5 Published Articles on Studies on the Notostraca

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STUDIES ON THE NOTOSTRACA

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by

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This thesis consists of a series of reprints of
publications in which are reported the results of researches
on the systematics of the Notostracan Crustacea. Studies were
made on the cytology, the biochemistry and the comparative ecology
of the group and were utilised in a systematic study of the
Notostraca.

This research was initiated after the finding by the
candidate of living Notostraca in a rain-pool in southern England,
which proved to be the only known locality for the group in the
British Isles in recent years, having been found there previously
by Professors Hobson and Fox. Success in culturing Triops cancriformis
from this pool under laboratory conditions stimulated efforts to
obtain cultures of other species, and finally cultures of all four
species of Triops and of two species of Lepidurus were maintained at
Bedford College. These, together with the collections of preserved
material in a number of European, American and Australian museums,
formed the basis of the study.

The cultures were utilised for investigations of the
development of exoskeletal characters during growth, for the
investigation of the variability of these characters in a single line
of individuals under differing environmental conditions, for cytological
studies resulting in some knowledge of the chromosome numbers within the
group, and for an investigation of the specificity of blood pigments in
different species and in different races of a single species.

The study was recorded in five publications, which are bound
together to form this thesis; a preliminary report of the discovery that
the so-called parthenogenetic forms are in fact hermaphroditic is bound
in as E in the thesis. The main paper, B, contains a review of
Notostracan literature, the analysis of the validity to systematics of
the exoskeletal characters used in the past, the chromosome counts,
the investigation of biochemical specificity, and the basic systematic
revision of the group. The conclusion reached in this paper was that

the Notostraca are composed of a small number of very widely dispersed species, all rather close to each other systematically but characterised by considerable individual variation. The number of species previously described was shown to be much too high.

A separate account of the details of the cytology and reproductive cycle which were elucidated incidentally in the investigation of chromosome numbers appears as D and describes in considerably more detail than hitherto the cytology of the gonads during reproduction.

An attempt was made in a separate publication, A, to explain the widespread nature of the distribution of Notostracan species and to relate it to the extreme longevity of the group in palaeontological terms, and an explanatory hypothesis is developed, derived from the ecology of the group.

Finally, under C, there is an account of the existence of what appears to be a most unusually high proportion of abnormal individuals occurring in populations of Notostraca compared with the proportion in other animal groups, and this again is referred to the palaeontological longevity of the Notostraca.

For convenience the constituent papers of the thesis are listed below:

A: Evolution in the Notostraca.   Evolution.
B: A review of the Notostraca.   Bull. Brit. Mus.   (N.H.)
C: Abnormal variation in the Notostraca.   Syst.Zool.
D: Reproduction in the Notostraca.   Proc. Zool. Soc. Lond.
E: Reproduction in the Notostraca.   Nature, Lond.

EVOLUTION IN THE NOTOSTRACA

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The Notostraca are phyllopod Crustacea in which the carapace is shield-shaped and covers the anterior part of the body; together with other phyllopods, they are considered to be relatively unevolved Crustacea—there is a high, but irregular, number of appendages (forty to sixty pairs are usual) and the segmentation of the body is anameristic.

It is characteristic of phyllopods that they occur in temporary rain pools, generally in arid or steppe country where such pools are common, and are unable to maintain themselves in the face of competition from higher Crustacea or Insecta (Ardö, 1947).

The survival of such primitive and vulnerable animals poses an interesting problem—the key to which may lie in their main adaptation to a temporary habitat, the drought-resistant egg. The possession of such an egg, from which hatching normally occurs only after desiccation, is an obvious prerequisite for the exploitation of a temporary fresh-water habitat by a group of animals which do not have the capacities of aerial migration which the Insects possess.

These drought-resistant eggs of phyllopods are the only possible means of dispersal for the group, for the pools in which the animals occur are isolated from one another, and are only rarely part of a stream system along which dispersal of adults would be possible.

The eggs are small, light in weight because of their dry alveolar shells, and are sticky when laid in at least one genus (*Triops*, Notostraca); further, the eggs of some Anostraca are known to retain viability after passing through the guts of Amphibia (Mathias, 1937). These facts suggest several possible means of dispersal—in or upon larger animals, attached to dry pieces of wind-blown vegetation, or airborne singly in wind currents (a desert dust-devil will whirl particles much denser than the eggs of phyllopods high into the air).

That these passive means of dispersal are effective is quite clearly shown by the ubiquitous occurrence of phyllopods in suitable pools wherever these occur. Notostraca occur on such isolated oceanic islands as the Hawaiian group, and in the few suitable pools that the rainy English climate permits. The phyllopods show another characteristic of passively distributed invertebrates—that of very widely spread, sometimes almost cosmopolitan species; in a recent study of the Notostraca for a systematic revision I found that *Triops longicaudatus*, which Linder (1952) showed was the only species of the genus in the Americas, extends from the West Indies through Central America and right across the Pacific to Japan by way of the Galapagoes, Oahu and New Caledonia. In all this area there is virtually no morphological change (Longhurst, 1955).

These facts of dispersal and geographical distribution seem to me to explain the survival of the phyllopods. The initial arthropod invasion of temporary pools may well have been performed by the primitive fresh-water Crustacean fauna and has radiated into the forms of phyllopods we see today—the carnivorous Notostraca, the "pelagic" Anostraca, and the burrowing, detritus-feeding Conchostraca. This early fauna would have spread and occupied at least a high proportion of the suitable pools, and such a cosmopolitan occupation would have effectively prevented any geographically iso-

lated, phyllopod-free, part of the environment from forming a place in which later, more highly evolved forms could have adapted themselves to life in temporary waters.

This is in line with modern theories concerning the primary importance of geographical isolation in, at least, speciation and adaptive radiation. The small amount of essential adaptation—drought-resistant eggs and a rapid rate of growth—would surely have been evolved in, say, Amphipods or Isopods if some such prohibitive factor were not operating. Here the essential adaptation to the unusual habitat seems to have enabled the pioneer arthropods to have retained possession of the habitat.

The lack of competition and the unchanging nature of the habitat would have produced no selection forces for further evolution in these phyllopods, and they have retained a primitive, unevolved form in consequence.

Fossil Notostraca are, unfortunately, sparse, but Guthorl (1934) illustrates what are certainly carapaces of these animals from the Permian deposits, although it is not possible to relate these to either of the modern genera. Trusheim (1938) found abundant remains of Notostraca in European Triassic material, and his figures leave no doubt that these forms were quite remarkably like one of the extant species; they were well preserved and Trusheim was able to make out details of the armature of spines on the exoskeleton—these are identical with those of *Triops cancriformis* except that the terminal spine on the dorsal carina was relatively small in the Triassic animals; I should consider these two forms to be conspecific if they both occurred today. *Lepidurus stormbergensis* (Barnard, 1929) from the Upper Triassic of South Africa is almost indistinguishable from some specimens of extant *L. arcticus* as far as one can see from Barnard's figures.

The systematics of the Notostraca accords very well with my hypothesis of their survival. There are only two genera, *Triops* and *Lepidurus*, each with a small number of very wide-spread species, as if the geographical barriers which are essential to speciation in less passively distributed animals are ineffective in the face of the efficient dispersal of the resting eggs.

Although Notostraca are normally characteristic of pools in arid regions, one species—*Lepidurus arcticus*—occurs only in the circumpolar arctic regions, where it lives in large lakes, stream systems and small permanent or temporary pools; possibly this is a case where adaptation to one habitat—desert pools—in which there is a premium upon rapid development and reproduction may have preadapted the animals to another, completely different, environment where conditions amicable to life occur seasonally for similarly short periods.

Some Anostraca exploit the period in very early spring when the temperature begins to rise, but before the predatory insects are active—*Branchipus vernalis* occurs in permanent pools in North America and is active only in this very short period at the end of winter; it then lays eggs which lie dormant until the same time in the following year, when they hatch and develop very rapidly before the pond arthropods generally are active. This is a way of life which is a conceivable step in the evolution of *Lepidurus arcticus* from a temporary pool animal to an inhabitant of boreal lakes.

There is some evidence that in *Triops* hermaphrodite reproduction is correlated with range extension; in *T. cancriformis* the European and North African populations fall into three categories—bisexual in the south, irregular occurrence of males in central Europe, and hermaphroditism in the north (Longhurst, 1954, 1955). During the glacial period the whole of Europe would have been untenable for all Notostraca except *Lepidurus arcticus* (which is known to have occurred in Britain at this time) and it may be that the post-glacial extension of *Triops cancriformis* from the refuges was performed by

hermaphrodites, which have the advantage that only a single egg is neccessary to effect a successful colonization, which must make lodgements very much more likely. Perhaps the sporadic male occurrence in central Europe reflects a spread to the north of bisexuality. The same species occurs in rice fields in Spain, the Carmargue, and North Italy and here the populations are composed, as far as present records show, entirely of hermaphrodites. Perhaps this is another case of a newly available habitat being colonized first by hermaphrodites.

Triops longicaudatus in North America is bisexual over most of its range, but in the Californian rice-fields no males occur (Rosenberg, 1947) and all the individuals present appear to be hermaphrodites (Longhurst, 1954). It may be significant that no males have been found in any of the outlying populations on the Pacific islands or Japan—although Linder (1952) examined hundreds of individuals from the Galapagoes, and Uéno (1927) 73 from south-east Japan. (The samples that I have seen from Oahu and New Caledonia, though small, contain no males.) This may be the result of another range extension from a central mass of population in America.

It must be emphasised that much of this account is, of course, hypothesis; but the survival of a very primitive Crustacean which is apparantly in a state of evolutionary stagnation calls for some attempt at explanation. The survival of 'living fossils' is not explicable by any general theory, but each case must be considered individually; the survival of Notostraca appears to be due to causes which are diametrically opposite to those which operated in the case of *Sphenodon*, in which the important factor was probably complete geoggraphical isolation on a remote land mass.

SUMMARY

The Notostraca have a passive means of dispersal, so effective as to enable them to occupy suitable temporary pools wherever they occur—even on remote oceanic islands. They are apparently in evolutionary stagnation.

Their method of dispersal may account for the survival of such primitive Crustacea, for they would have at all times fully occupied their habitat, leaving no geographically isolated, notostracan-free part of it in which later evolved forms could have adapted themselves to life in temporary pools. This is in accordance with modern theories of the paramount importance of geographical isolation in evolution.

It is suggested that life in temporary pools may have preadapted Notostraca to life in the arctic, where the growth period is similarly curtailed.

Hermaphroditism occurs in some species of Notostraca, and there is some evidence to show that this method of reproduction may be associated with range extension.

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A REVIEW OF THE NOTOSTRACA

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A REVIEW OF THE NOTOSTRACA

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SYNOPSIS

This paper reviews the known species of Notostraca on the basis of a large collection of museum material and on information from the literature. The genus *Triops* is reduced to four, and the genus *Lepidurus* to five species.

The species of *Triops* are separated on the armature of the telson and on the presence or absence of a second maxilla; in each species there is considerable variation in the segment number, and in the many structures whose variation is shown to be correlated with this number.

The segment number is more constant in *Lepidurus* and fewer structures are correlated with its variation; this genus appears to fall into two groups, as Linder (1952) suggested, on the basis of the segment number. A new species of *Lepidurus* is described from Russia.

In addition to the analysis of the validity of the systematic characters from work on preserved specimens, evidence derived from the growth and development of living animals, their cytology, their reproduction and their protein specificity are also considered.

INTRODUCTION

THE Notostraca are an order of Euphyllopod Crustacea with shield-shaped carapace, consisting of a single family with two genera; *Triops* (= *Apus*) and *Lepidurus*. They usually occur in temporary pools of fresh or brackish water, being most common in the drier parts of the world where the surface water is often of a temporary nature.

Their adaptation to a temporary habitat has enabled their drought-resistant eggs to become efficient agents of passive dispersal, so that populations occur on remote oceanic islands and are apparently found wherever there are suitable pools.

These animals are of interest to the general zoologist not only on account of their primitive nature, but also because they exemplify an animal in evolutionary stagnation. The family has been in existence since the Permian, and forms from the Triassic are almost indistinguishable from one of the extant species.

Individually Notostraca are notoriously variable and differences in the armature of spines on the exoskeleton, or in bodily proportions, can be found in any pair of animals, even those from the same pool. This, together with the lack of conspicuous morphological discontinuities within the genera, makes the group a " difficult " one systematically, and has resulted in the excessive number of descriptions—of specimens rather than species—with which the synonymies are now burdened.

There have been several revisions of the group as a whole, but none later than that of Simon (1886) who revised the species then known to him. Barnard (1929), Linder (1952) and Tiwari (1952) have reviewed regional material from South Africa, North America and India respectively, and have tended towards a reduction in the number of species recognized, placing many names into the synonymies. This trend has been general in recent years but has by no means prevented the description of new species on inadequate grounds.

Because of their interest from a systematic and evolutionary point of view, their geological age, their passive distribution, and their restricted habitat, it was evident that a review of the Notostraca based on a comprehensive collection of preserved specimens and on a study of the growth and cytology of living animals was desirable ; one of the points of agreement between recent authors on the group has been the need for such a revision.

MATERIALS

The preserved specimens of Notostraca on which this revision is based consist of more than 200 samples, of which about 160 are of *Triops* ; the number of specimens in each sample varies and the majority contain less than 10 individuals, although a few have more than 100 specimens from the same locality.

The bulk of this material is formed by the collections of the British Museum and of the Muséum Nationale d'Histoire Naturelle, Paris ; the remainder was on loan from the U.S. National Museum in Washington, the Western Australian Museum in Perth, the Zoological Survey of India in Calcutta, and the Museo de Ciencias Naturalis in Madrid. A few samples of preserved Notostraca were sent to me by private individuals.

The living material was reared in the laboratory from eggs in dried mud sent to me from phyllopod pools all over the world. Many contained no viable eggs, but successful hatchings were obtained from the following samples (collector's name in parentheses) : *Triops cancriformis*—Sweden (P. Ardö), England (A. R. Longhurst), France (D. Schachter), Italy (H. M. Fox) ; *T. granarius*—Johannesburg (van der Horst), Grahamstown (J. Omer-Cooper), Iraq (A. James) ; *T. longicaudatus*—California (L. E. Rosenberg) ; *T. australiensis*—Ayers Rock (I. Thomas, F. McNeill, A. L. Rose), Kalgoorlie, Ballodonia (A. R. Main) ; *Lepidurus arcticus*—Iceland (H. Moore) ; *L. apus*—New Zealand (A. Lysaght, E. Percival).

Living cultures of Notostraca were successfully maintained in the laboratory

under reasonably standard conditions. Larvae hatched readily from the mud samples when these were placed in a tank of clean water (either filtered pond water or dechlorinated tap water) which were maintained at about 20° C, air being bubbled through the water. If an excess of mud was put in a tank bacterial growth was very rapid and the culture was soon lost ; about $\frac{1}{4}$ in. on the bottom of a 24 in. by 12 in. tank proved suitable.

The larvae fed at first on the organic content of the mud and if the production of diatoms and Protozoa was poor in the culture in its early stages an addition of cultured *Chlorella* was very beneficial to the growth of the larvae. From about 1 cm. in length growth was more rapid if additional food was provided ; this consisted of chopped annelid worms (*Tubifex*), live *Daphnia* and an artificial food. This last was made up from equal parts by weight of dried *Daphnia*, grass-flour, and Bemax (a proprietary cereal food) ground together into a fine powder and suspended in calcium alginate jelly. This was then chopped and formed a satisfactory basic diet for adult Notostraca.

The eggs laid in the cultures were hatched by allowing the mud which contained them to dry out slowly ; on re-wetting, a high proportion of them hatched successfully. A more rapid and effective way of maintaining a culture was to collect the eggs as they were laid and to transfer them to a beaker of clean tap water with an addition of 30–50% of glass-distilled water ; this low osmotic pressure medium induced hatching after 12–14 days without prior drying, in the same manner as Hall (1953) has described for the eggs of *Chirocephalus diaphanus*. The larvae live for only a few moments in this water however, and must be removed from it at once.

I am most grateful to those who sent me samples of mud (including those from which I was unable to hatch Notostraca and which are not listed above) and to those people who collected and sent preserved specimens. My thanks are also due to the Authorities of the Museums listed above who lent me material, and especially to the Trustees and Staff of the British Museum (Natural History) and the Muséum Nationale d'Histoire Naturelle, who generously gave me facilities for examining their collections. I am particularly indebted to Dr. J. P. Harding of the British Museum who has given me invaluable help during the whole time that I have been studying the group.

The work on living animals was done in the Zoology Department of Bedford College, University of London under the supervision of Professor H. Munro Fox, to whom I am grateful for much assistance.

A maintenance grant from the Department of Scientific and Industrial Research, and a special grant from the Central Research Fund of the University of London were received during the work.

Abbreviations.—In the text the museums listed above are referred to by the following sets of initials :

BMNH	London.
USNM	Washington.
MNHNP	Paris.
WAM	Perth.
ZSI	Calcutta.

SYSTEMATIC CHARACTERS

The systematics of the Notostraca have been based almost entirely on characters of the setae and spines which comprise the armature of the exoskeleton, and on the proportions of various parts of the body—the endites, the furca and the carapace.

The validity of these characters was discussed in Barnard's revision of the South African forms (Barnard, 1929). More recently, the review by Linder (1952) further explored this field and has added several characters which prove useful in separating species. The description of new species from European and North African material by Ghigi (1921) initiated a discussion on the validity of the characters which he used, to which Colosi (1922), Gurney (1923), and Gauthier (1933, 1934) contributed.

Before any character can properly be used in systematics it is essential that its variation in adult individuals be known, and that its development or change during the growth of a single individual should have been studied ; in the present review the validity of as many as possible of the systematic characters has been studied and several new ones are proposed.

Previous authors have been concerned almost without exception with the variation of characters in samples of adult individuals, and it has been possible to extract much useful information about this from the literature, which has been combined with that obtained from the study of the museum material.

A pure line of individuals from a hermaphrodite *Triops cancriformis* from Britain was raised under standard conditions ; a large batch of eggs was collected from the parent, hatched, and reared at first in a single large culture dish, later being transferred to individual dishes, each with the same volume of water and mud ; the dishes standing in a room thermostatically controlled at 20° C ($\pm$ 1° C). A surplus of the artificial food was always available to the animals. From this culture 25 individuals were preserved and their variation studied ; all these animals were preserved after growth changes had ceased in the characters to be studied.

The change of several characters during growth was studied by Linder (1952) in museum material ; he based his conclusions on specimens which were about to ecdyse, in which both the old and the new exoskeletons could be observed. In the present review living material of all species of *Triops* was studied during growth from larva to adult ; the changes in relative proportions during growth have been examined and the size at which the exoskeletal armature becomes stable determined.

A start has also been made on the effects of environmental factors on morphology, but the experiments have not been very successful. *Triops* is a difficult animal to grow under precisely standardized conditions, for it has not been possible to rear them without a little mud in their dishes even when they are fed artificially. Main (1953) has suggested that so-called specific differences in Australian forms may be due to differences in the salinity of the medium ; I have made attempts to grow *Triops* at salinities near those that Main found in the field, but the animals have rapidly died each time. The temperature at which the animals were reared might be expected to have some effect on their form, and so a pure line of *T. cancriformis* was grown at a temperature (25–28° C) near their lethal point, but these animals showed little difference from those grown at normal temperatures.

Notostraca were grown in the laboratory under very diverse conditions of temperature, food, and vessel size, but all have remained remarkably uniform in their morphology. *Daphnia* under parallel conditions would show very marked morphological changes, and it is probably safe to assume that environmental factors can affect the morphology only after a very considerable number of generations—as salinity affects the form of *Artemia salina* only after several years (Schmankiewitsch, 1875).

The various characters which have been used in systematics are now examined separately.

(1) *Total size*

Samples of adult Notostraca usually contain individuals of very different sizes, and it is difficult to determine whether there is a normal adult size for any species. The growth rates of animals in a batch of *Triops* reared in the laboratory are also very variable (Fox, 1949) as the pure line of *T. cancriformis* showed very clearly; after a few days growth they varied enormously in size; 33 individuals were between 2·0 and 3·5 mm. carapace length, while one was only 1·5 mm., and another 5·0 mm. Spandl (1926) gives growth curves for individual *T. cancriformis*, maintaining that those which grow the fastest become the largest, which is what one would expect if the growth rate depended on the level of nutrition.

The usual adult size for all species seems to be between 15 mm. and 30 mm. in carapace length, the growth curve flattening out somewhere between these two figures.

The total size has occasionally been used as a systematic character.

Bowkiewicz (1923) suggests that giant *Triops* which he saw in Siberia might be a new species; large individuals of other species occur up to 40 mm in carapace length and probably correspond to the giant specimens of Anostraca, which Sellier and Morice (1946) have shown to be cytologically similar to normal individuals in one species (*Chirocephalus diaphanus*).

It is difficult to find a suitable measure of the total size of individuals in order that relative proportions of endites, etc. may be compared during growth in different samples. The total length has been shown to be quite useless in preserved specimens (Barnard, 1929; Sømme, 1934; Linder, 1952) and is difficult to measure in living animals, which have considerable powers of contraction. The measurements made on living animals also indicate that there is some increase in length during an instar. Sømme (1934) showed that the median carapace length is more reliable for it is little affected by the action of the preservative.

It has now been possible to show that the growth of the carapace is isometric and is therefore a valid measurement of size at all ages (p. 11).

Unfortunately, the ratio of carapace length/total length varies between samples and so this measurement is valid only in comparisons within a sample.

Generally, *Lepidurus* spp. tend to be smaller than *Triops* spp. and *Lepidurus arcticus* is usually smaller than the rest, but probably more rarely achieves its maximum size than the non-boreal species.

(2) *Colour*

Living Notostraca are frequently brightly coloured, the colours being due to two main pigments within the body and the brown colour of the exoskeleton.

The internal pigments are haemoglobin, which is present in solution in the blood (Régnard and Blanchard, 1883), and a dark blue-green pigment which occurs in connective tissue in many parts of the body ; this pigment is of unknown composition, but is similar in nature to that which occurs in some Ostracods (Fox, 1955).

The concentration of haemoglobin varies inversely with the oxygen tension of the medium in which the animal is living (Fox, 1949), and large animals in poorly aerated conditions may have so dense a concentration that the animal appears to be deep red in colour.

The blue-green pigment appears to be more abundant in *Lepidurus* than in *Triops* and the animal is sometimes deep green in colour (hence *Lepidurus viridis*, Baird). In *Triops* it may be completely absent, though a mid-dorsal patch on the carapace and smaller areas on the bases of the thoracic appendages are generally present. It seems to be more abundant in animals which have grown rapidly and under good conditions, when it forms a dark marbling on the carapace and is well distributed elsewhere. The only living specimens of *T. australiensis* that I have seen have been without this pigment, but this is unlikely to have any significance.

The newly hatched larvae of both genera may be densely coloured with a carotenoid pigment, as Fox (1949) reported for *Triops cancriformis* ; in successive generations of the same stock the colour of the larvae is very variable and probably depends on the feeding of the parents ; well fed females usually contain eggs which are pink with carotenoid, while in starved specimens they are white.

The egg shells of *Triops* are bright red in colour, for a red haemochromogen is present in them (Fox, 1955) ; this pigment is secreted by the follicle ducts of the ovary, and is brightest in colour in newly laid eggs, becoming duller after they have been dried.

A bright violet pigment occurs in the egg shell of *Lepidurus arcticus* (H. Moore, personal communication), while other species in this genus have eggs of the same colour as in *Triops*.

(3) *Body-length, segmentation, and number of appendages.*

The carapace of Notostraca is attached only to the head region, and the thorax and abdomen are completely free from it ; the post-carapace region is divided into a number of segments or body rings, which have considerable powers of telescoping. The first eleven segments, of which the first is incomplete dorsally, normally each bear one pair of appendages ventrally, and together comprise the thorax.

The number of post-thoracic, or abdominal, segments is variable and the series of appendages is continued along them ; a few segments at the posterior end of the abdomen bear no appendages.

Linder (1952) has analysed a great deal of North American material and has to a great extent elucidated the relationships between the number of segments, the number of appendages and the number of apodous segments posteriorly. He con-

cludes that the number of segments and the number of appendages are the results of two quite separate growth processes for a number of reasons : the production of segments and appendages in the larvae proceed at different rates ; the boundaries of the appendage bearing segments are not complete ventrally ; an aberration in which the segments are spiral instead of annular does not upset the arrangement of the appendages ; no correlation can be found between the number of appendages and the segments bearing them ; and the appendage series may end anywhere along the length of a segment.

While studying the development of the systematic characters during growth I found that the larvae of *Triops* complete their segmentation by the 5th or 6th instar, but that the series of appendages continue to increase and encroach posteriorly on to fresh segments until the 8th or 9th instar, after which the number of apodous segments remains constant. After this the number of appendages may continue to increase for a few instars but come to occupy no further segments. So after the 9th instar the number of segments and the number which are apodous may be taken as fixed in an individual, so that these could validly be used as characters in animals of more than 3–4 mm. in median carapace length.

The total number of segments varies in *Triops* from 32–44, and in *Lepidurus* from 26–34 ; these results are based on the museum material combined with information from the literature. Throughout this paper the figures given do *not* include the telson which is considered to be post-segmental, and incomplete segments are included in the count.

The figures for *Triops* show that the variation is continuous throughout its range, and separation into groups on the number of segments would be quite arbitrary ; the results for females from all sources illustrates this—

No. of segments	32	33	34	35	36	37	38	39	40	41	42	43
No. of occurrences	24	31	19	12	11	17	22	12	13	15	10	7

The bottom row of numbers—the number of occurrences—is obtained by counting the number of samples in which each segment-number occurs ; this prevents undue weight being given to large samples, which are not evenly distributed along the range of variation.

The apparent bimodality of these figures is due to the fact that one species—*Triops cancriformis*—has a range of segment variation which covers only a part of that of the other species. This species occurs in Europe and naturally predominates in the collections, thus increasing the number of occurrences at the lower end of the scale. *T. cancriformis* has a variation of 32–35, while the other species probably run from 32–43.

By far the greatest number of *Lepidurus* examined fall within the range of 25–29 segments ; I have seen only two samples with more, *L. lynchi* Linder and *L. batesoni* sp. n. This is in accordance with Linder's findings, for he suggested that there might be two groups of species within *Lepidurus* based on the number of segments.

The variation within samples bears out the theory that the number of segments may be of use in the systematics of *Lepidurus* but not of *Triops* ; in the pure line of *T. cancriformis* there was a variation of 3 in this character (33–35), and variations

of 2, 3, or 4 are usual in samples of preserved specimens. In *Lepidurus*, however, possibly because there are fewer segments, the variation is smaller, rarely being more than 2 in each sample, many samples showing none.

The number of appendages confirms the above grouping of *Lepidurus*; the shorter bodied group has from 35–48 appendages, the longer from 39–71; these figures are based on Linder's data with the addition of counts made on the material I have examined. But in *Triops* I can find no correlation between the number of legs and the number of segments, for high numbers of appendages occur in both short and long bodied specimens, and the converse is also true. In this genus I can find no significance in the numbers of appendages.

The number of apodous segments is a secondary character depending on the interplay of the processes which control appendage and segment formation (Linder, 1952). This is confirmed in my data, most commonly with males and females from the same sample; the males tending to have a smaller number of appendages, the same number of segments and so a higher number of apodous segments than the females. Similarly, *Lepidurus bilobatus* has 33 segments, 60 pairs of appendages and 6 apodous segments (Linder, 1952), while *L. batesoni* with the same number of segments, but only 39–52 appendages, has 8–9 apodous segments.

The apodous segments were frequently counted in early descriptions of Notostracan species, and several specific distinctions have been based on small differences in this number. It is now known that there is so much variation in this character in *Triops* that it is useless as a systematic character; the pure line *T. cancriformis* had a variation of three (5–7). It may be valid in some *Lepidurus*, and is of use in at least one specific distinction.

A few general rules can now be drawn from the data on segmentation and appendage number.

In both genera males often have a higher number of segments within a sample, while the reverse appears to be unknown. In 25 samples of *Triops* I found this to be the case, while in 21 the difference was insignificant.

Certainly in *Triops*, and probably in *Lepidurus*, the males tend to have fewer appendages and so a higher number of apodous segments than the females; in 44 *Triops* samples the males had a higher number of apodous segments, in 7 there was no difference and in 1 the female had more.

Specimens with high numbers of segments tend to have a high apodous number in both genera.

Thus, it is obvious that these characters can be used in systematics only with a great deal of caution, and appear to be of more use in *Lepidurus* than in *Triops*.

(4) *Carapace*

The shape and size of the carapace in Notostraca varies considerably and the differences found have frequently been used in the past by systematists to distinguish species. Ghigi (1921) used the carapace shape as one of his arguments in separating *Triops* into two genera: *Thriops* and *Proterothriops* (*sic*); Barnard (1929) considered the shape to be a distinguishing feature between South African species of *Triops*, particularly between his *Apus numidicus* and *A. namaquensis*. On

the other hand, Linder (1952) made no use of the carapace size and shape in his revision of the North American forms. The carapace is one of the structures which is usually described adequately in the earlier papers.

In each individual the growth of the carapace from the earliest larva is probably isometric ; a number of individuals of *Triops cancriformis* and *T. granarius* were measured during the whole of their growth period and it was found that the ratio of
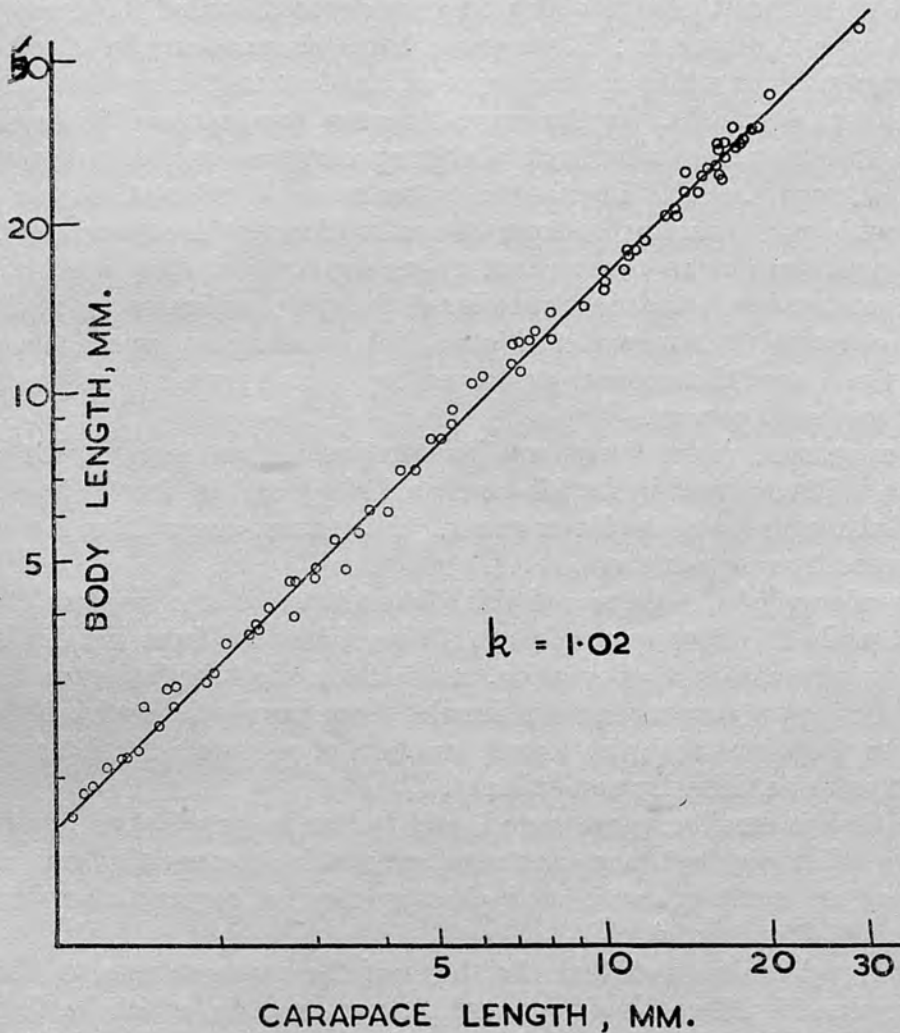

FIG. 1. Growth coefficient (*k*) of females of *Triops cancriformis* from Hampshire—five individuals.

carapace length to total length remained the same throughout growth. In the former species the growth coefficient (*k*) of the carapace was 1·02, while in the latter species *k* = 1·01 ; these results are shown graphically in Text-fig. 1.

The basic variation in the carapace is its size relative to the total length of the animal ; in some forms it covers a much greater length of the body than in others ; correlated with this relative size-difference are other differences in shape and strength

of the carapace ; in those specimens in which it is relatively small it is always more rounded in outline, flatter, and less strong than in those in which it is large. These differences hold good for both genera.

The relationship between carapace length and total length depends both on changes in size of the carapace—the number of segments that it covers—and on changes in the number of abdominal segments. A comparison between two species of *Triops* made on the living animals illustrates this ; British female *T. cancriformis* have about 33 segments of which about 19 are exposed behind the carapace, which thus covers some 14 segments ; *T. granarius* from Johannesburg have, in the female, about 38 segments of which 27 are exposed, so that in this species the carapace covers about 11 segments. In the second species the increase in the number of exposed segments comes both from a shorter carapace and a larger number of abdominal segments. It is impossible to make such calculations on preserved specimens with any accuracy, because of contraction in the preservative.

The carapace appears to cover about 11–14 segments in most specimens, for on these segments are borne the most anterior of the spines which occur on the margins of the segments in the exposed portions of the abdomen ; in all the specimens examined, the first of these spines appear on segments 11–14, regardless of the total number of segments present.

Within a species, males have smaller carapaces than females, although this dimorphism is less marked in *Lepidurus* than *Triops,* and in shorter bodied than in longer bodied specimens of the latter genus. This sexual dimorphism in the carapace has been noted by many authors.

The dependence of the degree of this dimorphism on the number of segments means that while it is usually possible to distinguish males from females at a glance on this character within a population, males from short bodied populations may actually have longer carapaces than females from populations with high segment numbers. In the forms with the lowest numbers of segments the dimorphism may be so slight as to be virtually non-existent.

The carapace is smaller, more round, and flatter in populations of both genera which have relatively high segment numbers ; this is especially well marked in *Triops* where the specimens with the highest numbers of segments have remarkably small carapaces (Text-fig. 2).

Barnard (1929) maintained that the shape of the carapace was an absolute difference between his *Apus numidicus* and *A. namaquensis,* which he found in the former species to be oval in shape and in the latter almost round ; he also gave data on the number of apodous segments which show that *A. namaquensis* is longer in the body than the other species, although some overlap occurred between the two. He was concerned only with South African material, but on examining specimens of these species—and of synonymous ones—from the whole of their range in Africa and Asia I find that there is no discontinuity in the variation of carapace-shape. The round carapaces and the oval are connected by populations of intermediate form (Text-fig. 2A–E). The differences that Barnard found were differences between the long and the short bodied forms of the same species.

I can find no differences in the carapace shape or size which are not correlated
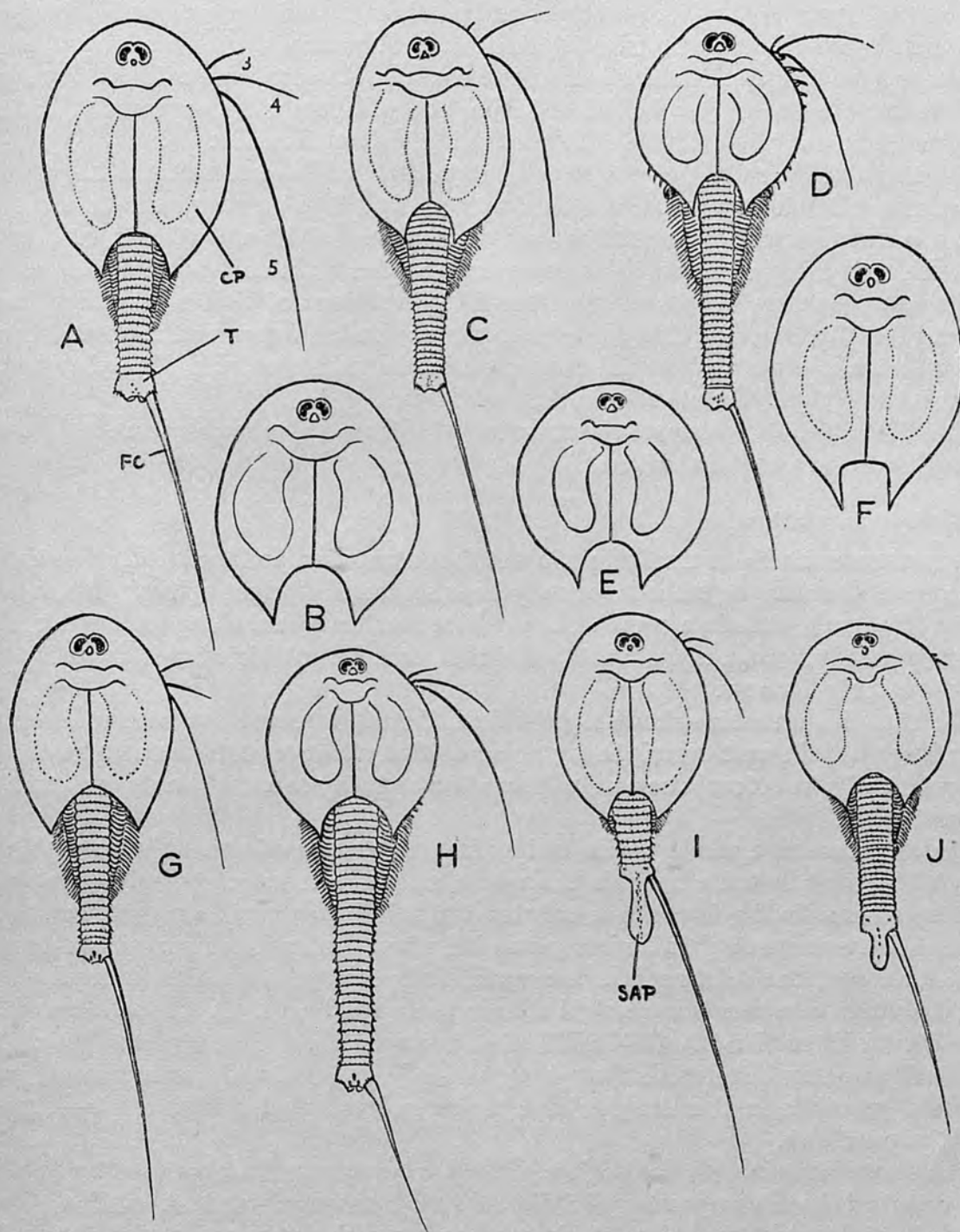
FIG. 2 Correlation of form with number of segments. A–E, *Triops granarius*, progressive increase of segments (32–42) ; F, squared sulcus on some specimens of *T. granarius* from South Africa ; G–H, *T. longicaudatus*, few and many segments respectively ; I, *Lepidurus apus* ; J, *L. batesoni*. (3, 4, 5, = endites of first thoracic appendage, *cp* = carapace, *t* = telson, *fc* = furca, *sap* = supra-anal plate).

with sex or the number of segments ; *Triops cancriformis* tends to have a lower number of segments than *T. granarius* and so its carapace tends to be longer, less flat, than in the other species ; and specimens of *T. granarius* with a low number of segments have carapaces similar in shape to those of *T. cancriformis*. *Lepidurus* spp. tend to have even shorter bodies and here the carapace may cover most of the abdomen, and may be so deep as to enclose the animal laterally.

The shape of the sulcus, or posterior emargination, of the carapace has frequently been described and importance attached to it ; I find it to be very variable and can see no correlation with other characters ; it may be shallow and wide in both long or short bodied forms, or small and round in similar animals. A peculiar squared sulcus has been seen in several short bodied populations of *Triops granarius* from Africa (Text-fig. 2F), but this grades into more rounded forms and is obviously of no significance. Wide, shallow sulcus shapes occur most frequently in *T. longicaudatus*, but this is of very doubtful value in the systematics.

The difficulty of an accurate classification of sulcus shapes makes it unlikely that this will ever be a useful character.

(5) *Carapace armature*

The carapace bears an armature of spines both scattered and localized. The whole outside surface may be smooth, or may bear scattered upright spines ; the dorsal carina frequently ends in a spine and may bear smaller spines along its length ; the sulcus generally bears a row of marginal spines, and the outside edge of the carapace may bear a similar row.

The carapace armature shows a great deal of variation, and has been referred to very frequently in past descriptions ; some of this variation does seem to be of use systematically, but it must be used with caution and only as a confirmatory character in most cases.

The armature as a whole varies in its strength and development even within a population, and in some animals the whole armature is more strongly developed than in others—in the former not only are the spines larger and stronger, but they are also more numerous. In *Triops granarius*, when the scattered surface spines are well developed, the sulcus spines are particularly strong, the carina is denticulate and the whole carapace is more rigid than in other specimens. In a population of *T. cancriformis* from Tunisia (MNHNP) the armature of the exoskeleton is extraordinarily weakly developed, though typical of this species in arrangement, and extreme examples in this sample have no carinal or sulcal spines at all—a most singular condition.

The scattered spines on the surface of the carapace were features used by Sars in the description of two species of *Triops* (*Apus trachyaspis* and *A. sculleyi*, Sars, 1899), but Barnard found that specimens bearing such spines occurred sporadically among South African material. I have found such specimens in samples of *Triops granarius* and *T. longicaudatus*, both as isolated individuals and as complete samples. Specimens in which this character is well developed are so conspicuous—the carapace having a prickly feel—that I shall refer to them as the *trachyaspis*-form of whichever species is involved.

The terminal spine of the carina is most prominent in larval *Lepidurus*; I have seen specimens of *L. arcticus*, *L. apus apus* and *L. apus viridis* in which it is relatively enormous in the second and third instars (Text-fig. 13A). In larvae of *Triops* it develops later and is never as large as in young *Lepidurus*. The growth rate of this spine in *Lepidurus* must be strongly negatively allometric, for although it is present in most adults, it is relatively very much smaller in these than in the larvae ; in *Triops*, when it occurs, this spine has a positively allometric rate for it is quite small when it first appears, and becomes, in the adult, of a size relatively similar to that of adult *Lepidurus*.

This terminal spine occurs in almost all adult *Lepidurus* and is absent in only a few. There appears to be no correlation between its absence and other characters ; *L. batesoni* and some specimens of *L. apus apus* and of *L. apus lubbocki* are without it, but these specimens of *L. apus* are otherwise quite normal. There is probably a variation in the growth rate of this spine to account for its disappearance in adults of a few populations.
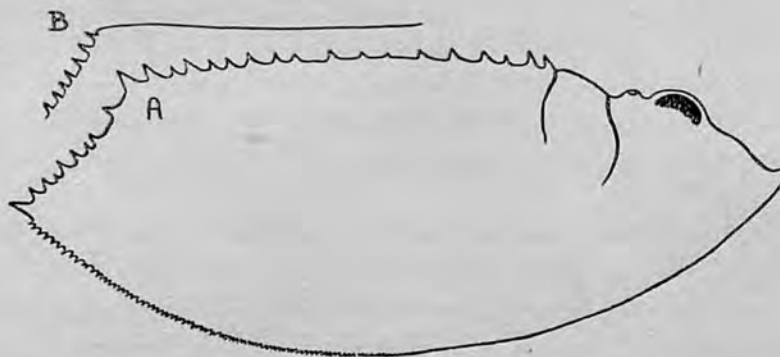

FIG. 3. Carapace of *Lepidurus lynchi*. A, typical form of carinal spines ; B, specimen with no carinal spines.

In *Triops* there is a loose correlation between the occurrence of the terminal spine and other characters ; within a species it is more commonly present in short than in long bodied forms. There is some difference between species, too, and as might be expected it is almost always present in the relatively short bodied species, *T. cancriformis*. It is present in the remaining species only in their short bodied forms.

The carina may bear a series of spines, most commonly at the posterior end just anterior to the terminal spine. These have frequently been used in the past for systematics (Ghigi, 1921 ; Linder, 1952) and they have proved to have value in certain cases. In *Triops* they may be present, or absent, in both long and short bodied forms, but there are some interesting differences within *T. cancriformis*. In this species a few small spines are generally present posteriorly, and these are more numerous and much stronger in specimens from Morocco and Southern Spain ; these are the populations referred to by Ghigi (1921) as *Thriops mauretanicus*, but they are now considered to comprise a sub-species (sens. Mayr, *et al*) of the more widespread *Triops cancriformis*. Another sub-species of this species is characterized by the complete absence of carinal spines.

In *Triops australiensis* and *T. longicaudatus* these spines are most frequently

completely absent, but in a number of populations, that from the rice fields of Biggs County in California, for example, the whole carina bears an even row of very small denticles.

Most specimens of *Triops granarius* are without carinal spines, and only a few of the short bodied specimens have an arrangement like that of *T. cancriformis*. Very rarely this species has a long row of very small denticles like those of *T. longicaudatus*.

The majority of specimens of *Lepidurus* have perfectly smooth carinae but a remarkable series of large teeth along the carina occurs in *L. lynchi*, quite unlike anything else in the Notostraca (Text-fig. 3).

The sulcus normally bears a marginal row of spines, the only exceptions being some of the specimens of *Triops cancriformis* from Tunisia mentioned earlier. There is a fairly clear correlation of the form of these spines with the number of segments in *Triops*, but not in *Lepidurus*; they are larger and fewer in number in short bodied forms of the former genus.

Their development in *Triops* is fairly clear; the spines at the outside angles of the sulcus appear first, in the 4th or 5th instar, at which time the rest of the sulcus has a finely granulated margin. The first marginal spines appear in the 7th or 8th instar, and increase in number until about the 10th instar, after which time the number is fixed, though in a few specimens small subsequent additions may occur. There is little variation in this character in an individual after it is about 5·0 mm. in carapace length.

Barnard (1929) considered that there was so much variation between individuals in the sulcus spines that their use in systematics was not justified, although earlier writers had placed much emphasis on them. Linder admitted this variation, but thought that in some cases specific differences could be found.

I can discover no differences of the sulcal spines in *Triops* which can have any value in systematics, most of them are correlated merely with body length; in *T. granarius*, short bodied forms have long, slightly curving spines and in longer bodied animals a larger number of small, blunt spines occurs. As in other characters *T. cancriformis* here resembles the shorter bodied *T. granarius* specimens.

In *Lepidurus*, a correlation with body length was not observed; some specimens with 28 and some with 33 segments had small squat spines, but the vast majority of samples of all body lengths have long spines similar to those of *Triops cancriformis*. An unusual arrangement occurs in *Lepidurus apus packardi* in which the margin is closely set with many small squat spines like those of larval *Triops*.

The outer margin of the carapace in both genera normally bears a series of denticles which produce a finely serrated edge; this is variable in development, and is normally stronger near the posterior angles of the carapace; in only one case are these marginal denticles of any value systematically; some specimens of *Lepidurus lynchi* bear a series of teeth along this edge which are very much larger than those of any other known form.

The amount of individual variation which may be expected in the carapace armature of a population was illustrated by the pure line of *Triops cancriformis*; here the number of posterior teeth on the carina varied from 2–10, the number of sulcus spines from 24–32, and all the specimens had a large terminal carina spine.

(6) *Supra-antennal crest*

On either side of the ventral surface of the head there is a ridge, behind which is set the first antenna ; this is the supra-antennal crest of Simon (1886), which Linder (1952) suggests may be worth study. I find it variable within a single species, in some specimens of *Triops c. cancriformis* it is denticulate and in others smooth and less prominent. It seems improbable that it is of importance systematically.

(7) *Eyes and dorsal organ*

In all adult Notostraca the dorsal surface of the head bears a pair of compound eyes, an ocellus, and the dorsal (or nuchal) organ.
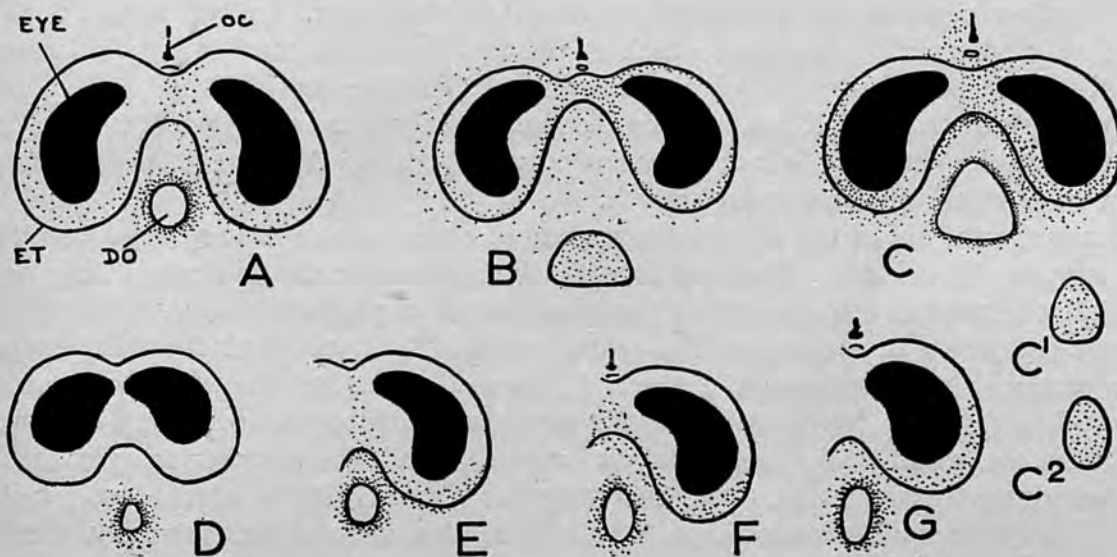

FIG. 4.   Eyes and dorsal organs.   A, *Triops cancriformis* ; B, *T. australiensis* ; C, C_1, C_2, *Triops granarius* ; D, *Lepidurus batesoni* ; E, F, *L. apus* ; G, *L. arcticus*.

The size and arrangement of these structures are given in most specific descriptions and considerable importance has been ascribed to them, in particular to the dorsal organ ; Barnard (1929) showed that the dorsal organ varied in South African material from a small round shape to a larger and triangular one. Further, he found that the small, round dorsal organs tended to be set on a tubercle in his animals, but that the triangular ones were less elevated and nearly flush with the surface of the head. These differences, to which he ascribed much importance in separating species, now appear to be another example of a character which is correlated with the number of segments, and which varies in a similar fashion in several species.

In all the species of *Triops* the specimens with a low number of segments tend to have small, round and elevated dorsal organs, and as the number of segments increases so the dorsal organ becomes larger, less elevated, and more triangular in shape (Text-fig. 4C–C_2).

This is well shown by *Triops granarius* ; in specimens from South Africa with only 33 segments the dorsal organ is small and round, or slightly pear-shaped, as it is in

specimens with 36–37 segments from Chufoo, China (both BMNH) ; in longer bodied specimens it is much larger and more triangular. In *T. cancriformis* the usual shape is round, but in some of the longer bodied individuals it approaches the triangular form of most specimens of *T. granarius*. *T. longicaudatus* is similar in this character to *T. granarius*, but in *T. australiensis* a peculiar wide shape, with a slight emargination of the posterior margin, occurs in a few specimens.

I have seen no specimens, and can find no records, of *Lepidurus* with triangular dorsal organs ; here the round shape seems to be usual but in most species it varies from round to oval (Text-fig. 4). In *L. arcticus* a peculiarly long, narrow oval shape is common and this does not appear to occur in other species (Text-fig. 4G).

The growth rate of the dorsal organ is very strongly negatively allometric and this further complicates its use as a systematic character. In the larvae it is a relatively enormous structure so that in the first instar its median length is commonly about half that of the carapace rudiment (Text-fig. 13B).

During growth to adult size its linear increase is only × 2 or × 3 while the relative growth of the carapace is naturally very much greater. This negative allometry appears to continue throughout growth.

Linder made use of the relative arrangement of the eyes and the dorsal organ in his species of *Lepidurus*. He found that *L. lynchi* has the dorsal organ placed well behind the posterior boundary of the eyes and of the tubercles over the eyes, in contradistinction to the rest of the genus in which he found that the dorsal organ was placed in part between the eyes. *L. batesoni* sp. n. has the first arrangement (Text-fig 4D), but *L. bilobatus*—the other member of the long bodied group—has not.

In *Triops*, almost all the specimens examined had the anterior margin of the dorsal organ between the eyes, the only exceptions being 8 of the 12 samples of *T. australiensis* examined, in which the arrangement was precisely similar to that of *Lepidurus lynchi* and *L. batesoni* (Text-fig. 4B) ; in the other four samples it was normal. This may indicate that not too much reliance should be placed on this character in either genus as a primary distinction between species.

(8) *Telson*

The telson bears an armature of spines on both dorsal and ventral surfaces, and variation of these have commonly been used in the past for separating species (Packard, 1883 ; Ghigi, 1921; *et al.*).

The important spines on the dorsal surface of the telson fall naturally into four groups to which it is convenient to apply names (Text-fig. 5) ; around the bases of the furca are rings of *furcal* spines ; on the posterior margin of the telson of the larvae the first spines to appear are large and are identifiable in the adult—the *posterior marginal* spines ; the median area of the telson may bear a row of large spines or scattered smaller ones—the *median* spines ; around the dorsal sensory setae are rings or arcs of *setal* spines.

The development, but not the origin, of these spines differs radically between the several species of *Triops* (Text-fig. 5), and the final arrangement is of the greatest importance in the systematics.

All the specimens of *Triops* which were available were examined on a geographical

basis, and no account was taken of previous determinations of the specimens; it was found that there was a strong correlation between the spine pattern of the telson and the geographical distribution of the animals, but none with the sex or the number of segments.
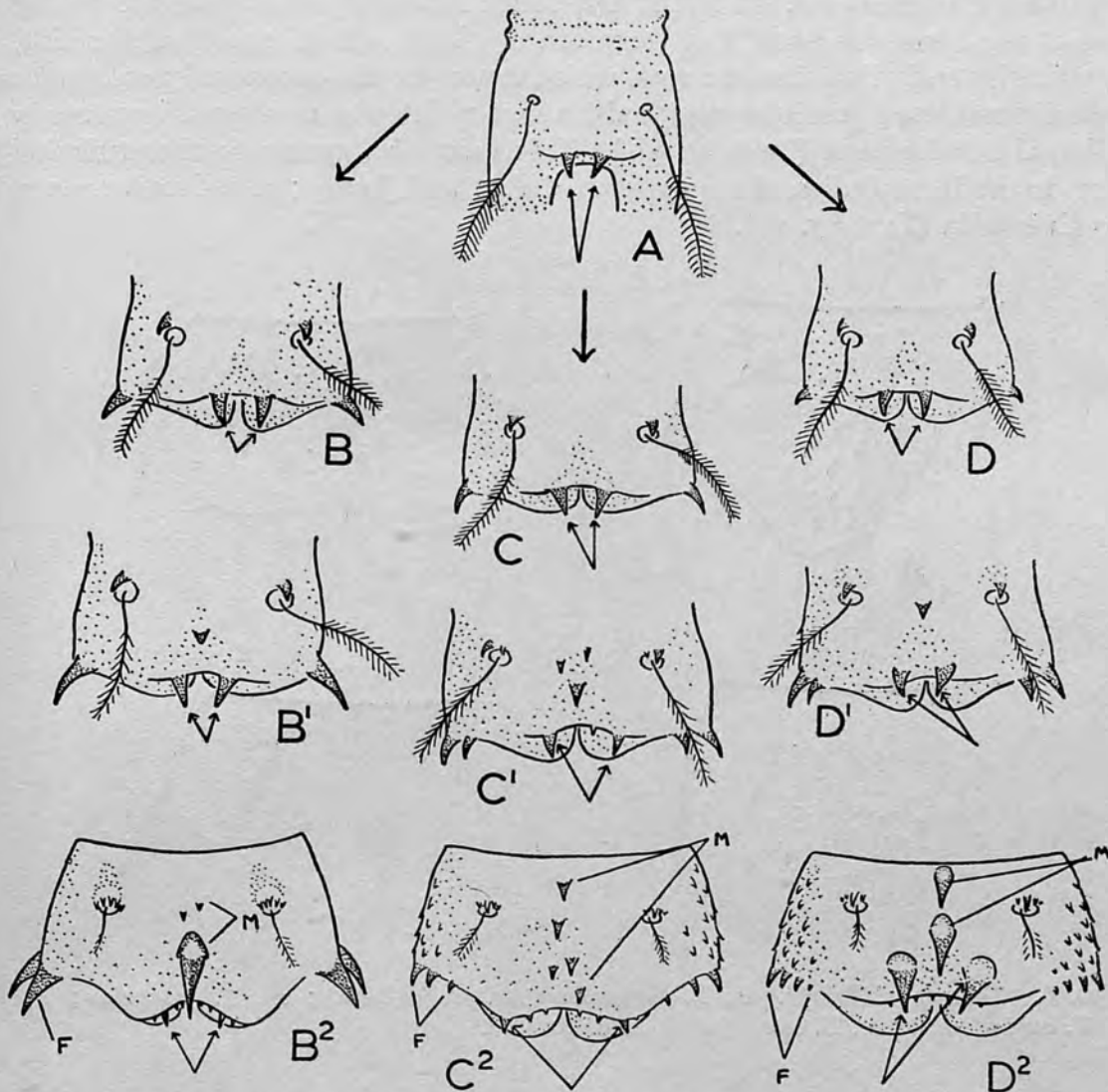

FIG. 5. Development of telson armature in *Triops*. A, larval stage (instar 2) common to all; B, C, D, instar 5–6; B_1, C_1, D_1, 3–4 mm. carapace length; B_2, C_2, D_2, adults. B_n, *T. cancriformis*; C_n, *T. granarius*; D_n, *T. longicaudatus* (the small arrows indicate the position of the posterior marginals in each case; f = furcal spines, m = median spines).

Without exception the specimens from Europe and western Russia have a small number of median spines arranged in an accurate row in the centre of the telson, the furcal spines are few and large, and the posterior marginals small, thin and remaining on the margin in the adult (Text-fig. 5A); this pattern occurs also in North Africa, the Middle East and northern India. In Africa south of the Palaearctic Region all

the specimens have a larger number of small, relatively scattered medians in the mid-dorsal region, small, numerous furcal spines, and small posterior marginals (Text-figs. 5C, 6A). This pattern overlaps the European type in North Africa and the Middle East without forming intermediates, and then spreads across Central Asia to the Chinese coast. In North and South America the medians are similar to those of the European form, but there are two large spines, one on either side, at the posterior end of the median row, which represent the enormously enlarged and forwardly migrated posterior marginals, a fact which was confirmed by a study of the larval development (Text-fig. 5D). This form also occurs to the exclusion of others in the West Indies, the Galapagos, Oahu, and Japan ; a derivative occurs in New Caledonia (Text-fig. 16).
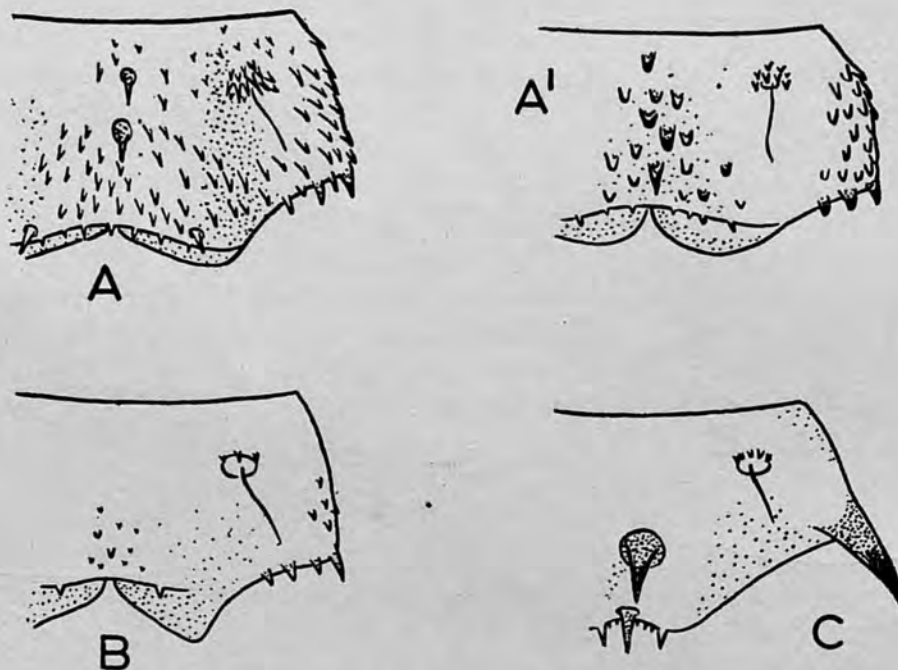

FIG. 6.   Telsons of *Triops*.   A, *T. granarius* (*trachyaspis*-form) ; A₁, *T. granarius* ; B, *T. australiensis* ; C, *T. cancriformis mauretanicus*.

The Australian forms have a very few small scattered medians, as in the African form, but they are so few in number as to be frequently absent (Text-fig. 6B) ; the rest of the armature is as in the African specimens.

This gives a picture of four large groups which are to a great extent allopatric, but forming where they overlap no intermediates. The descriptions in the literature completely confirm this grouping and are too numerous to list with profit.

As a systematic character this pattern appears to be perfect, there are no known intermediates, it is unlikely that it has any direct adaptive significance, and it is very easily seen in the specimens.

It must be remembered, however, that although the pattern is stable the numbers of spines which form it are very variable ; in the pure line *Triops cancriformis* there

were 1–4 medians, 2–4 furcals, and, once, small additional posterior marginals barely distinguishable from the primary pair.

The number of these spines is fixed from a size of about 5 mm. carapace length, but as Text-fig. 5 shows, their relative sizes forming the true adult patterns are not stable until a little later, and allowance must be made for this (e.g. *Apus mavliensis*
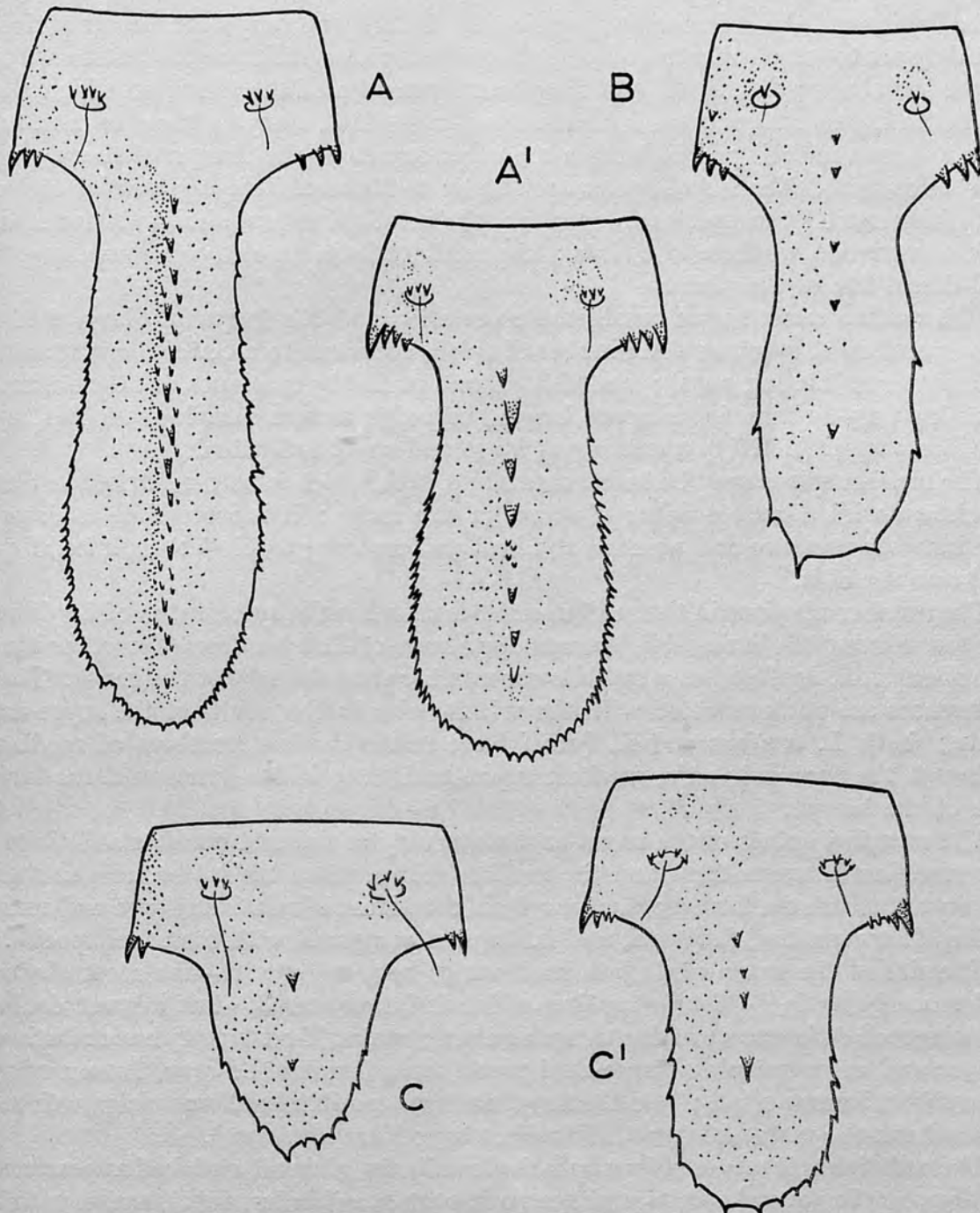

FIG. 7. Supra-anal plates of *Lepidurus*. A, *L. apus apus*; A₁, *L. apus lubbocki*; B, *L. batesoni*; C, ♀, C₁, ♂, *Lepidurus arcticus*.

Tiwari appears to have a different telson pattern from the other Indian forms, but this species was described on immature individuals in which the posterior marginals were still relatively very large).

The spines encircling the dorsal setae are very similar in arrangement, though not in number, in all specimens of *Triops* examined, and no importance is attached to them.

In *Lepidurus*, the spines corresponding to these four groups can be recognized, but they are to some extent modified ; the posterior marginals are the first to appear in the larval telson (*L. apus*) and the posterior margin of the telson on which they are borne expands rapidly to form the supra-anal plate, carrying them with it, and they are soon indistinguishable from the other spines on the margin of the plate in most specimens. The furcal spines are similar to those of *Triops granarius* and do not differ much from species to species ; the setal spines are similar in form and lack of variation to those of *Triops* ; the medians form an elongate row along the mid-dorsal line of the plate.

This median series shows considerable variation and has frequently been used in the separation of species ; the number of spines increases to a certain extent as the animal grows (Linder, 1952) ; and this process probably continues until the animal is at least 15–20 mm. in carapace length, to judge from a sample from Berlin of *Lepidurus apus* (BMNH) consisting of large and small individuals.

The median spines may be borne on a slight keel, which is better marked in those specimens with a large number of spines in this series ; it is impossible to draw a line between presence and absence of a keel and contrary to Linder's opinion, I can make no use of it.

The number of spines in the median series is useful in the systematics of *Lepidurus* species, serving to distinguish the nominate race of *L. apus* from the other three sub-species. *L. arcticus* has a much lower number than the rest of the genus. These differences are not connected with the relative size in the adults of the supra-anal plate ; both *L. arcticus* and *L. lynchi* have relatively low numbers of medians, although the former has the smallest supra-anal plate in the genus and the latter one of the largest.

The marginal spines of the supra-anal plate vary in size and number and there is a connection between them and the median spines, when the latter are small and numerous, so are the former ; the marginals therefore are relatively large and sparse in *Lepidurus arcticus*, *L. lynchi*, and *L. batesoni* compared with the other species.

The size of the supra-anal plate itself varies between species—the most obvious difference being in *Lepidurus arcticus* where it is very small—but a great deal of the observed differences are due to age and sex ; males (Text-fig. 7c) have relatively longer and more spatulate supra-anal plates than females (*L. apus*, Braem 1893 ; *L. arcticus*, Sømme 1934) ; and the structure has a positively allometric growth rate throughout the period of growth (Braem, 1893 ; Campan, 1929).

The end of the plate is occasionally incised medianly, giving it a bilobed appearance ; this appears in several species and has no importance (Linder, 1952), and it is to be expected that this will occur in species other than those in which it has already been recorded.

The shape of the telson was used by Packard (1883), but Linder has shown that this is an unreliable character in *Triops*, though he records relative differences in length and breadth in some *Lepidurus* species. The variation is such that no reliance is placed on it here.

The dorsal sensory setae are present, and similar in form, in all species of Notostraca that I have examined, and are longer in small than in large specimens.

(9) *Segmental armature*

Each segment which is exposed behind the carapace bears a series of spines on its posterior border; this series is interrupted by the appendages and is continued ventrally only on the apodous segments.

The form of these spines on the ventral surface of the apodous segments has frequently been used in the systematics of both genera; Ghigi (1921) considered them to be important in *Triops*, as did Linder (1952) in *Lepidurus*.
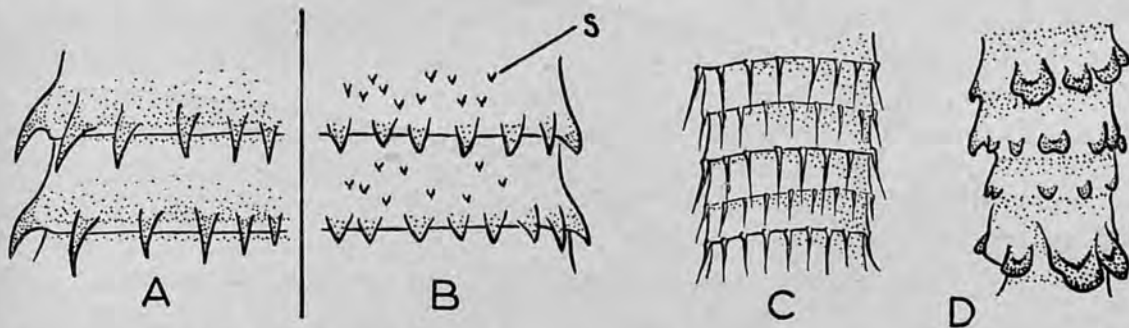

FIG. 8. Armature of apodous segments (A, B) and furca (C, D) of *Triops*. A, *T. cancriformis* without supernumeraries; B, *T. granarius* with supernumeraries (s); C, ♀ *T. cancriformis* or *granarius*; D, ♂, *T. granarius*.

On the ventral surface of these segments the spines near the midline are usually smaller and set more closely together than the lateral ones. Linder (1952) considers that the number and relative size of these centrals is diagnostic of certain species; he gives a variation of 13–28 teeth in *Lepidurus packardi, L. couessi,* and *L. bilobatus,* and only 8 in *L. lynchi*; I find the variation so great that this character is effectively useless even though the differences are at times striking.

In *Triops*, the shape of the marginal spines was used by Ghigi (1921), who found that they were squat in his *T. mauretanicus*, and finer in his other species; I find that the European and North African material—which Ghigi divided into species—shows continuous variation in this character although, as he described, there is a tendency for the Moroccan specimens to have squat spines.

These spines become rounded and heavy in males of *Triops granarius* in which the ventral armature of furca and telson are heavy; they are thus heavier in males than in females of the same species.

A more useful character on the apodous segments is the presence or absence of scattered supernumerary spines which occur between, and anterior to, the marginal spines and are much smaller than them (Text-fig. 8). In *Triops cancriformis* only one

specimen has been seen which possesses any of these spines, a female from Palestine (coll. Goldschmidt) which had 3–4 small supernumeraries on one of the apodous segments. In the other species of *Triops* it is most unusual to find a specimen which does not possess at least a few supernumeraries on each apodous segment, and in the main there are 10–12 per segment.

I have not seen these spines in *Lepidurus*.

(10) *Appendages*

The appendages have been described in considerable detail for one species (*Triops cancriformis*, Lankester 1881), but with the exception of one character have been little used in systematics. The endites of the first thoracic appendage are drawn
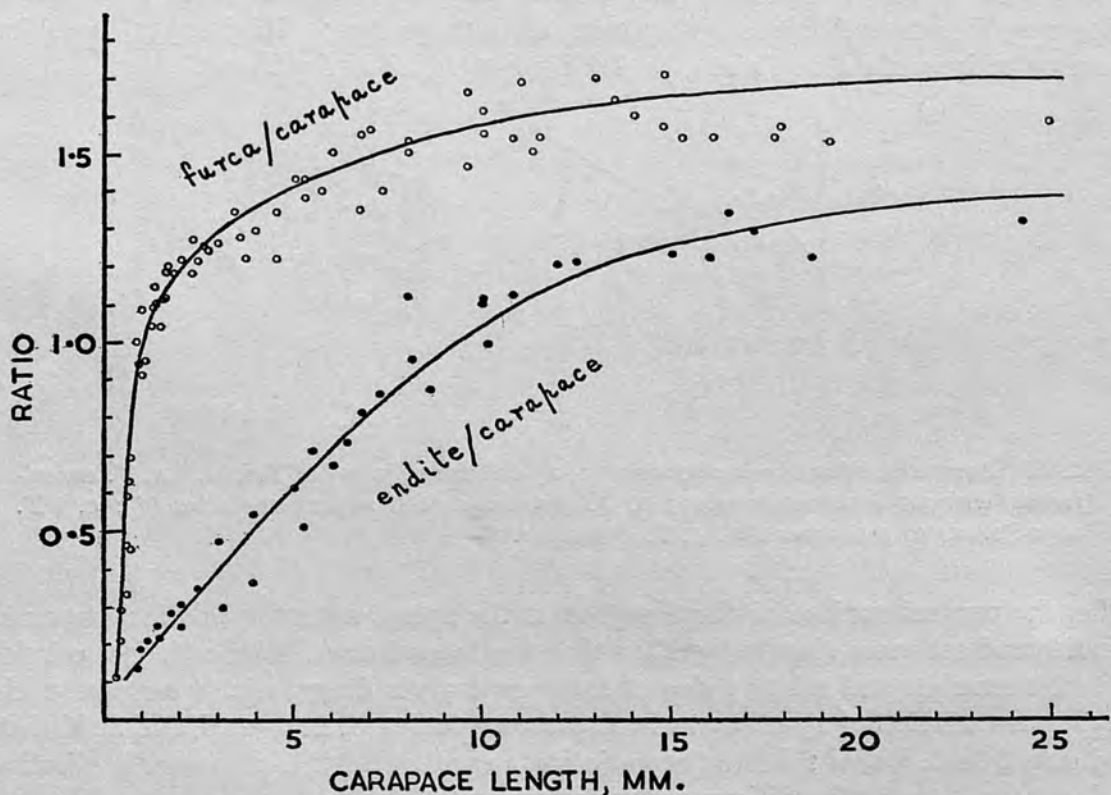

FIG. 9. Relative growth rates in *Triops cancriformis* from Hampshire. Furca and longest endite of first thoracic appendage expressed as ratios furca/carapace and endite/carapace for various carapace lengths. Any slope on the line thus indicates allometric growth, since the growth rate of the carapace is isometric.

out into filaments of which the longest endite (the fifth) forms an antenna-like structure in most forms. The length of the endite 5 and the number of segments of which it consists have been described by too many past authors to list. Even recently small differences in endite length have been considered to have significance (Tiwari, 1952).

A study of the developing endite of *Triops cancriformis* and *T. granarius* has shown

that it grows positively allometrically and that this rate continues, to some extent, throughout life (Text-fig. 9). So small differences in relative length are of no use in systematics without much more investigation of the growth rates of this structure in many populations.

It is likely that the length of the endites is not related to the size of the animal *per se*, but to the instar that the animal has reached. Specimens which have grown rapidly, with a large increment at each instar would have a different endite length at a particular size from individuals with low instar increments due to poor conditions; this is borne out by the great size and relative proportional differences seen in laboratory cultures.

In museum samples, perhaps for this reason, the individual differences in this character appear to be greater than those to be expected between large and small specimens; if a sample is arranged in order of carapace-length the endite/carapace ratio does not increase evenly up the series, as would be expected from the results obtained from the growth of single specimens, and the inference to be drawn must be that the specimens have grown at different rates and are of different sizes at each instar.

This is further supported by the occurrence of two samples taken from the same locality in different seasons; two such samples from a locality in the Saône area of France (MNHNP) collected two years apart consisted one of large, the other of small adult individuals, but the endite/carapace ratio was very similar in each; in the first, individuals of 29–31 carapace length had a carapace/endite ratio of 0·80–0·84; in the second sample the same ratio occurred in specimens of 9·5–10·8 mm. in length.

The situation is further complicated by the fact that there is sexual dimorphism in the endite length; in 26 bisexual samples of *Triops*, 24 showed higher endite/carapace ratio in the males. This may be due to the relatively shorter carapaces of males than to any real difference in endite length relative to the total size of the animals. In living specimens this appeared to be the case.

It is very noticeable that the endites are shorter relative to the body length in both sexes of the longer bodied forms, but it is not possible to give reliable figures for this because of the parallel differences in the relative carapace length which renders inter-sample comparisons very difficult.

The range of the endite/carapace ratio is very great within a species determined as such on other characters; in *Triops cancriformis* this varies from 0·55–1·28, and in *T. granarius* from 0·47–1·52. No correlation with the geographical distribution could be found.

In *Lepidurus* the endites are not as long as in *Triops*. *Lepidurus arcticus* and *L. apus* form a series from animals with very short endites which scarcely project beyond the carapace, to those in which they are relatively long. In *L. batesoni* the arrangement is unique; the 5th endite of the first appendage is little longer than that of the second appendage, and the 6th endite forms a claw in both appendages although in all other Notostraca it is reduced to a small, soft lobe at the base of the 5th endite in the first thoracic appendage, undergoing negative allometry during growth (Text-fig. 10).

Linder (1952) remarks " . . . the legs of various species are known to be very similar to each other . . . "; I can find no reference to a comparative study of the appendages of Notostraca, and so it seemed valuable to attempt at least a preliminary survey. Unfortunately, it is necessary to dissect the appendages from the specimen
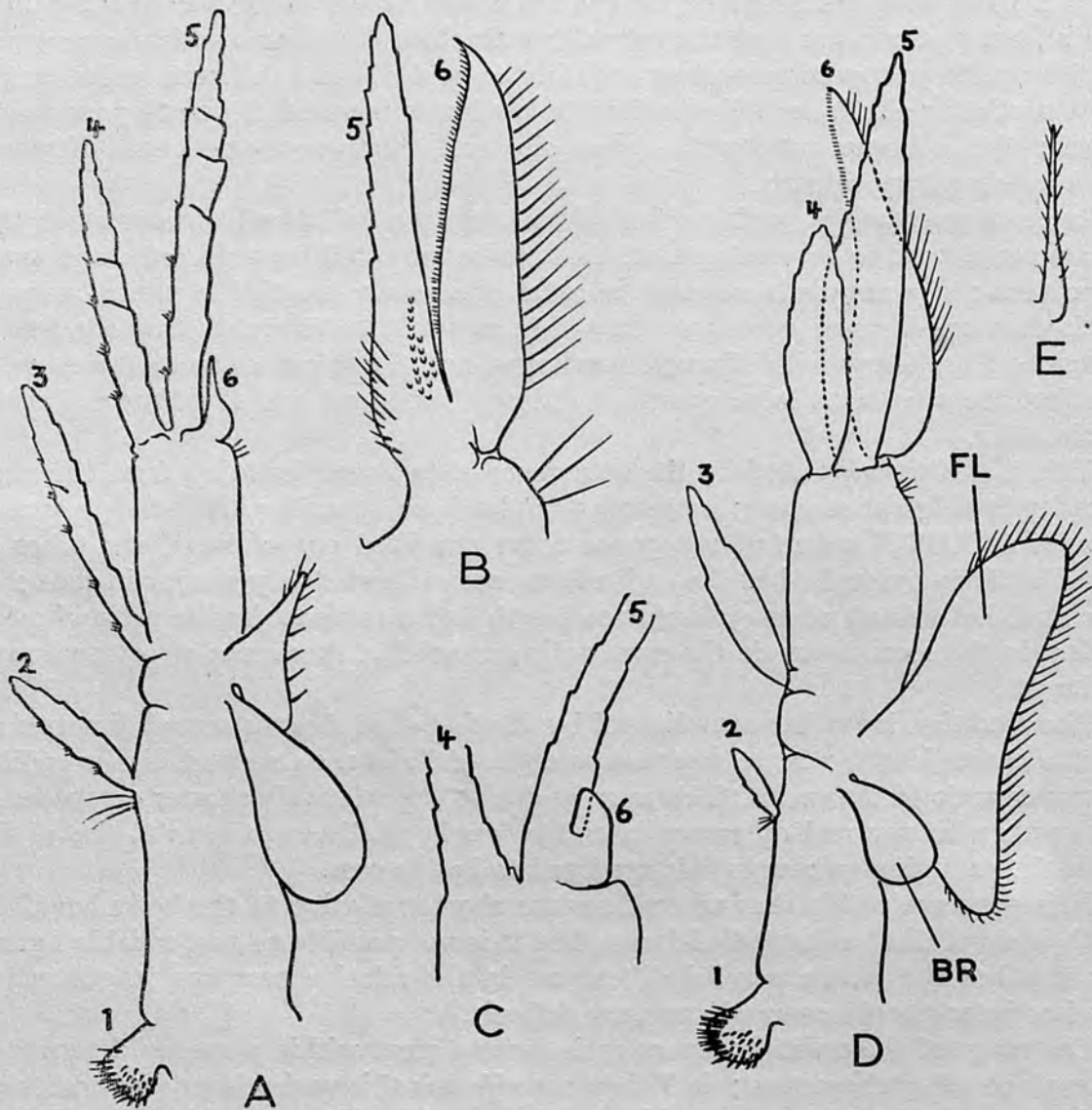

FIG. 10. Thoracic appendages: A, first thoracic appendage of *Lepidurus arcticus*; B, tip of second thoracic appendage of *Triops cancriformis*; C, tip of first thoracic appendage of *T. cancriformis*; D, first thoracic appendage of *Lepidurus batesoni*; E, endite 6 of first thoracic appendage of larval *Triops cancriformis*. (numbers = endites, *fl* = flabellum, *br* = bract.)

in order to examine them properly, and this has naturally been possible with only a few specimens. Appendages of representatives of both sexes of all four species of *Triops*, and of several of *Lepidurus* were examined after mounting in polyvinyl lactophenol.

The first antenna is present in all larvae and adults and is remarkably uniform in structure ; it bears at its tip three setae in all species that I have examined, although this number may be apparently altered by breakage. An aberration was seen in one specimen out of a sample of a *trachyaspis* form of *Triops granarius* from South Africa in which a pair of additional strong spines were present on one margin.

The second antenna must be present in all larvae, for in them it is the main locomotor organ ; the form and numbers of setae are identical in the larvae of all four species of *Triops*, but I have been unable to make comparisons in *Lepidurus* ; this appendage subsequently dwindles, due to negative allometry, and its locomotor functions are taken over by the thoracic appendages. It is often absent in large
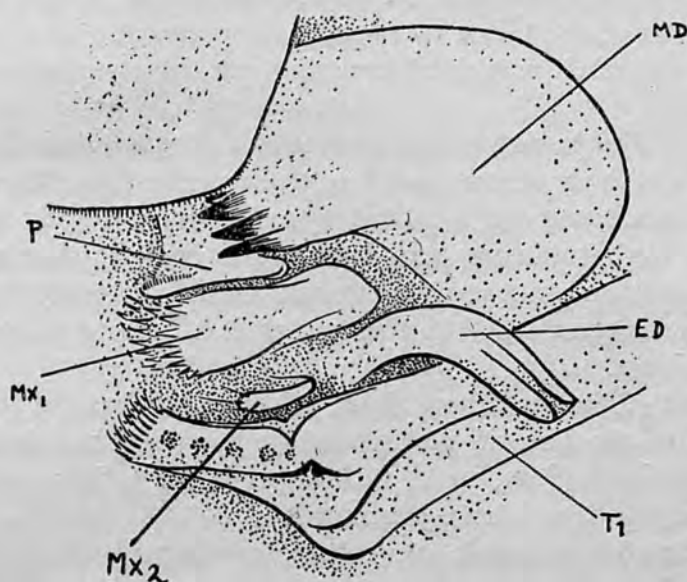

FIG. 11. Mouth parts of *Triops cancriformis* to show second maxilla. (*md* = mandible, *Mx*1 = first maxilla, *Mx*2 = second maxilla, *p* = paragnath, T_1 = first thoracic appendage, *ED* = efferent duct of shell-gland).

specimens, or it may be present (but very hard to detect) in the cleft in front of the mandible. I have found both conditions in large individuals of all species and can attach no importance to its presence or absence, contrary to the opinions of Linder (1952) and Spencer and Hall (1896).

Ghigi (1921) used the arrangement and relative sizes of the teeth on the triturating surface of the mandible as a systematic character in his division of European and North African material ; I have examined this character in many specimens conspecific with his material and there is so much variation that the invalidity of the character seems certain. Gauthier (1934) and Pérès (1939) found similar variation in their North African material.

The first maxilla has never been described comparatively ; I find the main variation to be in the row of spines on the ventral edge of the appendage. These tend to be fewer in number and finer in *Triops cancriformis* than in the other species in the

genus, but there is probably a complete gradation of intermediates, and I can make no use of the appendage in the systematics.

The second maxilla has received more attention than the previous appendage and seems to provide an important character (Text-fig. 11). Sars (1901) noted that the second maxilla was larger in *Lepidurus* than in *Triops* ; this is so, and this appendage is also larger in *T. cancriformis* than in the other species of the genus, but even in this species is so small that it can scarcely be of importance in the feeding mechanism. Linder (1952) reported that it was absent in large individuals of most species of *Triops* (*australiensis*, *granarius*, *numidicus*, *longicaudatus*), but that no dwindling occurred during growth in *T. cancriformis*. I cannot agree with this. The second maxilla is present in all samples that I have seen of *T. cancriformis* and *T. granarius*, and absent in all those of *T. longicaudatus* and *T. australiensis*. Even in very small specimens of the latter two species it is absent ; in a narcotized female from Morawa in Australia it was clearly missing, yet this specimen was only 7·5 mm. in total length.

In those species of *Triops* in which it is present it does not dwindle during growth ; in a *T. cancriformis* of 8·0 mm. carapace length the second maxilla was 0·2 mm. long and in one of 18 mm. carapace length it was 0·4 mm. long ; in a *T. granarius* of 7·5 mm. carapace length it was 0·13 mm. long, and in one of 13·8 mm. it was 0·33 mm.

Thus, the presence or absence of a second maxilla provides a clear character separating two species groups within *Triops*, but it is present and well developed in all species of *Lepidurus*.

The efferent duct of the maxillary gland arises at the base of this appendage, or from the position of the base if the appendage is absent ; this duct is longer in *Triops* than in *Lepidurus* (Sars, 1901) and longer in male than in female *Triops*, in all the bisexual samples that I have examined.

The endites of the first thoracic appendage have already been dealt with, and I could find no significant variation in the other lobes of this appendage, except that the flabellum was relatively larger in *Lepidurus batesoni* than in other species—another character of the 2nd thoracic appendage appearing on the 1st in this species.

In the second thoracic appendage, the form of the terminal " claw " (= exopodite, Lankester 1881 ; apical lobe, Borradaile 1926 ; endopodite, Linder 1952 ; which I shall call endite 6 from the precisely similar ontogeny in the early stages of this and the other endites) was used by Ghigi (1921) to differentiate between species of *Triops* ; I find great variety in the form of this lobe, but none that can be correlated with other characters. The relative lengths of endites 5 and 6 of this appendage show a sexual dimorphism ; in males endite 5 is commonly longer than endite 6, while in the females they are more nearly equal. This is well known and I have been able to confirm it in all the bisexual samples that I have seen.

In the remainder of the thoracic series there is considerable variation in the shapes of the lobes of the appendages, but I can find none that are of importance between species ; however, all the specimens that I have seen of *Triops granarius* from Central and Eastern Asia have endite 6 of the mid-thoracic appendages of a more rounded shape than is usual.

The armature of these appendages shows much variation in numbers of spines

but not in their arrangement—a situation common in the armature on other structures in these animals. The numbers of spines in any group tend to increase during growth, but I have not been able to follow this closely.

The abdominal appendages showed no differences which might be of use systematically except to demonstrate once again a similarity between *Triops cancriformis* and the *Lepidurus* species ; the flabellum of *Lepidurus* bears a number (20–30) of setae around its outer margin, and these are reduced in number in *Triops*. But *T. cancriformis* has a higher number (10–20) than the other species (e.g. *T. granarius*, 4–9).

Linder (1952) mentions an inflated condition of the flabella in some specimens ; this I find to be due to post-mortem changes, especially in those animals which have died just after moulting, when the flabella are commonly so turgid with fluid after a few hours that they have the appearance of small red balloons.

(11) *Furca*

The length of the furca has been considered an important systematic character and was often included in even the early descriptions, but recent authors have thought it unreliable (Linder, 1952).

The furca grow very rapidly in the larval stages of *Triops* but their positive allometry soon becomes less marked, though some relative increase probably occurs throughout life (Text-fig. 9). The furca are generally relatively longer in those specimens in which the endites of the first thoracic appendage are long, and are probably correlated in their development with the number of segments in the same way as the endites. That there is no direct correlation with the endite length is shown by *Lepidurus arcticus* in which the endites are very short, but the furca are similar in length to those of the other species.

Gurney (1924) showed that sexual dimorphism in the armature of the furca occurred in *Triops* ; the spines on the ventral surface of the proximal region of the furca tend to be broader in males than in females, in extreme cases forming protuberant scales (Text-fig. 8c, D). With few exceptions this dimorphism is more marked in long bodied forms, where the base of the furca tends to be relatively thick and rapidly tapering. In *Lepidurus* these spines are a little, but not much, thicker in males than in females.

PROTEIN SPECIFICITY

Oxyhaemoglobin has a characteristic absorption spectrum, and small differences in the wave-length at which the axes of the absorption bands occur have been demonstrated for several species of *Daphnia* by Fox (1945, 1946) ; similar differences in the position of the absorption band axes of the chlorocruorin of species and varieties of *Sabella* have been used systematically by the same author (1946).

The blood of Notostraca contains a considerable concentration of haemoglobin in solution and the size of the animals is such that a volume of blood sufficient for spectroscopic analysis can readily be withdrawn by a micro-pipette. It seemed profitable to determine the wave-lengths of the absorption bands of as many populations of Notostraca as were available, and to apply the results to the systematics.

A Hartridge reversion spectroscope was used to determine these wavelengths, in the manner described by Fox (1945), with a small refinement in technique to eliminate personal bias and errors due to parallax; the operator kept his eye to the instrument throughout a series of measurements and an assistant made the readings on the micrometer head and noted them down.

The wave-length of the axis of the oxyhaemoglobin-α band was determined by comparison with a sample of blood of similar optical density and of known wave-length (human blood, 5775Å). A number of readings were made on each sample of blood and the results were treated statistically.

Several cultures of *Triops cancriformis* from different European localities were compared, using several adults from each culture. The results (Table I) show that although there is little individual variation, the three populations are apparently different from each other; these differences gave a probability of significance of 0·02 when a *t* test was applied to them, and it may be taken that they are real and not referable to errors in the methods of measuring.

TABLE I.—*Wave-length of the axis of the oxyhaemoglobin-α band. Means of the readings taken on each animal, the averages of these means (X̄), the number of readings per sample(N), and the standard errors of the means (S.E.). The figures in parentheses indicate the distribution of the readings within a sample.**

| | Triops cancriformis | | | | T. granarius | | | T. longi-caudatus |
	Sweden	England	Italy		Johannes-burg	Grahams-town		Cali-fornia
Means per animal (Å)	5779·7 (30)	5778·3 (40)	5777·0 (20)	.	5776·7 (10)	5778·2 (30)	.	5777·3 (30)
	5778·9 (30)	5778·8 (30)	5778·2 (30)	.	5776·4 (30)	5775·5 (30)	.	5776·3 (30)
	5779·0 (30)	5778·6 (20)	5777·9 (30)	.	5776·8 (30)	5776·5 (30)	.	—
	5780·6 (30)	5778·8 (32)	5777·3 (30)	.	5777·3 (30)	5778·3 (30)	.	—
	5779·8 (28)	5778·9 (39)	—	.	5776·9 (30)	—	.	
X̄ (Å) . .	5779·6	5778·6	5777·6	.	5776·5	5777·1	.	5776·8
N . .	148	161	110	.	130	120	.	60
S.E. . .	0·356	0·305	0·281	.	0·340	0·370	.	0·255

This indicated that inter-specific differences must be considerably greater than these intra-specific ones to be of any value in systematics, and that many populations of a species must be tested before a value characteristic of that species could be determined.

In fact, subsequent inter-specific comparisons gave results (Table I) very little different from those obtained with *Triops cancriformis*.

The span between the axes of the oxyhaemoglobin and the carboxyhaemoglobin-α bands was also examined, for this is known to show differences between species in some cases (Fox, 1946). The results obtained with three species of *Triops* showed no differences which would justify further investigation. (span : *T. cancriformis* = 50·1 Å, *T. longicaudatus* = 48·2 Å, *T. granarius* = 47·5 Å).

The results of both these investigations are of no practical value in the systematics of these animals—the differences being much smaller than those found and used in *Sabella* by Fox—but do serve to demonstrate that in this character, as in others, the species of *Triops* form a remarkably closely related group.

* A single specimen of *T. australiensis* from Kalgoorlie was tested and gave a result of 5779·3 Å.

REPRODUCTION

It has long been known that some populations of Notostraca contain both males and females, and some only females. The occurrence of large populations in which no males could be found has generally been assumed to indicate parthenogenesis, especially since it was also known that isolated females from such populations could produce viable eggs.

Bernard (1889) found scattered testis lobes in the gonads of female *Triops cancriformis*, *Lepidurus apus* and *L. arcticus*, and reported these occurrences as cases of hermaphroditism. Zograf (1906) found ovarian tetrads developing in the testis
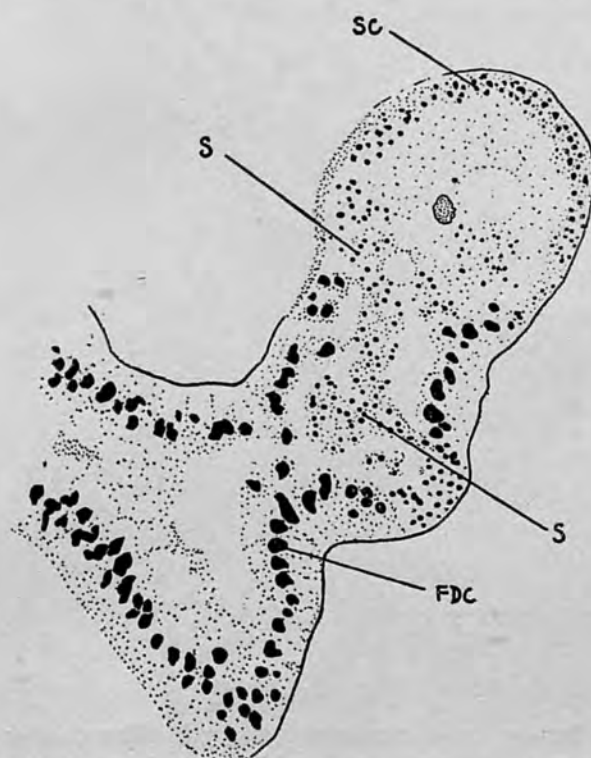

FIG. 12   Testis lobe in ovotestis of *Triops cancriformis*.   5μ section, Carnoy/Feulgen.
    (*S* = sperms ; *Sc* = spermatocytes ; *F.D.C.* = follicle duct cells).

walls of male *L. apus*, which must surely be an aberration of no use to the animal, for the oocytes subsequently degenerated. Spencer (1896) could find no testis lobes in the ovaries of *Triops australiensis*.

Bernards' findings, largely ignored since his account, have been confirmed in the present work during investigation of the cytology of *Triops* and *Lepidurus*, and have been reported elsewhere (Longhurst, 1954). Hermaphroditism has been found in three species—*Triops cancriformis*, *T. longicaudatus* and *Lepidurus arcticus*—and it was found that females of the first two laid viable eggs in isolation and contained ovotestes (Text-fig. 12) ; no *L. arcticus* reached adult size. Females of *Triops granarius* and *T. australiensis* were unable to lay eggs in the absence of males, but

did so readily as soon as males were put into the tanks with them and pairing had occurred ; this was presumably correlated with the fact that no testis lobes were present in the ovaries of the females of these species.

There is no evidence to show that these latter two species of *Triops* are ever anything but bisexual ; in all the material I have examined of these species the large samples invariably contained both sexes, and there are no records in the literature of females occurring in large numbers without males. In *T. cancriformis* there appears to be a complex situation : in the southern parts of its range bisexuality is normal, and a female from Algeria had no testis lobes ; but in the more northerly regions males occur sporadically, often in very low proportions, so that some of the females
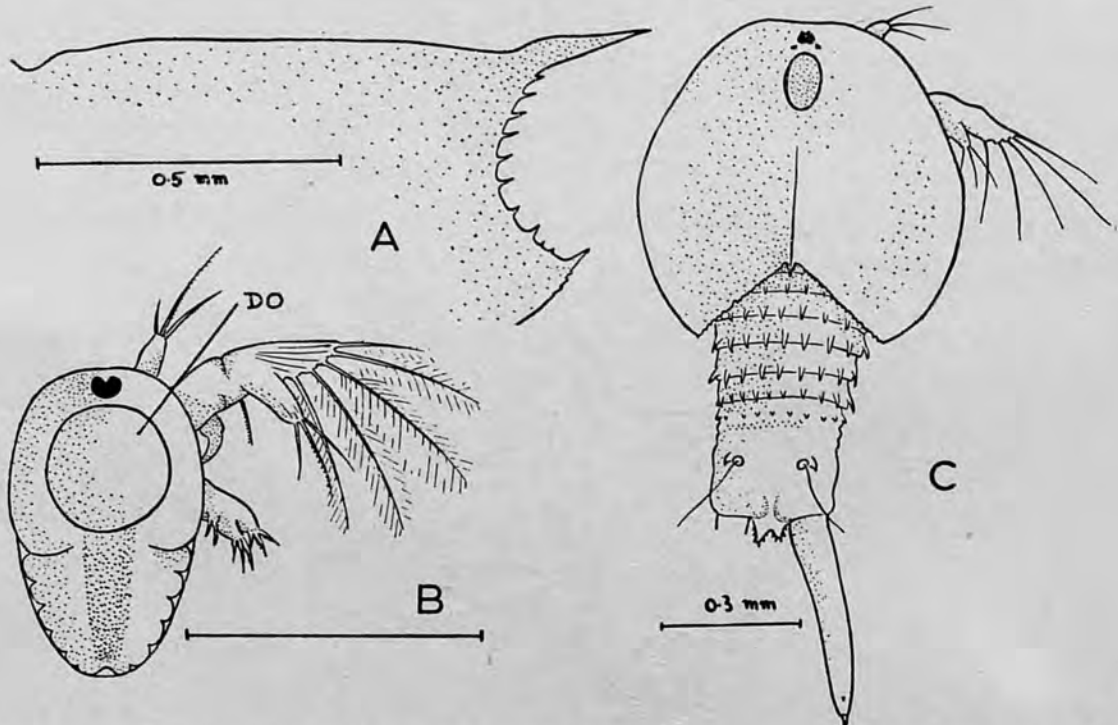

FIG. 13.   Notostracan larvae.   A = carina of instar 3 *Lepidurus apus* ; B, metanauplius of *Triops cancriformis* ; C, Neonatus of *Lepidurus arcticus*.   (*do* = dorsal organ.)

probably reproduce without fertilization.   In the extreme north of the range (Britain, Sweden) males are unknown and here females contain ovotestes.   Unfortunately I have not been able to examine the gonads of females from a population with sporadic male occurrence.   Mathias (1937) gives a review of the occurrences of males of this species.

In *Triops longicaudatus* the geographical distribution of males is not so clear; however, specimens from Californian rice fields where males are unknown contained ovotestes, and Linder (1952) reports examining many specimens from the Galapagos Islands without finding males.   Uéno (1935) records this species in Japan and found no males in 78 specimens.   It may be that all the populations of this species from the Pacific region are hermaphrodite, for the small samples that I have seen from Hawaii (Oahu) and from New Caledonia contained no males.

Reproduction in *Lepidurus* is less well explored ; it is known (above) that herma-phrodite individuals occur in some species, but males of these are also known in some populations although their geographical distribution is not clear. The three long bodied species all appear to be bisexual.

The size of the egg in *Triops* is variable, being larger in long bodied forms irres-pective of species ; with this is correlated a size difference in the mature follicles in
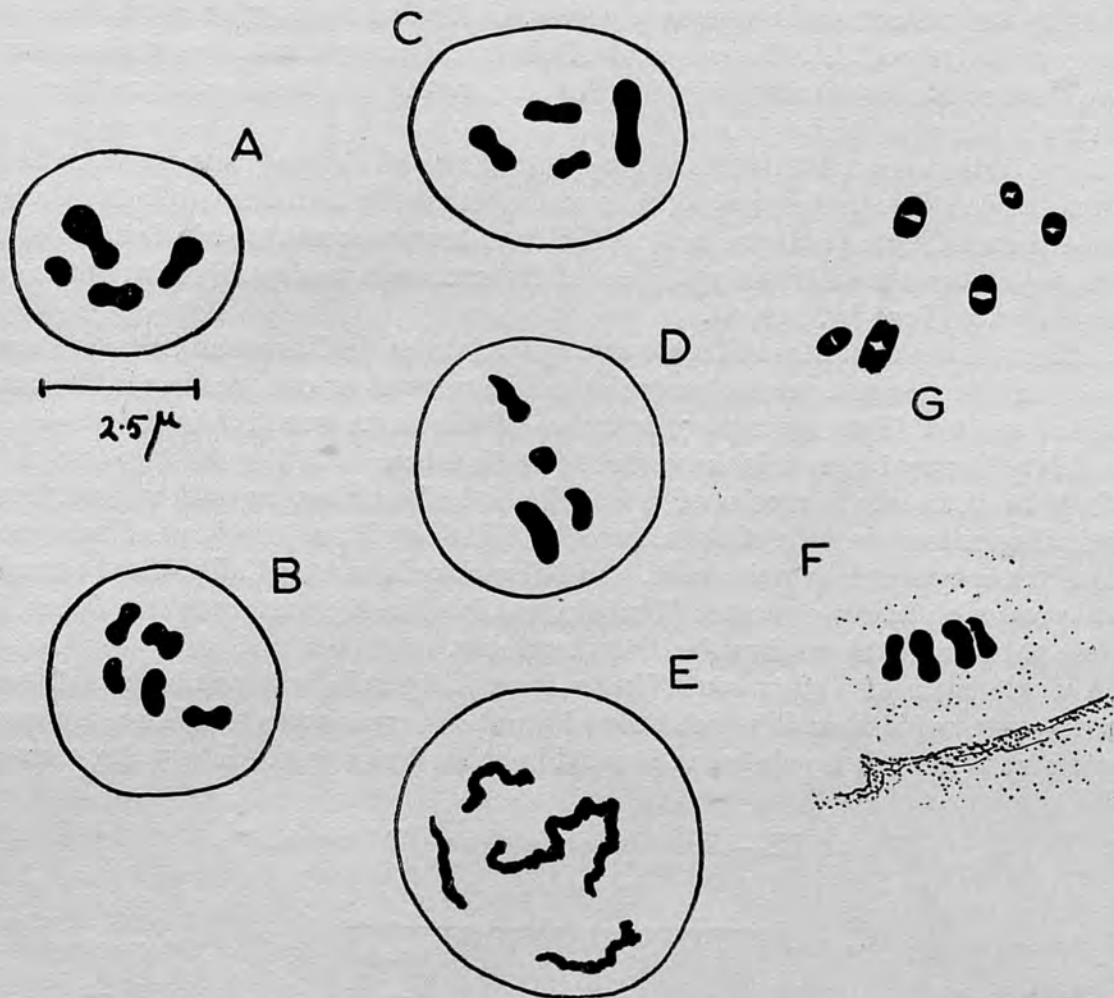

FIG. 14. Notostracan chromosomes. A–C, 2° spermatocyte telophase ; D–E, young oocyte ; F, resting unfertilized ovum ; G, spermatocyte diakinesis. A, *Triops longi-caudatus* ; B, *T. australiensis* ; C, D, E, *T. granarius* ; F, *T. cancriformis* ; G, *Lepidurus apus*. (G is half the scale of the remainder and is redrawn from Goldschmidt, 1953.)

the ovary : *T. cancriformis* (33 segments), 0·28 mm. ; *T. granarius* (38 segments), 0·45–0·52 mm. This size difference is correlated with size differences in the resultant eggs and larvae, the long bodied forms having the largest larvae. In *Lepidurus* the differences may be even more marked and are diagnostic of species in at least one case ; the larvae of *L. arcticus* hatch at a later stage of development than those of the other species (Text-fig. 13), and the eggs are very much larger, the ovarian

in this haploid set are all sub-equal in length (Text-fig. 14B), and it seems probable that this situation could have arisen by the fragmentation of one chromosome in a set of four, such as the other species possess, in which one is nearly twice as long as the other three.

My findings and those of Goldschmidt are summarized in Table II, and both agree in ascribing a low number of chromosomes to the Notostraca so far examined. Moore's account of amitosis may be true of the cells that he studied, but even that is doubtful in view of my chromosome counts in epithelial cells ; his inference of a single chromosome was obviously incorrect.

All the *Triops* material was fixed in Carnoy's or Susa's fluids and was stained with the Feulgen reaction.

BIOLOGY

Very many accounts of the ecology of the Notostraca and of their appearance in temporary pools have been published, and a clear picture of their biology can be derived from the literature.

There appear to be almost no ecological differences between the species of *Triops*, a slight difference between *Triops* and most species of *Lepidurus*, and a marked divergence between *L. arcticus* and the rest of the Notostraca.

So far as is known, *Triops* occurs only in waters which dry out regularly, and the eggs normally hatch in the field only after a period of dessication. The habitat itself may vary a great deal in size from tiny rain pools and cart-ruts to large temporary lakes (Main, 1953) and the water may be fresh as in the Hampshire locality (Hobson and Omer-Cooper, 1935), brackish as in the Scottish pools (Balfour-Browne, 1909), or saline as in the lakes on the Tibetan plateau (Schlagintweit, 1872) and in Australia (Main, 1953).

The farming practice of rice fields makes these ideal situations for *Triops*, which are sometimes present in enormous numbers and have been recorded as a rice field pest from many parts of the world (they uproot the rice seedlings).

Lepidurus may occur in temporary pools, but there seems to be a tendency for most species to live in waters which dry out less regularly than the *Triops* pools. Lundblad (1920) records that *Lepidurus apus* is a spring form which appears when the temperature rises early in the year in ponds or ditches which have held water all the winter ; Linder (1952), on the other hand, says that he has seen the same species in Sweden in temporary pools. *L. apus viridis* occurs in a pool near Christchurch, New Zealand, which dries out in normal years, but is only very rarely found in neighbouring permanent ponds (G. Parry, personal communication). *Lepidurus* spp. regularly occur in temporary, often alkaline, pools in North America (J. Lynch, in litt.). L. Glauert has sent me a map showing all the records for *Triops* and *Lepidurus* in Western Australia and it is clear that *Lepidurus* is restricted to the south-western coastal belt where there is regular winter rain and *Triops* to the arid interior where rainfall is, at the most, sparse.

Lepidurus arcticus is confined to the boreal and alpine regions of the Holarctic, where it may occur in large lakes and form an important food of Salmonidae and where the eggs could never be dessicated (Sømme, 1934), it is also in pools which

normally do dry out each year (J. Mohr, in litt.). The only other records of *Lepidurus* occuring in lakes refer to *L. lynchi* (Linder, 1952).

It has been thought that there is a difference between the two genera in the conditions necessary for the hatching of the eggs : Fritsch (1866) and Grasser (1933) thought that *Triops* eggs could hatch only after dessication, while Brauer (1877) believed that the eggs of *Lepidurus* were incapable of withstanding dessication. Schaeffer (1756) and Kozubowsky (1857) showed that the eggs of *Triops* were sometimes capable of hatching without drying out. This has been confirmed in the present work and it is now known that the eggs of at least three species of *Triops* can hatch out, after an interval for development, in the water in which they were laid, or will remain viable if dried out and will hatch when replaced in water. This accounts for the report by Mathias (1937) that *Triops* has two types of eggs : the one drought resistant and the other not.

Fox (1949) reported that the eggs of *Lepidurus apus viridis* were able to hatch after drying, and I have confirmed this with another mud sample from the same locality as his ; *L. arcticus* from Iceland were also hatched from dried eggs. The ecology of *Lepidurus* outlined above indicates that the eggs of this genus must in many cases be drought resistant.

The eggs of *Triops* probably do not often hatch out without prior dessication, as the water must have a low osmotic pressure for this to occur, a condition unlikely to be found on the bottom of a pool where the eggs are laid, but most likely when the pool refills with water after rain and the eggs float to the surface.

SYSTEMATICS

From the analysis of the characters used in the systematics of the Notostraca it is evident that many of the obvious differences between individuals must be correlated with differences in the number of body segments (Text-fig. 2) ; in *Triops* there is no discontinuity in the variation of this number, so that neither the number itself nor characters correlated with it can validly be used in the separation of species.

In this genus, as the number of segments increases to give a long bodied form so the carapace becomes smaller, rounder and flatter ; the number of legs remains about the same and consequently the apodous number becomes higher ; the furca, and the endites of the first thoracic appendage become relatively shorter ; the dorsal organ becomes larger, less elevated, and more often triangular in outline ; the sulcus spines become smaller and more numerous, and the terminal spine of the carina is more frequently absent ; sexual dimorphism becomes more marked.

Similarly, certain characters are correlated with the sex of the specimen ; males tend to have more segments than females and so the characters outlined in the previous paragraph vary from male to female within a population ; characters other than these also show sexual dimorphism : the efferent duct of the shell gland is longer in males than in females ; endites 5 and 6 of the second thoracic appendage are more nearly equal in length in females ; the 11th thoracic appendage bears a brood pouch in females ; the ventral armature of the furca of males is coarse, often forming scales rather than spines, and with this is correlated the ventral armature of the telson and apodous segments, which vary in the same way between males and females.

These two considerations then—segment number and sex—invalidate a number of characters in the systematics of *Triops*. With those that remain there appear to be good grounds for dividing the genus into four groups, each with a geographical basis. The valid characters appear to be : the armature of the telson, the presence or absence of the second maxilla, and the arrangement of the eyes and dorsal organ. Of these the most important is the armature of the telson, which is diagnostic for each group ; the other characters, together with a few less well-marked ones, confirm this primary grouping.

Two groups are partially sympatric, and here there is no tendency to hybridize and no intermediates have been found in the areas of overlap ; there is a record, moreover, of two species—which correspond to two of these groups—living in the same pools in several localities in Morocco (Pérès, 1939). These two forms, therefore, behave precisely as biological species (*sensu* Mayr, 1942) would be expected to do when they become sympatric ; it seems justifiable to consider them, therefore, as species and since the degree of morphological difference between all four groups is similar to that found between these two, then all four may equally well be regarded as species.

Each species, then, has a geographical basis and a clear cut character in the telson armature, but contains populations which are remarkably different in general appearance depending on the number of body segments in the specimens. What determines the body length is completely obscure, for there appears to be a general tendency for the longer bodied animals to occur in the warmer regions of a species range, but there are many blatant exceptions to this generality ; Barnard's *Apus ovamboensis* is a population of exceptionally short bodied *Triops granarius* from a very hot and dry part of Africa.

It is likely that an experimental study of the effect of environmental factors on morphology would throw some light on this problem, for perhaps the effects are seen only after a considerable number of generations.

Several species show some indications of the presence of geographical races ; the differences between these are much slighter than the specific differences, and their distribution indicates that the geographical barriers between them are very slight. *Triops cancriformis* will serve as an example ; the populations in Morocco and southern Spain differ in several respects from the rest of the species, even though in Spain there is no geographical barrier where the change occurs, and there is some evidence that intermediates occur where the races meet, for in Seville and near Gibralter the specimens are identical with the Moroccan ones and from Valencia they are similar to the specimens from the rest of Europe, but in Ciudad Real—midway between the two areas—the specimens are intermediate. A similar zone of intermediates seems to occur in Spanish Morocco east of Ceuta.

Ghigi (1921) considered these races of *Triops cancriformis* to be species and described them as such ; Colosi (1922) and Pérès (1939) referred to Ghigi's species as varieties of the single species *T. cancriformis* but Gauthier (1934) used a true trinomial nomenclature and considered them to be sub-species or geographical races ; I follow this nomenclature and believe them to be sub-species in the sense that Huxley (1942) and Mayr (1942) used the term.

The arrangement of the species seems to follow different principles in *Lepidurus* from that in *Triops*, and the following account owes very much to the work of Linder (1952) who demonstrated the existence of two species-groups within the genus, each group characterized by its segment numbers.

The variation in segment number in *Lepidurus* is not so great as in *Triops*, and many characters show no correlation with this number in *Lepidurus* though the correlation is obvious in *Triops* : the armature of carina and sulcus ; the endites of the first thoracic appendage ; the number of apodous segments and the size and shape of the dorsal organ. The segment number shows a marked discontinuity at about 30; the vast majority of specimens have less than this number, and those which have more are aberrant in other respects.

Within the short bodied group there is relatively little differentiation, but *Lepidurus arcticus* can be separated at once, and is distinguished by its range, its habitat, its relatively short supra-anal plate and endites. The remainder of the group appears to comprise a single species, with a few rather ill-marked, but very widespread, sub-species.

Linder (1952) showed that *Lepidurus couesii* was conspecific with specimens determined as *L. macrourus* Lilljeborg. I can find no differences between the specimens that I have seen of either of these species and those of the European *L. apus*. The ranges of variation in the segment number are similar, the size and armature of the supra-anal plate is the same, and so is the armature of the carapace.

In California a form occurs which is admitted as a species by Linder, *Lepidurus packardi* ; in these specimens there is usually a slightly higher number of segments than in the normal *L. couesii* (= *L. apus*), the apodous number tends to be higher, and the sulcus spines are very small, numerous and closely packed. In the Mediterranean region there occurs a form which diverges from typical *L. apus* in a similar way except that the sulcus spines are normal. Both of these forms replace the typical race over very restricted areas, but there appear to be no effective geographical barriers separating the several ranges from one another, and for these considerations I propose to consider these forms to be sub-species of the typical and widespread *L. apus*.

The Australasian forms do not differ from typical *Lepidurus apus* as much as do the above two sub-species, and many specimens would be indistinguishable if placed in a sample from Europe. However, I have seen no specimens which have the high number of central spines on the supra-anal plate which are very common in the typical *L. apus*, so that there is a slight degree of morphological differentiation and I propose to consider the Australasian form as another sub-species, *L. apus viridis*. The South American forms which I know only from descriptions must be considered as another sub-species of *L. apus*.

The rest of the genus comprises the few longer bodied specimens which are known. All have coarse and sparse marginal spines on the supra-anal plate—a character which they share with *Lepidurus arcticus*—and a low number of central spines on the same structure ; specimens from three localities bear uniquely large spines on the carina and the carapace margin and these are Linder's *L. lynchi*, typical form and var. *echinatus*. A small sample from Russia has a considerably higher apodous

number than the rest of this group and shares with *L. lynchi* a peculiar arrangement of the eyes and the dorsal organ, which resembles the arrangement in *Triops australiensis* where the anterior margin of the dorsal organ may be placed well behind the posterior margin of the eyes. A single specimen from Utah was placed in this species-group by Linder on account of its segment number and seems to agree with the description of *Lepidurus bilobatus* Packard, having a normal carapace armature and normal arrangement of the eyes and dorsal organ. The only possible arrangement at the moment is to consider all these three forms as three separate species, but it seems very probable that future work will be able to find a connection at least between *L. bilobatus* and the Russian sample (*L. batesoni* sp. n.) and perhaps between these and *L. apus*.

It will be noted from the foregoing account how widespread are the species of the Notostraca and this is probably accounted for, as it is in some other invertebrates, by their passive distribution ; the dried viable eggs must be blown around by wind, and transport by birds is not unthinkable, for the eggs when laid are extremely sticky and remain so for some days while the shell hardens, and so could presumably adhere to larger animals. The eggs of other phyllopods are known to be capable of passing unharmed through the guts of amphibia (Mathias, 1937), and birds are known to eat Notostraca ; starlings (Decksbach, 1924) and gulls (Balfour-Browne, 1909) are recorded as feeding on *Triops cancriformis*, and Summerhayes and Elton (1923) watched Arctic terns feeding *Lepidurus arcticus* to their young, and thought that they might drop them accidentally into fresh pools on their way to the nest.

A passive distribution such as this must mean that geographical barriers are not nearly so effective as they are for sedentary, or non-passively distributed animals, and has produced species with world-wide distribution in other animals, such as Tardigrades and Rotifers.

In addition, the group has a very long geological record and has had ample time to occupy all suitable areas ; fossils from the Permian (Guthorl, 1934) are clearly Notostracan carapaces, and forms from the Triassic of Europe (Trusheim, 1938) are certainly *Triops* and differ from extant *T. cancriformis* only in the small size of the terminal carinal spine. The upper Triassic *L. stormbergensis* (Barnard, 1929) from South Africa is very similar to recent species except that the supra-anal plate has, apparently, no central spines as in some extant *L. arcticus*.

It is impossible from these few fossils to give any account of the history of the group, except to point out how little evolution has occurred in the space of 170 million years since the Triassic forms were alive.

However, something can be deduced about more recent changes in distribution. During the Pleistocene glaciations *Lepidurus arcticus* was much more widespread in western Europe than it is now ; this species is known from lacustrine beds of that time from Scotland (Bennie, 1894) and from the Isle of Man (Geikie, 1894), and now shows in Scandinavia the typical distribution of a boreo-alpine relict occurring at sea level in the North and at progressively greater altitudes towards the South (Sømme, 1934).

Triops cancriformis must have been absent from much of its present range at the same period, and the post-glacial extension may have been performed largely by

hermaphrodites, which predominate in the northern parts of its range ; for these would be more efficient in dispersal as only a single egg would be required to effect a colonization. Perhaps the increasingly sporadic occurrence of males towards the north indicates a spread northwards of bisexuality.

All the known rice field populations consist entirely of females (or hermaphrodites if parthenogenesis is assumed not to exist in these animals) and this strengthens the above argument, for these are relatively new habitats for Notostraca, and a colonization by hermaphrodites ahead of the bisexuals seems to have occurred.

The westward extension of *Triops longicaudatus* across the Pacific from the largest area of distribution in North America, may also be of relatively recent origin and has apparently been performed again by hermaphrodites, for no males are known from the Pacific populations (p. 47).

Nomenclature

Keilhack (1909) and Fox (1949) have shown that the generic name *Apus* Schaeffer, 1756 should be rejected in favour of *Triops* Schrank, 1803 ; this practice will both accord strictly with the Rules of Nomenclature and will avoid further confusion in this genus, and in the avian genus *Apus* Scopoli, 1777. I therefore propose to follow Keilhack in the use of *Triops*.

The use of trinomials is necessary to describe formally the geographical sub-species recognized.

The lists of synonymies before each species are not complete lists of references to that species, for these would be too long and not very useful—but include (a) the names, and the various spellings of each name, that have been applied to that species, and (b) important descriptive works.

Apus has been applied to Crustacea other than Notostraca ; *Apus pisciformis* Schaeffer is an Anostracan and *Apus caudatus* De Kay, was a crustacean parasitic on a crab.

Identification

The following key should serve to identify specimens down to species, but the user must bear in mind the extent of variation in any character and not expect the figures to match the specimen in details of armature. It would be very valuable if the segment number, the apodous number, and the number of appendages were given in any future records.

It must also be remembered that every individual in a sub-species may not be typical of it ; many ornithologists consider a sub-species to be valid if 75% of its specimens can be placed in it without question. In *Triops cancriformis*, for example, it may be difficult to ascribe single specimens to the nominate race or to *T. cancriformis simplex*, for the smooth carina which is typical of the latter occurs in some individuals of the former, but I have no knowledge of whole samples of the nominate race with smooth carinas.

Key to species of Notostraca

1. Supra-anal plate present (Text-fig. 7) . . . . (*Lepidurus*) 2.
   Supra-anal plate absent . . . . (*Triops*) 6.

2. Segments more than 30 . . . . 3.
   Segments less than 30 . . . . 5.
3. Anterior margin of dorsal organ between eye tubercles (Text-fig. 4E)   *L. bilobatus* (p. 53).
   Anterior margin of dorsal organ well posterior to eye tubercles (Text-fig. 4D) . . 4.
4. Carina and/or lateral margins of carapace with large spines. (Text-fig. 3) Apodous
   segments 3–5 . . . . *L. lynchi* (p. 53).
   Without large spines on carina or lateral margin. Endite 6 of first thoracic appendage
   as in Text-fig. 10D. Apodous segments 8–9 . . . . *L. batesoni* (p. 54).
5. Supra-anal plate short, 0–5 spines centrally, marginals few (Text-fig. 7C). Endites
   scarcely project beyond edge of the carapace . . . . . *L. arcticus* p. 52).
   Supra-anal plate long (Text-fig. 7A, B), 4–100 central spines, marginals numerous.
   Longest endites with 3/4 of their length projecting beyond edge of carapace (Text-
   fig. 2i) . . . . *L. apus* (p. 50).
6. Second maxilla absent . . . . 7.
   Second maxilla present (Text-fig. 11) . . . . 8.
7. Posterior marginals sub-equal to medians and well forward of the margin (Text-fig.
   5D$_2$). Medians large, 1–4 in number, in a row . . . *T. longicaudatus* (p. 46).
   Posterior marginals reduced and marginal. Medians small, scattered when more
   than 3–4, often absent. (Text-fig. 6B) . . . . . *T. australiensis* (p. 48).
8. No supernumerary spines on the apodous segments (Text-fig. 8A). Medians large, 1–4,
   in a row (Text-fig. 5B$_2$) . . . . *T. cancriformis* (p. 41.)
   Supernumerary spines present on apodous segments (Text-fig. 8B). Medians of
   various sizes, scattered except when less than about 5 are present, when they form
   an irregular row (Text-figs. 5C$_2$, 6A, A$_1$) . . . . . *T. granarius* (p. 44.)

Genus *TRIOPS* Schrank, 1803

1756. *Apus* Schaeffer (in part).
1758. *Monoculus* Linn. (in part).
1803. *Triops* Schrank.
1921. *Thriops* (sic.) Ghigi.
1921. *Proterothriops* Ghigi.

Triops is at once separable from *Lepidurus* by its lack of a supra-anal plate ; even if a structure resembling a rudimentary plate (Text-fig. 7C) is found in some specimens of *Triops cancriformis* (Linder, 1952) there is never any doubt as to which genus a specimen belongs.

Proterothriops was erected by Ghigi for the reception of the long bodied forms of the genus ; he was struck by the great difference in general appearance between long and short bodied forms which I have now been able to show to be conspecific in a number of cases.

Binoculus Geoffroy, 1762 and *Apodis* Zaddach, 1841, are not in a strict binomial system and are ignored on this account.

Triopes Schrank, 1803, appears later in the publication than *Triops* and must be regarded as a spelling lapse.

TRIOPS CANCRIFORMIS (Bosc)

1756. *Apus cancriformis* Schaeffer (in part).
1758. *Monoculus apus* Linn. (in part).
1801. *Apus cancriformis* Bosc.

1801. *Apus viridis* Bosc.
1803. *Triops palustris* Schrank.
1816. *Apus montagui* Leach.
1871. *Apus himalayensis* Packard.
1885. *Apus halicienis* Fiszera.
1885. *Apus lublinensis* Fiszera.
1885. *Apus varsovianus* Fiszera.
1909. *Triops cancriformis* (Bosc) Keilhack.
1909. *Apus cancriformis bidens* Sidorov.
1909. *Apus cancriformis transcaucasicus* Sidorov.
1921. *Thriops simplex* Ghigi.
1921. *Thriops mauretanicus* Ghigi.
1921. *Thriops apulius* Ghigi.
1922. *Thriops cancriformis* var *simplex*, Colosi.
1953. *Triops cancriformis simplex* (Ghigi, 1921) Margalef.
1953. *Triops cancriformis mauretanicus* (Ghigi, 1921) Margalef.

TYPE. Original is unknown, and designation of neotypes desirable. A sample from Kirkudbrightshire is selected (BMNH, 1907.10.17.1–4) and consists of a number of neoparatypes.

RANGE. Western Europe (Spain to Sweden) east to Russia ; North Africa, Balkans, Asia Minor, Middle East to India. Individual records too numerous to list ; Lundblad (1920) gives many for Europe, Decksbach (1924) many for Asia. Does not extend beyond 60° N and range in Russia obscure, but no records authenticated for Eastern Asia.

HABITAT. Temporary fresh or brackish waters ; occurrence depends on the pools filling when the temperature is high enough for development, so usually summer form in Europe, spring form in N. Africa.

Rice field pest in N. Italy, Spain and La Carmargue.

DESCRIPTION. *Head.*—Dorsal organ round, oval or rarely triangular, small and with its anterior margin between the eyes. Second maxilla present in all specimens examined and relatively larger than in the rest of the genus.

Carapace.—Shape generally oval, more round in males. Carina with terminal equal to, or longer than, sulcus spines (Text-fig. 15) ; sometimes number of smaller spines on posterior carina. Sulcus spines long, 24–44, usually about 30.

Body.—Segments 32–35 in both sexes ; apodous 4–7 in ♀♀, 5–9 in ♂♂. Apodous segments without supernumerary spines on ventral surface.

Telson.—Median spines large, 1–4, in a single median row (Text-fig. 5B). Furcal spines large, number sometimes varying from side to side of a single animal, and with few scattered spines on lateral face of telson anteriorly.

Posterior marginals small, fine and marginal in the adult, and posterior margin of telson sometimes drawn out to resemble a rudimentary supra-anal plate (Text-fig. 6C).

Furca generally long.

Appendages.—48–57 pairs recorded, but variation probably greater. Endites of first thoracic appendage long.

Sexual dimorphism.—Not as well marked as in other species ; no males with furcal scales seen. Abonyi (1926) records two sets of males in one summer in the same pool

of which the second batch had very reduced sexual dimorphism—so a dimorphism of males may exist ?

Larvae.—Metanauplius (Text-fig. 13) ; dorsal organ of instar 1 generally round.

Reproduction.—Bisexual and hermaphrodite ; in the northern regions no males occur and such females as have been examined are hermaphrodite. In the South populations are bisexual and in central Europe males occur sporadically. Mathias (1937) reviews occurrence of males.

Geographical Races

1. *Triops cancriformis cancriformis* (Bosc)

RANGE. Whole of species range with exception of that occupied by the other two sub-species.

DESCRIPTION. Carina bears 0–10, generally 2–3, small teeth in front of the terminal spine (Text-fig. 15E) and no large samples without specimens showing these spines are known. Furcal spines small (Text-fig. 5B$_2$). Dorsal organ round-oval.

Hermaphrodite and bisexual. Chromosome number $2n = 8$.
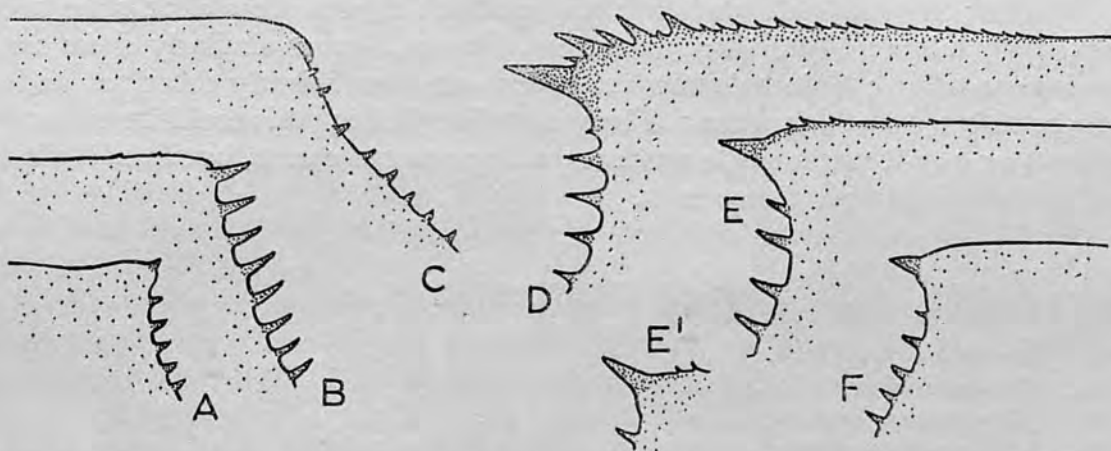
FIG. 15. Carinas of *Triops*. A–C, *T. granarius* ; D, *T. cancriformis mauretanicus* ; E, E$_1$, *T. c. cancriformis* ; F, *T. cancriformis simplex*.

2. *Triops cancriformis simplex* Ghigi

RANGE. North Africa, Ceuta to Egypt.

DESCRIPTION. Characters of *Thriops simplex* Ghigi. Carina quite smooth in front of the terminal spine (Text-fig. 15F) ; this is invariable in the specimens I have seen from this area, and in those seen by Gauthier (1934), Colosi (1922) and Ghigi (1921). Furcal spines small (Text-fig. 5B$_2$). These populations frequently show a tendency to a general weakness in the strength of the armature and include the sample from Kebili (p. 14) which has specimens with no carapace armature whatever. The terminal spine of the carina is frequently reduced.

Apodous segments frequently higher in number than the nominate race (♀♀ 5–7, instead of 4–6).

Bisexual.

3. *Triops cancriformis mauretanicus*, Ghigi

RANGE. N.W. Africa: French Morocco and Tangier. S. Spain and Balearics (Minorca).

DESCRIPTION. With the characters of *Thriops mauretanicus* Ghigi: armature very strongly developed; carina with a number of teeth posteriorly (Text-fig. 15D), the largest often sub-equal to the terminal spine. Furcal spines very large (Text-fig. 6C); ventral marginal spines on apodous segments very coarse. Apodous number is similar to that of sub-species 2. Dorsal organ oval.

Bisexual.

SYNONYMS

Apus viridis Bosc was applied to figures of Schaeffer (1756) which showed juvenile *Triops cancriformis; Triops palustris* Schrank is presumably of this species because of its N. European locality; *Apus montagui* Leach, type in BMNH and clearly of this species; *Apus himalayensis* Packard, author's figures show clearly the *cancriformis*-type telson; *Apus varsovianus*, etc. Fiszera, figures similarly show *cancriformis*-type telson; Sidorov's two sub-species are insufficiently described and can both be referred to this species; *Thriops apulius* Ghigi; this could be either sub-species 1 or 2 as it was a single specimen with a smooth carina, but from its Italian locality is probably of sub-species 1.

TRIOPS GRANARIUS (Lucas)

1864. *Apus granarius* Lucas.
1865. *Apus numidicus* Grube.
1877. ? *Apus dispar* Brauer.
1877. *Apus sudanicus* Brauer.
1880. *Apus dukeanus* Day.
1886. *Apus bottegoi* Prato.
1886. *Apus namaquensis* Richters.
1893. *Apus sudanicus* var. *chinensis* Braem.
1893. ? *Apus sudanicus* var. *braueri* Braem.
1893. *Apus numidicus* var. *strauchii* Braem.
1893. *Apus numidicus* var. *dybowskii*, Braem.
1895. *Apus somalicus* Wedenissow.
1899. *Apus bottegoi*, Bouvier.
1899. *Apus trachyaspis* Sars.
1899. *Apus sculleyi* Sars.
1899. *Apus namaquensis* Sars.
1899. *Apus granarius* Sars.
1907. *Apus elongatus* (nom. nov. for *namaquensis* Sars) Thiele.
1920. *Apus zanoni* Colosi.
1921. *Apus asiaticus* (nom. nov. for *granarius* Sars) Gurney.

1922. *Triops uebensis* (nom. nov. for *bottegoi* Bouvier) Colosi.
1924. *Apus ovamboensis* Barnard.
1927. *Apus numidicus* var. *sinensis* Uéno.
1929. *Apus cancriformis*, Barnard. (non Schaeffer, 1756).
1929. *Apus sudanicus*, Barnard. (? Brauer, 1877.)
1934a. *Apus granarius*, Gauthier.
1937. *Apus sudanicus*, Gauthier. (non Brauer 1877).
1939. *Apus numidicus*, Pérès.
1940. *Apus sinensis* Uéno.
1952. *Apus mavliensis* Tiwari.
1952. *Apus orientalis* Tiwari.

TYPE. MNHNP ; ♂ Holotype, unregistered other than label " Type *A. granarius* Lucas ".

RANGE. South Africa to China ; the whole of Africa except for unsuitable forest regions in west and centre ; Middle East, India, central and eastern Asia to the north Chinese coast. Single sample in MNHNP labelled " near Paris " almost certainly mistake in labelling.

HABITAT. Temporary fresh and brackish waters ; unknown from rice fields ; Pérès (1939) compares its distribution in North Africa with that of *Triops cancriformis* and finds latter in steppe zones (300 mm. annual rain) and in the sub-steppe (300–500 mm.) while present species is restricted to the sub-steppe.

DESCRIPTION. Shows great variation in body length and includes very short and long bodied forms with all the associated variation.

Head.—Dorsal organ triangular, oval or round in the short bodied forms, anterior margin between the eyes. Second maxilla present in all specimens examined except in one case (see below).

Carapace.—Shape variable, round to oval. Carina with terminal spine in short bodied forms only (Text-fig. 15), generally smooth. Sulcus round (or squared in some African short bodied forms), spines many, often reduced in size, 24–72.

Body.—Segments : ♀♀, 32–42 ; ♂♂, 32–43. Apodous : ♀♀ 4–13 ; ♂♂, 6–14. Apodous always with varying number of supernumerary spines ventrally (Text-fig. 8B).

Telson.—(Text-fig. 5c$_2$, 6A). Medians small, numerous, scattered, but when low in number may form a rough row medianly, though this never as accurate as in *Triops cancriformis*, and spines smaller. Furcals small and with many scattered in front of them. Posterior marginals small, squat and marginal. Furca variable with body length.

Appendages.—44–46 recorded, but variation probably much greater than this. Endites of first thoracic appendage variable with body length (Text-fig. 2).

Sexual dimorphism.—Strong in many long bodied specimens, males having strong scales on furcal (Text-fig. 8D).

Larvae.—Metanauplius, those seen having in instar 1 a trapezoid-shaped dorsal organ which later changes to triangular.

Reproduction.—Bisexual. Chromosome number $2n = 8$.

GEOGRAPHICAL RACES

With present knowledge not possible to recognize any with certainty. Some indications known—many South African (not S.W.A.) and Middle East (Bombay-Baghdad) specimens have reduced sexual dimorphism even in long bodied forms ; these correspond to *Apus asiaticus* Gurney and this name may eventually be applied to a race with a restricted range. Some specimens from Eastern Asia have reduced second maxilla, and this is even absent in few out of large sample (BMNH 1935. 6.18. 7–12) and these might be separated off as another race, but evidence too weak at present.

SYNONYMS

Apus sudanicus Brauer belongs here doubtfully as the description is inadequate and I have not seen the types, but Barnard's specimens determined as this are certainly *Triops granarius*. A number of species are placed here on evidence of original descriptions : *A. numidicus* Grube, Braem's varieties of *A. numidicus* and *A. sudanicus* (exc. var. *braueri* which is doubtfully here for it refers to Brauer's description of *A. sudanicus*), *A. somalicus* Wedenissow, Sars' three species (1899), *A. granarius* Sars and the nom. nov. *asiaticus* Gurney, Uéno's var. *sinensis* and *A. sinensis*. I have seen the types of *A. granarius* Lucas, *A. bottegoi*, Bouvier, *Apus ovamboensis* (= *cancriformis* sens Barnard), and of Tiwari's two species. *A. mavliensis* Tiwari, in spite of its odd appearance is clearly only a young form of this species. *A. bottegoi* Prato is insufficiently described and may belong here or to the previous species.

TRIOPS LONGICAUDATUS (LeConte)

1846. *Apus longicaudatus* LeConte.
1852. *Apus domingensis* Baird.
1871. *Apus aequalis* Packard.
1871. *Apus lucasanus* Packard.
1871. *Apus newberryi* Packard.
1907. *Apus frenzeli* Thiele.
1916. *Lepidurus patagonicus*, Bruch.   (non Berg, 1900).
1944. *Triops pampaneus* Ringuelet.
1947. *Apus biggsi* Rosenberg.
1947. *Apus oryzaphagus* Rosenberg.
1952. *Apus longicaudatus*, Linder.

RANGE. Western North America, south of 50° N, through Central to South America, where only very scattered records (Thiele, 1907 ; Bruch, 1916 ; Ringuelet, 1944 ; Linder, 1952). W. Indies, Galapagos Islands, Hawaii, Japan and New Caledonia.

HABITAT. Temporary fresh waters, rice fields in California and Japan.

DESCRIPTION. As variable as the preceding species, but not so many short bodied forms seen.

Head.—Dorsal organ usually triangular, round in short bodied forms, and anterior margin between the eyes. Second maxilla absent in all the specimens seen.

Carapace.—Text-fig. 2G., H). Shape varies from oval to round with segment number. Terminal spine of carina very small when present, but generally absent. Carina finely denticulate along whole length in some specimens. Sulcus tends to be broad and shallow, spines variable in size, 24–60.

Body.—Segments : ♀♀, 35–43 ; ♂♂, 35–44. Apodous segments : ♀♀, 5–12 ; ♂♂, 10–13 in material examined. Apodous segments with varying number of supernumerary spines on ventral surface.

Telson.—(Text-fig. 5 D_2·) Medians large, 1–3, in a single row in the midline. Furcal spines smaller than those of *T. cancriformis*. Posterior marginals very large, set in the adult well forward of the margin, often pointing vertically. This arrangement of marginals unique and all specimens of this species have it.

Appendages.—54–66. (Linder's data mainly) : endites of first thoracic appendage variable with segment number.

Sexual dimorphism.—Well marked in specimens with high segment numbers, males then having furcal scales.

Larvae.—Metanauplius, indistinguishable from that of *T. granarius*.

Reproduction.—Bisexual and hermaphrodite, the latter only in California and Pacific region populations.
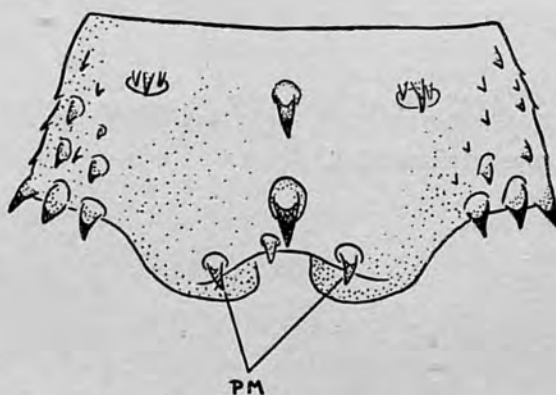
Fig. 16. Telson of *Triops longicaudatus intermedius*. (*pm* = posterior marginals).

GEOGRAPHICAL RACES

1. *Triops longicaudatus longicaudatus* (LeConte)

RANGE. That of species with exception of New Caledonia.

DESCRIPTION. With the characters described above. There may be a difference in the shape of the posterior margin of the telson on the forms from Galapagos and Hawaii as against continental American forms ; in the former the posterior margin is quite straight with no trace of an emargination in many specimens. This may well be evidence for a sub-species inhabiting these islands. Chromosome number $2n = 8$.

2. *Triops longicaudatus intermedius* subsp. n.

RANGE. New Caledonia. Two samples in MNHNP labelled " 93–1887 " and

" coll. Simon 25–96 " respectively are of this form and no others from the island are known to me. These specimens, all females, form the paratypes of the new sub-species. The name suggests that in their telson armature they are intermediate in form between their nominate race and the rest of the genus.

DESCRIPTION. Second maxilla absent, segments 39, apodous 8–9. Dorsal organ small, triangular to round. Carapace oval, terminal spine of carina very reduced, sulcus spines long, 24–30. Few supernumerary spines on apodous segments ventrally. Telson : medians large, 2–3, in mid-line, posterior marginals much smaller than in nominate race but well forward of the margin (Text-fig. 16). This is the most char-acteristic feature.

SYNONYMS

Apus obtusus James, 1823 and *Apus guildingi* Thompson, 1834 are clearly of this species on geographical grounds, but neither description is detailed enough to confirm this. Linder has shown that Packard's and Rosenberg's species are synonyms of this species. The diagrams of *A. frenzeli* and *Triops pampaneus* both show the *longicaudatus*-type telson, and Bruch's record of *Lepidurus patagonicus* is accom-panied by a figure which certainly shows a *Triops*, and probably *T. longicaudatus*, though the telson is not very clear.

TRIOPS AUSTRALIENSIS (Spencer and Hall)

1896. *Apus australiensis* Spencer and Hall.
1905. *Apus sakalavus* Nobili.
1907. *Apus madagassicus* Thiele.
1911. *Triops gracilis* Wolf.
1911. *Triops strenuus* Wolf.

RANGE. The drier regions of Australia, where it may be locally very common. Madagascar.

HABITAT. Temporary fresh water, sometimes (Wolf, 1911 ; Main, 1953) in saline or alkaline pools and lakes.

DESCRIPTION. Includes extremes of long and short bodied forms ; from Australia several samples have been seen with aberrations (not damage) to limbs and lobes of limbs ; both females in a sample from Ayer's Rock have reduced 11th thoracic appendages so that these are but a stump with a duct running through it on one side of each specimen. Several samples from W. Australia have endites 5 and 6 reduced to rudiments on one side of the thoracic series.

Head.—Dorsal organ triangular, ovoid or " wide ", often set with the anterior margin well behind the eyes (Text-fig. 4B). Second maxilla absent in all specimens seen.

Carapace.—Shape variable, terminal carinal spine usually absent and carina frequently denticulate along the whole length. Sulcus round, often small, spines variable in size, and numerous, 28–62.

Body.—Segments : ♀♀, 35–43 ; ♂♂, 36–44. Apodous : ♀♀, 5–12 ; ♂♂, 9–13. Apodous segments with varying number of supernumerary spines ventrally.

Telson.—Medians small, scattered, fewer than in *T. granarius*, often very few or even absent (Text-fig. 6B) ; furcal spines small, posterior marginals small, squat and marginal in the adult. Furca varies with the segment number.

Appendages.—48–66, but only few specimens counted. Endites variable with segment number.

Sexual dimorphism.—As in previous two species.

Larvae.—Metanauplius, indistinguishable from that of *T. granarius*.

Reproduction.—Bisexual.

GEOGRAPHICAL RACES

1. *Triops australiensis australiensis* (Spencer and Hall)

RANGE. Continental Australia.

DESCRIPTION. With the characters described above. Chromosome number $2n = 10$.

2. *Triops australiensis sakalavus* (Nobili)

RANGE. Madagascar.

DESCRIPTION. Very similar to the nominate race, but median spines are rather more numerous in the specimens I have seen in MNHNP, which otherwise are clearly of this species, and not of *T. granarius ;* the specimens have no second maxillae, the carinae are denticulate, and the median spines are relatively sparse compared with *T. granarius*.

SYNONYMS

Wolf's species are clearly *Triops australiensis*, showing the typical telson pattern and Main has already (1953) suggested uniting them with it. *T. madagassicus* and *T. sakalavus* are placed here on the assumption that only one species will occur in Madagascar, since sympatric species are the exception in the Notostraca, but future work will be needed to confirm this arrangement.

Genus *LEPIDURUS* Leach

1756. *Apus* Schaeffer (in part).
1758. *Monoculus* Linn. (in part).
1819. *Lepidurus* Leach.
1924. *Bilobus* Sidorov.

Distinguished at once from *Triops* by the presence of a supra-anal plate. In general, also, the segment number is lower, the carapace is longer and more compressed laterally, the sexual dimorphism is weaker than in the other genus.

Bilobus Sidorov was erected on the erroneous assumption that median incision of the posterior margin of the supra-anal plate was important systematically (see p. 22, and Linder, 1952).

LEPIDURUS APUS (Linn.)

1756. *Apus cancriformis* Schaeffer (in part).
1758. *Monoculus apus* Linn. (in part).
1801. *Apus productus* Bosc.
1819. *Lepidurus productus* Leach.
1850. *Lepidurus viridis* Baird.
1866. *Lepidurus angasi* Baird.
1873. *Lepidurus lubbocki* Brauer.
1875. *Lepidurus couessii* Packard.
1877. *Lepidurus macrourus* Lilljeborg.
1879. *Lepidurus viridulus* Tate.
1879. *Lepidurus kirki* Thompson.
1879. *Lepidurus compressus* Thompson.
1886. *Lepidurus packardi* Simon.
1893. *Apus extensus* Braem.
1900. *Lepidurus patagonicus* Berg.
1909. *Lepidurus apus* Keilhack.
1911. *Lepidurus hatcheri* Ortmann.
1921. *Lepidurus barcaeus* Ghigi.
1952. *Lepidurus couessii*, Linder.

RANGE. Europe (excluding Britain), North Africa, Palestine, Asia Minor, Russia ; North and South America ; New Zealand and Australia.

HABITAT. Temporary fresh waters, but perhaps less restricted to those which regularly dry out than, for instance, *Triops cancriformis*. Occurs in alkaline pools in North America.

DESCRIPTION. This species has the largest range of any known Notostracan and shows very little variation over the whole area.

Head.—Dorsal organ round or oval (Text-fig. 4E, F), anterior margin between the eyes with the possible exception of the specimens seen by Ortmann (1911) from Patagonia. Second maxilla present in all the specimens seen by me.

Carapace.—Oval, fairly compressed laterally but not so markedly as in next species. Terminal spine of carina only rarely absent. Sulcus spines usually long, rarely (*packardi*) reduced. Normally 35–50 in number.

Body.—Segments, 26–29 ; Apodous, 4–6. No supernumerary spines on apodous segments.

Telson.—Supra-anal plate relatively longer than in next species, the ratio carapace/ supra-anal plate being about 4–6 in adults. The marginal spines of the plate are small and numerous in all except the South American forms. Central spines 4–100 or more, the higher numbers being borne on a distinct keel (Text-fig. 7A).

Appendages.—35–48 ; endites of first thoracic appendages reach to the end of the carapace in some, in others little longer than *L. arcticus*.

Sexual dimorphism.—Males occur, and the supra-anal plate is longer and more spatulate in these ; otherwise the dimorphism is weak.

Larvae.—Metanauplius in the European and New Zealand forms and probably in all. May differ from that of Triops by presence of rudiments of paired eyes in the first instar (Bernard, 1892 : 158).

Reproduction.—Bisexual and hermaphrodite.

GEOGRAPHICAL RACES

1. *Lepidurus apus apus* (Linn.)

RANGE. Europe (exc. range of next ssp.), Asia, North America (exc. California).
DESCRIPTION. Segments, 26–28; apodous, 4–5; supra-anal plate with 20–100 spines generally borne on a keel; marginal spines of plate fine and numerous. Bisexual and hermaphrodite.

2. *Lepidurus apus lubbocki* Brauer

RANGE. N. Africa, Palestine, Syria, Italy, Sicily.
DESCRIPTION. Segments, 27–29; apodous, 5–6; supra-anal plate (Text-fig. 7B) with fewer central and marginal spines than above ssp (3–20 centrals) and keel less prominent. Specimens from eastern part of the range tend to have the fewest central spines; endites relatively longer than nominate race. Bisexual. Chromosome number, $2n = 12$ (Goldschmidt).

3. *Lepidurus apus packardi* Simon

RANGE. California.
DESCRIPTION. Segments and supra-anal plate similar to sub-species 2. Sulcus differs from that of all other forms by having very many small spines forming a granulated margin. Bisexual.

4. *Lepidurus apus patagonicus* Berg

RANGE. South America (Chubut Territory, Patagonia).
DESCRIPTION. Segments, 29; apodous, 5. Marginal spines of supra-anal plate coarser and fewer than previous forms, central spines few. Sulcus spines as typical race. Bisexual.

5. *Lepidurus apus viridis* Baird

RANGE. New Zealand, Tasmania, and coastal or better watered regions of Australia.
DESCRIPTION.—Very similar to nominate race. Segments, 27–28; apodous, 4–5. Generally with low number of central spines on the plate (5–10), but one specimen from Tasmania had more than 20; average is much lower than in nominate race, however. I have seen no males.

SYNONYMS

I have examined the following types, and am satisfied that they are correctly placed here : *L. packardi, L. extensus, L. barcaeus, L. angasi, L. compressus, L. kirki, L. viridulus*. The rest are included on the basis of the original descriptions or on material previously determined.
Lepidurus lemmoni (Holmes, 1894). Holmes' description does not enable determination of his specimens with any here recognized, yet contains nothing to indicate

good differences from them ; the types are lost (Linder, 1952), and therefore it is advisable to abandon the species.

LEPIDURUS ARCTICUS (Pallas)

1793. *Monoculus arcticus* Pallas.
1883. *Lepidurus glacialis* Packard.
1892. *Lepidurus spitzbergensis* Bernard.
1893. *Apus productus* var. *glacialis* Braem.
1896. *Lepidurus glacialis*, Sars.
1927. *Lepidurus ussuriensis* Sidorov.

RANGE. Circum-polar Arctic regions ; Aleutians, North America ; Alaska to Labrador, Greenland, Iceland, Bear Island, Spitzbergen, Northern Palaearctic ; Scandinavia to Siberia.

HABITAT. Temporary fresh-water pools, the streams connecting pool systems, and large lakes which are permanent. A reservoir in the Norwegian mountains (Sømme, 1934).

DESCRIPTION. *Head.*—Dorsal organ oval, sometimes very elongated, anterior margin just between the eyes (Text-fig. 4G). Second maxilla present.

Carapace.—Oval, laterally very compressed. Terminal carina spine present, long. Rest of carina smooth.

Body.—Segments, 26–28 ; apodous, 4–5. Apodous without supernumerary spines on ventral surface.

Appendages.—41–46, but variation probably greater. Endites of the first thoracic appendage very short, scarcely reaching beyond margin of carapace (Text-fig. 10A).

Telson.—Supra-anal plate very small ; carapace/plate = about 12 in adults of 20 mm. carapace length. Median spines very sparse (0–5) and marginals few and coarse (Text-fig. 7C).

Sexual dimorphism.—Males rare, but known to have longer and more spatulate supra-anal plates.

Larvae.—Post-metanauplius (Poulsen, 1940, and my cultures), equivalent to about instar 3 of *Triops* larvae (Text-fig. 13).

Reproduction.—Bisexual and hermaphrodite. Males known from Bear Island in very low proportion of the population. (Sømme, 1934).

GEOGRAPHICAL RACES

None could be recognized in the material available, nor could Linder (1952) find any subdivisions of his material. *Lepidurus ussuriensis* Sidorov appears to be of this species, for the endites are shorter than is usual in other species, and the supra-anal plate is small (carapace/plate = about 9) and typical of this species in its armature. However, the endites are projecting more beyond the carapace than is usual in *L. arcticus* and may indicate a difference between this East Siberian form and the typical Arctic forms. The weakness of the carina and the elongate form of the dorsal organ confirm the placing of this species in *L. arcticus*.

LEPIDURUS BILOBATUS Packard

1883. *Lepidurus bilobatus* Packard.
1952. *Lepidurus bilobatus*, Linder.

RANGE.   North America ; Utah, Colorado, probably Arizona (Linder, 1952).
HABITAT.   Not known, but occurs in arid areas so presumably in temporary pools and lakes.
DESCRIPTION.   Known only from Packard's description, and two further specimens ascribed to the species by Linder.
Head.—Dorsal organ round or oval, anterior margin set between the eyes.
Carapace.—Arrangement of sulcus spines normal.
Body.—Segments, 33 ; apodous, 6.
Telson.—Supra-anal plate with numerous small marginals, 4–6 centrals.
Appendages.—60 ; endites of first thoracic appendage as in *Lepidurus apus.*
Sexual dimorphism.—Males unknown.
Larvae, Reproduction.—Unknown.

LEPIDURUS LYNCHI Linder

1952. *Lepidurus lynchi* Linder.
1952. *Lepidurus lynchi* var. *echinatus* Linder.

TYPES.   Holotype (♀) and allotype (♂) in Uppsala Museum ; paratypes USNM 82101 ; var. *echinatus*.   Holotype (♀) USNM 82068, allotype (♂) USNM 82069.
RANGE.   North America ; Washington, Nevada, and Oregon.
HABITAT.   Apparently in lakes (Linder, 1952 . . . North end of Goose Lake in water two feet deep, muddy), but probably also in temporary pools.
DESCRIPTION.   Long bodied form with unique carapace armature.
Head.—Dorsal organ round with the anterior margin set well behind the eye tubercles.
Carapace (Text-fig. 3).—Oval.   Carina absent except when it bears series of unusually large spines.   Specimens from first two localities have 0–20 of these carinal spines.   Some of those from Oregon have series of large spines along posterior part of lateral margin in addition to carinal spines and carapace shape may be more round in these.   But no useful purpose is served by the formal term var. *echinatus* for these latter forms ; *L. lynchi* is obviously characterized by the possession of large spines on carina and margin and there is much variation in the distribution of these spines ; even in the specimens from the first two localities the margin of the carapace bears larger spines than is usual in *Lepidurus.*
Body.—Segments, 31–34 ; apodous, 3–5.
Telson.—Supra-anal plate about same size as in *L. apus*, central spines 2-7, marginals very large and sparse.
Appendages.—60–71.   Endites as in *L. apus.*
Sexual dimorphism.—Normal for the genus.
Reproduction.—Bisexual.

LEPIDURUS BATESONI sp. nov.

TYPES. Holotype (♂) and two paratypes in BMNH (1911.11.8, 23542–4, Norman collection). Collected by W. Bateson.

RANGE. Russia. Probably collected at Chilik Kul in the Kazak region, where Bateson made a collection of other fresh-water entomostraca also in the Norman collection.

DESCRIPTION. Males only known. Long bodied form in general appearance (Text-fig. 2J).

Head.—Eyes and dorsal organ similar to those of *Lepidurus lynchi*. Second maxilla present and typical of the genus.

Carapace (Text-fig. 2J). Oval-round, more rounded than in *Lepidurus apus*. Carina and its terminal spine absent in all specimens seen ; position of carina demarcated only by the light streak of the dorsal blood channel of the carapace which follows the line of the carina in normal forms. Sulcus wide, rounded, with small sulcal teeth.

Body.—Segments 33, apodous 8, in all. Apodous ventral marginal spines very small and widely separated centrally, no supernumeraries.

Appendages.—49–52. Endites of first thoracic appendage (Text-fig. 10D) unique in known Notostraca ; endites 4 and 5 very short ; much more reduced than in *Lepidurus arcticus* and can scarcely have projected beyond carapace margin in life ; endite 5 of this appendage is little more developed than endite 5 of the second appendage. Endite 6 of the first appendage is fully developed and claw-like as in the subsequent appendages (in all other Notostraca the 6th endite of the first thoracic appendage is reduced to a small soft lobe at the base of the 5th endite).

Telson (Text-fig. 7B).—Supra-anal plate very similar to that of *Lepidurus lynchi*, central spines few (4), marginals few, coarse.

Sexual dimorphism.—Females unknown.

Reproduction.—Bisexual.

Note.—One of the paratypes has an abnormality of the supra-anal plate, which is reduced in size, soft, and lacks its armature.

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Abnormal Variation in the Notostraca

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Abnormal Variation in the Notostraca

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MUCH recent work on the systematics of the Notostraca (Crustacea, Phyllopoda) has included comment on the great range of the variation in each systematic character in comparison with other animal groups, and the consequently unsatisfactory nature of a classification which must be based upon such characters; Linder (1952) has reviewed a number of these comments and has analysed the extent of the variation in many of the important characters. Data derived from the culture of a pure line of hermaphrodite *Triops cancriformis* has been presented by Longhurst (1955*a*) and it was thereby demonstrated that much of the recorded variation can be of little significance systematically or, probably, adaptively.

In a percentage of specimens variations occur which fall far outside the statistical normal distribution of the character for the remainder of the sample. For instance, in a sample of 12 specimens of *Triops cancriformis simplex* from Kebili in Tunisia (MNHNP)[1] there is one individual in which the sulcus spines are completely absent; in the remainder, though these spines are rather small, they are quite normal in number for the subspecies, having a mean of 33.8±3.9. In the same category are the cases of abnormal body segmentation recorded by Barnard (1929) and Linder (op. cit.) where the normal sequence of exoskeletal annuli is disturbed by the formation of incomplete rings or by spiral growth. These abnor-

malities have been described from several species of both *Triops* and *Lepidurus* and appear to occur sporadically among normal specimens; this was confirmed in the present work.

During a recent examination of *Triops* material from several localities near Khartoum which had been collected by Dr. J. Rzóska—to whom I am much in debt for the specimens and for pointing out to me some of their peculiarities—it became obvious that such abnormalities may occur even in exoskeletal characters which are of primary importance in the classification of the group and may thus render the general systematic key presented in the recent review of the Notostraca misleading. In view of this, a survey of the abnormalities recorded in the literature and in the material examined for the review seems desirable; the characters in which abnormalities have been recognised are all exoskeletal and are concerned either with variation in the armature, the body rings, or with the absence of appendages in whole or in part.

In four of the 75 samples of *Triops cancriformis* which were examined in these investigations there was a reduction, or absence of part of, the armature of spines on the carapace; one of these samples is from the Saône (MNHNP), and the remaining three from North Africa. In the French sample the sulcus spines are normal in number (mean, 29.2±2.35) in all except one specimen which has only three spines on the right side, two on the left— that is, approximately 10 standard deviations from the mean. The most extreme of the North African specimens, that from Kebili, is described above; in another sample from Ghardaya, Algeria, the termi-

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[1] The following abbreviations have been used in the text. BMNH—British Museum (Natural History), London. MNHNP—Musée Nationale d'Histoire Naturelle, Paris. WAM—Western Australian Museum, Perth. MCNM—Museo Ciensas Naturalis, Madrid.

nal carina spine is absent in three of the four specimens, and in the fourth is very reduced; another sample, from El Abiod Sidicheik, Algeria, has the telson armature extremely reduced, so that the median spine is about one quarter of its normal length. The relationship between these abnormal Tunisian and Algerian specimens and the general tendency towards a weak armature shown by the subspecies (*Triops cancriformis simplex*) that occurs in this area requires investigation.

The converse, where there is duplication or multiplication of the normal armature, is most clearly exemplified by those specimens that were regarded in the review as the *trachyaspis*-form of several species. In these specimens (as in the original *Apus trachyaspis* Sars, 1899) the normally smooth surface of the carapace is shagreened by very minute denticles; Barnard (1924) found that such specimens occurred sporadically in his South African material, and in the present material they have been recognised in samples of both *Triops granarius* and *T. longicaudatus*. There are two samples of the latter species which are composed entirely of individuals of this type—one from Montana, the other from Arizona; two samples of *Triops granarius*, one from S.W. Africa, the other from Algeria, contain only a proportion of spiny individuals, while two from Grahamstown and from Kosti (Sudan) contain only the *trachyaspis*-form

A specimen of *Triops cancriformis* from Christchurch, England, (BMNH, Mus. Leach), has a duplication of one of the primary carapace spines, the terminal spine of the carina being double; a sample of three specimens of the same species from Paris have three, instead of the normal two, posterior marginal telson spines.

Linder (1952) and Gauthier (1934) have recorded specimens of *Triops cancriformis* from North Africa in which there is a rudimentary supra-anal plate resembling a very reduced form of that characteristic of *Lepidurus*. In the present material,

two specimens from Laguna da Janda, Southern Spain (MCNM), of the same species, show the rudimentary plate. This has been recorded only from the small area of the Western Mediterranean and Moroccan littoral in which the subspecies *T. cancriformis mauretanicus* occurs; in other characters this subspecies is less *Lepidurus*-like than the nominate race from the rest of Europe.

The second maxilla of *Triops* has been found to be of basic systematic importance and it was thought that it occurred in all specimens seen from Africa and Eurasia (*T. cancriformis* and *T. granarius*) but was apparently absent in all specimens from the Americas, Oceania, Australia, and Madagascar (*T. longicaudatus* and *T. australiensis*). However, the examination of Rzóska's material showed that in some specimens, otherwise referable to *T. granarius*, there was reduction or even absence of this appendage. A re-examination of all the available material showed that the above generalisation was valid (Fig. 1) but that in ten Old World samples there were some specimens in which a reduction occurred amongst other normal individuals.

The reduction of the appendage is irregular and often asymmetrical; although it was not possible to dissect the specimens it was clear that all stages of reduction were present, from the normal appendage, through loss of the terminal setae, to a simple lobe of decreasing size until a stage is reached where it is virtually impossible to decide whether a small lobe is, or is not, present. For the purposes of analysis three arbitrary stages of this reduction are recognised—the normal appendage, a lobe without setae, and complete absence.

In only one sample of *Triops cancriformis* was a reduction found; three specimens from Vienna (BMNH) include one in which the right second maxilla was reduced to a small lobe. In the normal specimens of this species the appendage is larger than in the remainder of the genus

FIG. 1. The distribution of the material of *Triops* available for re-examination of the nature of the second maxilla, showing type of appendage present in each sample. The stippled areas are the remainder of the range of the genus from which no specimens were available.

and most nearly approaches the state in *Lepidurus*.

The remaining reduced samples are of *Triops granarius* from Africa and from Eastern Asia; the greatest reduction occurs in three samples from Khartoum and in one from Chinwangtao, China. The Khartoum sample collected by Rzóska included both *T. cancriformis* and *T. granarius* from the same pools, but reduction was found only in the latter species.

Rzóska's *T. granarius* consist of 37 specimens from a number of pools and of these only three have no reduction of the appendage on either side, while in ten there was complete absence on both sides; in the remaining 24 specimens the various stages of reduction were found. Two earlier samples from Khartoum (BMNH, coll. Grabham 1907) show a very similar state of reduction; in two specimens the appendage was completely absent while various stages of reduction occurred in the remaining four.

A sample from Berbera, British Somaliland, (BMNH) consists of seven normal specimens and two in which there is reduction; another from Eburru, Kenya

(BMNH) contains one normal specimen, two reduced; samples from Kimberley and Grahamstown (BMNH) each have a few reduced specimens.

These African samples with reduced second maxillae occur as relatively isolated occurrences among a preponderance of entirely normal samples from the same general areas. There are seven samples from South Africa in the present material in which the appendage is entirely normal, of which one is from the vicinity of Grahamstown; another 14 samples from Northern Africa with normal appendages include some from places as close to the Sudan as the Siwa oasis and Somalia.

In two samples from China (BMNH) a proportion of the individuals have reduced second maxillae, but in no specimens do they appear to be completely absent on both sides; about 20 per cent of the very large Chufoo sample consists of normal individuals. Between the Sudan and China there are many samples from Arabia, the Middle East and India of *Triops granarius* all of which are completely normal in this respect.

The various stages in reduction and

their asymmetry in the specimens are laid out in Table 1; there appears to be no evidence of greater reduction on the right or the left sides, nor of any significant difference between the sexes.

From a taxonomic point of view it is important to note that in the samples of *Triops cancriformis* and *T. granarius* in which the second maxilla is reduced there is always a proportion of specimens, even if a minority, in which normal or reduced second maxillae are present on at least one side of the individual; in the majority there are a few specimens in which the appendage is completely normal. This contrasts very strongly with the samples of *T. longicaudatus* and *T. australiensis* in none of which have any specimens been found with even reduced second maxillae; in these species the appendage is apparently absent even in the young individuals.

The Australian samples in the present material include specimens which show very remarkable abnormalities of the post-maxillary appendages; three of the eleven samples examined from this continent include specimens in which appendages or parts of appendages are unilaterally absent. Damage to the exoskeleton of Notostraca results in a thickening and dark-ening at the site of the damage at subsequent moults and there can be little doubt that there is here no confusion between loss by damage and the inherent absence of appendages or endites.

A sample from Western Australia (BMNH) contains three specimens of which two are apparently quite normal, while the third lacks the terminal endites on the fourth and fifth thoracic appendages. Another sample from Wiluna (WAM) consists of a single male and female; the latter is normal but the former lacks endites 5 and 6 from the thoracic appendages 1 to 3 on the right side, while the left abdominal appendages lack their distal epipodites.

Two females from a pool on Ayers' Rock, Central Australia (WAM) each lack the brood pouch formed by the right eleventh thoracic appendage which is represented merely by a slight prominence below which the efferent oviduct opens; that on the left side in both specimens is quite normal. Both left and right ovaries are present but on the abnormal right side the longitudinal oviduct contains eggs which are pale and shrivelled compared with those on the normal left side.

It is perhaps relevant here to consider the extraordinary sample of three speci-

TABLE I—REDUCTION OF THE SECOND MAXILLA IN NINE SAMPLES OF *TRIOPS GRANARIUS* FROM AFRICA AND EASTERN ASIA.

	Abs/Abs	Abs/lobe	Abs/Normal	lobe/lobe	lobe/normal	Normal/Normal
1. Khartoum (Rzóska)	12	11	1	12	—	—
2. Khartoum (BM 1912.11.11)	2	1	—	—	—	1
3. Khartoum (1913.9.10)	—	1	—	2	—	—
4. Berbera (1956.8.17)	—	—	1	—	1	7
5. Eburru (1949.2.24)	1	—	—	1	—	1
6. Kimberley (1932.2.25)	—	—	—	—	1	2
7. Grahamstown (1932.2.25)	—	—	—	—	2	3
8. Chufoo (1935.6.18)	1	3	7	1	4	4
9. Chinwangtao (1910.12.7)	—	—	3	—	1	—

mens in the BMNH described as *Lepidurus batesoni* (Longhurst, 1955a); there is, apparently, more than normal variation in some characters—for instance, one specimen has a supra-anal plate which is less than half the length, relatively, of those on the other specimens and, in addition, has no marginal armature. The main characteristics of the species are (1) a relatively high number of apodous segments, (2) a complete lack of the specialisation of the distal endites of the first thoracic appendage which is found in all other known Notostraca, and (3) the complete lack of a dorsal keel, or carina, on the carapace. In view of the occurrence of structural abnormalities in other species of Notostraca it seems desirable to consider the possibility that these characters of *Lepidurus batesoni* may indicate that this is a highly aberrant and long-bodied sample of, perhaps, *L. lynchi;* even if further specimens with these characters are collected in the Kazak steppe of southern Russia from which the original sample is thought to have come, how is it possible to distinguish between a localised occurrence of aberrated characters and a localised subspecies with abnormal characters?

The decision appears to rest on the rather arbitrary recognition by the systematist of what is to be considered normal variation and what an aberration. It is a compromise to regard this sample as a new species of *Lepidurus;* on the one hand it might be held that the important characters were, in fact, simply aberrations, while on the other hand the possession of a first thoracic appendage which closely resembles the second—on both sides, in all three specimens—might well be considered to be a character of at least generic importance.

From this survey of Notostracan abnormalities a pattern emerges. In some cases the abnormality occurs in isolated specimens from otherwise normal samples, or in a low percentage of populations spread over a wide geographic region; in other cases the abnormality occurs prevalently in a relatively restricted geographical area, and in a relatively high proportion of samples.

In the material under review, some 12 percent of the samples of *Triops* include specimens showing one or more of these major aberrations, while many more contain specimens that appear to fall well outside the statistical normal distribution in respect of one character or another; that is, surely, a considerably higher percentage of abnormal specimens than would be found in a comparable survey of most animal groups, and it is clear that few of the aberrations are likely to have any adaptive significance—the occurrence of female *Triops* in Australia whose egg production can be little more than 50 percent of the normal is extremely interesting. Is there any connection between the survival in Notostracan populations of so high a percentage of abnormalities and the two facts (Longhurst, 1955b) of their exceedingly long evolutionary stagnation, and the current lack of any important ecological competition?

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THE REPRODUCTION AND CYTOLOGY OF THE NOTOSTRACA (CRUSTACEA, PHYLLOPODA)

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The reproduction and cytology of the Notostraca (Crustacea, Phyllopoda).

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(With 5 figures in the text.)

CONTENTS.

INTRODUCTION.

The gonads of the Notostraca (Crustacea) have been described and figured by several previous authors, but in papers which are all old and rather incomplete, giving little account of the cytology. Almost two hundred years ago Schæffer (1756) published his remarkable monograph based on material of *Triops* and *Lepidurus*, in which the gonads were described and figured for the first time, together with many stages in the hatching of the eggs and the development of the larvæ. Zaddach (1841) gave further figures of the general appearance of the gonads, and these—together with Schæffer's drawings—have been widely copied in textbooks.

In 1857 Kozubowski recorded and figured the testes of *Triops cancriformis* (Bosc) for the first time, noting that the sperms were round and non-motile. Siebold (1871) furnished the most complete account of the oogenesis of a notostracan, and this was later supplemented by the work of Bernard (1892), Moore (1893) and von Zograf (1906). Our knowledge of these organs, however, is still far from complete.

During systematic work on the Notostraca chromosome counts were made and it was found necessary to make a further investigation of the gonads before the nature of the chromosomes could be elucidated. This study confirmed the occurrence of hermaphroditism in several species of *Triops*—first found by Bernard—and a preliminary account of this has already been published (Longhurst, 1954). It has not been possible, however, to analyse the complete reproductive cycle and many points remain obscure; the present work is a contribution, not a complete account.

Cultures of all four species of *Triops* were available to me and the sources of these, together with culture methods, have been given in a systematic review (Longhurst, 1955). The material was examined by sections and squashes of the ovaries and ovotestes, and by smears of the testes; fixation was in Carnoy or Susa, and staining was with Feulgen.

Dr. J. P. Harding of the British Museum (Natural History) has given me invaluable advice throughout, and has supplied several important specimens; I am very grateful to him for his help. The work was done in the Zoology Department of this College, under the supervision of Professor H. Munro Fox.

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OVARIES.

The general appearance of the ovaries of Notostraca is well known ; the gonads are paired and lie in the haemocoel on either side of the alimentary canal, extending from the anterior end of the thorax to the region of the apodous segments.

Each ovary consists of a main *longitudinal oviduct* which is elastic, packed with resting eggs in the adult, and connected with the cavity of the brood pouch by an *efferent oviduct*. Attached to the longitudinal oviduct there are many branching *follicle ducts* (fig. 1A) at the tips of whose branches are borne *germinal regions* in which arise tetrads of cells—one *oocyte* and three *nutritive cells*. The tetrads swell, in succession, to form the large follicles, in which the development of an ovum from the oocyte occurs.
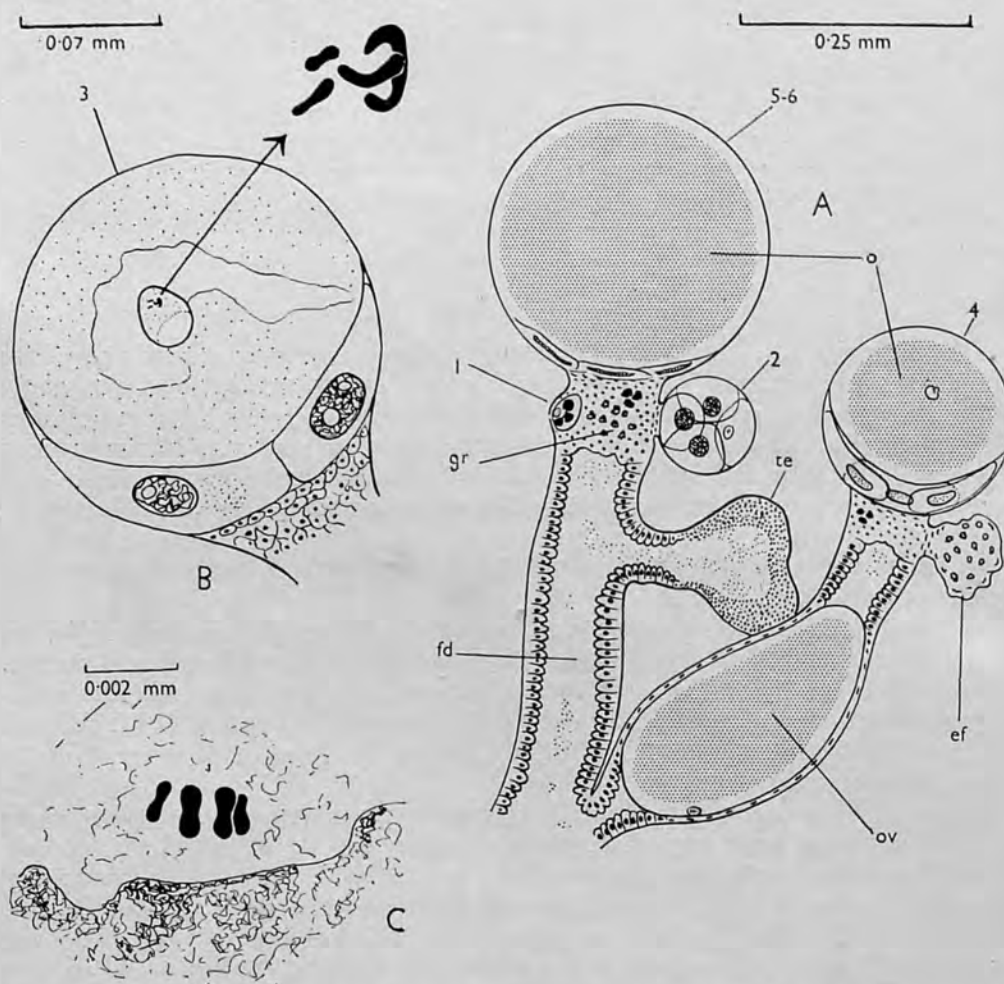

Fig. 1.—Ovotestis of *Triops cancriformis*; A, Part of follicle duct system, somewhat diagrammatic; B, Stage 3 follicle; C, Haploid (*n*=4) set of chromosomes of resting ovum in the longitudinal oviduct. (ov=ovum, o=oocyte, gr=germinal region, fd=follicle duct, tl=testis lobe, ef=empty follicle; numbers indicate stages of follicles.)

The gonad is ensheathed in a transparent membrane, which becomes considerably stretched over each follicle as this increases in size. The walls of the follicle ducts are composed of a regular epithelium of columnar cells which secrete the egg-shell substance. These cells are capable of great distension into a flattened form as an ovum passes down the follicle duct on its way to the longitudinal oviduct (fig. 1A, ov).

The longitudinal oviduct consists of an epithelium of flat cells, rather smaller and with smaller nuclei than those of the follicle duct. This longitudinal duct is probably no more than a storage sac for the eggs and I can find no evidence that its walls assist in the secretion of the egg-shell substance.

At the tips of the follicle-duct branches, the regular epithelium gives place to smaller, irregularly rounded, cells which crowd into and apparently occlude the lumen of the duct ; this mass of cells forms the germinal region (fig. 2, grc).
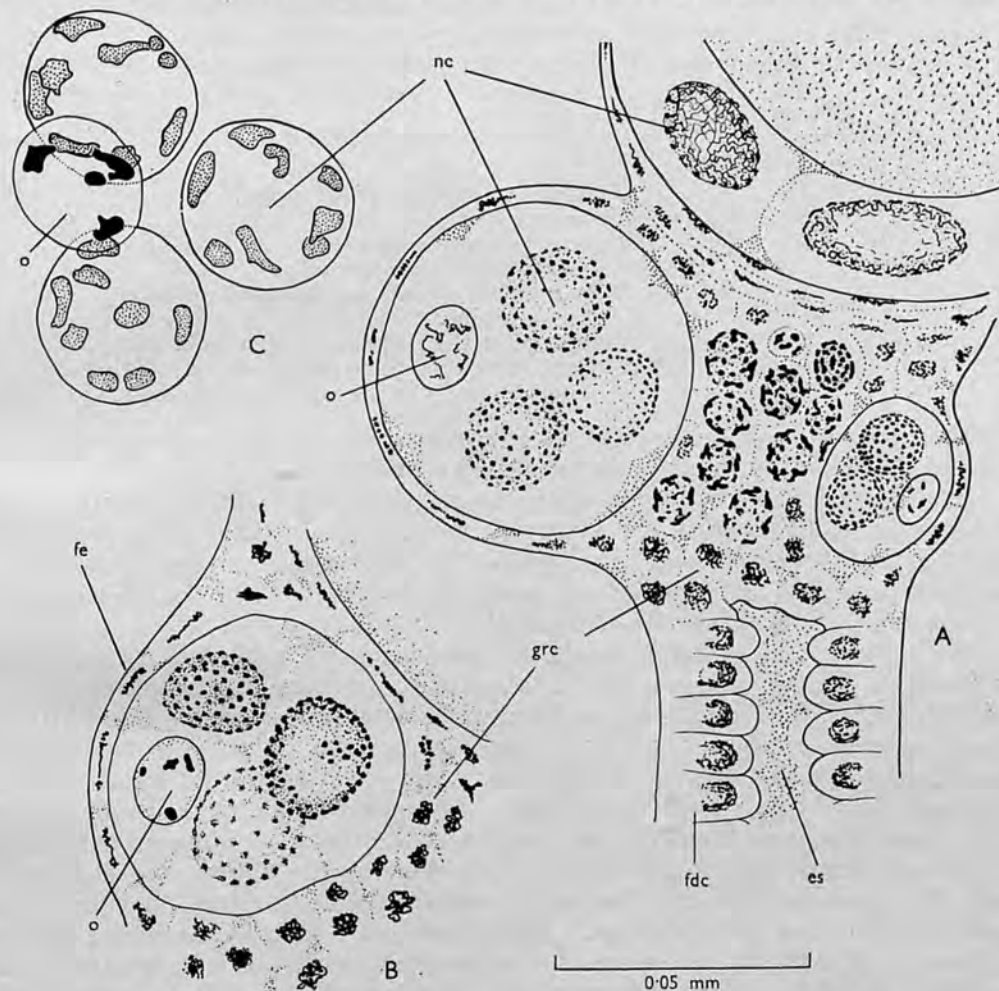

Fig. 2.—Oogenesis of *Triops granarius* ; A, Details of germinal region ; B, Stage one
follicle ; C, Nuclei of pre-stage 1 tetrad. (o=oocyte nucleus, nc=nutritive cell
nucleus, grc=germinal region cells, fdc=follicle duct cells, es=egg-shell substance,
fe=follicular epithelium.)

Scattered within the germinal region are the cells which will give rise to the follicular tetrads. It has unfortunately not been possible to discover the origin of these cells, for in the earliest stages that I have found they are already differentiated into oocytes with a haploid, and nutritive cells with a diploid, set of chromosomes (fig. 2C). The nuclei of the nutritive cells enlarge during development and the number of discrete Feulgen-positive bodies within them becomes very much greater. If the earliest diploid nutritive cells were the first step on a process of polyploidization it is possible that the oocyte and the three nutritive cells could arise from the division of a single precursor.

As the tetrad develops, its members increase in size, come to lie near the surface of the germinal region, and later begin to form a lateral bulge (fig. 2A). This swelling is covered by a single layer of the small somatic cells which form

the mass of the germinal region, and these become enormously stretched and flattened as the swelling increases in size and comes to form a spherical follicle (fig. 2B, fe).

At first the nutritive cells grow more rapidly than the oocyte, and their nuclei become relatively enormous and progressively more diffuse, or less densely Feulgen-positive. Later the oocyte grows more rapidly and becomes greater than the combined nutritive cells, while its cytoplasm becomes charged with ovoid yolk granules—except peripherally—and finally crushes the remains of the nutritive cells into the base of the follicle (fig. 1A, 4, 5–6).

The stages in the growth of a follicle can usefully be tabulated :—

Stage (See numbers on fig. 1. A, B)	Form of follicle
1	Bulging out from germinal region.
2	Becoming stalked.
3	Oocyte becomes larger than the combined sizes of the nutritive cells.
4	Yolk granules appear, squashing of nutritive cells begins.
5	Clear area at the periphery of the yolk.
6	Mature, nutritive cells almost obliterated, oocyte ready to pass down follicle duct.

The appearance of the haploid set of chromosomes in the developing oocytes differed considerably in the material at my disposal.

In the ovaries of *Triops granarius* (Lucas) from South Africa a haploid set of four was readily seen in the youngest oocytes and in those of early stage 1 (fig. 2C) ; in late stage 1 and in early stage 2 they became progressively longer, and then appeared to fragment and to disappear (fig. 2A, o). In later oocytes I could find no Feulgen-positive material.

In European *Triops cancriformis*, on the other hand, a haploid set could not be found in the early stages, but in late stage 2 or stage 3 a rather small and indistinct set of four chromosomes became discrete and stainable (fig. 1, B), to disappear again subsequently. In *Triops longicaudatus* (leConte) from America, the situation seems to be the same as in *T. granarius* (fig. 4, D) but successful preparations of this species were rare ; no chromosomes were visible in the only female specimen I was able to examine of *T. australiensis* (Spencer & Hall).

New germinal regions arise on a follicle duct by the appearance of a small mass of germinal-region cells among the epithelium of the duct, and from this mass the first new follicle arises. Each germinal region is associated with a succession of follicles, of which the most mature is borne terminally, the remainder laterally ; when the ovum from the most mature follicle passes down the duct, the next in the series takes its terminal position.

The epithelium around the follicle is derived from the somatic cells of the germinal region which the follicle pushed outwards as it began its expansion, and its cells became enormously stretched and their nuclei flattened (fig. 2B, fe). In stage 2 follicles of a few specimens in which the staining was especially dense the nuclei of these cells contained eight discrete Feulgen-positive bodies—thus confirming the diploid, somatic, number of eight, but occasionally there were sixteen or about thirty of these bodies in larger nuclei. Nuclei of these cells in later stages are filled with a mass of quite uncountable Feulgen-positive bodies. This may indicate a process of polyploidization as the cells increase in size during the growth of the follicle that they surround.

The process by which the egg passes down the oviduct is completely obscure ; no continuation of the lumen of the duct can be seen in the germinal region, yet the relatively enormous egg passes through this region into the follicle duct, leaving the germinal region still functional ; the remains of the follicle membrane and epithelium remain as a crumpled and deflated sac.

The ovum becomes coated with the egg-shell substance as soon as it passes into the lumen of the duct, which is filled (fig. 2A, es) with a red hæmochromogen-containing liquid (Fox, 1955 ; Longhurst, 1955). The passage of the egg down the duct is probably rather rapid, for in opening fresh, unnarcotized females, I have frequently found a follicle distended with an egg on passage and have watched this being pressed down the duct by active, though irregular, contractions of the wall of the duct. I can, however, find no trace of muscle elements in this wall.

The longitudinal oviduct contains a mass of resting eggs, soft-shelled and distorted by mutual pressure; clear haploid sets of four chromosomes were found in these ova in *Triops cancriformis* but not in any other species.
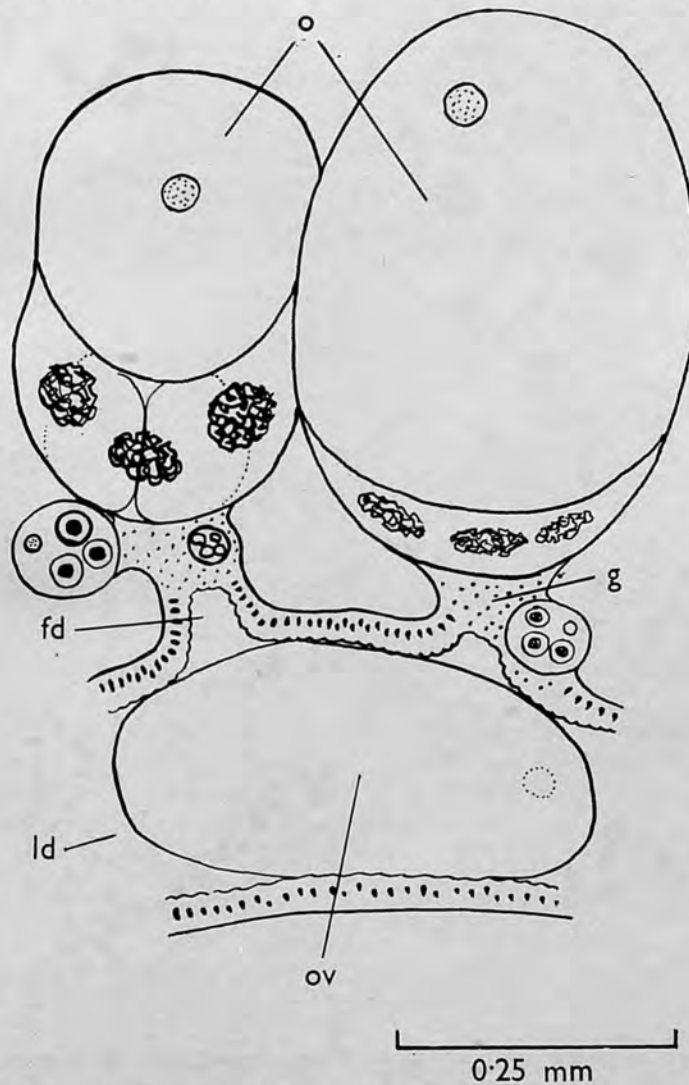

0·25 mm

Fig. 3.—Part of the ovotestis of *Lepidurus arcticus*. (o=oocyte, ov=ovum in longitudinal duct, fd=follicle duct, g=germinal region, ld=longitudinal oviduct.)

The above account is based on *Triops*, but there is no reason to suppose that most species of *Lepidurus* differ greatly from it ; in *L. articus* (Pallas) the ova when laid tend to be a little larger than those of the rest of the genus and contain a larva corresponding to about instar 3 of the rest of the genus ; the mature follicles are fewer in number in an individual in this species, longer in form, and borne on much shorter follicle ducts (fig. 3).

In the Notostraca that I have cultured, the eggs are carried for a complete instar in the brood pouches on the eleventh thoracic appendages, and released

from these almost immediately before ecdysis ; they are then sticky, and adhere firmly to plants, pieces of stone, sand grains, and the bottom of the aquaria. A new batch of eggs is laid into the brood pouches within a few hours of the completion of the ecdysis. This process was described for *Lepidurus apus* (L.) by Desportes & Andrieux (1944).

TESTES.

The testes, like the ovaries, are paired and lie in the haemocoel on either side of the gut, attached to the ventral body wall ; in fresh specimens they are transparent and difficult to see.
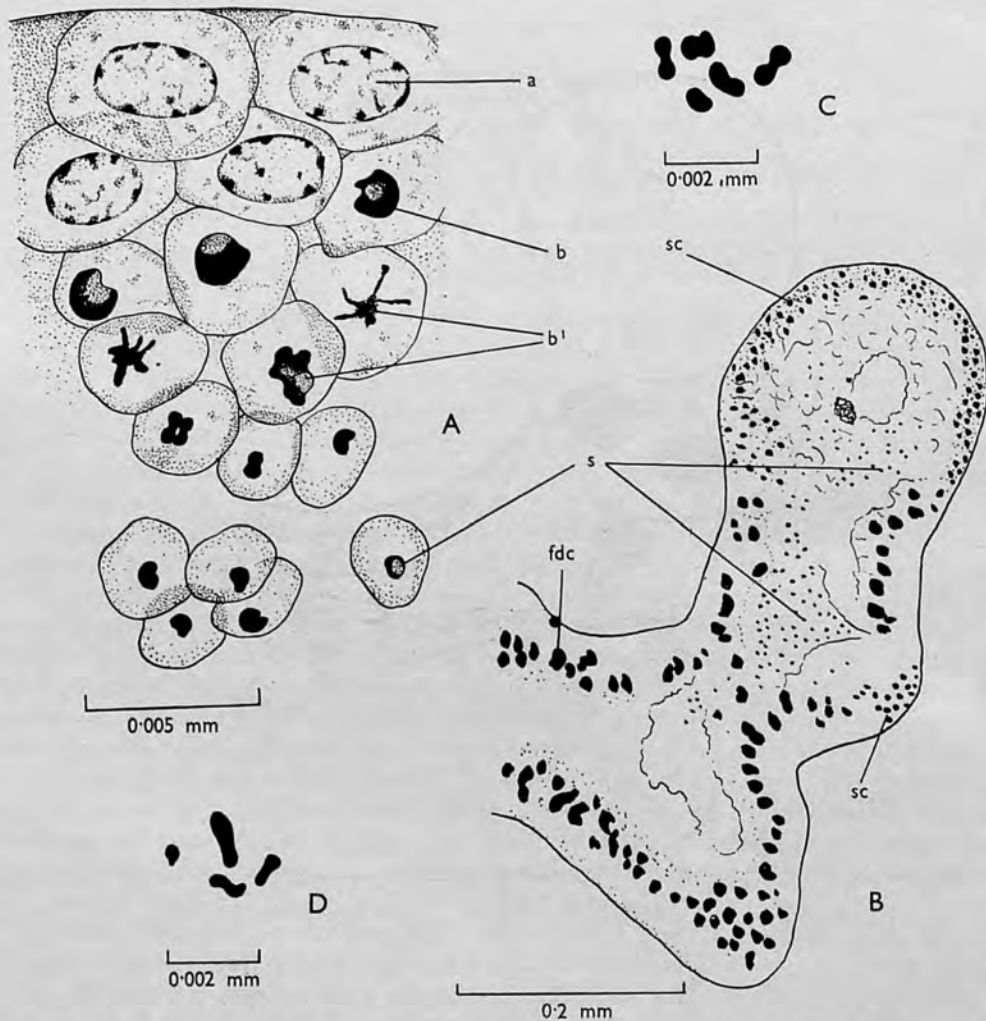

Fig. 4.—A, Part of testis wall of male *Triops granarius* ; B, Section of testis lobe in ovotestis of *T. cancriformis* ; C, Haploid set of chromosomes ($n=5$) of *T. australiensis* ; D, Haploid set ($n=4$) in early oocyte of *T. longicaudatus*. (a=1° spermatocyte, b=2° spermatocyte, b′=division of b, s=sperms, sc=spermatocytes, fdc=follicle duct cells.)

Each consists of a highly lobulated sac, with a main longitudinal duct meandering throughout its length ; this duct is joined to the efferent duct which opens on the base of the eleventh thoracic appendage.

The lumen of the gonad—both lobes and duct—is filled with sperms in mature animals ; as Kozubowski described, they are round non-motile cells with a small dense central nucleus.

As would be expected, the histology of the gonads differs considerably between the mature and the immature animals; the whole organ is bounded by a thin transparent membrane within which is a wall of cells four or five deep, arranged irregularly. In this wall are two types of inactive cells and various stages of their division (fig. 4A).

The first type of cell—the "A" cell—has large ovoid nuclei that are weakly Feulgen-positive, while the second type—the "B" cell—has smaller, very densely staining nuclei. The "A" cells are in a much higher proportion in the immature males.
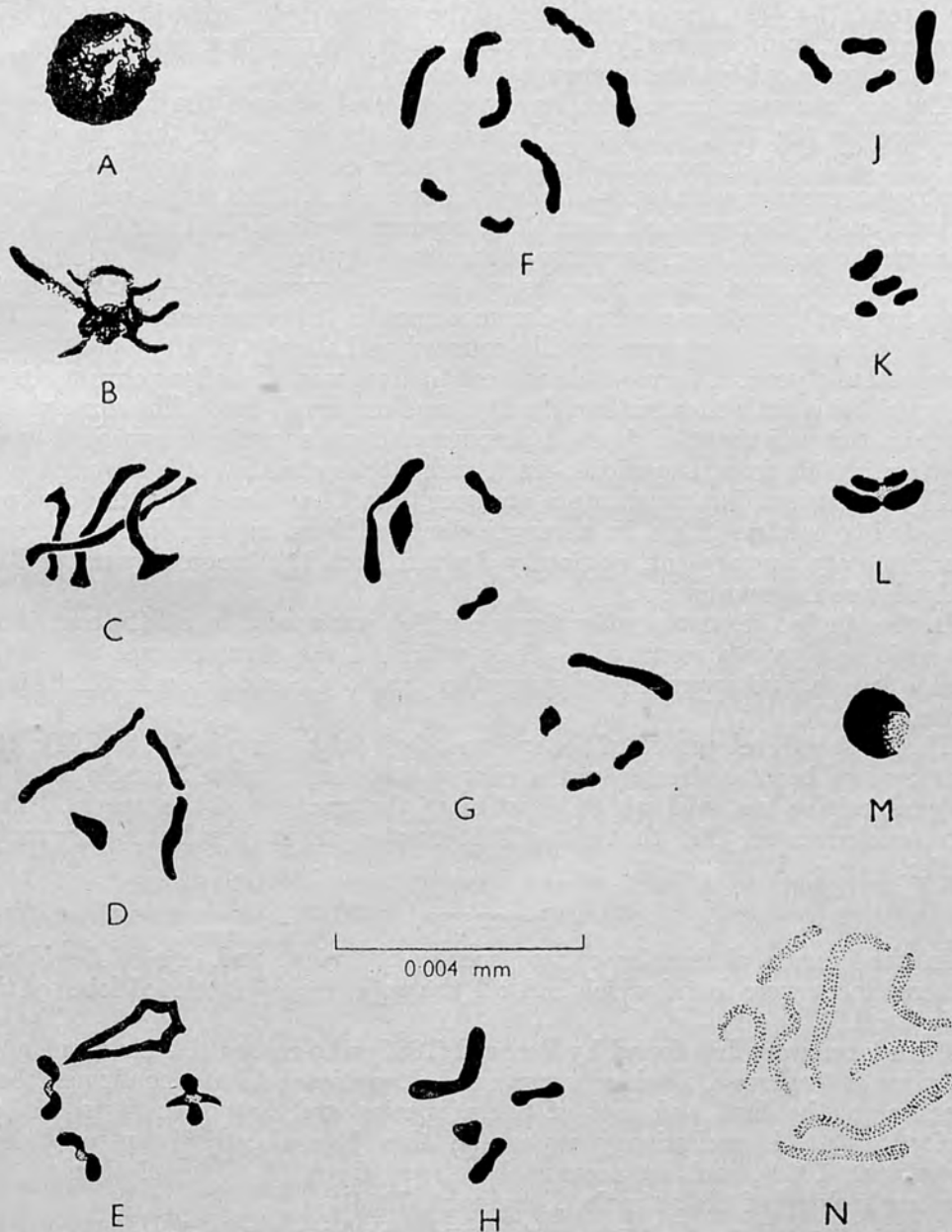

Fig. 5.—Spermatogenesis of *Triops granarius*; A, 2° spermatocyte nucleus; B, prophase beginning; C, prophase completed; D, metaphase; E, early anaphase; F, telophase; G, two spermatids from telophase; H, another spermatid; J–M, condensation of chromosomes in spermatid to form definitive sperm nucleus; N, metaphase of 1° spermatocyte.

Divisions of both types of cell have been observed. Type "B" cells are conspicuous in division in near mature and mature gonads, and by their division give rise to a pair of haploid spermatids. "A" cell divisions are more rare, and difficult to analyse when found, but a number of diploid sets of weakly Feulgen-positive chromosomes are taken to represent such divisions.

It is thought, then, that the testis wall is composed of 1° spermatocytes ("A" cells), 2° spermatocytes ("B" cells) and various stages of their divisions.

The division of the 2° spermatocytes has been followed fairly closely and deserves further description. The first sign of division is the appearance of small prominences on the periphery of the nucleus which proceed to grow out into threads (fig. 5B); the central mass of the nucleus dwindles as these prophase threads grow, and eventually disappears, when the prophase chromosomes fill the whole space within the nuclear membrane (fig. 5C).

The nuclear membrane then breaks down and releases the haploid set of chromosomes (fig. 5D). A few of the stages of the division of these have been seen (fig. 5E) but in none are there any traces of spindle formation. Many telophases were seen with twice the haploid number within a single cell (fig. 5F), but were easily distinguished from the 1° spermatocyte diploid sets (fig. 5N) by their smaller size and their property of staining very deeply.

The division products of these telophases—the spermatids—were the most numerous and conspicuous sets of chromosomes in the testis smears (fig. 5G, H). In *Triops granarius* they were readily counted and a series of fifty-one sets was drawn and analysed. The most characteristic form was of one long chromosome, two equal but a little shorter than the first, and one small one. The main variation from this was that the shortest chromosome was sometimes subequal to, or indistinguishable from, the middle-sized ones ; it may be that this is evidence of an XY mechanism, but much more analysis than I have been able to do would be needed to confirm this. In a very few sets of these haploid chromosomes a supernumerary was present, obviously derived from the longest by natural or manipulative fragmentation.

In the single *Triops australiensis* male which was available, all the countable spermatid sets gave a result of $n=5$, in which all the chromosomes were subequal in length, and approximately equal in size, to the middle ones of the other species (fig. 4C).

The further development of the spermatids is fairly simple (fig. 5, J, H); the chromosomes become shorter and condense together to form a single mass of Feulgen-positive material which constitutes the nucleus of the sperm. This sperm-nucleus is very like that of the 2° spermatocytes in form but is very much smaller.

OVOTESTIS.

In the gonads of females of two species of *Triops* and one of *Lepidurus* scattered lobes were found which had all the appearance of isolated lobes of the testis (fig. 4B).

Such lobes were first found by Bernard (1892) who recorded their occurrence in *Triops cancriformis*, *Lepidurus apus* and *L. arcticus* ; I have confirmed their presence in the first and last of these species and found them in *Triops longicaudatus*. A preliminary report of this has already been published (Longhurst, 1954), and an account has been given of their relation to the breeding biology of the animals (Longhurst, 1955).

Precisely similar cell-types were found in these testis lobes in *Triops granarius* as in the true testis, but the lobes in the ovotestes were much less successfully seen in preparations, for smears are spoilt by the great quantity of yolk which spills out from the oocytes, and in squashes it is difficult to obtain a single layer of isolated testis-lobe cells ; however, spermatid haploid sets of chromosomes (e.g. fig. 4D) were found in the two species of *Triops* (both n=4) but not in *Lepidurus arcticus*,

FERTILIZATION.

The copulation of *Triops cancriformis* has been described by Hotovy (1937) and that of *Lepidurus apus* by Desportes & Andrieux (1944) ; it is similar in both species and I find the process to be identical in *Triops granarius*.

It is a rapid process, in which the male approaches the female laterally, and arches its body so that it grips that of the female in such a way that the ventral surfaces of the posterior regions of the thorax are opposed ; for a few seconds the male moves convulsively, and then breaks away.

Copulation appears to occur successfully only when the female has just completed ecdysis, and has yet to pass a batch of eggs to the brood pouches, although males may attempt to copulate with females in any condition or even with other males if no females are present.

In bisexual populations copulation is necessary before the females will pass eggs into the brood pouches ; females of such populations of *Triops granarius* and *T. australiensis* will lay no eggs in the absence of males. One female of the latter species reared in isolation was found to have the longitudinal oviduct ruptured and the haemocoel packed with masses of aborting eggs, so presumably egg production, but not egg laying, will proceed in the absence of males.

The sperms (fig. 4A, s) are non-motile ; this was confirmed by observations on living cells with the phase-contrast microscope. Fertilization is presumed to occur in the brood pouches, for no sperms were ever found in the longitudinal oviducts of bisexual animals, even when these had been reared with males and were producing eggs normally.

Isolated hermaphrodite females readily lay viable eggs, and it was found that sperms were present in the lumen of the longitudinal duct in all mature females examined. The lumina of the follicle ducts and of the testis lobes are confluent and sperms pass into the duct in small aggregations which are then found throughout the duct system, even in the blind ends near the germinal regions. These small packets of sperms become embedded in the semi-liquid egg-shells of the ova resting in the longitudinal duct.

No fertilization stages were found in these races of *Triops cancriformis* and *T. longicaudatus* in which ovotestes replace ovaries : the ova resting in the oviduct appear still to be in a haploid condition, with sets of four chromosomes —seen particularly clearly in the former species (fig. 1C). This is a re-appearance of the haploid set which occurs in the early oocyte and becomes unstainable in the stage four follicles of these species. Attempts to find chromosome sets in ova after deposition in the brood pouches failed, for the egg-shell then hardens and renders manipulation very difficult.

The inference that these two species are at times hermaphrodite, rather than parthenogenetic, is based on the negative correlation between the occurrence of males and of ovotestes, and on the inability of females isolated from bisexual populations to lay eggs (Longhurst, 1955). It is unlikely that the sperms from the ovotestes act only as a stimulus to egg-laying, for they are absent from the oviducts of " bisexual " females, even in immediately post-fertilization stages.

There appears to be a general tendency towards sex reversal in Notostraca. von Zograf (1906) found, in the testes of *Lepidurus apus*, incipient ovarian tetrads—quite recognizably like those of the normal follicles of the females—but these aborted before development had proceeded very far.

In the present work a few cells with nuclei very similar to those of the nutritive cells of the tetrads were found in the lumina of testis lobes of hermaphrodites ; these were scarce and by no means universal and are taken to be aberrations rather than any form of testis nurse cells.

SUMMARY.

Both bisexual and hermaphrodite reproduction occurs in the Notostraca. The form of the gonads is described and the cytological cycle of ovaries and testes reported briefly.

The most successful chromosome counts were made on the early spermatid nuclei, seen abundantly in smears of nearly mature tests. These counts were confirmed by chromosomes found in the testis lobes and ovaries of other animals.

An account of copulation is given and methods of fertilization are discussed.

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Reproduction in Notostraca (Crustacea)

IN some species of Notostraca, populations occur in which no males are found and these have generally been considered to reproduce by parthenogenesis ; the European *Triops* (=*Apus*) *cancriformis* (Bosc.) exhibits a geographical variation in the occurrence of males, which are less common, or absent, in the north of its range, so that the species has been supposed to show parthenogenesis in colder, bisexuality in warmer regions, in the same manner as *Trichoniscus* (Isopoda, Crustacea)[1].

The account in the year 1889 by Bernard[2] of the discovery of testis lobes in the gonads of female *Triops cancriformis* has been overlooked by recent writers ; but during systematic work, in which this genus is being investigated cytologically, I have found testis lobes in the gonads of all the specimens which were examined from so-called parthenogenetic races of *T. cancriformis*. These lobes can readily be seen in sections, smears and whole mounts of the ovotestes.

No living males of *Triops cancriformis* are yet available, and in order to confirm the nature of the lobes in the ovotestis of the hermaphrodites, testes of male *Triops granarius* (Lucas) (syn. *T. numidicus* (Grube)) have been examined for comparison. In each species the spermatocytes in all stages and round, non-flagellate sperms were found to be identical.

It has been possible to obtain evidence from chromosome numbers to show that the sperms produced in the ovotestis are functional. In *Triops cancriformis* both oocyte and spermatocyte nuclei have a haploid number of four chromosomes, while dividing cells of the follicle epithelium show that the diploid number of the species is eight. Precisely similar chromosome numbers occur in the same cells of bisexual *T. granarius*, in which cross-fertilization takes place. The hermaphrodites appear to be self-fertilizing, for pairing does not occur and sperms are present in the oviducts and follicle ducts throughout adult life.

Hermaphrodites are able to lay viable eggs in the absence of males, a fact long known for the so-called parthenogenetic races of *Triops cancriformis*, and it has now been possible to confirm this with *Triops longicaudatus* (Le Conte) from a Californian rice-field population consisting entirely of 'females', which lay viable eggs into their brood-pouches in the absence

of males. Their gonads proved to be ovotestes, similar to those of *T. cancriformis*.

In other species bisexuality appears to be invariable, for in examining many samples of *Triops granarius* from Africa and Asia, I have found no instance where a large number of females without males might indicate hermaphroditism. The ovaries of this species were found to contain no testis lobes, a fact correlated with the inability of the females to lay eggs in isolation, and confirmed abundantly with cultures from two South African localities. A single female of *Triops australiensis* (S. and H.) reared in isolation laid no eggs, thus fitting in with the account of Spencer[3], who examined ovaries of this species shortly after Bernard's report and found no testis lobes.

The populations of *Triops cancriformis* present an interesting problem ; in some parts of the range the species is hermaphrodite, in others males occur sporadically, while bisexuality appears to be normal in North Africa. Brauer[4] showed that females from a central European population with sporadic occurrence of males were able to produce viable eggs in isolation, but they copulated normally when reared with males. I have not been able to obtain females from such a population to find out what mechanism enables them to produce viable eggs without mating. A female from a bisexual population from Algeria had no testis lobes in the ovaries, and it appears likely that the normally bisexual *T. cancriformis* reproduces in the same manner as *T. granarius*.

Bernard[2,5] also described an ovotestis in *Lepidurus arcticus* (Pallas) and in *Lepidurus apus* (L.). Specimens which I have examined of the former species from Alaska have, as he described, testis lobes crowded at the posterior end of the gonad, but no further investigation of this genus has yet been possible.

Hermaphroditism appears to be rare in Crustacea[6], having previously been known only in the Cirripedia, although in some Decapoda and some parasitic Isopoda a sex-change occurs during life.

Systematic and cytological work is being continued on *Triops* and will be described fully elsewhere when it is completed.

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