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The Hymenopterous Insects of the superfamily Chalcidoidea developing within the receptacles of Figs.

THEIR LIFE-HISTORY, SYMBIOSES AND MORPHOLOGICAL ADAPTATIONS

(Discourse delivered at the Zurich Polytechnic School on the 13rd of April 1958 on the occasion of the Centenary of the Entomolocical Society of Switzerland (1)).

[In questi ultimi anni è andato aumentando il numero dei ricercatori che, nelle regioni orientali estraeuropee, si occupano degli Insetti dei Fichi. Per tali ricercatori la lettura di memorie scritte in lingua italiana costituisce un ostacolo grave e, talora, insormontabile. Mi è sembrato pertanto utile tradurre in lingua inglese il discorso da me tenuto nel 1958 al Politecnico di Zurigo, il quale riassume lo stato attuale delle nostre conoscenze sul comportamento biologico della *Blastophaga psenes* L. e della *Philotrypesis caricae* L.].

The Insects which develop within the receptacles (syconia) of Figs, in antagonistic reciprocal and mutualistic symbioses with the host plants are Hymenoptera Apocrita Terebrantia, belonging for the most part to the superfamily Chalcidoidea. At present, however, we know a very small numbers of them. Indeed, if among them we take into consideration only the primary sycophiles, surely able to develop within the inflorescences of *Ficus* (without depending upon the previous intervention of other representatives of the superfamily), that is the *Agaonidae* included in the sub-family *Agaoninae*, we find that the species described do not reach a hundred and a half (arranged in a dozen of genera), besides a few tens of entities, on which it is not yet possible to express one's opinion objectively. I have temporarily relegated them into a group of uncertain nature or doubtful value (1). This in comparison with the seven hundred or so species belonging to the gen. *Ficus* recognized for the various regions of the Earth. Therefore, the amount of our knowledge in the taxonomical field is reduced to the determination of the existing species.

Another reason of perplexity as regards the taxonomic arrangement of the forms is given by the difficulty of associating the opposite sexes. Va-

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rious species of Chalcidoidea, belonging also to different genera, may develop within the receptacles of the same species of *Ficus*. Usually (as we know) we find within them a single Agaonine, frequently associated with a Sycophagine, but the Idarninae are often numerous. In the Fig-insects sexual dimorphism is highly developed and when a species, as it happens in most cases, has only heteromorphic and even polymorphic males (having discontinuous unisexual polymorphism), it is not always easy to associate with a certainty a given female with her « legitimate husband » without a biological study « in loco ». This is proved by the fact that many « marriages celebrated on paper » by the speciographers have been to be dissolved, even after many years of « seemingly regular conjugal life » (2). Still as concerns taxonomy there is an important lacuna inhibiting the possibility to consider in the whole the general situation of the faunules living in the Fig receptacles and this serious lack regards the members of the family *Agaonidae* belonging to the subfamily *Sycophaginae*. The twenty species or so of this group that we know are arranged in about ten genera, and only the female sex is known for almost all of them. We know little or nothing about them. In the first place we ignore whether they are really primary or secondary sycophiles (that is depending for their development within the receptacles of the host plants on other synoecetes); we are not able to realize the structural characteristics of their males (the few things lately discovered have entangled rather than disentangled the matter (3); at last we observe such a variability of morphological behaviours that we are compelled to increase the number of the generic groups and present the subfamily in a particular position, which may also be a stage of evolutional arrangement (4).

The Chalcidoidea which are secondarily sycophiles are almost all included in the family *Torymidae* and subfamily *Idarninae*. I think, however, that a thorough study of their structures will induce us to revise their classification completely. They are even less known than the forms before mentioned, because the researches that I made and am making into other branches of Entomological knowledge have only allowed me to begin inquiries into the rich materials owned by me, coming from all the countries of the World.

If our taxonomical knowledge is little satisfactory, biological information is almost completely lacking. The only Agaonid sufficiently known to us is a European species, *Blastophaga psenes* L., which lives as a guest of *Ficus carica* L.; several years ago I devoted a big paper (5) to its morphology, anatomy, development and ethology. The only Torymid almost equally known is another species of Europe, *Philotrypesis caricae* L. living is symbiosis with the *Blastophaga* of which I studied thoroughly the structure and habits (6); from this inquiry I inferred its character of cleptoparasite lately confirmed by J. Joseph Kuttamathiathu (7-9). Few other data have been found on some exotic species; these data, however, give a vague notion of very interesting habits and life-cycles.

This is all we know on the matter so far.

Now, in order to accept the invitation made by the Direction of this Society, which was so kind as to receive me as an « honorary fellow » and to request me to speak before YOU on the occasion of the happy event of the first centenary of its foundation, I shall briefly synthetize our knowledge on the habits and morphology of these extraordinary Insects, showing incidentally the general problems involved in their behaviours.

Let us begin this account considering how *Blastophaga psenes* L. and *Philotrypesis caricae* L. live and develop, which are the mutual relations between the two species and those established with the host plant.

Blastophaga psenes L. (in the places where I made my observations on it, that is in the surroundings of Naples) has three generations a year within the three cycles of receptacles (respectively called in Italian: « fioroni », « forniti » and « cratiri »), which follow each other on the Caprifig (*Ficus carica* L.) (1). It is a proterandrous and polygynic species. The males are apterous, depigmented, solenogaster. They emerge from the galls (derived from the generally brevistylar female flowers) where they developed, making their way with the mandibles; then they get up on the galls containing the newly emerged females, gnaw again with their mandibles a hole, introduce inside the tubular portion of the abdomen and fertilize their mates, which are still doubled upon themselves within the little dark case. After repeating the operation several times in as many gynophorous galls, they, die within the receptacle being exhausted. The female, instead, having come out from the cecidium through the hole made by the male (if it is necessary she widens it) leaves also the receptacle (by this time a mature collective fruit) through the ostiolar canal; its scales (squamiform phyllomes) easily yield and allow the insect to go out. Thus the females get out perfectly undamaged; they fly off and go in search of the inflorescences of the following cycle and penetrate into them again through the ostiolar canal. Here, however, they find conditions differing from those of the collective fruits. The scales lining the ostiole and, particularly, the more external ones, turgid, resisting and imbricated as they are, quite imperforable compel the hymenopteron to a long, hard and tiring work. The *Blastophaga* wedges its head under the free edge of the outer scales, then goes on laboriously through the scales and overcomes the obstacles by giving up its wings (particularly the fore wings), which almost always remain entangled on the way, and often cutting off its antennae (beginning from the 4th-5th antennomere). Having thus reached the interior of the receptacle (in some cases the female does not achieve her purpose and dies half-way), the *Blastophaga* sets up oviposition: she introduces her short terebra into the bifid asymmetrical stigma of each galligenous female flower, follows at first the stylar canal, then bores the funicle and lays the long-pedunculate egg between the inner integument of the ovule and the nucellus so as to leave it fastened with its

(1) In other places, two or four generations have been reported.

peduncle to the tissue of the funicle, and, therefore, to prevent its possible shifting in consequence of the development of the gall. On the whole a female may lay 300 to 400 eggs and after oviposition dies in the interior of the syconium; but together with each germ she discharged, according to what I discovered in 1920, a little of the secretion elaborated by the remarkable glandular complex annexed to the genital apparatus; at the emergence of the insect this secreted material is completely stored in an enormous reservoir. Obviously the secretion acts on the secondary nucleus of the embryo sac and makes it enter on segmentation as if the normal double fertilization and its fusion with one of the two spermatic nuclei had occurred. Thus the endosperm, as half a century ago the botanist B. LONGO (1906-1909). first pointed out (10-11), has parthenogenetically origin (1). Afterwards it will serve as a food to the larva of the *Blastophaga*. The flower is trasformed into a gall and the embryonic development is inhibited since the beginning (parasitic castration) (12, 13). The larva of the hymenopteron emerges from the egg after a few days' incubation and takes a time ranging according to the season from two to many months to reach full-growth. Metamorphoses occur within the gall. The females, on leaving the receptacles of the first cycle, come out through the ostiole of the pseudofruits and are compelled to pass over the crown of the male flowers so that they are laden with the adherent pollen discharged by the anthers. Therefore when they penetrate into the inflorescences of the receptacles called « forniti » they pollinate some normal flowers and allow the formation of some seeds. Later on the Fig-wasps which develop and come out from the collective fruits called « forniti » (that is containing few male flowers) gain admission into the inflorescences of the « cratiri », where the insect will overwinter as a full-grown larva; the females leaving in spring the inflorescences of the « cratiri » containing few male flowers come into the inflorescences of the « fioroni » and thus begin again the yearly cycle. In plant biology the procedure of fertilizing the flowers of a cycle with the pollen of the foregoing cycle is a unique rather than a rare method. In fact we have to notice a synchronical development of both male and female flowers belonging to two different generations and, on the contrary, a paradoxically precocious proterogyny (12, 13).

Also *Philotrypesis caricae* L. has three generations a year within the Caprifig and is a proterandrous and polygynic species too. The males which are stenopterous, brachypterous, micropterous or subapterous (in a word meiopterous), depigmented, polymegetical and polymorphic, leave the galls where they developed gnawing a way through the walls with their mandibles and fertilize the females arisen from the galls opened by them in the cavity of the receptacle. It seems that they may mate also within the galls before the fe-

(1) LONGO thought that it was the simple deposition of the egg to determine the phenomenon.

males leave them. Certain is it that, as soon as the males perceive the females, they seize and possess them and at times do not give them even the time of coming completely out of the cell where they developed. The female walks quickly in the dark cavity of the collective fruit, carrying the « hot-tempered cavalier », who clings to her side, to her back and also ventrally in a very curious way. The males, as those of the *Blastophaga* do, die within the receptacles; on the contrary the females leave the syconia through the ostiolar canal; therefore they behave in the same way as the *Blastophaga* does. However, in order to lay eggs (long pedunculate and exhibiting at the opposite side a particular process (6)) within the galligenous flowers of the inflorescences belonging to the following cycle, they do not penetrate, in conformity with the habit of the Agaoninae, into the same inflorescence, but remain outside the receptacle and after running over the urn in various directions, perform oviposition; during this operation they graze the surface of the receptacle with the distal end of the antennae bent at right angle between the first and the second segment (6). Having found out the suitable point, the insect rises on its legs, sets upright its gaster, bends down its long terebra and, making it pass between its hind legs, points the sting forward putting the distal end of the valves into contact with the support where they stop. Then it pierces the wall of the receptacle with its stylets, which penetrate very deeply and reach the interior of the galligenous flowers.

Where does the larva of the *Philotrypesis* develop and on what does it feed? Is it a parasite or a simple synoecete of the *Blastophaga*? As far back as 1920-1921 when I began the researches on the biology of Fig-insects in the surroundings of Naples, being still assistant to the great entomologist Filippo Silvestri, I had been struck by various facts which I shall enumerate briefly. I could no longer continue my researches in regard to *Blastophaga psenes* L. and *Philotrypesis caricae* L. because in 1926 I left for ever Southern Italy returning to my Northern region to direct the Entomological Institute of the University of Bologna.

1. - The anatomical study of the *Philotrypesis* had allowed me to point out that the glandular apparatus annexed to the female reproductive organs is noticeably reduced having one of the glands (the gland that in the *Blastophaga* is provided with an enormous reservoir for the storage of the secretion) very small and without reservoir and the other subatrophic.

2. - The morphological study had allowed me to enlighten a continuous unisexual polymegetism involving eumegetical, epimegetical and hypomegetical forms; this phenomenon was wider and more conspicuous in the males, whose determinism seemed presumably to be of trophic nature (I pass over the complex polymorphic behaviour of the males and other discontinuous meaningful variations the discussion of which is here out of place).

3. - After all, the ethological study had showed clearly to me that the females of *Philotrypesis* may live much longer than those of *Blastophaga*; if some inflorescences of the Caprifig containing only females of *Philotrype-*

sis are isolated, after some time the receptacles fall (which does not happens, if we let in also members of *Blastophaga*); that, at last, it never happens to find syconia infested only by the *Philotrypesis*, while it is possible, and even easy, to find syconia infested only by the *Blastophaga* (6).

The discovery of these facts made me believe that the *Philotrypesis* was a parasite of the *Blastophaga*. Now it was a question of determining the type of parasitism performed by it. The careful examination of the clear and incontrovertible facts found out by me and the procedure leading in the field of reflection to reject what is unlikely or unsustainable (I learnt this procedure at the school of other two great zoologists, CARLO EMERY and BATTISTA GRASSI) led me in 1930, when I brought out the monograph on the gen. *Philotrypesis* Forst. (6), to formulate, the following hypothesis, which I affirmed would agree with all the facts discovered: « *Philotrypesis caricae* is a parasite of *Blastophaga psenes*; its larva, however, does not feed on the body of the host in any stage of its postembryonic development, but on the supplies that the Agaonine has prepared for its offspring ». Therefore it would be a question of a true « cleptoparasitism » (14). My hypothesis were fully confirmed about twenty five years later. Mr. J. JOSEPH KUTTAMATHIATHU (7, 9) coming from India, who in France under the direction of my friend Prof. P. P. GRASSÉ has studied again *Philotrypesis caricae*, has been able to see that the larva of this species, after living for a short time in harmony with that of its synoecete, enters eagerly into trophic competition with it; it devours a great part of the albumen formed parthenogenetically in consequence of the injection of the genital glands secretion discharged by the mother *Blastophaga* and actually lets the « legitimate owner » of the pabulum starve (1). Therefore the unisexual polymorphism could be explained with the different amounts of food that are left at the disposal of the larva of the *Philotrypesis* and the wider extent of the phenomenon observed in the males could be accounted for with the differential mortality of both sexes, as the males (haploid) survive more than the females (diploid) (2) (9).

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(1) I had supposed that the larva of the *Philotrypesis* suppressed the egg or the newly hatched larva of the *Blastophaga*. KUTTAMATHIATHU in his first note (1955) (7) affirms the same thing, in the third (1957) (9) points out the report above mentioned.

(2) In his third note (1957) J. JOSEPH KUTTAMATHIATHU refers the following words of mine: « I said that it is unknown whether the *Philotrypesis* and other allied genera are parasites of *Agaoninae* or merely their inquilines, or in other words synoecetes, that is whether they are carnivorous or phytophagous in the larval stage ». After quoting these words, he stopped! Now I must inform that these words were immediately followed by the following ones: « In 1930, and regarding *P. caricae*, I discussed as a working hypothesis the possibility that the larvae of *Philotrypesis* have a phytophagous diet, but, nevertheless, are compelled to develop within the flowers where an Agaoninous female has laid an egg and a little secretion of the glands annexed to her genital apparatus, determining ... » etc.

The first words, quoted by JOSEPH KUTTAMATHIATHU, were, obviously, suggested by the prudence that must always restrain the researcher mindful of the objectiveness of his work. The others made my idea clear immediately.

Considering the above mentioned facts concerning the case of *Ficus carica* L. we can notice the existence of a symbiosis between three symbionts: the host plant, *Blastophaga* and *Philotrypesis*; that is between a plant and two Insects. The *Blastophaga*, indeed, has contracted a very binding mutualistic symbiosis with the Fig. In fact the insect acts by hormonal way on the secondary nucleus of the embryo sac of the flowers of the plant and causes the (parthenogenetic) formation of the albumen on which its own larva will feed, but at the same time fertilizes some normal flowers with the pollen taken by itself passing over the anthers of the male flowers of the preceding receptacle from which it came out. The *Philotrypesis* on the contrary is an antagonistic symbiont and therefore a parasite of the *Blastophaga*, but belongs to the group of the « cleptoparasites ». Owing to the reduction of its genital glands cannot induce in the flower the same phenomena as the *Blastophaga* does and thus profits by the work of the former and lays eggs where the Agaonine has prepared the pabulum for its offspring. The larva of the *Philotrypesis* which is more fit for this work will steal the food from its antagonist and bring the latter to death. At the end the result of the competition is the same as it would be if the larva of the *Philotrypesis* were zoophagous and fed on that of the *Blastophaga* the more females of *Philotrypessi* emerge from a syconium, the fewer females of *Blastophaga* come out from it.

Now, a question rises spontaneously; can the behaviours pointed out laboriously in the two European species and the relationship between either of the species and between both and the host plant be extended to all the representatives of the faunules of Figs existing on the Earth? In other words, must we think it likely that all the sycophilous Idarninae are cleptoparasites of their synoecetes Agaoninae? Or is it possible that the things proceed in a different way, at least as regards particular groups? Prudence the daughter of wisdom, advises us to wait before expressing our opinions until our knowledge is more advanced in extent and depth.

In the mean time it is necessary that the biologists of the various countries of the World (of the continents and islands) should make up their minds to investigate seriously and conscientiously the habits of the various species in the various-sized and various-formed receptacles of the many existing species of *Ficus*. In this regard, as I said, we know almost nothing. It is known to us (PEMBERTON, 1921) (15) that the females of an Australian Agaonine, *Pleistodontes Froggatti* Mayr, after emerging do not come outside through the ostiole, but from any point of the wall of the receptacle, through which they make their way by force; nevertheless they leave the receptacle laden with adherent pollen, as in the receptacles of the host Fig (*Ficus macrophylla* Desf.) the male and female (brevistylar and longistylar) flowers are promiscuously associated and distributed everywhere; it is known to us (GRANDI, 1932) (2) that the females of an Idarnine of Sumatra (if it can be considered an Idarnine), *Neosycophila omeomorpha* Grnd. leave likewise the receptacles of *Ficus gibbosa* Bl. through

the walls passing straight from the galls where they developed to the outside, after excavating the peduncle of the galligenous flower; at last it is known to us (GRANDI, 1923) (2) that the females of a *Sycophila* Walk., developing in Sumatra within the syconia of *Ficus ampelas* Bl. finds its way to freedom boring the walls or the ostiolar scales of the receptacle. But how many and what secrets are still concealed in the inviolate cases of the receptacles belonging to so many *Ficus*? Those, for instance, of *Ficus linearis* Becc. of Borneo, which are smaller than a chick-pea or those of *Ficus callicarpa* Mig. of Borneo too, having the size of a big lemon? And those of *Ficus Beccarii* King, *F. stolonifera* King, *F. uncinata* Becc., which are half-hidden in the ground of the damp forests where plants grow or are inserted on subterranean flagelliform branches spreading around from the base of the tree (BECCARI, 1921) (16)?

In this rapid excursion throughout the wonderful world of the sycophil Terebrantia let us give up biology to pass to the structures. Let us set, namely, to show the somatic modifications undergone by the insects in question during their particular evolution and in relation to the very particular environment where they develop and live at least for a part of their life; and, therefore, to enlighten the extraordinary « morphological adaptations » they have to submit to. Now, however, many pages of condensed writing and a very long speech would be necessary in order to deal properly with so complex an entanglement of facts. Of course I have no intention of submitting my kind audience to such a test of endurance. Therefore I shall confine myself to a concise survey of the subject and to some conclusive considerations. Those who are interested in getting a more thorough knowledge of the subject can consult the works published by me in 1923 (17), 1925 (18), 1955 (19, 20) and 1959 (21); the last in « Atti dell'Accademia Nazionale dei Lincei », in « Mémoires de la Société Royal d'Entomologie de Belgique » and in the volume edited by the « Smithsonian Institution » in honour of Dr. R. SNODGRASS (19-21).

Let us bear in mind that the female imagoes after emerging may live: either completely out of the receptacles in the forms that lay eggs remaining outside the inflorescences, as almost all the Idarninae do, or partly outside (from the moment in which they leave the collective fruit to the time that they come into the inflorescence of the following cycle) and partly inside (from this time until their death) in the forms which (like the Agaoninae) must penetrate into the inflorescences to lay eggs. Likewise let us remember that the males imagoes after emerging, may live: either outside the receptacles in the homeomorphic winged forms (which, however, are a little minority); or completely in the interior of the collective fruit, where at the end of their sexual activity they die, in the apterous or meiopterous heteromorphic forms (which are the greatest majority).

Well now the females belonging to the first group (that is living outside) do not exhibit, to speak morphologically, other modification than a more or

less exceptional development of their terebra, joined sometimes to peculiar behaviours of the last urites or other portions of the gaster. Instead the females belonging to the second group are remarkably transformed.

Some of the modifications undergone are characteristic of all the taxonomic groups considered; others are peculiar to determined genera or species. Both seem to be related to the work the insect has to accomplish in order to penetrate into the interior of the inflorescences and lay eggs. Some of them, however, turn out to be unnecessary, but such as to facilitate the female's efforts. For instance we can mention the flattening, disintegration and, therefore, the deformability of the head-capsule; the characteristic structure of the first three joints of the antennae and the toothlike setae bent backward that cover the dorso-median face of the 2nd joint; the rise of a new organ, that is the particular laminar process of the mandibles exhibiting crosswise many keels or many denticles, which overlap outside the ventral face of the cranium (the process is very long in the species having a much elongated head); we mention also some series or complexes of minute tegumentary processes sharp-pointed and bent forward, confined to various regions of the body or its appendages; the strenghtening of the fore – and hind – legs, the shortening of the tibiae and their rich armament including spine-like or tooth-like setae; the transformation of the maxillary stipites in sclerotized plates shaped like a chisel and so on. Other changes are the consequence of the involution or rudimentation of some organs; among them the atrophy of the upper lip, the noticeable reduction of the maxillae and lower lip, the atrophy or disappearance of the ocelli, the more or less advanced obliteration of the marginal, post-marginal and stigmatic veins of the wings, and so on. Other changes can be considered « inventions », which generally are hyperplastic and seemingly meaningless. We may take as examples of them the exceptional lenghtening of the cranium, the turning upward of the mandibles or their transformation in somewhat strange and complex gnatites; the rising finally of new, enormous, odd organs as, for instance, the plates placed at the end of the fore tibiae to differentiate the series of microspinules turned backward, which in other species are placed elsewhere.

Like the females, the males belonging to the first of the two above mentioned groups (that is the winged homeomorphic ones), which as imagoes live outside, do not appear modified. On the contrary the males belonging to the second above mentioned category (that is those which emerge and die within the receptacles where they developed) are deeply modified and, sometimes, to such an extent as to lose also some important characteristics of the order and even of the class they belong to. Also in this case some modifications are common to the representatives of the various taxonomic groups, others are characteristic only of some genera or species. All, anyway, are related to determined functions (opening of their own galls from the inside and those of the female from outside; peculiar ways of mating, and so on) or to the microhabitat (the interior of the receptacles of the host plant) where they pass

their life from the time they emerge until they die, mostly, without knowing the sun's light (1). Among the modifications in question we observe some, as in the females, which seem to be of some use (shortening of the antennae by oligomery and fusion of articles, the sensillae of which are gathered at the distal end of the last joint; strengthening of the mandibles; particular behaviours of the thorax; solenogastria; special structure of the 9th urite; strengthening of the fore and hind-legs and so on); some which can be included among the phenomena of involution and rudimentation (atrophy of the upper lip; reduction, atrophy or obliteration of the maxillo-labial complex; reduction or disappearance of the intergnathal cavity and oral opening (which leads to astomia and aphagia); involution, atrophy and disappearance of the middle legs (which leads to the formation of tetrapod individuals); involution, atrophy and disappearance of two wings (which leads to the formation of dipterous individuals) or of all four wings (which leads to the formation of meiopterous or apterous individuals); disappearance of the cerci; and so on. We observe also some which, on the contrary, present themselves as hypertelic behaviours (a sometimes paradoxical hypertrophy of the antennary scape, mandibles, cranium, first and last tarsomere, and so on); some which also we may include among the last two categories now considered and which seem to be correlated to other modifications undergone by the organ (antennary and tarsal oligomeries; malformation of some portions of the legs and ankylosis of the articulations; more or less advanced coalescences of thoracic nota and the propodeum; disintegration of the cranium and pronotum into sclerites articulated to each other, and so on); some, finally, which obviously are (maybe indirectly) related to the special microhabitat where the insects live (depigmentation of the tegument, disappearance of the ocelli, particular localization of the antennae inside fossae, or even inside cranial pockets dorsally open or closed, and so on).

Moreover it is necessary to fix our attention on a triple series of phenomena, that is: 1) the fact that the heteromorphic males of many Idarninae show us a noticeable variability, sometimes complex, continuous or not, megetical and morphological, etc.; 2) that the heteromorphic males of the various species belonging to a given genus may exhibit so uniform a constitution as to make their discrimination extremely difficult, or, on the contrary, may be so different as to be discerned very easily; 3) that a biological cycle based on the laying of the eggs inside the pistillate flowers of Figs (at least of some species) which give rise to the galls, where the insect performs its ontogenetical (embryonic and postembryonic) development, may normally take place without interference of any modification in the species adapting themselves to haunt such an environment.

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(1) Sometimes the males availing themselves of the way made by the females through the ostiole, come out from the receptacles and fall to the ground where, however, they die at once.

What may we conclude in regard to the morphological « adaptations » of Fig-Insects?

In a paper of mine before mentioned, the one issued in 1955 in « Memorie dell'Accademia Nazionale dei Lincei » (19), I studied rather deeply and widely the morphological « adaptations » in the Insects having a specialized diet, taking into consideration a noticeable number of species belonging to various orders of Holometabola in their imaginal or larval stages. On that occasion I affirmed that the results of my researches were such as to permit, perhaps, a general examination of the data and an attempt to interpret the phenomena of the morphological adaptation. These phenomena constitute one of the most entangled and incumbent problems of general biology. I added, however, that I did not intend for the moment to enter into such a question, as I thought that our knowledge regarding this subject was not sufficient to permit a serious and objective endeavour; which did not prevent me from presenting in the meantime the general conclusions from the results of my researches and their coordination. These conclusions are arranged in 18 units.

Allow me, Gentlemen, to end the lecture I have had the honour to deliver before You, reporting only the conclusions regarding the Fig-Insects. They are the following:

1) The modifications undergone by the sycophile Chalcidoidea are always related to the function the organ or the groups of concerned organs must perform, and, on the whole, to the work the whole organism must fulfil in the particular environment where it lives.

2) Approximately these modifications can be arranged in five groups: *a*) involutions, rudimentations, or disappearance of organs or portions of them, *b*) abnormal (hypertelic) developments of organs or portions of them; *c*) displacements of organs or portions of them; *d*) transformations of organs or portions of them; *e*) development of new portions of pre-existent organs and even of new organs.

3) When it is question of new organs we always observe more or less advanced modifications of determined somatic regions, which organize in special formations what elsewhere is a characteristic of the regions themselves.

4) The modifications undergone by a species (or by a taxonomic group of higher rank) are generally numerous and complex and often functionally co-ordinated, as they may concern many organs, each of which of course, performs its own function, correlated with the functions of the others, within the limits of the general behaviour.

5) The modifications concerning the same organ may be in the various species of a genus (or of taxonomical groups of higher rank) different (though all correlated to the same function) and more or less advanced in a determined sense.

6) An organ modified in such a way as to acquire an inconvenient form and size, viz. hypertelic, may exhibit other corrective modifications, which

seem to attenuate, or actually attenuate, the functional inconveniences depending on its abnormal structure.

7) The modifications undergone by the sycophile Chalcidoidea and always related, as we have said before, to the function the organ or the concerned organs must perform, do not seem, however, to be generally necessary, often not at all useful, sometimes even inconvenient (if not disgenic).

8) Indeed species belonging to the same taxonomic group live and develop in environments like those haunted by the modified forms, perform functions fundamentally alike and on the contrary have undergone no modification.

9) All the modifications examined seem to be included in a class the representatives of which exhibit characteristics similar to those evocable from the processes of the so called exogenous adaptation, which however are hereditary and, therefore, susceptible of becoming manifest independently.

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Nota Bene - The papers published by me on the Fig-Insects amount to 51; those regarding Insects with specialized diet to 21. The whole list of them can be found in my paper of « Lincei » (n. 19 of the preceding list).

APPENDIX

After the publication of this lecture, the work in full of J. JOSEPH KUTTAMATHIATHU (*Recherches sur les Chalcicidiens* Blastophaga psenes (*L.*) *et* Philotrypesis caricae (*L.*) *du Figuier* (Ficus carica *L.*). - Ann. Sc. Nat., Zool. et Biol. Animale, XX, 2, 1958, pp. 197-260, 20 figg.) has been published. As regard him no comment: all my data are explicity or implicity confirmed.