Figs 1 and 3 in Pl. IV). Outside the crown, radii are only slightly marked, narrow (Pl. IV, Fig. 1; Pl. VI, Fig. 3c) or even almost completely disappear. Orifice is small, shaped like a thick lens, displaced from the middle of the crown towards the carina along the carino-rostral line, and situated somewhat obliquely to the horizontal level, higher on the side of carina and slightly descending towards the rostrum (Pl. IV, Fig. 1).

On the inside of the crown, both the sheath and septa are pronouncedly developed (Pl. I, Fig. 1; Pls. II and III; Pl. V, Figs. 1 and 3; Pl. VI, Fig. 2). Since it is steeper, the sheath considerably stands out from the inner side of the crown and approaches it only in the middle part of the carina, where it is sharply bent. Between the wall of the crown and the sheath, there occur septa, some of them projecting below the lower edge of sheath. These septa are not, however, fused to the edge of sheath which remains free and, in a way, hanging from the central parts of septa. This edge descends as a rule below the lower edge of the crown which in fact is caused by a relatively flat shape of the crown. Sutures in the sheath are very distinct and along them there are visible narrow alae (of carina and lateralia), gradually extending towards the top of the crown, becoming arcuate and disappearing in this place which causes the appearance of radii (Pl. III, Fig. 2). Growth ridges on the sheath incurve, close to sutures, towards the top of the crown.

Individual compartments of the crown are connected with each other by an ala being overlapped by a radius on the side of sheath and; afterwards, an arcuate ledge, bent towards carina and mostly reaching its nearest septum, continue from both processes (radius and ala). At the septum to which the ledge runs from the ala, there is developed a row of fine and sharp pectinate denticles. This row is enmeshed with an analogous row of thicker and distinctly macelike denticles which grow out on the extension of the ledge running from the radius and fused with the adjacent septum (Pl. V, Fig. 3). This extension is pronouncedly marked, on the external surface of the radius-bearing compartments, in

the form of an external radius (comp. Figs. 3 in Pls. IV and V). The external radius is, therefore, displaced in relation to the internal one towards carina to a distance, mostly equalling a double interseptal distance. This is a direct reason why the rostrum, that is, a compartment having radii on both its sides, reaches the largest width of all the compartments outside the crown (Pl. IV, Figs. 1 and 3). On the other hand, within the sheath, the parts of all the four compartments of the crown are almost identical and particular sutures divide the sheath into more or less equal quarters (Pl. I, Fig. 1; Pl. V, Figs. 1 and 3). Such a development of the radial portion which causes a distinct displacement of the position of the external part of the radius in relation to its internal part, deviates, therefore, from the conditions predominating, in this respect, in acorn barnacles in which both parts of the radius usually correspond to each other and enable the individualization of the radius as an almost independent part of a definite compartment. It should be emphasized that, despite such a modification, the arrangement of growth ridges of both sides of the radius remains in the specimens examined identical with that in acorn barnacles, i.e. parallel to the suture in the external part (cf. the right laterale, Pl. IV, Fig. 3) and slightly oblique to it in the internal part (Pl. V, Fig. 3). In the specimens under study, the denticles on the radius are more knoblike (Pl. V, Fig. 3) and seem to be more prominent than in common acorn barnacles.

Septa are uniformly covered with fine ridges, running parallel to the sheath, that is, obliquely to the wall of the crown. On the lower termination of septa the ridges are expressed in the form of fine denticles, often situated opposite each other on both sides of a given septum which causes — in such a way — a beaded feature of these terminations.

Particular septa run over the entire distance from the sheath to the wall of the crown and, resting on this wall, cause — in the place they contact it — bends in the form of folds. These are precisely the ribs visible on the outside of the crown and, thus, septa enter the internal parts of particular folds (ribs). Now, in turn, the lower ends of septa, detaching from the sheath and descending below it, enter analogous bends of the basis (Pl. III, Fig. 2) which on the outside of it occur as ribs which make up a continuation of the ribs of the crown. The bends of the basis, entered by the ends of septa, are of a character of narrow grooves which in a way are a trace of the gradual upward shifting of septa during the animal's growth. This type of the relation of septa to ribs determines the numbers of both of them as equal to each other. The newly formed septa, which are developing in the place where the sheath adheres to the wall of the crown, reach at once the growth zone of the shell and cause the formation of new folds (ribs) of the shell which are developed simultaneously in two directions, that is, towards the crown and towards the basis. New-yielding septa, however, do not

reach the lower edge of the sheath which is, usually, situated below the growth zone. As a result, only part of septa, i.e. the oldest of them (Pl. III, Fig. 2) project from below the sheath. On the other hand, the numbers of ribs on the shell are identical on the crown and on the basis and equalling the number of all septa.

Opercular valves, terga and scuta are free and do not display any traces of fusing together (Pl. IV, Fig. 2; Pl. V, Fig. 2 — holotype).

Terga are relatively narrow which is caused by the possessing of the carinal margin shorter than the scutal margin and by a considerable length of the basal margin between the spur and the basi-carinal angle. Both parts of the basal margin around the spur are slightly concave. Still less distinct is the concavity of the scutal margin. On the other hand, the carinal margin is pronouncedly convex and the apex is nearly sharp and slightly bent towards the scutal margin. Spur, comparatively wide, situated approximately one-third the distance from the basi-scutal angle, relatively slightly projects from the basal margin. The latter character is partly a result of an almost tangent contact of the basal margin and both sides of the spur at the very end of it. In the longitudinal furrow which runs from the spur to the apex, both lips are distinct, more prominent being the carinal lip which is slightly overhanging. The entire furrow is relatively shallow. Growth ridges are more distinct in the scutal part and towards the basal margin. On the internal side, there is visible a fairly wide articular furrow limited by a distinctly projecting and nearly sharp articular ridge which vanishes at less than one-third the distance from the basi-scutal angle. The longitudinal-furrow ridge is prominent and with a strongly protruding carinal edge which runs as far as the end of the spur. It is also visible that the scutal margin is framed with a narrow ledge and, together with it, slightly tucked up inwards. No distinct tergal depressor muscle crests are present. Scuta are relatively strongly elongated due to a considerable length and arcuate bent of the basal margin. The occludent margin is straight and slightly withdrawn near the apex. Tergal margin is very slightly convex, except close to the apex where this convexity is somewhat more distinct. Together with a slight recession of the occludent margin, this causes a more distinct accentuation of the apex. Growth ridges are very distinct and having the character of sharp ledges, inclined towards the apex and terminating in fine serratiform denticles. Occludent margin is denticulate, slightly bent in towards the inner side where it terminates in a distinct ridge. The denticles of the occludent margin represent a continuation of successive pairs of growth ridges. Articular ridge, prominent and slightly overhanging towards the tergal margin, descends at less than one-third the distance from the basitergal angle and, further on, rapidly disappears. Articular furrow is narrow, covered with fine ridges which make up a continuation of growth ridges of the outer surface which run obliquely

towards the apex. Adductor ridge starts slightly below the apex from which, strongly prominent and almost straight, it runs as far as the basal margin and contacts the latter almost half-way its length. Close to the basal margin, near which it disappears, the adductor ridge bends very slightly towards the rostral angle. The adductor muscle scar is mostly relatively poorly developed, although — in some specimens — it is very distinct (Pl. V, Fig. 2). Strongly elongated, it stretches over a considerable area close to the adductor ridge and, at both ends, terminates in a flat-oval manner which gives the entire scar an almost rectangular appearance. The lateral depressor muscle scar is, as a rule, very distinct and deep, sometimes even rimmed with a prosecting, very fine edge. It is semi-oval in outline and slightly elongated towards the basal margin it reaches. In some specimens, above the lateral depressor scar, there is developed a fine and narrow ridge whose trace continues, parallel to the tergal margin, towards the apex. In other specimens, the area between the occludent margin and adductor ridge is slightly uneven and, in a way, swollen.

A pigmentation of the shell is a characteristic feature, preserved in all specimens (cf. Pl. IV and Pl. VI, Figs. 1, 3c). It is expressed in the presence of darker transverse stripes, greyish-violet, blueish-cherry or

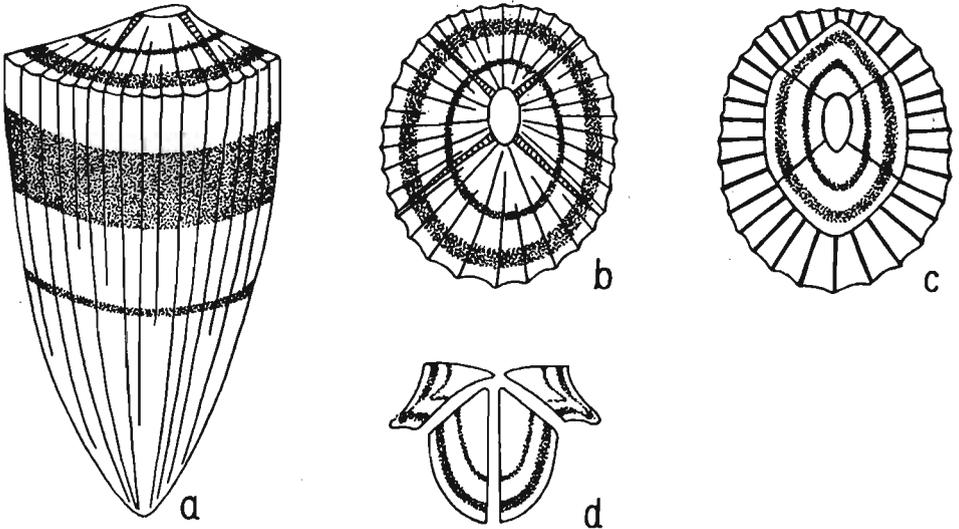


Fig. 3.—Pigmentation of the shell in *Creusia sanctacrucensis* n.sp. presented by an individual bearing the same pattern of coloured stripes  $\times 6$ ; a entire shell, b crown from the outside, c crown from the interior, d opercular valves.

slightly pinkish in colour, distinctly contrasting with the whitish shell. The width of the stripes is varying in individual specimens, the same of their number which may reach 4—5, but usually 2—3 stripes are most distinctly marked. In specimens with preserved fragments of all parts

of the shell, it is visible that the intensity of colouration, width and succession of individual stripes are identical on the basis, on the external side of the crown, on the sheath (where they are slightly brighter) and on the opercular valves (Fig. 3). As may be judged by faded colour traces, originally these stripes were probably cherry-coloured or purple, like in many Recent *Creusiinae*. In extant forms, however, the colouration of the shell is rather uniform, without any definite pattern (Darwin, 1854a; Hiro, 1935). In a fossil state, the traces of pigmentation were recorded by Darwin (1854b, p. 36) in the Pliocene *Creusiinae* and by Sakakura (1934) — in the Pleistocene *Creusiinae*. On the other hand, they were never observed in the Miocene forms. The pigmentation, preserved in the species under study is not anything peculiar in the Korytnica deposits, since it occurs in many specimens of other fossils, mostly gastropods.

*Remarks.* — The described species *Creusia sanctacrucensis* n. sp. differs from all other representatives of the genus *Creusia* in its ribbing, as well as in the shape and morphology of opercular valves.

#### REVISION OF MIOCENE SPECIES OF THE GENUS *CREUSIA*

As it has already been mentioned above, the knowledge of individual species of *Creusia*, occurring in the Miocene of Europe (in the Miocene, they are known only from this continent), is very inaccurate and their nomenclature considerably varying. Of the works, referred to above, which display a sufficient degree of reliability, only two dealt with the forms from the Miocene of Europe. These are monographs by Seguenza (1876) and Procházka (1893). Revising the Miocene *Creusiinae*, one may base the considerations on these authors' documentation.

Of the forms, described by Seguenza (1876) as pyrgomas, an actual value may be ascribed to the species *Creusia costata* (Seguenza) and *C. multicostata* (Seguenza). The remaining forms (one species and two varieties) are not fit to any detailed specific determination (see p. 483).

Of five new species, described by Procházka (1893) the following three are of a true value: *Creusia sturi* Procházka, *C. miocaenica* Procházka and *C. darwiniana* Procházka. The remaining two species, as pointed out by de Alessandri (1910), are identical with the above mentioned species described by Seguenza (1876) whose work was unknown to Procházka.

The subsequent species of the creusoid barnacle has a rather long history. It was erected by Kramberger-Gorjanović (1889a) who gave it a specific name of *costata* Kramberger-Gorjanović and considered it as a new species of hippurites. It is true that this author, after getting to know Seguenza's (1876) work he did not know originally, have soon corrected his error, finally (Kramberger-Gorjanović, 1889c) assigning his species to cirripeds and to the genus *Creusia*. On the other hand, Kram-

berger-Gorjanović, considering Seguenza's species to be a pyrgoma, did not believe the specific name he introduced to be an actual junior homonym. Soon, it brought about a complete entanglement and confusion in the synonymy not only of both these species given the identical name, but also of other species of Seguenza and Procházka which we discuss in detail below. The present authors (Bałuk & Radwański, 1967a) have applied to this species a new name of *Creusia krambergeri* Bałuk & Radwański.

All these six species, referred to above, close the list of actual species of *Creusia* from the Miocene of Europe which are known so far. All others previously distinguished, are either contained within the synonymy of these six species, or are not suitable for the specific determination, although they undoubtedly belong to the genus under study. A correct synonymy of these six species, arranged according to the order of their erection, is presented below. The occurrence of other Creusiinae in the Miocene will be discussed at the end.

On the other hand, forms that cannot really be assigned to Creusiinae, which has already been pointed out by other authors, will be omitted from discussion. Here belong such forms as, "pyrgomas" from the Miocene of Aquitaine, described by de Alessandri (1922) and whose erroneous nature was shown by Withers (1929); some forms, mentioned long ago by Michelotti (*vide* Darwin, 1854b) which were called in question by de Alessandri (1894, p. 247) about their being cirripeds at all; finally, there was also an enigmatic structure from the Sarmatian of Hungary, described as resembling pyrgomas and figured by Kolosváry (1949, Fig. 4) who called it *Andromacheia Noszkyi* n.gen., n.sp.foss., also later mentioned by this author (Kolosváry, 1951a), although recently omitted from the list of Hungarian balanids (Kolosváry, 1959) and which also arouses doubts about its being a cirriped at all. Similar doubts are also aroused by forms, previously mentioned by Mayer (1872) from the Alpine molasse.

#### 1. *Creusia costata* (Seguenza, 1876)

This species has been erected by Seguenza (1876) who figured some fragments of its shells as well as the entire scuta. Its terga were illustrated by Procházka (1893) who, not knowing Seguenza's work, once more described analogous forms as a new species whose synonymy with that erected by Seguenza was pointed out by de Alessandri (1910).

The structure of crown and the shape of opercular valves, stated either by Seguenza (1876), or Procházka (1893) and subsequent authors, indicate that this species belongs to the genus *Creusia*.

This species is widely distributed in the European Miocene (cf. items, cited below in the synonymy). Forms described by Seguenza came from deposits he considered to be Pliocene which, stratigraphically, have not been definitely solved so far (cf. below).

Under the name of "*Pyrgoma costatum* Seguenza", this species was mentioned only from Italy (Seguenza, 1876; de Alessandri, 1894, 1906), whereas from other countries, it was cited as either other, or new species. The illustrations, enclosed in the papers discussed, indicate that these are undoubtedly identical forms. The synonymy of this species is as follows:

1866. *Creusia Rangii*; C. des Moulins, Liste des..., p. 302 (nom. dubium).  
 1876. *Pyrgoma costatum* Seguenza; G. Seguenza, Recherche..., Pl. 2, Figs. 5, 5 a-c (non Fig. 5d).  
 1893. *Creusia moravica* n.sp.; V. J. Procházka, O zkamenelych..., Pl. 2, Fig. 2 a-e.  
 1894. *Pyrgoma costatum* Seguenza; G. de Alessandri, Contribuzione..., Pl. 2, Fig. 3.  
 1906. *Pyrgoma costatum* Seguenza; G. de Alessandri, Studi monografici..., Pl. 18, Fig. 24 (non Fig. 23).  
 1910. *Pyrgoma* cf. *anglicum* Sow.; G. de Alessandri, Die Cirripedier..., Pl. 48, Fig. 15 a-b (non Fig. 14).  
 1922. *Pyrgoma Rangii* (Des Moul.); J. Duvergier, Note complémentaire..., Fig. in p. 228.  
 1929. *Creusia rangi* des Moulins; T. H. Withers, The phylogeny..., Pl. 11, Fig. 3c, 4.  
 1949. *Creusia spinulosa* forma *praespinulosa* n.f. foss.; G. Kolosváry, New balanids..., Fig. 5 (non Figs. 2—3).  
 1957. *Creusia rangei* des Moulins; L. Bogsch, Eine fossile..., Figs. 4—5.  
 1962. *Creusia spinulosa* Leach forma *praespinulosa* Kolosváry; G. Kolosváry, Balanids..., Pl. 1, Fig. 12; Pl. 3, Fig. 2.  
 1962. *Creusia spinulosa* Leach forma *kojumdgievae* n.f.; G. Kolosváry, *Ibid.*, Pl. 1, Figs. 9—11; Pl. 2, Fig. 21.  
 1962. *Creusia rangi* (Desmoulins); G. Kolosváry, *Ibid.*, Pl. 3, Fig. 6.

The discussion of the synonymy, listed above and of the views, expressed in particular items, cited in this synonymy, is a rather thankless task. The observation of Duvergier that French collections include specimens, determined — after des Moulins (1866) — as "*Creusia Rangii*" was a primary fact which contributed to a complete confusion in this synonymy. "*Creusia Rangii*" is, however, nomen dubium or, as results from Duvergier's information, also nomen in collectione. Duvergier himself was not quite certain of the taxonomic value of this name and, at first, he asked Professor de Alessandri for an opinion on this problem, sending the latter a few French specimens. De Alessandri (*vide* Duvergier, 1922) stated that the specimens sent in are identical with the Italian "*Pyrgoma multicostatum* Seguenza". Now, it is difficult to make sure which specimens were actually sent to de Alessandri. It remains a fact, however, that, soon after de Alessandri's death, Duvergier (1922, Fig. in p. 228) illustrated the opinion, referred to above, with specimens undoubtedly different from *Creusia multicostata* (Seguenza) and identical with the forms "*Pyrgoma costatum*" of Seguenza and "*Creusia moravica*" of Procházka which are synonymic, as it has previously been confirmed by de Alessandri (1910) and which are different from the species *Creusia multicostata* (Seguenza), discussed below. Thus, Duvergier did not reject nomen dubium *Creusia Rangii* des Moulins but, moreover, he

accepted it as a priority name in relation to the name of "*Pyrgoma multicostata* Seguenza" and he illustrated it with another species — *Creusia costata* (Seguenza). This led to the confusion of concepts, concerning a few species of *Creusia*. Soon, Duvergier's error was repeated by Withers (1929) who, under the name of *Creusia rangi* des Moulins, illustrated the specimens undoubtedly identical with *Creusia costata* (Seguenza) but, at the same time, he placed the species "*Pyrgoma multicostata* Seguenza" in the synonymy. Withers, considering the synonymy he accepted to be absolutely sure and attaching no importance to original statements of previous authors, ascribed (1929, p. 563) the view on the identity of "*Pyrgoma rangi*" with "*Pyrgoma fuchsi*" to de Alessandri (1910, p. 126), although the latter expressed, on the page cited, the view on the identity of "*Pyrgoma multicostatum*" with "*Creusia Fuchsi*" and did not mention "*Pyrgoma rangi*" at all. Duvergier's (1922) and Withers' (1929) erroneous synonymy was later repeated by Abel (1935), Kolosváry (1949, 1959) and Bogsch (1957) who, at the same time, became confused as to the problem of a mutual relationship between *Creusia rangii* des Moulins and *Creusia costata* (Seguenza). It is true enough that these authors correctly identified these species with each other but, unfortunately, they erroneously identified them simultaneously with *Creusia multicostata* (Seguenza) and, at the same opportunity, also with the species *costata*, described by Kramberger-Gorjanović (1889a), which is quite different from all species, referred to above and, in this number, from the identically called *costata* Seguenza. As a matter of fact, Kramberger-Gorjanović (1889c) was himself aware of the difference between his species *costata* and the same named species *costata* Seguenza (cf. below).

Of the forms we have included in the synonymy of the species *Creusia costata* (Seguenza), an explanation is only required by small forms, described by Kolosváry (1962) as *Creusia spinulosa* Leach forma *kojumdgievae* Kolosváry and which really represent juvenile individuals of the species under study.

## 2. *Creusia multicostata* (Seguenza, 1876)

This species has been erected by Seguenza (1876) who figured complete shells, as well as terga and scuta.

Both the structure of crown and the shape of opercular valves, stated by Seguenza (1876), Procházka (1893) and subsequent authors, indicate this species belongs to the genus *Creusia*. Procházka (1893), not knowing — as it has already been mentioned above — Seguenza's work, once more described identical forms as a new species which was already pointed out by de Alessandri (1910).

This species is widely distributed in the European Miocene (cf. items, cited in the synonymy). Its synonymy is as follows:

1876. *Pyrgoma multicostatum* Seguenza; G. Seguenza, Ricerche..., Pl. 2, Figs. 7, 7 b-f (non Fig. 7a).
1893. *Creusia Fuchsi* n. sp.; V. J. Procházka, O zkamenelych..., Pl. 2, Fig. 1 a-d.
- ?1894. *Pyrgoma multicostatum* Seguenza; G. de Alessandri, Contribuzione..., Pl. 2, Fig. 2.
1906. *Pyrgoma multicostatum* Seg.; G. de Alessandri, Studi monografici..., Pl. 18, Figs. 15—22.
1928. *Pyrgoma costatum* Seguenza; O. Abel, Parasitische..., Fig. 1.
1935. *Creusia multicostata* Seguenza; O. Abel, Vorzeitliche..., Fig. 444 (the same as Abel, 1928, Fig. 1).
1949. *Creusia spinulosa* forma *praespinulosa* n.f. foss.; G. Kolosváry, New balanids..., Figs. 2—3 (non Fig. 5).
1952. *Pyrgoma multicostatum* Seg.; S. Charalambakis, Contribution..., Pl. 9, Fig. 2.
- ?1962. *Creusia spinulosa* Leach forma *cladangiae* Kolosváry; G. Kolosváry, Balanids..., Pl. 1, Fig. 13; Pl. 3, Fig. 4.

In view of the inaccuracy of illustrations, a few of the forms, named above, cannot be assigned here without any reservation. The same might apply to Charalambakis' (1952, Pl. 9, Fig. 2) illustration itself but, by the courtesy of Prof. M. K. Mitzopoulos (Athens), the present writers had the opportunity to examine this specimen which turned out to be identical with those of Seguenza.

The forms, mentioned as "*Pyrgoma multicostata* Seg." by previous Hungarian authors (Vadász, 1919; Noszky, 1925), most probably belong to the species under study. On the other hand, here do not belong the forms, determined as "*Pyrgoma multicostatum*" or included under this name to the synonymy by Duvergier (1922), Withers (1929), Abel (1935, the text in p. 535) and Kolosváry (1949, 1959) which actually represent, as mentioned above, *Creusia costata* (Seguenza) or the species "*costata*", described by Kramberger-Gorjanović (cf. below p. 480).

### 3. *Creusia sturi* Procházka, 1893

This species has been erected by Procházka (1893) who figured complete shells, as well as terga and scuta, thus correctly identifying on this basis its being a species of the genus *Creusia*. It occurs in Moravia, in the Vienna Basin and in Styria from where it was described by Procházka (1893). It is mentioned only by Procházka:

1893. *Creusia Sturi* n. sp.; V. J. Procházka, O zkamenelych..., Pl. 1, fig. 1 a-r.

and only these forms may be referred to the species under study since no other similar ones have ever been illustrated so far.

### 4. *Creusia miocaenica* Procházka, 1893

This species has been erected by Procházka (1893) who illustrated complete shells and scuta and who correctly identified it as belonging to the genus *Creusia*. The terga of this species were figured by the present writers (Bałuk & Radwański, 1967a).

This species occurs in the Vienna Basin and in Croatia (Procházka, 1893; Bałuk & Radwański, 1967a). Its synonymy is as follows:

1893. *Creusia miocaenica* n. sp.; V. J. Procházka, O zkamenelych..., Pl. 2, Fig. 3 a-d.  
 1910. *Pyrgoma* cf. *anglicum* Sow.; G. de Alessandri, Die Cirripedier..., Pl. 48, Fig. 14 (non Fig. 15 a-b).  
 1967. *Creusia miocaenica* Procházka; W. Bałuk & A. Radwański, Genus *Creusia*..., Fig. 1; Pls. 1—2.

### 5. *Creusia darwiniana* Procházka, 1893

This species has been erected by Procházka (1893) who figured complete shells and correctly assigned it to the genus *Creusia*. Opercular valves were never recorded. This species was mentioned only by Procházka:

1893. *Creusia darwiniana* n. sp.; V. J. Procházka, O zkamenelych..., Pl. 2, Fig. 4 a-g. and only these forms may be assigned to it. It occurs only in Styria (Procházka, 1893).

### 6. *Creusia krambergeri* Bałuk & Radwański, 1967<sup>3</sup>

Forms, assigned to this species have been described and figured by Kramberger-Gorjanović (1889a) as a new genus and species of hippurites, *Ceratoconcha costata*. This author, on getting to know Seguenza's (1876) work, stated that the species actually belongs to cirripeds and determined it first (Kramberger-Gorjanović, 1889b) as a species of the genus *Pyrgoma* and then (Kramberger-Gorjanović, 1889c) — correctly — as that of the genus *Creusia*. Considering the genus *Creusia* as a separate from *Pyrgoma*, Kramberger-Gorjanović (1889c) was aware of the distinction of his species „*Creusia costata* (Kramberger-Gorjanović)” in relation to “*Pyrgoma costatum* Seguenza”.

Taking into consideration the fact that both these species, i.e. *costata* Seguenza 1876 and *costata* Kramberger-Gorjanović 1889, are actually those of the genus *Creusia* and, therefore, are homonymic, whereas Kramberger-Gorjanović's (1889a) name — as a junior homonym — must be rejected, the present writers (Bałuk & Radwański, 1967a) introduced for the specimens, illustrated by Kramberger-Gorjanović, a new specific name of *Creusia krambergeri* Bałuk & Radwański.

Two specimens, illustrated by Kramberger-Gorjanović (1889a) from Croatia, are the only and sole specimens which may be assigned to this species. Opercular valves have never been recorded. The better preserved one of these two specimens (Kramberger-Gorjanović, 1889a, Pl. 1, Fig. 1) was many times presented in different works as an example of fossil “pyrgomas” (*Creusiinae* sensu the present authors') and, in fact, named

<sup>3</sup> Bałuk & Radwański (1967a).

by different names (Stromer v. Reichenbach, 1912; Abel, 1920; Dacqué, 1921; Termier & Termier, 1953). Some of the authors cited (Termier & Termier, 1953, Fig. 19; Ziegler, 1963, Fig. 29h), at this opportunity, modified the illustration, thus losing the similarity to the original (cf. discussion in Bałuk & Radwański, 1967a).

The species under study, i.e. *Creusia krambergeri* Bałuk & Radwański, was described, illustrated (explained with a reproduced illustration), or discussed as follows:

1889. *Ceratoconcha costata* Kramb.-Gorj.; D. Kramberger-Gorjanović, Über einen..., Pl. 1, Figs. 1—2.
1889. *Pyrgoma (costata)* Kramb.-Gorj.; D. Kramberger-Gorjanović, Berichtigung bezüglich..., p. 142.
1889. *Creusia costata* (Kramb.-Gorj. non *Pyrgoma costatum* Seguenza); D. Kramberger-Gorjanović, Berichtigung zu..., p. 231.
1893. *Creusia costata* Kramb.-Gorj.; V. J. Procházka, O zkamenelych..., p. 19.
1912. *Pyrgoma costata* Kramberger; E. Stromer v. Reichenbach, Lehrbuch..., Fig. 232 D.
1920. *Pyrgoma costata* Kramb.; O. Abel, Lehrbuch..., Fig. 136 (nach Stromer).
1921. (Balanidenkrebs, *Pyrgoma*); E. Dacqué, Vergleichende..., Fig. 91 B (aus Gorjanović-Kramberger).
1926. *Creusia costata* (Kramberger-Gorjanović) non *Pyrgoma costatum* Seguenza; T. H. Withers, Barnacles..., p. 5.
1928. *Pyrgoma costatum* Seg. = *P. costatum* Kramb.-Gorj.; O. Abel, Parasitische..., pp. 13—38.
1935. *Creusia multicostata* Seguenza = *Pyrgoma costatum* (Kramberger-Gorjanović, nec non Seguenza); O. Abel, Vorzeitliche..., p. 535.
1949. *Creusia Rangii* (des Moul.) = *Pyrgoma multicostatum* Seguenza = *Pyrgoma costatum* Gorjanović-Kramberger; G. Kolosváry, New balanids..., p. 111.
1953. *Pyrgoma costata* Kramberger; H. Termier & G. Termier, Sous-classe..., Fig. 19 (d'après Gorjanović-Kramberger) (erroneously modified picture!).
1957. *Creusia rangei* des Moulins; L. Bogsch, Eine fossile..., p. 29.
1960. *Creusia costatum* (Gorjanović-Kramberger); H. K. Brooks & A. Ross, *Pyrgoma*..., p. 362.
1967. *Creusia krambergeri* sp.n.; W. Bałuk & A. Radwański, Genus *Creusia*..., p. 145, Fig. 2 (after Kramberger-Gorjanović, 1889a, Pl. 1).

The complex synonymy of this species results from the previously discussed fact of including erroneously by some authors (Abel, 1935; Kolosváry 1949; Bogsch, 1957) the species "*costata* Kramberger-Gorjanović" into the species "*rangii* des Moulins" which in fact is otherwise taxonomically invalid. As a result, through an erroneous synonymy of the species "*rangii* des Moulins", the species "*costata* Kramberger-Gorjanović" was identified (Abel 1935, Kolosváry 1949) with *Creusia multicostata* (Seguenza), the problem of the priority name being in fact variously interpreted (cf. synonymy).

Independently of these facts, there existed another cause of further errors which resulted from the existence of two homonymic species, i.e. *costata* Seguenza, 1876 and *costata* Kramberger-Gorjanović, 1889. Only Kramberger-Gorjanović (1889c) himself and Withers (1926) were

aware of the separateness of these species and these two authors considered them to belong to two separate genera, *Pyrgoma* and *Creusia* resp. The subsequent authors, who in fact did not accept the separateness of these genera and called a single genus by the name of either *Pyrgoma* or *Creusia*, became completely confused and did not understand that within thus understood genus there are in fact two homonymic species, one of which being a junior homonym (Abel, 1920, 1928, 1935; Kolosváry, 1949; Termier & Termier, 1953; Brooks & Ross, 1960). Consequently, both these species were either identified with each other (Abel, 1928, 1935), or — for unknown reason — Kramberger-Gorjanović was considered to be the author of an only taxonomically correct specific name of “*costata*” (Stromer v. Reichenbach, 1912; Abel, 1920; Termier & Termier, 1953; Brooks & Ross, 1960).

#### SPECIFICALLY INDETERMINABLE FORMS OF *CREUSIA*

The specific assignment of several forms, illustrated from the European Miocene, is indeterminable. Most of them, as indicated by the illustrations enclosed in papers, undoubtedly belong to the genus *Creusia*. These are primarily numerous forms from the Vienna Basin, described by Abel (1927, 1928) who gave them a new generic and specific name of *Paracreusia Trolli*. The material, presented by Abel (bases and crowns viewed from the inside), do not allow one to determine any species and all the more to erect a new species and genus. In addition, the characters of the new species are rather vaguely described by Abel who, at the same time, erected a new genus on the basis of the presence of growth ridges occurring on the inner side of the crown (sheath), that is, on the basis of a character which occurs in all the Balanidae (sic!). As a matter of fact, the genus “*Paracreusia* Abel” was soon questioned by Withers (1929), as well as by Hiro (1938, p. 414) and Krüger (1940, p. 452). All these forms, described by Abel may be determined only as *Creusia* sp. which also applies to certain specimens, later excluded by Abel himself (1935, p. 535) from his “*Paracreusia Trolli*” (specimens from Lapugy and Forsttechnau).

Specifically indeterminable are also certain specimens, illustrated and given different names by Kolosváry (1949, Fig. 1; 1962, Pl. 2, Fig. 22; Pl. 3, Fig. 3), the first of which (Kolosváry, 1949, Fig. 1) is even a holotype of a new taxon — *Creusia spinulosa* forma *cladangiae* n.f.foss. All these specimens also may be determined only as *Creusia* sp.

The localities, from which the discussed specimens have been recorded, are shown in the map which presents the distribution of the genus *Creusia* as an entity in the European Miocene (Fig. 7). This map also contains a locality in the environs of Marseilles, mentioned by Gourret (1890), although it is not absolutely sure to concern *Creusia* (cf. p. 483). On the other hand, several Italian sites are omitted which were mentioned

by Seguenza (1876) and de Alessandri (1894, 1906), since the age of findings is rather debatable (Miocene, Pliocene or even Pleistocene) and the Creusinae forms, found there, difficult to identify. If de Alessandri (1894) determined certain newly found forms as one of "pyrgomas", discussed below, Seguenza (1876) erected several new taxons which, as a matter of fact, were never recorded later by any other authors. Forms, illustrated by Seguenza as:

*Pyrgoma costatum* var. *elargatum* Seg. (Seguenza, 1876, Pl. 2, Fig. 5d; the same specimen *vide* de Alessandri, 1906, Pl. 18, Fig. 23 as *P. costatum*),  
*Pyrgoma multicostatum* var. *latum* Seg. (Seguenza, 1876, Pl. 2, Fig. 7a),  
*Pyrgoma diploconus* Seg. (Seguenza, 1876, Pl. 2, Figs. 6 and 6a), and  
*Pyrgoma costatum* Seg. (Seguenza, 1876, Pl. 10, Fig. 23) — are not suitable for identification. All these specimens were irretrievably lost for science during the earthquake at Messina in 1908 (Dr. M. A. Moroni Ruggieri's communication).

Forms, mentioned by older Austrian authors as pyrgomas (Hilber, 1877, 1878; Toula, 1882; R. Hoernes, 1884, *fide* Procházka 1893) were already identified by Procházka (1893) as individual species of *Creusia*.

#### PROBLEM OF A SHAM OCCURRENCE OF *PYRGOMINA ANGLICA* (SOWERBY) IN THE MIOCENE

The Recent species *Pyrgomina anglica* (Sowerby, 1823) was described in the fossil state from the English Pliocene by Darwin (1854b) and Withers (1926), as well as from the Pleistocene of Japan (Sakakura, 1934). It results from these authors' studies (*vide* also Withers, 1929; Krüger, 1940, p. 485) that this species does not occur in formations older than the Pliocene.

The recording of *Pyrgomina anglica* (Sowerby) by de Alessandri (1894, 1906, 1910, 1922) in the Miocene most probably departs from truth. Formerly illustrated forms (de Alessandri, 1894, Pl. 3, Fig. 11; 1906, Pl. 18, Fig. 14) are unfit for identification. They represent rather some creusoid barnacle and are surely different than *Pyrgomina anglica*. Specimens, illustrated as conformis (de Alessandri, 1910, Pl. 48, Figs. 14 and 15) belong to *Creusia* (cf. previous synonymies). Later illustrated specimens (de Alessandri, 1922, Pl. 1, Fig. 3) actually belong — as shown by Withers (1929) — to acorn barnacles. Probably to *Creusia* belong also the forms mentioned by Gourret (1890).

Thus, no obvious facts have so far been presented which might testify to the occurrence of the species *Pyrgomina anglica* (Sowerby) in the Miocene, the same as of any other species which might be assigned to the genera *Pyrgomina* or *Pyrgoma*. In the present writers' opinion, in the light of the data available so far, these genera do not occur in both the European and extra-European Miocene.

## TAXONOMY OF CREUSIINAE

The taxonomy of Creusiinae, we present below, comprises both Recent and fossil forms, assigned to this subfamily and properly documented in literature. All forms which, following the suggested taxonomy and the revision, presented above, may be assigned to these genera, have been taken into account in examining *Creusia* Leach and *Pyrgomina* Bałuk & Radwański. Only the most important species have been discussed in an exemplary manner for the genus *Pyrgoma* Leach which represents only recent forms.

Genus *Creusia* Leach, 1817  
Subgenus *Creusia* sensu stricto

Crown consisting of 4 compartments (Fig. 8b), terga and scuta free and of the *Balanus* type. The Miocene species are:

- Creusia* (*Creusia*) *costata* (Seguenza, 1876)
- C.* (*Creusia*) *multicostata* (Seguenza, 1876)
- C.* (*Creusia*) *sturi* Procházka, 1893
- C.* (*Creusia*) *miocaenica* Procházka, 1893
- C.* (*Creusia*) *darwiniana* Procházka, 1893
- C.* (*Creusia*) *krambergeri* Bałuk & Radwański, 1967<sup>4</sup> and
- C.* (*Creusia*) *sanctacrucensis* n. sp.

Two of these species, *Creusia costata* and *C. multicostata*, were also recorded from Pliocene deposits (Seguenza, 1876; de Alessandri, 1894, 1906; Charalambakis, 1952) but, in view of the uncertainty of the stratigraphical position of the outcrops in Italy and Attica where these specimens came from, this problem cannot be considered as definitely explained. These findings may, for the time being, be generally determined as Mio-pliocene without a preclusion of a possibility of their Miocene age. In the general list (Fig. 7), they have been included in the remaining Miocene findings.

*Creusia* (*Creusia*) *prefloridana* (Brooks & Ross, 1960),

is a Pliocene species well characterized by Brooks & Ross (1960) from the Pliocene (*vide* Ross & Newman, 1967) of Florida and corresponding to the diagnosis of the genus *Creusia*. On the other hand,

“*Creusia spinulosa* Leach, 1824” and  
*Creusia* (*Creusia*) *floridana* (Pilsbry, 1932)

are Recent species, the former of which, including forms with a various sculpture, as well as a various morphology and structure of opercular valves, is suitable for a separate revision which has already been suggested by Darwin (1854a).

<sup>4</sup> Bałuk & Radwański (1967a).

All the other species or forms which have been reported from the European Miocene, either are to be included into the synonymy of the above discussed species or they cannot be determined specifically (*Creusia* sp.).

Subgenus *Withersia* n. subgen.

Rostral sutures in a four-compartment crown are very indistinct or even disappearing in particular species of a given population; terga and scuta free, of the *Balanus* type, although seeming to display a stronger manner of junction than that in typical forms of the genus *Creusia*, which makes possible their preservation in the undisjoining form (*vide* Withers, 1926). Here belong well characterized and accurately described species,

*Creusia* (*Withersia*) *barbadensis* Withers, 1926 and  
*C.* (*Withersia*) *oulastreae* (Utinomi, 1962)

the former of which, considered by the present writers as typical of the new subgenus, is a Pleistocene species from the Barbados Island (Withers, 1926) and the latter — a Recent species (Utinomi, 1962).

Genus *Pyrgomina* Bałuk & Radwański, 1967<sup>5</sup>

Crown built of two compartments (Fig. 8c), playing a role analogous to carina and rostrum<sup>6</sup>, terga and scuta free, of the *Balanus* type. The following fossil species from the Pliocene of the Crete Island is a type species of the genus, erected by the present writers (Bałuk & Radwański, 1967b):

*Pyrgomina sequenzai* Bałuk & Radwański, 1967

in addition to which a species, first described among Recent forms, i.e.

*Pyrgomina anglica* (Sowerby, 1823)

has been included by the present writers (Bałuk & Radwański, 1967b) in the genus under study.

The latter species described by Sowerby (1823) was earlier known as "*Adna anglica* Leach" (nom. in coll. — *vide* Sowerby, 1823) which caused

<sup>5</sup> Bałuk & Radwański (1967b).

<sup>6</sup> In the light of the ontogeny of certain pyrgomas (Utinomi, 1943) this rostrum („R" in Fig. 8c) should be interpreted as R+2L, fused together. Analogously, we may consider the shell of the genus *Pyrgoma* Leach to consist of at least C+R compartments, fused together. Most probably, 2L may also be parts of this shell. However, it is difficult to state whether or not this supposition is correct in the case of all pyrgomas. On the other hand, it should be pointed out that the diagrams of the structure of the shell in *Pyrgoma* in use so far are erroneous. In Withers' (1928, Fig. 52) presentation, repeated with a slight modification by Krüger (1940, Fig. 36), there is visible a single compartment with a suture in a position corresponding to a half of the rostrum; on the other hand, in Pilsbry's illustration (1916, Fig. 5), repeated with a significant modification by Davadie (1963, Fig. 5), there are visible four vestigial compartments, two of which are in C and R positions, but the remaining — in those of the rostrolateral (RL) compartments, never observed by any author and in any *Creusiinae*.

that both in previous years and even most recently (e.g. Moyse, 1961), Leach was considered to be the author of this species. In the light of the discussion, precluded above, there are no arguments testifying to the occurrence of this species in the Miocene from which it was mentioned several times. Doubts are also aroused by some specimens of this species, found in younger formations. It was mentioned from the Pliocene by Darwin (1854b), Seguenza (1876), de Alessandri (1894, 1906) and Withers (1926) but only the specimens, illustrated by the latter author (Withers, 1926, Pl. 1, Figs. 1, 2) were identical with Recent ones. The specimen, illustrated by Darwin (1854b, Pl. 2, Fig. 7a) differs from all illustrations of Recent forms of *Pyrgomina anglica* (Sowerby) and, according to the present writers, it probably does not belong to this species. It has already been pointed out by Darwin (1854a) that specimens from the Pliocene of England are larger and differ in their habitat (completely embedded in coralla) from the Recent ones. All specimens from the Pliocene of England recorded by Darwin, require revision. The same is true of Italian forms which, in addition, occur in the formations of a rather vague stratigraphic position. It is also difficult to take a firm view, concerning Pleistocene findings of this species, described by de Alessandri from Italy. On the other hand, it is quite certain that it occurs in the Pleistocene of Japan (Sakakura, 1934).

It is equally difficult to form an opinion as to the occurrence of the species, described by Darwin (1854a) as "*Pyrgoma Stokesii*" since Darwin's illustration does not allow to solve this problem. The specimen he illustrated considerably differs from the well-known illustrations (Sowerby, 1823; Darwin, 1854a; Withers, 1926; Hiro, 1935) of the species *Pyrgomina anglica* (Sowerby), although Darwin claimed a considerable similarity of both these species and even contemplated the advisability of separating them. The presence of carinal sutures in this species was stated by Withers (1926).

#### Genus *Pyrgoma* Leach, 1817<sup>7</sup>

Crown indivisible (in fact built of a single compartment, Fig. 8d), terga and scuta distinctly modified and displaying a different degree of fusing which justifies the division of the genus into three subgenera.

#### Subgenus *Pyrgoma* sensu stricto

Terga and scuta free but clearly modified and departing from the *Balanus* type. Among other species, *Pyrgoma cancellatum* Leach, which is

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<sup>7</sup> In regard to grammar, the name *Pyrgoma* is of a neuter gender, which was observed by Darwin (1854a, b) and most of his successors and which was not accepted by Leach and some of later authors who considered this name to be of a feminine gender like *Creusia*, *Daracia*, *Nobia*, etc. and like *Pyrgomina* and *Withersia* erected by the present writers.

a type species of the genus, belongs to this group. Only the following Recent species (Sowerby, 1823; Darwin, 1854a; Hiro, 1935, 1938) are known:

- Pyrgoma (Pyrgoma) cancellatum* Leach, 1824  
*P. (Pyrgoma) crenatum* Sowerby, 1823  
*P. (Pyrgoma) milleporae* Darwin, 1854 and  
*P. (Pyrgoma) dentatum* Darwin, 1854.

#### Subgenus *Nobia* Sowerby, 1839

Terga and scuta fused together, forming a pair of tergoscutal valves with a discernible outline of the tergal and scutal parts. Sowerby and not Leach was the author of this subgenus which was explained by Darwin (1854a, a footnote on p. 354). Leach used this name in an unpublished manuscript and even Sowerby himself referred to it.

In addition to typical forms without the traces of any sutures on the sheath (Darwin, 1854a; Hiro, 1935) such as:

- Pyrgoma (Nobia) grande* (Sowerby, 1839),

within the subgenus, including Recent species, there also occur species having slight traces of two sutures on the sheath (Darwin, 1854a; Hiro, 1934, 1935), as:

- Pyrgoma (Nobia) conjugatum* Darwin 1854 and  
*P. (Nobia) orbicellae* Hiro, 1934,

as well as that with the traces of four sutures on the sheath (Annandale, 1924; Hiro (Utinomi), 1935, 1943, 1962), i.e.

- Pyrgoma (Nobia) indicum* Annandale, 1924.

In the case of the last-named species, having a complex synonymy (*vide* Utinomi, 1962, p. 227) which, among other varieties, includes from Darwin's work *Creusia spinulosa* (var. 11), the presence of four sutures was a result of persisting doubts as to the relationship between *Creusia* and *Pyrgoma* which, among other authors, may be observed even in Darwin himself (1854a).

#### Subgenus *Daracia* Gray, 1825

Terga and scuta strongly fused with each other, completely modified in the form of two longitudinal tergoscutal valves which do not resemble at all opercular valves of other Balanidae (Darwin, 1854a; Hiro, 1931, 1935, 1938). The species:

- Pyrgoma (Daracia) monticulariae* Gray, 1831 and  
*P. (Daracia) elongatum* Hiro, 1931

may be included here. Both last-named species of this subgenus are also known only as Recent ones.

## ECOLOGY OF CREUSIINAE

Ecological problems, concerning Creusiinae will be examined on the example of *Creusia sanctacrucensis* n.sp. Correlations, stated in this species, may surely be found — as concluded from bibliographical data — in all representatives of the genus *Creusia* Leach and, in most cases, also in all remaining Creusiinae. If here exist some divergences or a lack of certain data, e.g. those on Recent forms, we emphasize such facts, at the same time, indicating which data concern only *Creusia* and which — all Creusiinae.

## MORPHOLOGICAL ADAPTATION TO THE SUBSTRATUM

The cuplike shape of the basis and, consequently, of the entire shell of *Creusia* and other Creusiinae, is a result of its constant outgrowing above the corallum of a live anthozoan. The degree of this outgrowing is, in truth, not great but all the same sufficient for the growth zone of the shell to be situated above the corallum and soft parts of the anthozoan. Thus, the substratum never exerts its influence on the growth zone and, consequently, on the sculpture and a general shape of the shell which, therefore, are elements, completely independent of the substratum. Hence, the ornamentation develops in creusioid barnacles on the outer surface of the basis. In other balanomorphous cirripeds (Balanomorpha), in particular in balanids, the growth zone of the shell directly contacts the substratum which sometimes exerts its influence on the shape and sculpture of the shell to such an extent that a relatively very accurate repetition of the details of the substratum sculpture may be brought about in the morphology and ornamentation of the shells. In extreme cases even the phenomenon occurs known as mimicry (de Alessandri, 1894, 1906, 1910; Bieda, 1931) which in fact has already earlier been observed (Darwin, 1854a; Seguenza, 1876), although it has nothing in common with a well-known mimicry in e.g. insects (Joleaud, 1910; Pilsbry, 1916; Davadie, 1963).

The cuplike extension of the basis in Creusiinae is, therefore, a result of the growth within the coralla (Fig. 4). This is the only habitat of the development of these animals and hence, such a shape is the only one possible for them. Creusiinae cannot develop on a substratum that does not gradually ascend and, therefore, they cannot live on, for instance, the coralla of dead anthozoans. This correlation significantly determines the necessity of the presence of live anthozoans, for the development of Creusiinae what will be discussed in detail below.

A certain relatively slight differentiation of the shape of shell of *Creusia*, following a different degree of elongation of bases, is — within a given population — most probably a result, as also interpreted by Abel (1928), of a different growth rate of corallites which surround particular

individuals of *Creusia* within a given anthozoan colony. In the case of a faster rate of growth of certain corallites, a given individual of the creusoid barnacle also faster outgrow above the surrounding part of the corallum and, therefore, its ultimate shape was more elongated. On the other hand, the diameter of such a specimen often reached a value

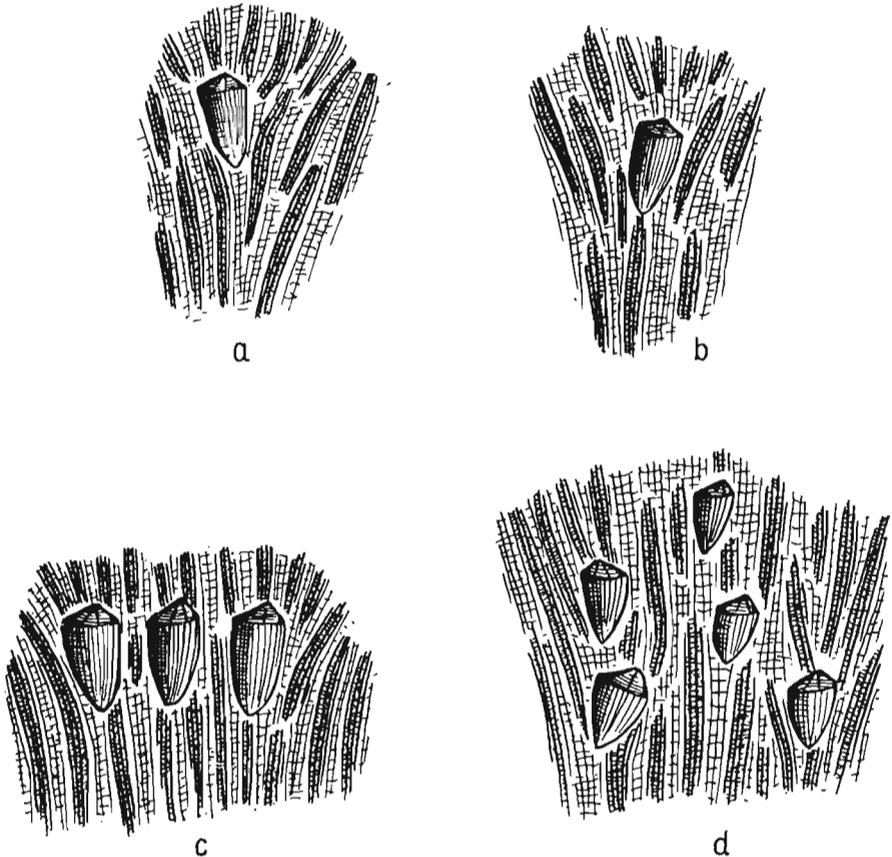


Fig. 4—Influence of shells *Creusia sanctacrucensis* n. sp. on the pattern of corallites within coralla of *Tarbellastraea reussiana* (Milne-Edwards & Haime); nat. size.

analogous to that in individuals average in shape (cf. Fig. 2). A different degree of elongation of shells in the representatives of a given species of creusoid barnacles from various findings results, on the other hand, most probably from their growth within different anthozoans of a different growth rate. Thus far, this phenomenon has only been recorded (Bałuk & Radwański, 1967a) in the species *Creusia miocaenica* Procházka.

The process itself of the modification of the basis and its transformation into a cupshaped form is not a phenomenon peculiar in balanids. In

many acorn barnacles, especially in those growing in uneven places of the substratum or those which grow in dense clusters, the basis adapts itself more than once to the shape of depressions, thus acquiring a convex or even a short cuplike form (*vide* Pilsbry, 1916; Abel, 1928; Withers, 1929; Hiro, 1938; Krüger, 1940; Termier & Termier, 1953, Fig. 17; Davadie, 1963).

An exact homology of the shell of *Creusia* and of *Balanus* also including the opercular valves, and which is expressed in the lack of far reaching structural transformations in *Creusia*, indicates that the shell of the latter creusioid barnacles is of a general functional significance, identical with that in *Balanus*, i.e. the shell protects the body against the contacts with the environment which thus does not exert any direct influence on the development of the animal. In the case of *Creusia* developing only within live anthozoans, such a statement is of an essential significance since it indicates a physiological independence of *Creusia* and an anthozoan. *Creusia* does not derive any observable physiological profit from the surrounding anthozoan which only plays the role of an indispensable substratum. In *Pyrgoma* which displays a greater degree of structural transformations and — as it seems — a different function of opercular valves which has already been mentioned above, this problem is not definitely solved. Certain correlations observed between pyrgomas and anthozoans (Hiro, 1935, 1938) need not necessarily be elucidated by the existence of physiological correlations which will be the subject of a further discussion.

#### OVERGROWING BY ANTHOZOANS

In the case of *Creusia sanctacrucensis* n.sp., a similar diameter of different shells (Fig. 2), hidden inside coralla, indicates that the adult individuals were overgrown by the corallum. Except for certain sporadic cases (Pl. VI, Fig. 2), tiny juvenile individuals were found only on the upper surface of one corallum (Pl. I, Fig. 2) which, in fact, contained inside only adult individuals (a similar case among Recent forms is cited by Kolosváry, 1948). The corallum discussed was surely buried in sediment during the growth period of the creusioid barnacle and of the anthozoans, i.e. it was buried jointly with the live anthozoan.

The manner of overgrowing of adult creusioid barnacles by the anthozoan may be traced on several specimens, contained in the examined material. The corallum gradually spread from the slopes of the crown of *Creusia* towards its top and, at the moment when it reached the orifice, it started to stop it up gradually, mostly forming a characteristic stopper (Fig. 5; Pl. I, Fig. 1; Pl. V, Fig. 1). A similar course of this phenomenon was observed in different Recent Creusiinae (*vide* Abel, 1928, Fig. 4; Pilsbry, 1932, Fig. 1; Korschelt, 1933, Fig. 23; Hiro, 1938, Pl. 1, Fig. 3; Krüger, 1940, Fig. 328a and 330). Such a stopper closing the orifice in

Creusiinae is, therefore, an indubitable product of the anthozoan. Thus, these are not transformed opercular valves as Abel (1928) believed. This author's observation that, sometimes, the stopper maintains a bilateral symmetry (maybe corresponding to terga and scuta), was most probably made in the case when the stopper was deposited so deeply inside the shell of a (live?) creusioid barnacle that it reached the opercular valves, which maybe left their imprint on its lower surface.

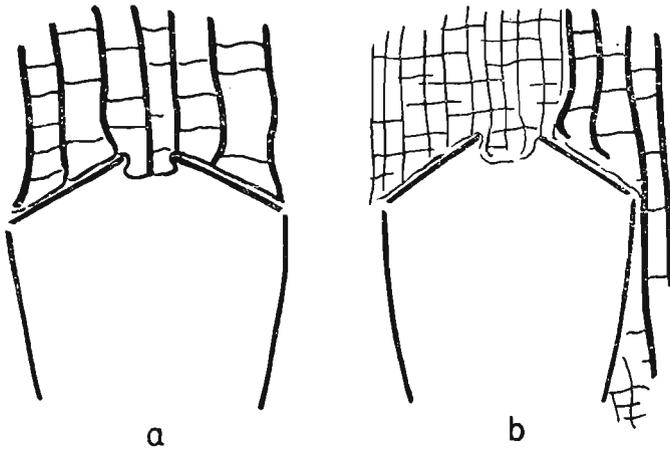


Fig. 5. — Stoppers made by the anthozoan and bolting orifices of *Creusia sancta-crucensis* n. sp.,  $\times 6$ ; stopper made: a by corallite, b by coenosteum.

In the case of the fossil material, the solving of the problem whether these were live individuals of adult creusioid barnacles that were subject to overgrowing which caused their death, or only already dead ones, does not seem to be possible. Besides, no appropriate observations are available concerning the recent material.

In the case of other balanids, analogous stoppers were also observed in mutually overgrowing acorn barnacles (Abel, 1928) which allows one to generalize the statement that similar stoppers may be produced by any animal which overgrows the balanomorphous cirripeds.

#### BIOLOGICAL RELATIONSHIP OF CREUSIROID BARNACLES TO THEIR HOSTS

As it has previously been shown, all Creusiinae are adapted to the life only within the coralla of live and constantly growing anthozoans. Most probably, their development on any other organic substratum is impossible. Likewise, in the case of the death of the host anthozoan, a further development of Creusiinae is impossible.

The fact of recording loose shells of creusioid barnacles in fossil deposits which seems to be fairly frequent, although it is distinctly emphasized only in some works (Kolosváry, 1949; Bałuk & Radwański, 1967a), corresponds — in the present writers' opinion — to the cases in

which the creusioid-barnacle bearing coralla were subject to a complete disintegration on the sea bottom and only the shells of creusioid barnacles, as the hardest part, reached the sediment. Such a disintegration, caused by hydromechanical agents, was probably a result of a different chemical composition of coralla (built of aragonite, easily undergoing chemical transformations) and shells of Creusiinae (built of calcite). Similar cases were also recorded under recent conditions (Ladd's oral communication in: Cloud, 1959, p. 392).

It results from the relationship of Creusiinae to the anthozoans that the presence of an anthozoan is indispensable for the development of these cirripeds. Creusiinae benefit, therefore, to a considerable extent by the presence of the anthozoans, although this profit is limited in fact only to obtain a substratum, essential to their life. On the other hand, as indicated above, there is no evidence for a supposition that Creusiinae derived physiological profit from the anthozoans.

In the case of colonial anthozoans — and, with some exceptions, only such provide a habitat for Creusiinae — certain corallites may of course suffer considerable loss resulting from the development of these cirripeds and even be destroyed but the colony as an entity does not suffer any observable loss (compare Cloud, 1959, p. 392). The relationship of some individual of Creusiinae to a single corallite on which it may settle is, therefore, quite different than that to the entire colony.

Determining with some term the relationship of Creusiinae to the anthozoan colony as a whole requires the adoption of a definite classification since the range of understanding of sometimes apparently identical definitions by individual authors happens to be rather wide. Adopting a detailed classification, presented by Ager (1963), this relationship should be termed as a commensalism (0 +) with which one organism derives profit (Creusiinae: +), whereas the other neither gains, nor loses (anthozoan colony: 0).

The relationship of particular individuals of Creusiinae to a single corallite which, as a result of the growth of cirripeds, becomes annihilated should be termed, according to Ager's (1963) classification with the name of exploitation (- +) with which an individual of Creusiinae gains (+) and a corallite loses (-). This relationship might be more accurately determined as the smothering which, however, was not distinguished by Ager within the exploitation relationships, since it consists in the destruction of one organism not as a result of deriving physiological profits by the other (in Ager, predation and parasitism), but as a result of the settlement on its body.

The relationship of Creusiinae to anthozoans is still different when we examine the case in which all corallites would be destroyed by cirripeds, which of course would cause the death of the anthozoan and, consequently, also the death of cirripeds. According to Ager's clas-

sification (1963), this would be an instance of competition (— —) in which both organisms suffer only losses as an ultimate effect of their relationship. In the material from Korytnica, there was no such case, although theoretically it was quite possible. A somewhat similar case was observed by Abel (1928, Pl. 1, Fig. 6) which induced him to state that the relationship of creusoid barnacles to anthozoans should be termed as parasitism (*vide* also Abel, 1927, 1935).

To sum up, the relation of Creusiinae to anthozoans should, therefore, be determined — with the entire anthozoan colony in mind — as commensalism. The remaining two cases should be treated individually with a strong emphasis put on the fact that this is either a relationship to a single corallite (exploitation, smothering), or to the entire destroyed colony (competition).

In the case of Creusiinae, settling on solitary anthozoans which is primarily characteristic of *Pyrgomina anglica* (Sowerby), actually living, e.g. along the British coasts, and settling on caryophyllias (Sowerby, 1823; Darwin, 1854a; Gosse, 1860; Holdsworth, 1860 and others), we also have of course to do with commensalism, unless developing Creusiinae cause the death of such an anthozoan (exploitation which soon passes into competition).

It is clear from the data, cited above, that the relationship of Creusiinae to anthozoans may be fairly variable, although in the case of a pronounced majority of forms, settling on colonial anthozoans, there is only the question of commensalism.

On the other hand, attention should be paid to the fact that similar relationship, i.e. commensalism also occurs in several other cases of different cirripeds settling on anthozoans or other type of biological substratum.

Cirripeds *Endosacculus moltkia* Voigt of the order Ascothoracica, living in the coralla of the Upper Cretaceous anthozoans *Moltkia*, which were studied in detail by Voigt (1959), may serve as an instance in this respect. Distending the corallum of *Moltkia* by *Endosacculus* is quite similar to that of the corallites of a given colony by Creusiinae. *Endosacculus* did not derive any physiological profit from *Moltkia*. Instead, it only secured sufficient place for its development. On the other hand, *Moltkia* neither gained, nor lost anything, except of course for the fact that it was compelled to tolerate the interloper, making itself at home. Voigt (1959) interpreted this relation in a somewhat wider range, calling it commensalism or Synökie (in Ager's classification, the latter corresponds to toleration).

An identical case of commensalism is also observed in cirripeds of the subfamily Coronulinae of the balanids which develop on the skin of whales and either partly ingrow in it as in the genus *Coronula* Lamarck, or completely penetrate it, as in the genus *Tubicinella* Lamarck, whose

individuals transform its crown into long tubes which deeply ingrow in the skin of some species of southern whales (Sowerby, 1823; Darwin 1854a; Pilsbry, 1916; Korschelt, 1933; Krüger, 1940). This matter stands similarly in the case of several balanids growing on turtles and other animals which makes up the subject of a rich literature (in addition to the above cited, *vide* Zullo & Bleakney, 1966; Ross & Newman, 1967).

#### DISTRIBUTION OF CREUSIOID BARNACLES ON ANTHOZOANS

In the examined material from Korytnica, the distribution of the individuals of *Creusia sanctacrucensis* n.sp. within particular coralla is on the whole variable but rather small indeed. Mostly, creusoid barnacles occur in groups of a few individuals, situated near each other (Fig. 4c) and much less frequently as single specimens, scattered within some larger part of a corallum (Fig. 4d). The cases of a numerous domiciling of *Creusia* in a given corallum are rare (e.g. a specimen in Pl. I, Figs. 1 and 2, which in fact represents the case of burrying in the sediment of a live anthozoan together with creusoid barnacles, as it has previously been examined). In the Korytnica clays there may be also found the coralla completely devoid of creusoid barnacles.

In view of a small amount of coralla, contained at all in the Korytnica clays, it is difficult to decide whether the quantitative relations are a result of a not uniform distribution of creusoid barnacles in the basin, or of some ecological causes. The fact that all specimens of *Creusia sanctacrucensis* n.sp. were found only in the coralla of *Tarbellastraea reussiana* and that they were lacking in other anthozoans, embedded in clays, might have suggested some biological correlations. With regard to the occurrence of these correlations, consisting in choosing by particular Creusiinae, especially pyrgomas, of a definite species or of several definite species for a substratum, fairly divergent opinions may, however, be found in literature (*vide* Darwin 1854a; Annandale, 1924; Abel, 1928, 1935; Hiro, 1935, 1938; Krüger, 1940; Kolosváry, 1951a; Cloud, 1959 and others).

On the analysis of the material from Korytnica and data from literature, it seems that a decisive role in such a distribution of the examined species *Creusia sanctacrucensis* n.sp., as well as in the distribution of other Creusiinae, should be ascribed to simple ecological rules, primarily to the principle (Volterra-Gause) of exclusiveness of one species within a given population, as well as to the rule which is in force in the sessile benthos, i.e. that the successive generations settle in the neighbourhood of their parents. In the case of Creusiinae, the latter possibility was pointed out by Hiro (1938). Both rules, referred to above, seem to sufficiently elucidate the facts of the occurrence of either only one species of Creusiinae on a given corallum, or of a given species of Creusiinae on

the coralla of different anthozoans from different sites, as well as a dense settlement by Creusiinae of only certain, definite coralla of the same species in a given environment. At present, there is no convincing proof for the existence of any close correlation between a given species of Creusiinae and a given species of anthozoans which was suggested by Abel (1928, 1935) and Hiro (1935 and, less emphatically, 1938). The cases of a simultaneous occurrence of different species of Creusiinae on the same corallum are rather rare (Darwin, 1854a; Hiro, 1935) and do not contradict the general explanation, presented above. Besides, they mostly concern the concurrence of pyrgomas and creusias and, less frequently, particular "varieties" of *Creusia spinulosa* Leach or individual species of pyrgomas.

#### TAPHONOMY OF CREUSIROID BARNACLES FROM KORYTNICA

Individual coralla, containing species of *Creusia sanctacrucensis* n.sp. were buried in sediment mostly after the death of cirripeds whose shells became completely overgrown by anthozoans (Pl. I, Fig. 1; Pls. II and III; Pl. V, Fig. 1; Pl. VI, Fig. 3). Sometimes, live anthozoans were buried together with still living creusioid barnacles (a specimen, discussed above, Pl. I, Fig. 2). Most coralla, probably after the death of anthozoans, rested for a long time on the bottom or were rolled and dragged over its surface,

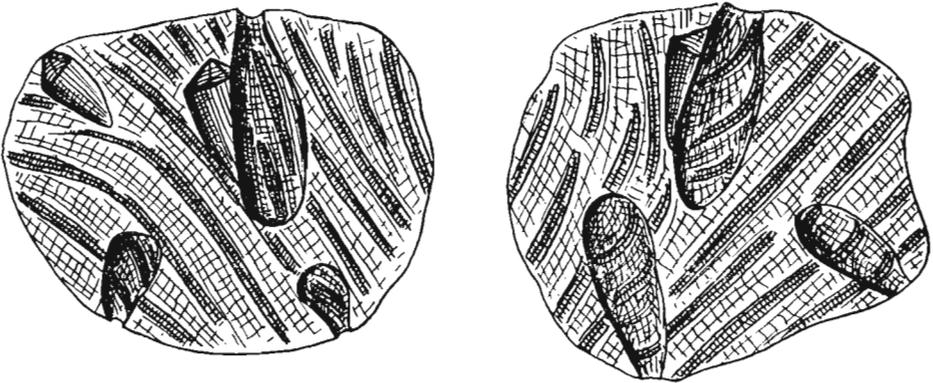


Fig. 6. — General appearance of coralla with *Creusia sanctacrucensis* n. sp. in the Korytnica clays; coralla are preserved as pebbles, bored by pelecypods, *Lithophaga lithophaga* (Linnaeus) destroying more than once also the shells of cirripeds domiciled within;  $\times 1.5$ .

crushed and rounded, or destroyed by different boring animals such as sponges *Cliona celata* Grant, polychaetes *Potamilla reniformis* (O. F. Müller) and pelecypods *Lithophaga lithophaga* (Linnaeus). As a result, many coralla occur in the form of pebbles cut on several sides by lithophags (Fig. 6). More than once, some larger lithophags, in particular *Lithophaga lithophaga*, boring the corallum, simultaneously cut the shells of creusioid

barnacles contained in them (Fig. 6). Some shells of *Creusia* are also destroyed by very fine borings probably made by polychaetes whose accurate taxonomic position cannot be determined.

#### BATHYMETRIC AND CLIMATIC REQUIREMENTS

As a bathymetric index, the value of the considered species *Creusia sanctacrucensis* n.sp. from Korytnica is not very great. It is beyond any doubt that the bathymetric range of Creusiinae depends on the distribution of anthozoans and, in addition, of only colonial ones in which these cirripeds domicile. Hence Recent Creusiinae are recorded primarily under very shallow marine conditions, mostly within the range of coral reefs (*vide* Darwin, 1854a; Annandale, 1924; Hiro, 1935, 1938; Krüger, 1940; Cloud, 1959; Newman, 1960 and several authors cited in: Hiro (Utinomi), 1935, 1962; Brooks & Ross, 1960). An exceptional position is taken only by *Pyrgomina anglica* (Sowerby) for a long time noted at much larger depths, ranging 80 m (Darwin, 1854a) and more (200 m according to Broch's data, *vide* Hiro, 1935).

Cloud's (1959) more accurate studies on the Mariana Islands have revealed that the local Creusiinae requirements were even extremely shallow marine. These cirripeds live there only in the shallowest, lago-ward parts of reefs, at depths smaller than 2 m.

Examining the material from Korytnica and in fact also any other fossil material, one may only state, therefore, that the presence of Creusiinae indicates the shallow marine or even extremely shallow marine conditions. The bathymetric distribution of these cirripeds should be considered the same as the distribution of anthozoans they domicile.

With regard to climatic conditions, the requirements of a pronounced majority of Creusiinae, as forms associated with colonial anthozoans, concern tropical and subtropical conditions (Darwin, 1854a; Nilsson-Cantell, 1921; Annandale, 1924; Pilsbry, 1932; Hiro, 1935, 1938; Krüger, 1940; Brooks & Ross, 1960; Moyses, 1961). It is only *Pyrgomina anglica* (Sowerby) that lives also under such mild climate as of the Mediterranean Sea from where it was known long ago and recorded from the coast of Sicily (Philippi, 1836, *vide* Darwin, 1854 a, b; Seguenza, 1876; de Alessandri, 1894, 1906; Kolosváry 1951b). As a matter of fact, of all Creusiinae, this is the most eurybathic and eurythermic species (*vide* Hiro, 1935, 1938), recorded besides as far north as the coasts of England and Ireland (Sowerby, 1823; Darwin, 1854a; Moyses, 1961). Except the last-named species, all other Creusiinae should be considered indicative of zones warmer than the Mediterranean. In interpreting any fossil material, the value of Creusiinae as a climatic index does not seem, however, to be larger than that of the colonial anthozoans. Nevertheless, a frequent presence of these cirripeds in the European Miocene seems to be remarkable.

In the Miocene, the genus *Creusia* Leach is common not only in Mediterranean countries such as France, Italy and Yugoslavia, but also in Bulgaria, Rumania, Austria, Hungary and Moravian part of Czechoslovakia (Fig. 7). The occurrence of this genus at Korytnica, on the southern slopes of the Holy Cross Mountains in Central Poland (Fig. 7) extends its range in the European Miocene distinctly northwards.

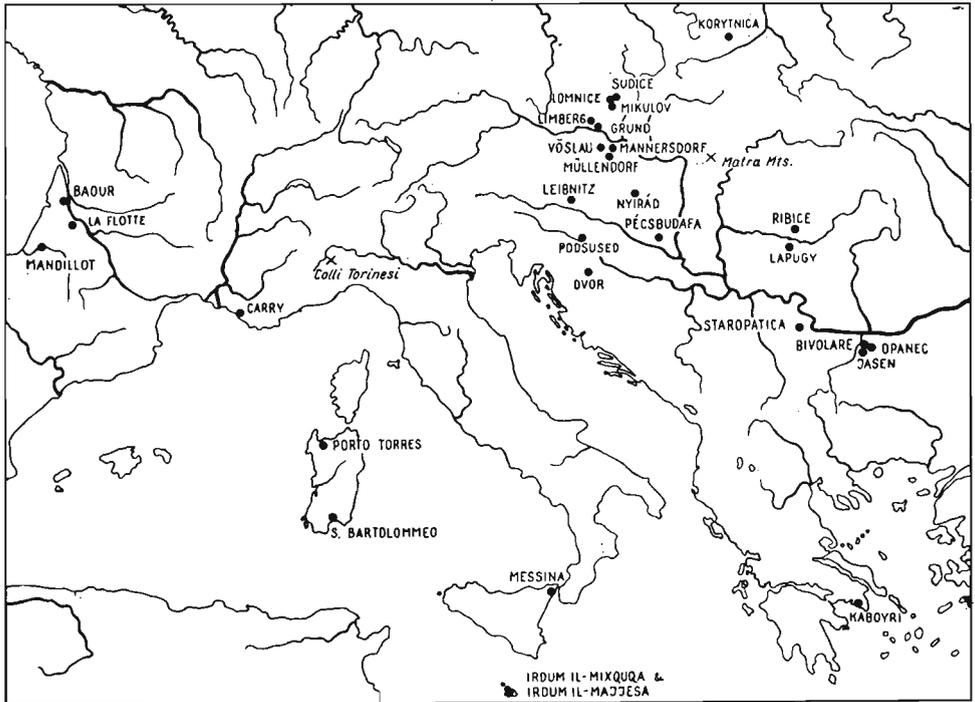


Fig. 7.—Geographical distribution of *Creusia* Leach in the European Miocene. Most important localities only have been compiled, smaller ones and situated nearby those—omitted. Localities from the Mio-Pliocene of Sicily and Attica included, some other ones from Italy of vague stratigraphical position—omitted. Compilation based on data by: Seguenza (1876), Kramberger-Gorjanović (1889a), Gourret (1890), Procházka (1893), de Alessandri (1894, 1906, 1910), Withers (1926, 1929), Abel (1928), Kolosváry (1949, 1962), Charalambakis (1952), Bogsch (1957), Bałuk & Radwański (1967a) and Dr. G. Zammit-Maempel (pers. communication, 1966).

As shown by the analysis of the entire fauna, in the Miocene (Tortonian) sea which covered southern regions of Poland, there predominated the conditions which on the whole were comparable with the present Mediterranean or even slightly warmer conditions. Besides, there are no essential differences in relation to the conditions, predominating in e.g. Vienna Basin and which might be caused by climatic factors. The sea of the Polish Tortonian was undoubtedly included in the same zone as the Vienna Basin, as well as south-Carpathian and Balkan basins which were directly connected with the area of the Mediterranean Sea. It seems

that within this system of basins no different climatic zones were more significantly marked. Such a conclusion may also be supported by a uniform distribution over this area of various species of creusioid barnacles without any more distinct predominance of zones situated more to the south (Fig. 7). If we refer to the present distribution of Creusiinae, the conclusion may be drawn that the presence of the creusioid barnacles under study in the Miocene Mediterranean-Carpathian basins would indicate the existence in those times of warmer climatic conditions than those, observed now in the Mediterranean zone. Nowadays, except for *Pyrgomina anglica* (Sowerby), none other Creusiinae are known in the basin of the Mediterranean Sea, although colonial anthozoans are still fairly numerous and flourishing in this sea.

It seems, therefore, that the species *Creusia sanctacrucensis* n.sp. may, in the Polish Miocene, be considered as a more philothermic element than a Mediterranean one. The presence of such forms in the Polish Miocene is all the more interesting since they represent the benthos. More philothermic forms, known so far in the Polish Miocene, are represented only by nectonic fish, in particular Elasmobranchii among which as a matter of fact there also occur indicative tropical forms (*vide* Radwański, 1965).

#### DISTRIBUTION OF CREUSIOID BARNACLES IN THE KORYTNICA BASIN

Palaeogeographically, the Korytnica basin represented in the Tortonian a terminal part of a large bay cut from the south-east in the Holy Cross land, subsequently along older valley patterns. The shores of this land were, therefore, of the Dalmatian type (Radwański, 1964, 1967).

The distribution of creusioid barnacles in the Korytnica basin is confined to its central part where the colonial anthozoans lived and where the clays, uncommonly rich in fauna of different systematic groups, were formed. In this area, among other cirripeds, there also occur the genera *Verruca* Schumacher, *Chthamalus* Ranzani and *Balanus* da Costa, which probably lived on the shells of different animals, mostly gastropods and pelecypods.

In the littoral zone of the Korytnica basin, no colonial anthozoans and, consequently, creusioid barnacles are recorded. In this zone, there were formed mainly lumachelles composed of the oyster detritus with relatively abundant cirripeds. These are the genera *Scalpellum* Leach, *Balanus* da Costa and *Acasta* Leach. The former two probably lived attached to oyster shells. At the base of lumachelles, within littoral rubbles and the abrasion surface, there lived boring cirripeds *Zapfella pattei* Saint-Seine of the order Acrothoracica.

The assemblage of cirripeds from Korytnica is the richest and, in practice, the only one in the entire Polish Miocene. The other occurrence,

only of acorn barnacles is that of a single outcrop of littoral oyster lumachelles in Cracow-Zwierzyniec (*vide* Bieda, 1931; Radwański, 1964).

#### PROBLEM OF HOMOEOMORPHY OF CREUSIINAE

The growth of Creusiinae which only and solely takes place within the coralla of live and constantly growing anthozoans, mostly causes a distinct and even strong elongation of their shells. The slender, cuplike shape acquired by these cirripeds was the reason, why they were more than once cited as an example of homoeomorphy in relation to the cup-shaped representatives of various taxonomic groups of animals primarily of hippurites (Abel, 1920; Dacqué, 1921; Termier & Termier, 1953; Müller, 1963; Ziegler, 1963).

The structure of shells of fossil and Recent Creusiinae indicates, however, that actually no Creusiinae, even the species *Creusia krambergeri* Bałuk & Radwański and *Pyrgoma grande* (Sowerby) which have the most elongated shells, have characters distinctly homoeomorphic with hippurites. In all Creusiinae, the cuplike, extended bases, i.e. the largest parts of the shell, are inside devoid of any mineral structures. In addition, these animals live single and within the anthozoans and, therefore, they contact the water environment only with their crown. A much greater similarity in the mode of life—a gregarious life on the sea bottom, a development of a spongy mass in the elongated part of the shell and, consequently, a much more pronounced homoeomorphy—is displayed among cirripeds, which has been pointed out by Abel (1935), by forms once described as *Tamiosoma gregaria* Conrad from the Miocene of the U.S.A. (*vide* Pilsbry, 1916, Pl. 29; Abel, 1935, Fig. 348). At first, these forms were considered by Conrad to be rudists (1856, *vide* Pilsbry, 1916). Nowadays, they are considered (Zullo, 1964) as a mere ecological modification of the species *Balanus aquila* Pilsbry.

On the other hand, low Creusiinae as e.g. *Creusia miocaenica* Procházka, sometimes display such a strong flattening of the shells that they acquire characters more homoeomorphic to inarticulate brachiopods of the genus *Crania* Retzius than to any other animals (Bałuk & Radwański, 1967a).

#### STRATIGRAPHICAL RANGE OF CREUSIINAE

As it is clear from the taxonomic review of Creusiinae, the oldest forms, assigned to this subfamily, appear in the Miocene and represent only the genus *Creusia* Leach which as a matter of fact has been extant until the recent times. All Miocene forms known so far, and not only

early Miocene ones, as believed by Withers (1929, p. 565) and Hiro (1938, p. 402), belong therefore to the genus *Creusia* as it has already been assumed by Krüger (1940). The subgenus *Creusia (Withersia)* appears in the Pleistocene and persists up to the present.

The genus *Pyrgomina* Bałuk & Radwański occurs from the Pliocene to the present.

The genus *Pyrgoma* Leach includes only Recent forms. Here, one may emphasize once more that such forms have never been reported in the fossil state. All previous records of fossil *Pyrgoma* either concern the new established genus *Pyrgomina*, or are simply erroneous (in the case of illustrated forms, they are mostly those of the genus *Creusia*).

The stratigraphical range of Creusiinae may be presented in the following tabular form:

Miocene	Pliocene	Pleistocene	Holocene																																				
C		R		E		U		S		I		A																											
				P				Y				R				G				O				M				I				N				A			
												PYRGOMA																											

#### PHYLOGENY OF CREUSIINAE

As it has been presented above, in the stratigraphical range of Creusiinae the oldest representative of this subfamily, i.e. *Creusia* Leach appears in the Miocene. It is true enough that the occurrence of various "pyrgomas" — this term should be understood as a synonym of Creusiinae — in the formations stratigraphically older than Tertiary was mentioned in several works but, as it has already been shown by many authors, such cases are contrary to fact (criticism or discussion in: de Alessandri, 1906, p. 319; Pilsbry, 1916, p. 12; Withers, 1928, p. 20; Abel, 1928, pp. 16—17, 1935, pp. 537—538; Krüger, 1940, p. 486; Termier & Termier, 1953, p. 306; Voigt, 1959, p. 216; Ladd, 1959; Brook & Ross, 1960, p. 362).

The next genus, i.e. *Pyrgomina* Bałuk & Radwański, appears in Pliocene, whereas the third one, assigned to the subfamily under study, *Pyrgoma* Leach, occurs only as a Recent form and in the fossil state has never been known so far. Since the appearance of individual genera

of Creusiinae is accompanied by certain consistent differences in the structure of shell, there occurs a possibility of treating these changes as links in the evolutionary phylogenetic process.

Although the genera *Creusia* Leach and *Pyrgoma* Leach themselves were — in the literature known so far — differently understood and the forms assigned to the genus *Pyrgomina* Bałuk & Radwański were not taxonomically distinguished, more than once attention was paid to the differences in the structure of Tertiary (Miocene) and Quaternary (Pleistocene and Recent) Creusiinae. The number of compartments was

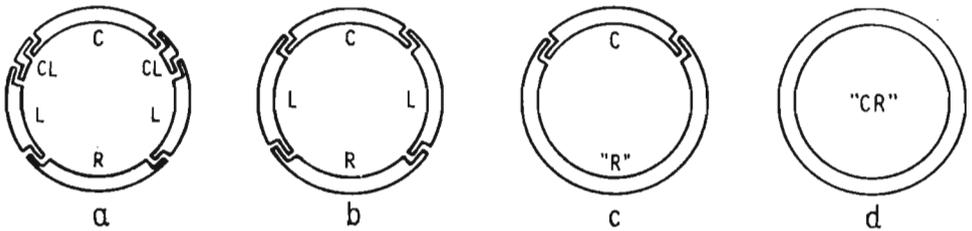


Fig. 8. — Schematic structure of the crown of *Balanus* and of the representatives of Creusiinae n. subfam.; a *Balanus* da Costa, b *Creusia* Leach, c *Pyrgomina* Bałuk & Radwański, d *Pyrgoma* Leach. Compartments: C carina, CL carinolaterals, L laterals, R rostrum; in *Pyrgomina* „R” compartment analogous to the rostrum of *Balanus* and *Creusia*, in *Pyrgoma* „CR” — analogous both to the carina and rostrum of *Balanus* or *Creusia*, and compounding all the crown.

considered to be the most characteristic difference, whereas the development of opercular valves was paid much less attention to. At the same time, the structure of Creusiinae was compared with that in acorn barnacles, i.e. in the genus *Balanus* (cf. Fig. 8), known from stratigraphically still older formations and which display characters of structure more similar to those in *Creusia* than in *Pyrgoma*. Consequently, the phylogenetic relationship and sequence were suggested from *Creusia* to *Pyrgoma* and mostly also from *Balanus* through *Creusia* to *Pyrgoma*. A gradual reduction of compartments from 6 in *Balanus*, through 4 in *Creusia* to 1 in *Pyrgoma* was believed to take place during such a phylogenetic development. Such a view, accepted as a whole or partly in numerous works (Pilsbry, 1916; Krüger, 1940; Kolosváry, 1951a; Termier & Termier, 1953; Zullo, 1961; Davadie, 1963) was, however, much more cautiously expressed by palaeontologists who more accurately dealt with this problem (Withers, 1926, 1929; Hiro, 1938). There always existed certain factual difficulties in a literal acceptance of such a phylogenetic series, as e.g. the lack of obvious passage forms and persistence of three out of four genera, mentioned above, until the present-day times (*Balanus*, *Creusia*, *Pyrgomina*), i.e. at least a partly simultaneous existence of these genera. In authors, who considered certain Miocene forms to be pyrgomas, this problem was yet vaguer.

Of the authors who more accurately dealt with this problem, it was Withers (1926) who paid attention to the fact that the forms morphologically "transitory" from creusias to pyrgomas, occur virtually as late as in the Pleistocene and, in addition, outside of Europe (where Tertiary forms are only known from), namely on the Barbados Island. Despite previous authors' opinions, Withers (1926) also noticed that the species *Pyrgomina anglica* (Sowerby), considered by him as one assigned to *Pyrgoma* and morphologically departing from all Miocene forms, appears as late as the Pliocene, although, on the other hand, he believed certain other Miocene species to be pyrgomas. On the basis of his observations, Withers (1926, *vide* also 1929) concluded that *Pyrgoma* might be developed from *Creusia* in different evolutionary lines, independent of each other. As one might guess from the entire text of Withers, this author was convinced that the *Creusia*- or *Pyrgoma*-stage could be evolved regardless of different ancestors which, however, developed within balanids. Withers' considerations were somewhat differently understood by Krüger (1940, p. 502) who wrote about a parallel development of *Creusia* and *Pyrgoma* from some balanoid ancestor which of course may negate the development of pyrgomas from creusias. Somewhat earlier, Hiro (1938) submitted several arguments which, in his opinion, testified to the polyphyletic nature of pyrgomas. Besides, Hiro (1938) believed that *Creusia* and *Pyrgoma* are not directly derived from *Balanus*, but from some older, common ancestor. A similar view was recently expressed by Zullo (1961).

Taking into consideration that the oldest creusioid barnacles, which appear in the Miocene, morphologically depart from *Balanus*, and that in the pre-Miocene formations there are no transitory forms between them, the view, referred to above should be reckoned as very likely. Attention should be paid that the problem of gradual reduction of the number of compartments in the phylogeny of balanids is not quite clear since the morphological type of a 4-compartmental crown appears also in other subfamilies of balanids (genus *Elminius* Leach in Balaninae Darwin, genus *Tetraclita* Schumacher in Tetraclitinae Gruvel), as well as in the genus *Chamaesipho* Darwin in the family of chthamalids (Chthamalidae).

Summing up the present state of knowledge related to the phylogeny of the genera *Creusia* and *Pyrgoma*, it is clear that both these genera, taxonomically separate, do not by any means succeed each other. The view on their mutual independence (Krüger, 1940), or on their polyphyletic (according to Hiro, 1938) nature are to a certain extent likely and do not at all preclude each other. The problem of the polyphyletic nature itself is not quite clear since the view on it (Hiro, 1938) was formed on the basis of the relations which exist among Recent forms and there is no definite and concrete phylogenetic evidence and no data

are available on a possible taxonomic separateness of the ancestor of particular pyrgomas. In addition, it is possible that all links which might compose the genus *Pyrgoma*, even in the case of their separateness, might, however, be derived from the same balanid stock. Besides, although all pyrgominas and pyrgomas might indeed develop from *Creusia*, there are no convincing proofs for the existence of a continuous process of reduction of the compartments in the phylogeny of balanids, since there are also no proofs for such a reduction in the preceding part of the hypothetical sequence: an 8-compartmental ancestor — 6-compartmental *Balanus* — 4-compartmental *Creusia* (cf. below).

In the ontogeny of *Pyrgoma indicum* Annandale, an only species of pyrgomas in which the development of the settled stage was examined, the oldest settled stage observed (Utinomi, 1943) has already a 4-compartmental crown of the creusioid type (R+2L+C) with opercular valves not fused together. In a later stage, the compartments fuse together, much the same as the tergum-scutum pair which forms fused tergoscutal valves. Thus, the ontogeny of *Pyrgoma indicum* indicates that it is at least this species among the pyrgomas which might be derived from creusioid barnacles. As presented below, an identical stage with an identical structure of the crown occurs, however, also in the ontogeny of *Balanus* (cf. Runnström, 1925, Fig. 11 and Utinomi, 1943, Fig. 1). In the ontogeny of *Pyrgoma indicum*, this stage may therefore indicate a pre-*Balanus* ancestor and not the *Creusia*. Besides, so far it is not certain if a similar stage also occurs in the ontogeny of other pyrgomas. Thus, forming any final and firm opinion on the problem of evolution of the genus *Pyrgoma* within the subfamily Creusiinae and on its supposed polyphyletic nature seems to be premature.

On the other hand, the studies of the literature, devoted to this subject, allow to express different views than those accepted so far concerning the phylogeny of the genus *Creusia*. Taking into consideration that this genus stratigraphically precedes the remaining Creusiinae, the views expressed may be considered as those, concerning the entire subfamily Creusiinae.

Facts observed in the ontogeny of *Balanus* indicate a possibility of another explanation of the phylogeny of the genus *Creusia*. Runnström's (1925) detailed studies indicate that in the ontogeny of *Balanus balanoides* (Linnaeus), at the moment of the settling of pupa (cypris), there occurs a distinct "germinal" stage of 4 compartment-bearing crown which consists of R+2L+C (Runnström, 1925, Fig. 11; *vide* also Krüger, 1940, Fig. 263i) and, therefore, without the CL compartments which develop later as the last ones. The crown in juvenile acorn barnacles consists therefore, in the stage under study, of these same compartments as those in adult *Creusia*. Consequently, one may say that acorn barnacles pass, in their ontogeny, through a sui generis *Creusia*-stage. If we assume

that the biogenetic principle is applicable to this case, *Creusia* cannot be a link derived from acorn barnacles (*Balanus*) and phylogenetically younger. On the other hand, *Creusia* should be considered to take its origin from a certain stage, occurring in the ontogeny of acorn barnacles and most probably representing some still older phylogenetic link which, however, is already characteristic of the family Balanidae since *Creusia* displays strikingly many characters in common with them and testifying to a close relationship. Here occurs the possibility that *Creusia* developed from some stock of balanids through the evolution of the 4-compartmental stage under study, keeping for a certain period of the phylogeny as neotenic forms. Applying such a presentation of this problem, one should assume that CL compartments in *Creusia* did not develop at all, which has previously been supposed by Withers (1928) and Zullo (1961), and, therefore, the lack of such compartments would not be explained by their fusion with the remaining ones in the crown.

The fact of a stratigraphically sudden appearance of *Creusia* in the Miocene and its persistence in an unchanged form until the present, may be explained by the hypothesis on the neotenic development of this genus. Considering that the genus *Balanus* da Costa appeared in the Eocene (Darwin, 1854a; Krüger, 1940; Davadie, 1963), it would be rather strange that, during a brief period (Oligocene), such a sudden qualitative change, i.e. the reduction of 6 to 4 compartments, took place in a mere single evolutionary branch of Balanidae, and then, this process would be stopped at least in a certain part of this branch which enabled the existence of the genus *Creusia* in an unchanged form until the present-day times.

In fact, no evidence for such a reduction of compartments from 6 to 4 have been found so far. In our opinion, the *Creusia*-shaped 6-compartmental acorn barnacles domiciled in anthozoans as, e.g. *Balanus duvergieri* (de Alessandri), considered by Withers (1929) to be forms phylogenetically transitory from acorn to creusioid barnacles and ecologically "starting" forms for the latter, cannot provide such evidence since they occur in the Miocene of Aquitaine together with creusioid barnacles (Withers, 1929) and analogous forms are also known recently (Zullo, 1961). The latter, represented by the species *Balanus (Hexacreusia) durhami* Zullo, living from the Pliocene to the present, are distinguished by Zullo (1961) even in the form of a separate subgenus, *Hexacreusia* Zullo, of acorn barnacles. In the present writers' opinion, all these forms are only an example of a morphological convergence of Balaninae with Creusiinae, and not phylogenetical ancestors of the latter.

Adopting the hypothesis on the neotenic development of *Creusia* from some Balanidae, we should imagine that the formation of the genus *Creusia* took place in early Tertiary (Oligocene?) as a result of the adaptation of the representatives of some line of balanids to specific

environmental conditions, existing within the coralla of live anthozoans and, besides this environment was not in fact inhabited by cirripeds in their previous history. Larvae of such a line of balanids, here settling, developed normally only to the stage of a 4-compartmental crown which assured them a sufficient possibility of functioning. A further development consisted only in the modification of the basis by its cuplike extension which was an indispensable condition for the preservation of cirripeds (a constant necessity of outgrowing above the corallum and the body of live anthozoans). A normal process of a further development of the crown and, therefore, a formation of the CL compartments was arrested in view of a change in the functions of particular parts of the shell. The function of the accommodation of the body, performed in acorn barnacles precisely by the crown, was completely taken over by the cuplike extended basis, whereas the crown itself began to transform itself into an apparatus, containing and protecting the opercular valves. The individuals of a given population which did not display such transformations were biologically eliminated. Only those individuals that underwent modification of the shell and, therefore, adapted themselves to new conditions, survived in the environment. The process of fixing adaptive characters and transmitting them to next generations without reaching the final form of an adult, "normal" balanid, i.e. through the neoteny, took place at a fast rate since it determined a possibility of a further existence of balanids in the coralliferous environment. A rapid realization of a new type of balanids, individualized in the form of a new genus *Creusia*, explains a sudden appearance of this genus in the Miocene and a lack of fossil transitory forms from the "normal" balanids (with the structure of the acorn barnacle type).

The process of the phylogenetic development of the genus *Creusia* from the neotenic forms of some balanids was most probably a factor which allowed the cirripeds under study to flourish in the environment abounding in anthozoans, since *Creusia* and the remaining, later *Creusiinae* are almost only cirripeds met with in such environment. From the times of Darwin (1854a; *vide* also Krüger, 1940; Newman, 1960) it has been a well-known thing that the environments, abounding in anthozoans, in particularly the reef species, were not, perhaps for some biological reasons, suitable for cirripeds which usually avoided them. Only *Creusiinae* which, in the present writers' opinion, passed through a specific phylogenetic development and reached a highly specialized adaptability to the anthozoan substratum, domiciled in such environments. The adaptation to the development on such a very specific substratum as a corallum of a live and constantly growing anthozoan, was probably a factor which considerably facilitated the persistence in the environment under study, but this does not on the whole elucidate the fact itself of the settlement of a certain group of cirripeds in the coralliferous environ-

ment. This fact has not also been explained by an interesting hypothesis of Newman (1960) who tries to elucidate the lack of cirripeds in the coralliferous environment by the formation of a complex ecological chain, determined by the activities of herbivorous fishes which — together with algae constituting their food and settling on dead parts of the coralla and on other objects — scratched away all settled larvae and juvenile individuals of cirripeds. These fishes live and have their feeding grounds precisely within anthozoan communities since these are the only places where they can find shelter and protection against piscivorous animals.

In the present writers' opinion, the modification itself of the basis of the shell in Creusiinae which causes their deviation from "normal" balanids was a factor which only facilitated — during their phylogenetic development — the adaptation to the coralliferous environment in which, probably as early as in the Lower Tertiary (Palaeogene), there predominated conditions, indicated by Newman (1960) or similar ones which even then eliminated other cirripeds from coralliferous environments. On the other hand, the neotenic development of a certain line of balanids which led to the formation of the genus *Creusia* with a 4-compartmental crown, was a principal and key reason why cirripeds could invade this environment and form within it a distinctly individualized group of the Creusiinae. Only such a development promoted a considerable plasticity in acquiring new, adaptive characters by particular individuals of a given population of balanids settling on anthozoans, as well as a rapid transmission of acquired characters to next generations. In the result, it facilitated a cirriped survival in this environment and, consequently, a final phylogenetic establishment of a character which consisted in the development of such balanids only and solely within the coralla of live and constantly growing anthozoans.

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WACŁAW BAŁUK & ANDRZEJ RADWAŃSKI

## WĄSONOGI MIOCEŃSKIE ŻYJĄCE W KORALOWCACH

### *Streszczenie*

Przedmiotem pracy są zagadnienia dotyczące budowy skorupy oraz systematyki i filogenezy stosunkowo rzadkiej i słabo dotychczas poznanej grupy aberantnych wąsonogów, żyjących w koralowcach. Grupa ta należy do rodziny *Balanidae* Leach, 1817, lecz wykazuje w porównaniu z jej typowymi przedstawicielami wyraźną odrębność morfologiczną.

Część analityczna pracy opiera się na zbadaniu materiału, zebranego w koralowinach *Tarbellastraea reussiana* (Milne-Edwards & Haime) z dolno-tortońskich ilów Korytnicy (południowe zbocze Gór Świętokrzyskich). Materiał ten, obejmujący ok. 60 okazów, reprezentuje nowy gatunek — *Creusia sanctacrucensis* n. sp.

Diagnozę nowego gatunku ustalono na podstawie szczegółowych badań morfologii skorup, zachowanych wraz z płytkami operkularnymi. Z uwagi na znaczne rozbieżności w literaturze dotyczącej rodzaju *Creusia* Leach, 1817, przeprowadzono rewizję wszystkich jego taksonów znanych w stanie kopalnym. Gatunek *Creusia sanctacrucensis* n. sp. (Fig. 1-3 oraz Pl. I-VI) wyróżnia się spośród innych odmienną morfologią płytek operkularnych i pewnymi szczegółami rzeźby korony. Charakterystyczną cechą badanych okazów jest zachowana pigmentacja skorupy (Fig. 3), nieznana u kopalnych przedstawicieli rodzaju *Creusia*.

Z uwagi na skomplikowane szczegóły budowy skorup omawianych wąsonogów, opis nowego gatunku poprzedzono krótkimi wiadomościami, dotyczącymi wykształcenia i sposobu wzrostu skorup u rodzaju *Creusia* Leach. Zagadnienia dotyczące ekologii *C. sanctacrucensis* n. sp. przedstawiono w dalszej części pracy

na podstawie badanego materiału oraz dyskusji dotychczasowej literatury. Istotną cechą, rozpatrzoną dokładniej, jest wzrost tych wąsonogów, dokonujący się wyłącznie w obrębie koralowin żywych i stale wzrastających koralowców. Wzajemny stosunek omawianych wąsonogów i koralowców należy określić mianem komensalizmu.

Część ogólna dotyczy systematyki i filogenezy całej rozważanej grupy wąsonogów. Oparta jest ona, prócz przedstawionego materiału analitycznego, również na wynikach badań nad innymi przedstawicielami tej grupy (Bałuk & Radwański, 1967 a, b). Zdaniem autorów, grupa ta obejmuje — prócz rodzaju *Creusia* Leach, 1817 — także rodzaj *Pyrgoma* Leach, 1817, który był niejednokrotnie łączony z *Creusia*, oraz nowy rodzaj ustanowiony poprzednio: *Pyrgomina* Bałuk & Radwański, 1967. Cała rozważana grupa wąsonogów charakteryzuje się pewnymi cechami wspólnymi, a mianowicie: obecnością co najwyżej 4 płytek w koronie, wyciągnięciem płytki podstawowej i wykształceniem na niej własnej rzeźby, a także rozwojem swoim jedynie w obrębie żywych koralowców. Grupa ta wyróżnia się w obrębie rodziny Balanidae Leach, 1817, i odbiega od podrodziny Balaninae Darwin, 1854, do której była dotychczas zaliczana. Zdaniem autorów, stanowi ona nową podrodzinę — Creusiinae n.subfam., w obrębie rodziny Balanidae Leach.

Przedstawiona systematyka Creusiinae n. subfam. obejmuje poszczególne rodzaje i gatunki w kolejności ich stratygraficznego występowania. Ponieważ kolejność pojawiania się poszczególnych rodzajów: *Creusia* Leach, *Pyrgomina* Bałuk & Radwański i *Pyrgoma* Leach, następuje równocześnie z pewnymi konsekwentnymi zmianami planu budowy skorupy, który coraz bardziej odbiega od pospolitych Balaninae (Fig. 8), przedyskutowano zagadnienie filogenezy Creusiinae i wyodrębnienia się ich z głównego pnia Balanidae. Zdaniem autorów, zasadniczą przyczyną, powodującą indywidualizację Creusiinae, był neoteniczny rozwój pewnej gałęzi Balanidae, który nastąpił przypuszczalnie w oligocenie. Hipoteza takiego rozwoju opiera się na analizie cech, widocznych w ontogenezie pąkli (*Balanus* da Costa) — najstarszego filogenetycznie rodzaju w obrębie tej rodziny. Neoteniczny rozwój umożliwił zdomowienie się pewnych Balanidae w środowisku koralowcowym i prowadził do nabycia cech przystosowawczych (wyciągnięcie płytki podstawowej), warunkujących dalszy rozwój tych wąsonogów w obrębie żywych koralowców.

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ВАЦЛАВ БАЛУК & АНДРЖЕЙ РАДВАНЬСКИ

## МИОЦЕНОВЫЕ УСОНОГИЕ ПОСЕЛЯЮЩИЕ КОРАЛЛЫ

### Резюме

В настоящей работе обсуждаются вопросы строения раковины, а также систематики и филогенезиса относительно редкой и слабо до сих пор изучен-

ной группы аберантных усоногих, поселяющих кораллы. Группа эта принадлежит к семейству Balanidae Leach, 1817, но по сравнению с его типичными представителями обнаруживает заметное морфологическое отличие.

Аналитическая часть настоящей работы основана на изучении материала, собранного в полипниках *Tarbellastraea reussiana* (Milne-Edwards & Haime) из нижнетортонских илов Корытницы (южный склон Свентокржиских Гор). Материал этот, включающий ок. 60 экземпляров, представляет новый вид, *Creusia sanctacrucensis* n. sp.

Диагноз нового вида установлен на основании детального изучения морфологии раковин, сохраненных вместе с оперкулярными пластинками. Принимая во внимание большие разногласия в литературе, касающейся рода *Creusia* Leach, 1817, проведено ревизию всех его таксонов известных в ископаемом состоянии. Вид *Creusia sanctacrucensis* n. sp. (фиг. 1-3 и Пл. I-VI) отмечается от других иной морфологией оперкулярных пластинок и некоторыми деталями скульптуры короны. Характерной чертой изученных образцов является сохранённая пигментация раковины (фиг. 3), не наблюдаемая до сих пор у ископаемых представителей рода *Creusia*.

Учитывая сложные детали строения раковин изучаемых усоногих, перед описанием нового вида представлено краткие сведения относительно строения и способа роста раковин рода *Creusia* Leach. Вопросы касающиеся экологии *Creusia sanctacrucensis* n. sp. представлено в дальнейшей части работы на основании изучаемого материала. Кроме этого проведено дискуссия существовавшей до сих пор литературы. Существенной чертой, которая обсуждается более подробно, является рост этих усоногих, происходящий исключительно в пределах полипняков и постоянно возрастающих живых кораллов. Взаимное отношение обсуждаемых усоногих определено как комменсализм.

Общая часть работы посвящена систематике и филогенезе целой обсуждаемой группы усоногих. Основана она, кроме представленного аналитического материала, также на результатах исследований иных представителей этой группы (Bałuk & Radwański, 1967 a, b). По мнению авторов, группа эта включает, кроме рода *Creusia* Leach, 1817, род *Pyrgoma* Leach, 1817, неоднократно соединяемый с предыдущим, а также новый род установленный раньше, *Pyrgomina* Bałuk & Radwański, 1967. Вся обсуждаемая группа усоногих характеризуется некоторыми совместными признаками, а именно: присутствием не более чем 4 пластинок в венце, удлинением основной пластинки и образованием на ней своеобразной скульптуры, а также своим развитием только в пределах живых кораллов. Эта группа очень четко выделяется в семействе Balanidae Leach, 1817, и уклоняется от подсемейства Balaninae Darwin, 1854, к которой до сих пор была причислена. По мнению авторов, становится она особое подсемейство *Creusiinae* n. subfam., в пределах семейства Balanidae Leach.

Представленная систематика *Creusiinae* n. subfam. вмещает отдельные роды и виды в порядке их стратиграфического распространения. Так как последовательность появления отдельных родов: *Creusia* Leach, *Pyrgomina* Bałuk & Radwański и *Pyrgoma* Leach, наступает одновременно с некоторыми последователь-

ными изменениями плана строения раковины, постепенно всё больше отклоняющимися от обыкновенных *Balaninae* (фиг. 8), продискутировано вопрос филогенезиса *Creusiinae* и выделения их из главного ствола *Balanidae*. По мнению авторов, основной причиной, вызывающей индивидуализацию *Creusiinae*, было неотеническое развитие какой то ветви *Balanidae*, которое состоялось вероятно в олигоцене. Гипотеза такого развития основана на анализе признаков выступающих в онтогенезе *Balanus da Costa* — филогенетически самого старшего рода среди этого семейства. Неотеническое развитие сделало возможным прижиться некоторым *Balanidae* к сообществу кораллов и привело к приобретению адаптированных свойств (удлинение основной пластинки), обуславливающих дальнейшее развитие этих усоногих среди живых кораллов.

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## PLATES

Plate I

- Fig. 1. Five individuals of *Creusia sanctacrucensis* n. sp., growing more or less simultaneously within the corallum of *Tarbellastraea reussiana* (Milne-Edwards & Haime) and partly prepared from it; bases removed, crowns visible from their internal side. Creusoid barnacles were completely overgrown by the anthozoan which bolted the orifices of particular shells, forming a prominent stopper;  $\times 5$ .
- Fig. 2. Upper surface of the corallum of *Tarbellastraea reussiana* (Milne-Edwards & Haime) with 6 fragments of bases of *Creusia sanctacrucensis* n. sp. Different sizes of the individuals of creusoid barnacles indicate that they were buried in sediment during their growth and, therefore, together with a live anthozoan;  $\times 5$ .

Lower Tortonian, Korytnica.

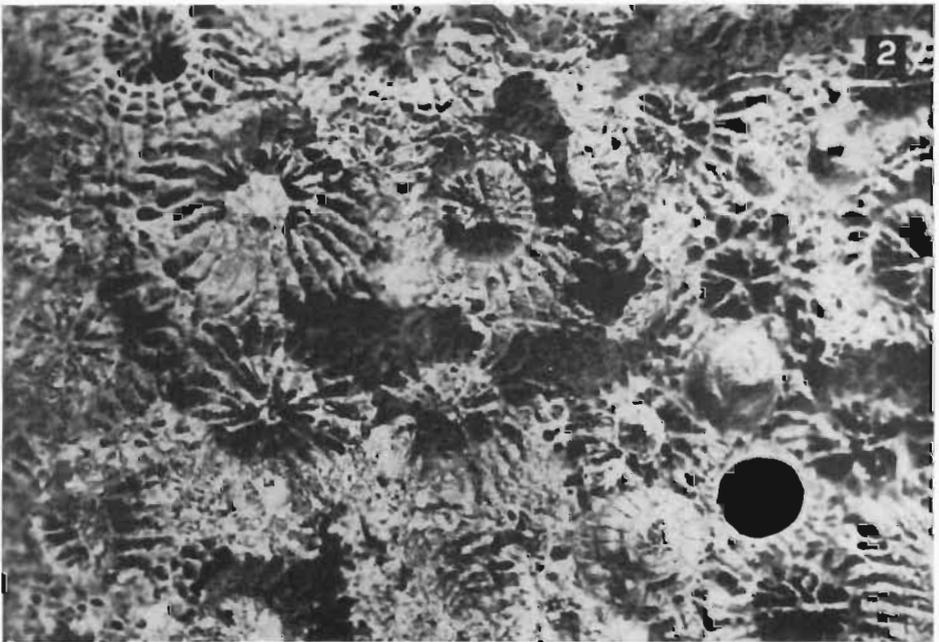
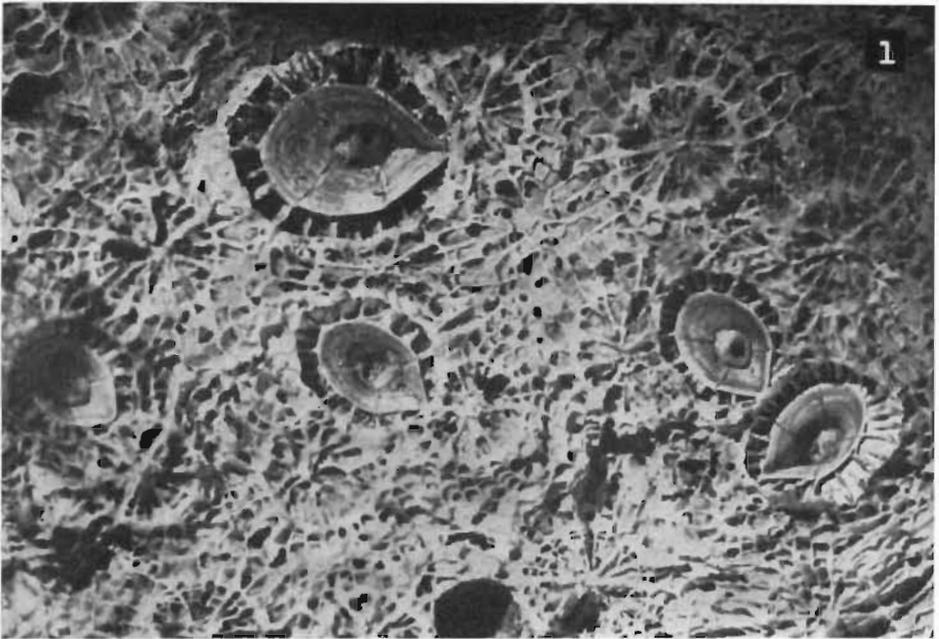




Plate II

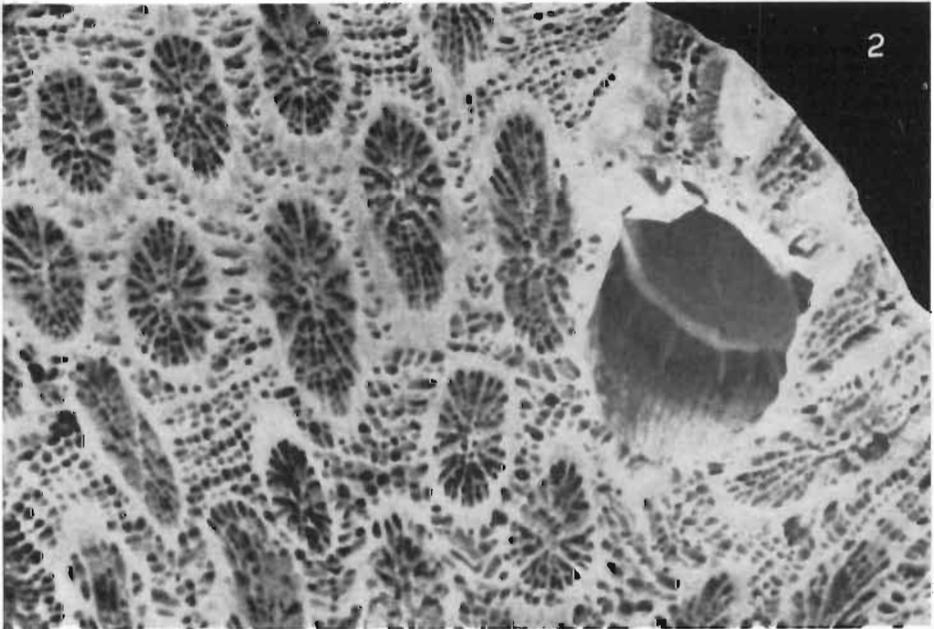
Spreading of corallites of *Tarbellastraea reussiana* (Milne-Edwards & Haime)  
around a shell of *Creusia sanctacrucensis* n. sp., longitudinal section;  $\times 4$ .

Lower Tortonian, Korytnica.

Plate III

Figs. 1-2. Other examples of spreading of corallites of *Tarbellastraea reussiana* (Milne-Edwards & Haime) around a shell of *Creusia sanctacrucensis* n. sp. Sections oblique to the vertical axis of the shell;  $\times 4$ .

Lower Tortonian, Korytnica.



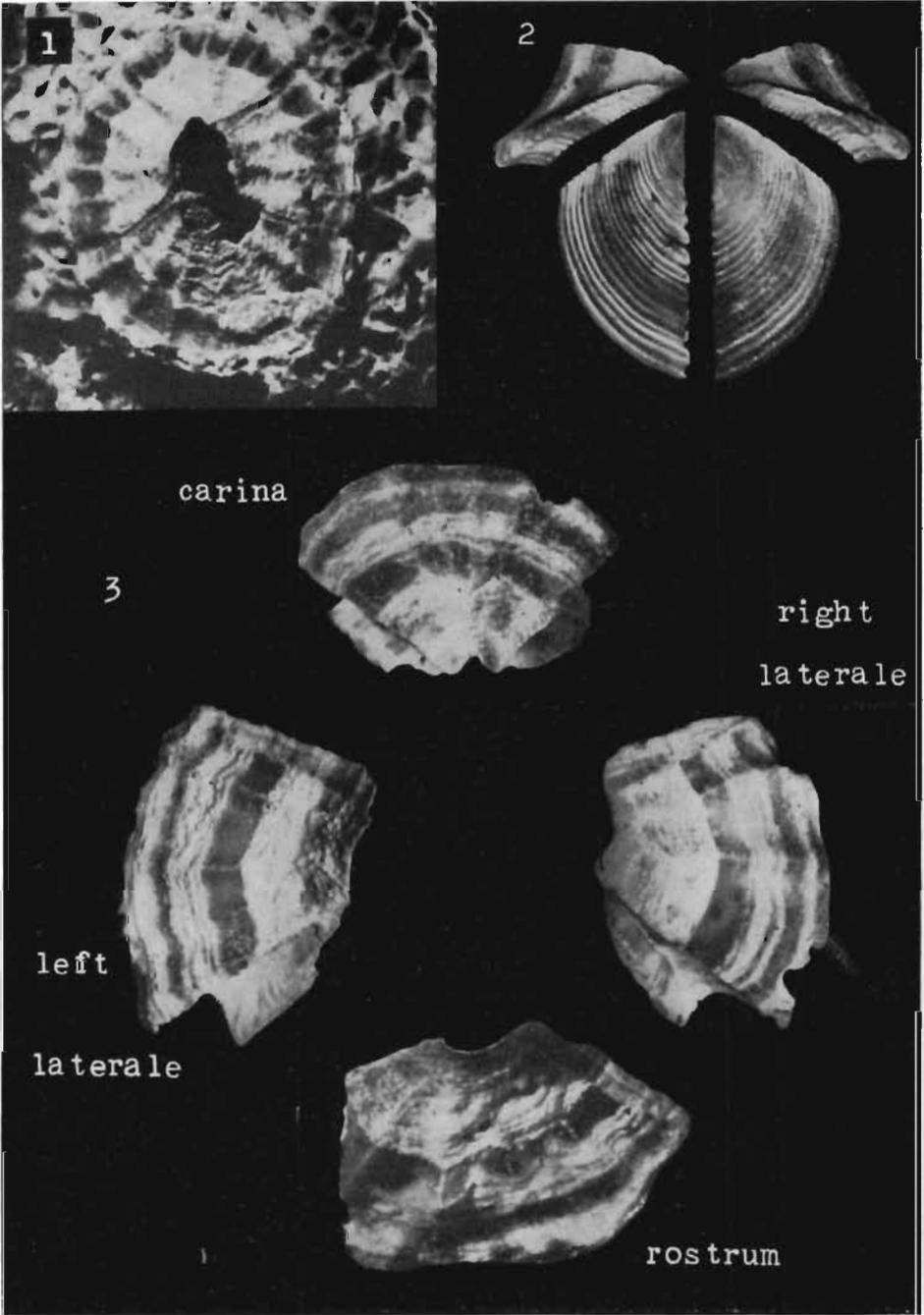


Plate IV

*Creusia sanctacrucensis* n. sp.

- Fig. 1. Complete crown (edge of rostrum slightly damaged near the orifice). A wide, coloured stripe visible near the crown edge;  $\times 10$ .
- Fig. 2. Opercular valves of another individual (constituting holotype of the species). Two coloured stripes visible, one narrower near basal margins in terga and scuta, and another, a wider one,—in the central part of valves;  $\times 15$ .
- Fig. 3. Separated compartments of another individual (rostrum damaged on the left side). Position of compartments identical with that in Fig. 1; individual compartments explained by inscriptions. Five coloured stripes, different in width, visible (most distinctly on the right laterale and carina);  $\times 15$ .

Lower Tortonian, Korytnica.

Plate V

*Creusia sanctacrucensis* n. sp.

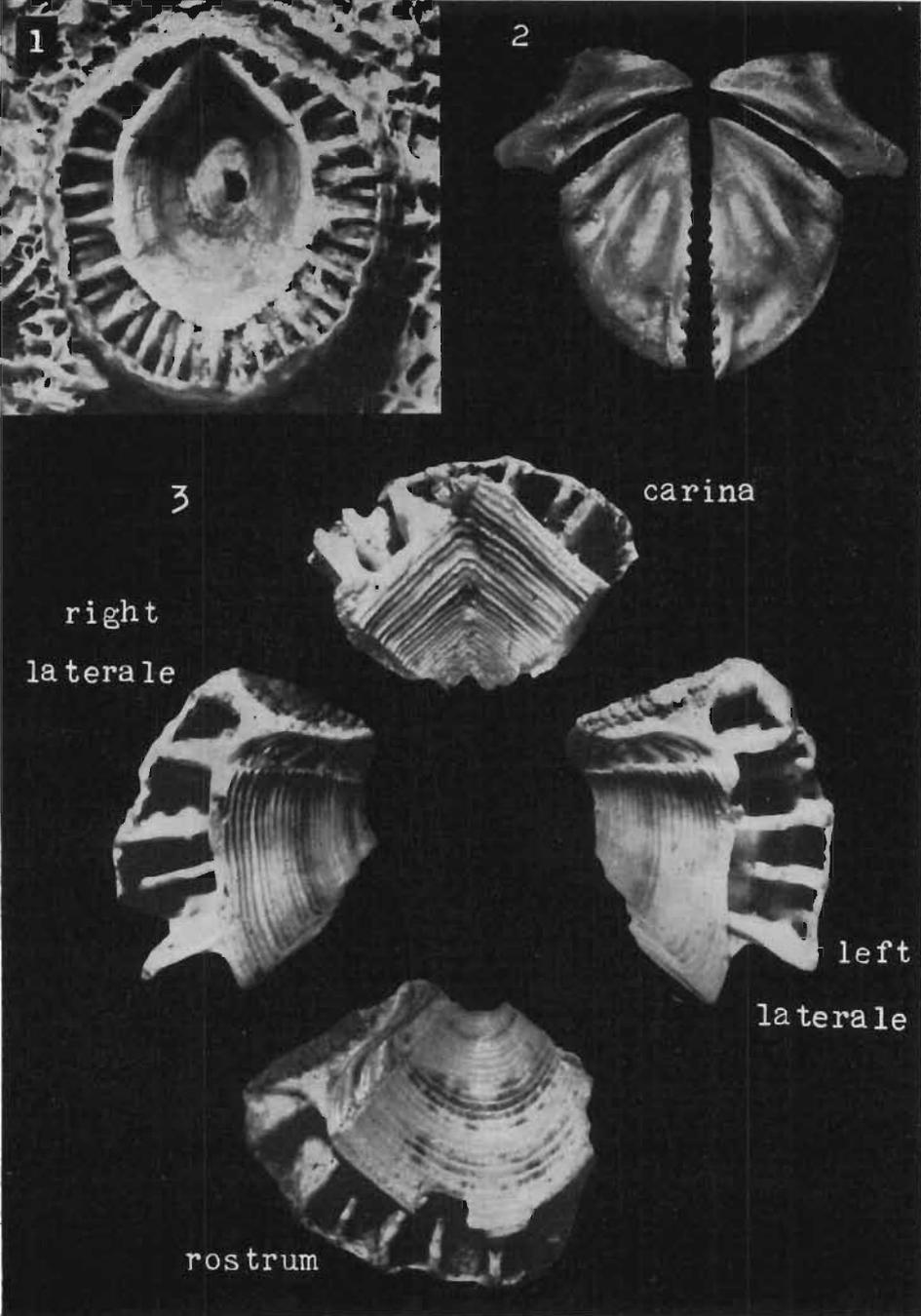
The specimens, the same or analogous ones to those of Plate IV, but viewed from their internal side.

Fig. 1. Complete crown of an individual marked by a rounder outline of the crown and greater number of ribs (visible at the very edge of the crown where a fragment of basis is preserved, their number is equal to that of corresponding septa);  $\times 10$ .

Fig. 2. Opercular valves of the holotype presented in Plate IV, Fig. 2.

Fig. 3. Separated compartments, the same as in Plate IV, Fig. 3.

Lower Tortonian, Korytnica.



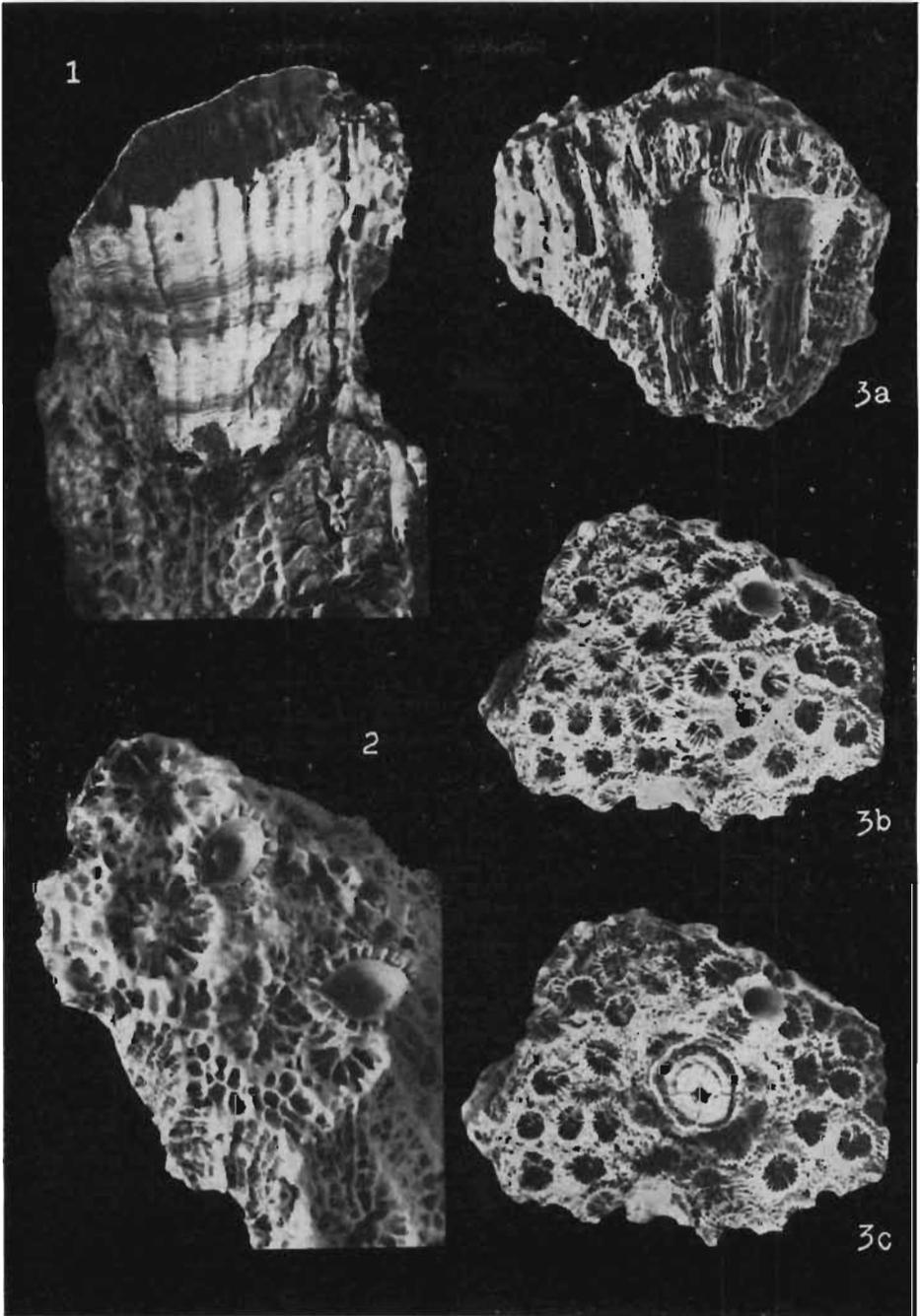


Plate VI

*Creusia sanctacrucensis* n. sp.

within the coralla of *Tarbellastraea reussiana* (Milne-Edwards & Haime)

- Fig. 1. Prepared fragment of basis; three coloured stripes visible;  $\times 7$ .
- Fig. 2. Two juvenile individuals overgrown probably alive by an anthozoan. In one of them tergum is visible embedded in a stopper formed by the overgrowing anthozoan;  $\times 7$ .
- Fig. 3. Influence exerted by the shell of the cirriped on the arrangement of corallites overgrowing it;  $\times 2$ .
- a* lateral view, the swelling visible on the surface of corallum (in addition, three other individuals of creusoid barnacle growing near each other);
- b* the same specimen—top view, irregular arrangement of corallites, visible within the same swelling (in addition to swelling, a fragment of basis of another individual growing at the surface of corallum);
- c* crown of the cirriped situated below the swelling, visible after removal of the latter.

Lower Tortonian, Korytnica.