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RELATIVE GROWTH IN SOME ANTARCTIC PYCNOGONIDA

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Master of Science

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by
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INTRODUCTION

Work on the systematics of a large collection of Antarctic Pycnogonida has revealed very forcibly the limitations of existing systems of classification of this group. In an attempt to rectify some of these shortcomings for a monograph on the pycnogonid fauna of the Ross Sea area, the author has been led to seek new characters and character states which will be useful in taxonomy.

Virtually nothing is known of pycnogonid behaviour and ecology, and it seems unlikely that additional knowledge in these fields will be forthcoming in the near future. Our knowledge of pycnogonid comparative anatomy and histology is also very slight. However, the Pycnogonida do lend themselves very readily to mensural description of much of their form. It is true that the expressions of some characters are more simply described by the traditional vocabulary of experts in the field (e.g., ovigeral spine shape), but for other characters this self-same vocabulary may be a source of confusion, as, for instance, in the description of proboscis shape.

A morphometric study involving some 160 specimens of three species revealed that certain simple statistical hypotheses on relative growth can readily be proposed. The values to practical taxonomy and the possible functional interpretation of these hypotheses, in the light of existing information on pycnogonid anatomy, are discussed in the following pages.

The author wishes to express his gratitude to Dr. Joel W. Hedgpeth, whose knowledge of Pycnogonida, and whose patient consideration of the many problems that arose, ensured the completion of this work.

Dr. Ralph G. Johnson criticised the manuscript, and his criticisms and comments are very highly valued.

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CHAPTER I

THE CHOICE OF SPECIES

The three species studied were *Ammothea australis* Hodgson (Figure 1), *Austropallene cornigera* Möbius (Figure 4), and *Colossendeis megalonyx*[1] Hoek (Figure 7). Morphological variation is bound to be observed whatever the nature of the samples studied, but the choice of three such morphologically very distinct species, from supposedly widely separated genera, has ensured that in this study the variation encountered is always below the specific level. This is important in view of the emphasis placed here upon the taxonomic usefulness of a knowledge of relative growth rates.

Additional considerations in the choice of the three species were their frequencies in the collection, and their absolute size ranges. The former consideration is of obvious statistical importance, while for the latter it was felt that the magnitude of errors of measurement of very small specimens would be such as to negate any conclusions that could be drawn from the data.

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[1] For the special significance of this epithet, see p.13.

CHAPTER II

CHOICE OF STRUCTURES AND MEASURING TECHNIQUES

As there are no data available on relative growth in any pycnogonids, it was considered advisable to begin analyses with the largest structures and appendages. Accordingly, the following structures were chosen for the study: third leg; left palp; trunk; proboscis. Of the three species, *Austropallene cornigera* possesses no structures homologous with palps in the size range with which this study is concerned.

Growth of three groups of leg segments relative to total leg growth was also considered. The groups are composed of those segments which appear to fall into natural groups from the point of view of locomotion. They are the three coxal segments, the three long middle segments (femur, tibia 1, and tibia 2), and the three distal segments (tarsus, propodus, and terminal claw). While other terminologies are used, especially by general arthropodists, the author prefers Sars' usage of names for the leg segments because they imply the functional subdivision of the leg.

Measurements of all but the largest structures were obtained by use of a calibrated microscope eyepiece micrometer. The largest structures were measured manually.

It was found necessary to pay particular care to the dimensions chosen to represent the length of any structure.

It is rare for any segment of a structure to be bilaterally symmetrical in all planes passing through its long axis, and differences of as much as 30% can be obtained by measuring different aspects of the same coxal segment in some species. Again, the insertion of the proboscis onto the trunk is at an oblique angle in all species, so that measurements of these structures from the dorsal and ventral views vary widely.

To overcome this problem, certain arbitrary procedures were adhered to rigidly. In the first place, a structure was always measured from the same aspect, for all specimens of all species. Secondly, the length of any segment or structure was taken to be the distance between the centres of the intersegmental membranes at its two ends. In the case of a distal structure, the length is the distance between the centre of its proximal intersegmental membrane and its distal extremity--no distal spines being included. The proboscis and trunk were always measured from the dorsal aspect, the palp from the ectal, and the leg segments from the postero-lateral aspects.

CHAPTER III

STATISTICAL METHODS AND PRESENTATION

Throughout this study, the data were analysed in their original state, and regression equations are all of the form $y' = bx + a$. Although it would have been possible to use the more highly refined techniques which have been developed for the study of allometry, it was felt that the nature of the study did not warrant this.

The specimens did not belong to successive stages in a particular ontogeny, which precluded a study of allometry of growth--as defined by Teissier (1960), and there was no great advantage in treating them as individuals of varying sizes at some specific stage of development, when allometry of size could be studied. Rather, the purpose was to determine whether there are specific stages of development whose boundaries could be detected by changes in relative growth.

Above all other considerations for the method of presentation, it was felt more advisable to leave the data and hypotheses in such a state that they could be tested by subsequent application of additional data, with an absolute minimum of mathematical effort. It is hoped to assemble similar hypotheses about a large number of other species, for use in keys and other classification forms, and the ideal kept in mind is that these hypotheses should be as easily selectable and comparable as are the other character states used in such keys and classifications.

The choice of the third leg as a reference dimension was purely arbitrary, as indeed the choice of any one dimension must be, since no structure is totally independent of any other. The considerations for practicality, described above, for the present preference for non-allometric methods, are equally applicable to the choice of an arbitrary reference organ, rather than some general factor such as Teissier's "general growth factor".

The plotting of regression lines to find regression equations was performed by the simplified method suggested by Tate and Cleland (pp. 78-80). 95% probability confidence limits for the slope and the origin of the curves were obtained with the use of the equations recommended by these authors.

Although existing knowledge of pycnogonid morphology indicates that no radical morphological changes occur, once the full complement of legs is realised, the preliminary hypothesis tested throughout this study was that there are differences in relative growth between sexually mature and immature forms.

This hypothesis was tested by comparison of the two regression equations of the slopes for juveniles and adults, using the methods suggested by Tate and Cleland (pp. 80-81). Rejection or acceptance of the null hypotheses was based on the 95% probability of χ^2_r with two degrees of freedom.

Where the null hypotheses proved mutually acceptable, the 95% confidence limits for the two parameters for the adult data alone were calculated. Disparities in the sizes of the samples of adults and juveniles suggested prudence in the matter of proposing confidence limits for the parameters of the relative growth of juveniles.

I. RELATIVE GROWTH IN *AMMOTHEA AUSTRALIS*

The data were obtained from eighty-four specimens, and their analyses provided the hypotheses given below in Table I. Data and hypotheses are depicted in Figures 1, 2, and 3.

TABLE I[*]

Plot	Regression Equ^{ns}	Confidence Limits	
		a	b
Trunk / Total Leg	$y'=0.088x+0.93$	0.78 to 1.00	0.076 to 0.095
Palp / Total Leg	$y'=0.15x+1.88$	1.72 to 1.92	0.133 to 0.163
Coxal Sg^{ts} / Total Leg	$y'=0.18x \pm 0.0$	-0.10 to 0.05	0.178 to 0.187
Middle Sg^{ts} / Total Leg	$y'=0.703x-0.55$	-0.50 to -0.65	0.701 to 0.710
Distal Sg^{ts} / Total Leg	$y'=0.10x+0.80$	0.78 to 0.92	0.10 to 0.104
Proboscis(J)[**] / Total Leg	$y'=0.166x+0.30$	—	—
Proboscis(A)[**] / Total Leg	$y'=0.109x+1.45$	1.30 to 1.52	0.100 to 0.111

[*] Here, as in Tables II and III, (J) signifies juveniles and (A) signifies adults.

[**] See pp. 5 and 6.

From this table may be deduced the following relative magnitudes of growth:

All Specimens:

Leg. Middle segments >[1] Coxal segments > Distal segments,

Adults:

Leg > Palp > Proboscis > Trunk,

Juveniles:

Leg > Proboscis > Palp > Trunk.

In this sample, the only detectable change of relative growth at the onset of sexual maturity occurs in the relative growths of the leg and proboscis. At sexual maturity, growth of the leg, relative to that of the proboscis, increases. The 95% confidence limits for the parameters of these two slopes are found to be discontinuous.

Attainment of sexual maturity, in the sample, is seen to occur during the following size ranges:

When the *Leg Length* is between 17.5 and 21.2 mm. (the middle segments being 11.47 to 14.7 mm.);
Proboscis Length is between 2.9 and 4.0 mm.;
Trunk Length is between 2 and 7 mm.;
Palp Length is between 4.8 and 5.8 mm..

The determination of size ranges at attainment of sexual maturity may prove to be very useful in investigations

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[1] Throughout this treatment, this symbol denotes "greater than".

of intrageneric ranges of variation and the delimitation of species, and especially so in the Ammotheidae.

In the genus Ammothea, some species appear to retain "perfect" chelae throughout life, while in others the chelae atrophy at a fairly early stage, and this character has been used in the separation of species. The criterion of "perfect", as applied to chelae, is difficult to appreciate. Atrophy is apparently gradual in this genus, and it is not always easy to determine whether or not the chelae are perfectly functional. The degree of atrophy of the chelae is not necessarily correlated with degree of completeness of the ovigers and the presence or absence of genital pores. A knowledge of the size ranges of a number of structures at the attainment of sexual maturity might be a satisfactory substitute in specific diagnoses of the single criterion of perfection of the chelae.

II. RELATIVE GROWTH IN *AUSTROPALLENE CORNIGERA*

Data were obtained from twenty-seven specimens, and the hypotheses depicted in Figures 4, 5, and 6 are given below:

TABLE II

Plot	Regression Equ^{ns}	Confidence Limits	
		a	b
$\frac{\text{Trunk}}{\text{Total Leg}}$	$y'=0.183x + 0.5$	0.42 to 0.72	0.169 to 0.212
$\frac{\text{Coxal Sg}^{\text{ts}}\text{(A)}^{*}}{\text{Total Leg}}$	$y'=0.106x + 1.55$	0.86 to 2.40	0.073 to 0.140
$\frac{\text{Coxal Sg}^{\text{ts}}\text{(J)}^{*}}{\text{Total Leg}}$	$y'=0.128x + 0.3$	—	—
$\frac{\text{Long Sg}^{\text{ts}}}{\text{Total Leg}}$	$y'=0.666x - 0.4$	-0.80 to 0.68	0.651 to 0.677
$\frac{\text{Distal Sg}^{\text{ts}}}{\text{Total Leg}}$	$y'= 0.12x + 0.90$	0.70 to 0.90	0.081 to 0.130
$\frac{\text{Proboscis}}{\text{Total Leg}}$	$y'=0.10x + 0.58$	0.40 to 0.85	0.079 to 0.117

*See pages 5 and 6 and Table I.

From this table, it can be seen that the structures studied have the following relative magnitudes of growth:

All Specimens:

Leg > Trunk > Proboscis,

Adults:

Leg. Middle segments > Distal segments > Coxal segments,

Juveniles:

Leg. Middle segments > Coxal segments > Distal segments.

In this sample, the only detectable change in relative growth at the onset of sexual maturity occurred in the relative growth of the total leg and the coxae, when the growth rate of the three coxae together diminished. No coincident increase of relative growth was detected for either of the other two groups of leg segments, indicating that the absolute growth rate of the total leg diminishes at this stage. The fact that such a dimunition of leg growth rate was not observed relative to the trunk and the proboscis suggests that either a similar dimunition for these two structures occurs simultaneously with the dimunition for the leg, or else that the statistical methods employed were not sufficiently fine enough.

When the slopes defining the relative growth rates were drawn for the adult and juvenile data, the suspicion became apparent that the actual change in growth rate occurs not at the attainment of sexual maturity, but at a greater leg length. There is no biological or morphological data which might suggest the position of such a point of flexure, and so no hypothesis could be tested.

Two possible explanations for the existence of such an apparently belated change of relative growth rate come to mind. Firstly, the attainment of physiological sexual maturity may not coincide with the attainment of the adult oviger form and genital pores, but may instead coincide with the second (and real) point of flexure of the slope. In this case, there is a stage, in this species, comparable with the prepubertal molt of some crustaceans.

Secondly, the attainment of physiological and morphlogical maturity may be simultaneous, while there occurs an over-all dimunition of absolute growth rates correlated with some process of aging. If this is so, then it is strange that such a dimunition should not be apparent in the relative growth rates of the middle and distal leg segments.

In the absence of any clear interpretation of the phenomenon, it was decided to retain the original hypothesis, which subdivides the sample into adults (!) and juveniles.

Bearing in mind the limitations affecting the definition of sexual maturity, this stage is reached, in the sample, at a size when the structures considered have the following dimensions:

Total Leg length	10.5 to 12.6 mm.
Coxal segments, length	2.0 mm.
Middle segments, length	6.9 to 7.7 mm.
Trunk length	2.7 to 3.3 mm.
Proboscis length	1.4 to 1.8 mm.

III. RELATIVE GROWTH IN COLOSSENDEIS MEGALONYX

The study of relative growth has so far proved itself most fruitful for the taxonomy of the genus *Colossendeis* Jarzynsky. Within this genus, there has been a considerable confusion in the synonymy of a supposed complex of Antarctic species, which we may initially consider as the "megalonyx complex".

No less than four species have been proposed within this complex. They are *C. megalonyx* Hoek 1881, *C. frigida* Hodgson 1907, *C. rugosa* Hodgson 1907, and *C. scoresbii* Gordon 1932. Recent treatments of the complex have included discussion of the possibility of complete synonymy of the species defined within the complex. However, while the combinations of characters used for the separation of the latter three species appear inconstant, the doubts on synonymy have not had very objective expression.

The heterogeneity of the complex was, in part, tested by the application of all available mensural data, on three of the four species, to the hypotheses proposed for the sample from the present collections. No suitable data from *C. scoresbii* are available, while data from eight specimens of *C. megalonyx*, *C. frigida*, and *C. rugosa* were taken from texts and figures.

In all the structures studied, the data from the eight specimens were found to fit within the 95% confidence limits for both parameters, of both juvenile and adult regression equations. In view of this, the complete synonymy of *C. megalonyx*, *C. frigida*, and *C. rugosa* is proposed. Confirmatory reasons for this synonymy are given in a general taxonomic survey of the Ross Sea Pycnogonida, now in preparation.

Evaluation of the status of *C. scoresbii* must await the availability of specimens of this species.

The hypotheses given in Table III are based on forty-nine specimens from the present collection and the eight specimens from previous collections. The data and hypotheses are shown in Figures 7, 8, and 9.

TABLE III

III. RELATIVE GROWTH IN *COLOSSENDEIS MEGALONYX*

Plot	Regression Equ^{ns}	Confidence Limits	
		a	b
Trunk / Total Leg	y'=0.094x + 0.9	0.50 to 1.20	0.079 to 0.085
Proboscis / Total Leg	y'=0.187x - 0.3	-0.8 to 0.1	0.160 to 0.196
Palp (A)* / Total Leg	y'=0.271x ± 0.0	-0.8 to 0.6	0.266 to 0.282
Palp (J)* / Total Leg	y'=0.381x - 4.9	--	--
Coxae / Total Leg	y'=0.064x ± 0.0	0.0 to 0.7	0.064 to 0.073
Middle Sg^{ts}(A) / Total Leg	y'=0.622x + 4.7	4.0 to 5.3	0.607 to 0.622
Middle Sg^{ts}(J) / Total Leg	y'=0.688x - 1.0	--	--
Distal Sg^{ts}(A) / Total Leg	y'=0.297x - 3.7	-3.1 to -5.1	0.288 to 0.305
Distal Sg^{ts}(J) / Total Leg	y'=0.255x + o.6	--	--

* See pages 5 and 6 and Table I.

The hypotheses given in Table III indicate that the structures considered have the following magnitudes of relative growth:

<u>Adults</u>: Leg $>$ Palp $>$ Proboscis $\gg$ Trunk
Middle segments $>$ Distal segments $>$ Coxae
<u>Juveniles</u>: Leg $>$ Palp $\gg$ Proboscis $>$ Trunk
Middle segments $>$ Distal segments $>$ Coxae

Changes in slope at attainment of sexual maturity were found in no less than three out of the six structures considered. The scatter of data appear normal around the curve fitted to the adult data in the three changing growth rates.

The criteria used in deciding the degree of sexual maturity are the presence or absence of genital pores and the completeness of the fields of special spines on the four terminal segments of the ovigers. Each field is found in three conditions; the presence of the final condition is completely correlated with the presence of genital pores.

Sexual maturity appears to be attained when the organs considered have the following lengths:

<u>Total Leg</u> length	44 to 45 mm.,
<u>Middle segments</u>, length	37.2 to 37.7 mm.,
<u>Trunk</u> length	5.75 to 6.25 mm.,
<u>Proboscis</u> length	8.5 to 10.5 mm.,
<u>Palp</u> length	14 to 16 mm..

One specimen with juvenile characteristics has a leg length of 83.5 mm. (middle segments 55.6 mm.), a trunk length of 9.5 mm., a proboscis length of 19.6 mm., and a palp length of 21.6 mm..

Enquiry into the relative growth in this species has proved of additional worth in casting new light on the _megalonyx_ complex. In the collections under investigation, there were two specimens, from separate stations, which are obviously closely allied to _C_. _megalonyx_,—if not actually to be included in that species. However, examination of the specimens suggested that, in addition to an unusually attenuated appearance of all structures, the proboscis appeared abnormally long for the species.

The data from these two specimens are shown in Figures 8 and 9, and it can be seen that, in respect of the growth rates (in relation to that of the total leg) of the trunk, coxae, and palp, the data lie outside the 95% confidence limits of the regression lines for the species. In all three cases, the leg appears to have a faster growth rate than does _C_. _megalonyx_. In respect of the other growth rates studies, these two specimens lie within the 95% confidence limits. In addition, the smaller of the two specimens is immature, and in respect of leg length is markedly larger than all but one of the juvenile _C_. _megalonyx_.

In view of the fact that the two specimens were collected from separate stations, and are presumably not--because of size differences--of the same brood, and since the two stations are in a more easterly part of the Ross Sea than has been sampled before, it seems reasonable to consider the specimens as members of a breeding population isolated from that of C. megalonyx. Whether allopatry or sympatry is involved is impossible to tell.

IV DISCUSSION

I. TAXONOMIC IMPLICATIONS

Some particular instances of the usefulness to taxonomy of a knowledge of relative growth rates have been discussed for each of the three species, but certain general points are worthy of mention.

Since the statistical procedures used have been methods of inference from small samples to whole populations, the nature of the samples and of the populations should be discussed.

In purely practical terms, the populations are here envisaged as consisting of all specimens of the three particular genera which can be identified with the use of keys, and other published information, as the "species" in question (the synonymy of C. megalonyx must be borne in mind in this context). It is particularly emphasised that the statistical hypotheses proposed rest on the basic assumption that the populations (species) are essentially static from an evolutionary point of view. Only by subsequent testing of the hypotheses with additional data can the directions of morphological variation, and the degrees of continuity in space of such variations, be ascertained.

Since the hypotheses proposed are to be applied to studies of intrageneric variation, a complete range of intraspecific variation is desirable if the confidence limits are to be fully meaningful. Whether this condition is satisfied here is impossible to tell, although the fit of the previously published data on the megalonyx complex and the distinctness of the two specimens discussed on page 17 provide a slight insight into the geographical distribution of the population of C. megalonyx. The previously published data are from specimens from a wide geographical range, while the two differing specimens occur within this range.

All three species have a superficially continuous distribution around the Antarctic continent, while the three samples have been taken essentially within the Ross Sea area. Since the degree of geographical continuity of variation is unknown, we cannot be sure that the complete range of morphological variation is present in each sample.

In each of the three species considered, changes in relative growth of at least two structures are shown to occur at or near the attainment of sexual maturity. However, in no two of the three species do the sites of the changes coincide completely. It is of interest to know whether or not this difference persists between species of the same genera, and how a knowledge of relative growth fits pre-existing schemes of pycnogonid classification and views on phylogenies within the groups. Relative growth should prove to be a useful tool for identifying juveniles and, with some refinement, larvae. In addition, an understanding of relative growth in juveniles may help to provide an understanding of morphological radiation and relationships.

In all, the amount of information in terms of additional characters and character states, of use in both analytical and synthetic taxonomy, which can be obtained by the simple statistical procedures described above, appear to far outweigh in value the additional time required for obtaining and analysing the data.

Although some of the types of data discussed in this paper are already incorporated in different form in specific definitions and keys, more detailed statistical analysis renders them far more biologically meaningful.

II. FUNCTIONAL INTERPRETATIONS

In the three species considered in this paper, the legs and the three middle leg segments show much faster relative growth than do any of the other structures. Since the morphology of the larvae of A. australis and A. cornigera are known (that of the larvae of C. megalonyx can only be surmised, since neither eggs nor larvae have ever been found), it is no surprise to find that this is so, nor to observe that changes in relative growth show a dimunition of the relative growth of the leg. What is perhaps surprising is the small size of the dimunition in each instance. An immediate biological interpretation of this phenomenon might be sought in terms of locomotory adaptations, were it not for certain anatomical peculiarities of the Pycnogonida.

The Pycnogonida appear to be unique among arthropods in that they lack well-organised and localised respiratory and excretory tissues, while at the same time the major parts of the gonads and the gut are borne within the walking legs. The gut diverticula extend to the end of the second tibiae. The femora tend to have greater diameters than either of the two tibiae.

Nitrogenous excretion is generally supposed to occur via the whole hypodermis or else via certain small "cutaneous" glands scattered over the entire body surface. The first supposition involves a theory of storage of nitrogenous excretory products in the hypodermis with liberation only during ecdyses, but, whichever of the two explanations is correct, loss of excretory products is accomplished over the whole surface of the adult animal. This is not true for the larvae, in which a small number of anteriorly-placed glands apparently account for excretion.

Respiratory exchange, in so far as it has been discussed, is considered to occur by diffusion across all integumental surfaces.

Our admittedly limited knowledge of the comparative physiology of marine invertebrates suggests that the lack of two such important sets of tissues as those for respiration and excretion will impose strict conditions upon morphological variation. Amongst such conditions will be the maintenance at all times of a high surface to volume ratio, and an integument permeable to respiratory and excretory products. However, these conditions need not apply to the whole animal, nor to all areas of the integument. The degree of localisation of regions with high surface:volume ratios and high integument permeability will be influenced by the efficiency of circulation and transport of a blood. The Pycnogonida possess an elongated dorsal heart and a fairly well-defined system of blood channels. Various blood cells have been reported, some apparently containing respiratory pigment, although no pigments have been reported free in the blood.

Even the most cursory examination of most Pycnogonida suggests that the legs comprise a large part of the total volume and total area of the animal and, at the same time, possess a high surface:volume ratio. This supposition was confirmed for an Antarctic species of Nymphon. Volumes and surface areas of certain gross structures were calculated and are given in Table IV. It should be noted that the inaccuracies of the measurements on which these data are based will tend to make areas smaller, and volumes larger, than they really are. The specimen from which the data in Table IV are derived had a fresh wet weight of 0.14 gm., and a maximum leg length of 24.6 mm. No tissues were further than 0.35 mm. from the exterior.

TABLE IV

	Areas as % of total	Volumes as % of total	Area:Volume
Total Legs	77.0	81.9	6.4
Middle segments	55.3	40.8	9.25
Coxal segments	18.5	26.2	3.7
Distal segments	7.5	14.9	3.5
Body*	11.5	13.0	6.0
Others**	11.5	5.4	14.3
Total	232.2 sq. mm.	33.9 cu. mm.	6.84

*Includes trunk, proboscis, and abdomen.

**Includes ovigers, chelae, and palps.

In general, we may consider that the attenuated appearance of many of the larger species of pycnogonids is connected with the need to maintain a high ratio of surface area to volume. Among larvae and smaller species (e.g., *Austrodecus* spp., *Rhynchothorax* spp., *Tanystylum* spp.), it is unlikely that surface to volume ratios are limiting to morphological variation, since all tissues are considerably less than 1 mm. from the exterior. There are some fairly large species (e.g., *Pycnogonum* spp.) which are compact and stout in form, but such behavioural data as we possess indicates that they are extremely sluggish creatures. The almost sedentary life of adult *P. littorale* and *P. stearnsi* suggests that these forms are near the lower limit for surface to volume ratios.

As an animal increases in mass (dry weight), the efficiency of processing of food by the gut must also increase, unless growth is accompanied by a general lowering of metabolic rates. The gut of the Pycnogonida, with its eight diverticula, performs digestion largely intracellularly. Therefore, to increase its ability for food uptake and digestion, it must have a very high internal surface area in relation to the animal's total mass; more so than if digestion were performed extracellularly in the gut lumen.

Similarly, as an animal increases its mass, it must also increase its respiration and nitrogenous excretion.

Again, increased size requires increase in muscle mass, with consequent increase of volume to house the muscles. Finally, the onset of sexual maturity requires additional volume for the formation, maturation, and storage of genital products. The conflict during growth, between the need for increased volume and the maintenance of a high surface to volume ratio, appears to have been resolved in the pycnogonids by a continued high relative growth of the three middle segments of the leg.

The gut volume might be increased in the trunk, but the trunk also contains part of the gonads, a relatively very large central nervous system, a heart, and the muscles necessary for moving the trunk segments and the coxae. Generally speaking, the trunk volume increases during growth by one of two ways in larger pycnogonids. In the first instance, there appear varyingly sharp dorsal and dorso-lateral projections, while the trunk stays short and increases in lateral diameter, the articulations of the trunk somites being maintained (e.g., _Ammothea_ _gigantea_, _A. stylirostris_). The effect of this is to alter very little the surface to volume ratio of the trunk. The second method involves a greater increase of length than of diameter, while no dorsal processes are developed, and the failure of the trunk segment articulations to develop, or their secondary fusion (e.g., various species of _Colossendeis_, _Austropallene_, and _Endeis_).

In both cases, the trunk maintains a very low relative longitudinal growth. Whereas the growth of the trunk involves considerable modifications of shape and muscle disposition if surface to volume ratio is to remain satisfactory, such is not the case for the legs. The conflicting needs for increased volume and a high surface to volume ratio are neutralised by great elongation of the legs. A slight increase of volume of each of the eight legs is equivalent to an increase of volume of the trunk, requiring drastic morphological andanatomical changes within the trunk. Increase of the leg volume can be achieved by an increase in length, with only a slight increase in diameter sufficient to accomodate the increased muscle masses.

Of the nine segments of the leg (the variably present accessory claws do not affect the discussion), observations on locomotion have shown that the three coxal segments are important in controlling limb posture, while the three distal segments are used in grasping the substrate. For either of these functions, relatively small segment length and high mobility are desirable. The femur, tibia 1, and tibia 2 act as levers in locomotion, and as such are not theoretically as limited in relative length as are the other two types of segments. It is not surprising, then, that this lack of limitation of elongation is exploited for the housing of the gut and gonads. The maintenance of a high surface to volume ratio of these three segments has the result that these segments bear a very large part of the total surface area of the animal (see Table IV), and it may be that they have come to act as the "gills" of the animal.

The efficiency of blood circulation through the legs is uncertain. There is a definite pattern of ventral centrifugal flow and dorsal centripetal flow in all structures but the proboscis, but speed and continuity of this flow seem to be affected by the peristalsis of the gut diverticula.

The possibility that the legs of pycnogonids are acting as gills is indicated by the morphology of one or two very large species of the family *Colossendeidae*. *Dodecolopoda mawsoni*, *Decolopoda australis*, and *Colossendeis scotti* are members of a group in this family with very stout compact trunks lacking dorsal projections. The surface to volume ratios of the trunk in these species are relatively low, while the actual mass is high. The legs are very long, sometimes in excess of 150 mm., and it seems likely that this morphological type is an exploitation of the possibilities of the gill function of the leg. In these species --none of which have ever been critically studied while alive--we would expect to find a highly efficient circulation of blood through the legs.

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APPENDIX

KEY TO FIGURES

CONVENTIONS

Throughout the figures, certain conventions have been used systematically. Male specimens are represented by the conventional symbol (♂); females by solid circles (•); unsexed forms by open circles (•); juveniles by crosses (+).

In all scatter diagrams, abscissae represent length of leg.

In Figures 8 and 9, the solid squares represent the data from the literature on the "megalonyx" complex; data from females have no sign, while data from males are designated by an arrow. In these two figures, the solid triangles indicated with a large open arrow are the data discussed on pages 21, 22, and 23.

The solid curves in each scatter diagram represent the originally calculated regression slopes, while the broken lines show the 95% confidence limits of the slope only.

Where the slopes for the total data are drawn, but no confidence limits for the slope indicated, the 95% confidence limits were so closely approximate to the original regression slope that they would have confused the figure, or else would not be visible. The algebraic forms of the missing 95% confidence limits for the slope and those for the origins, are given in Tables I, II, and III.

Figure 1. *Ammothea australis*: A, dorsal view of trunk; B, lateral view of trunk; C, 3rd right leg.

Figure 2. *A. australis*: A, trunk length on leg length; B, Proboscis length on leg length; C, palp length on leg length.

Figure 3. *A. australis*: A, length of coxae on total leg length; B, length of three middle segments of leg on total leg length; C, length of three distal leg segments on total leg length.

Figure 4. *Austropallene cornigera*: A, anterior view; B, dorsal view of trunk; C, 3rd right leg.

Figure 5. *A. cornigera*: A, distal leg segments on total leg length; B, middle leg segments on total leg length; C, length of coxae on total leg length.

Figure 6. *A. cornigera*: A, trunk length on total leg length; B, proboscis length on total leg length.

Figure 7. *Colossendeis megalonyx*:

Figure 8. *C. megalonyx*: A, trunk length on leg length; B, length of three middle leg segments on total leg length; C, length of three distal leg segments on total leg length; D, length of three coxae on total leg length.

Figure 9. *C. megalonyx*: A, palp length on total leg length; B, proboscis length on total leg length.

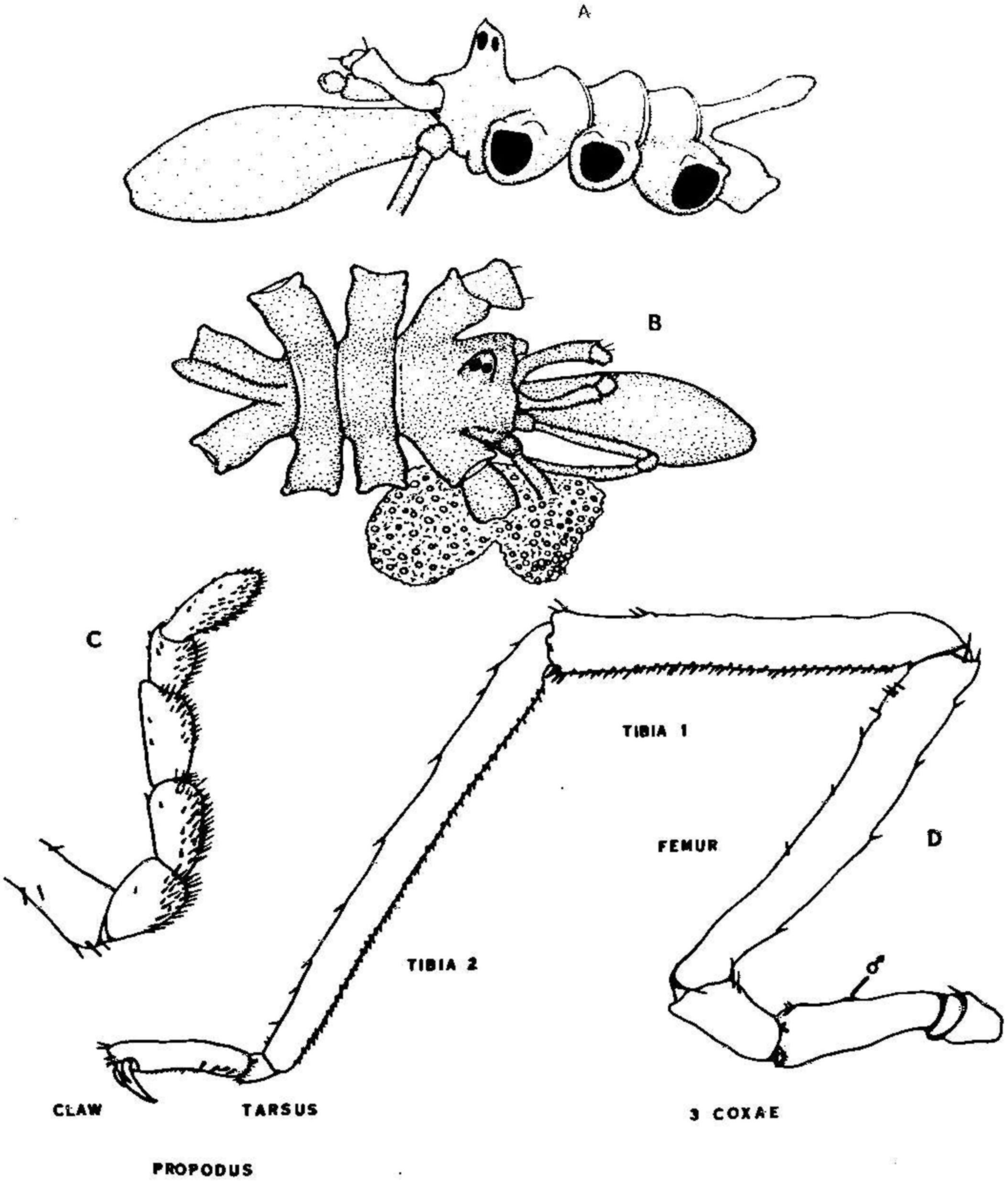
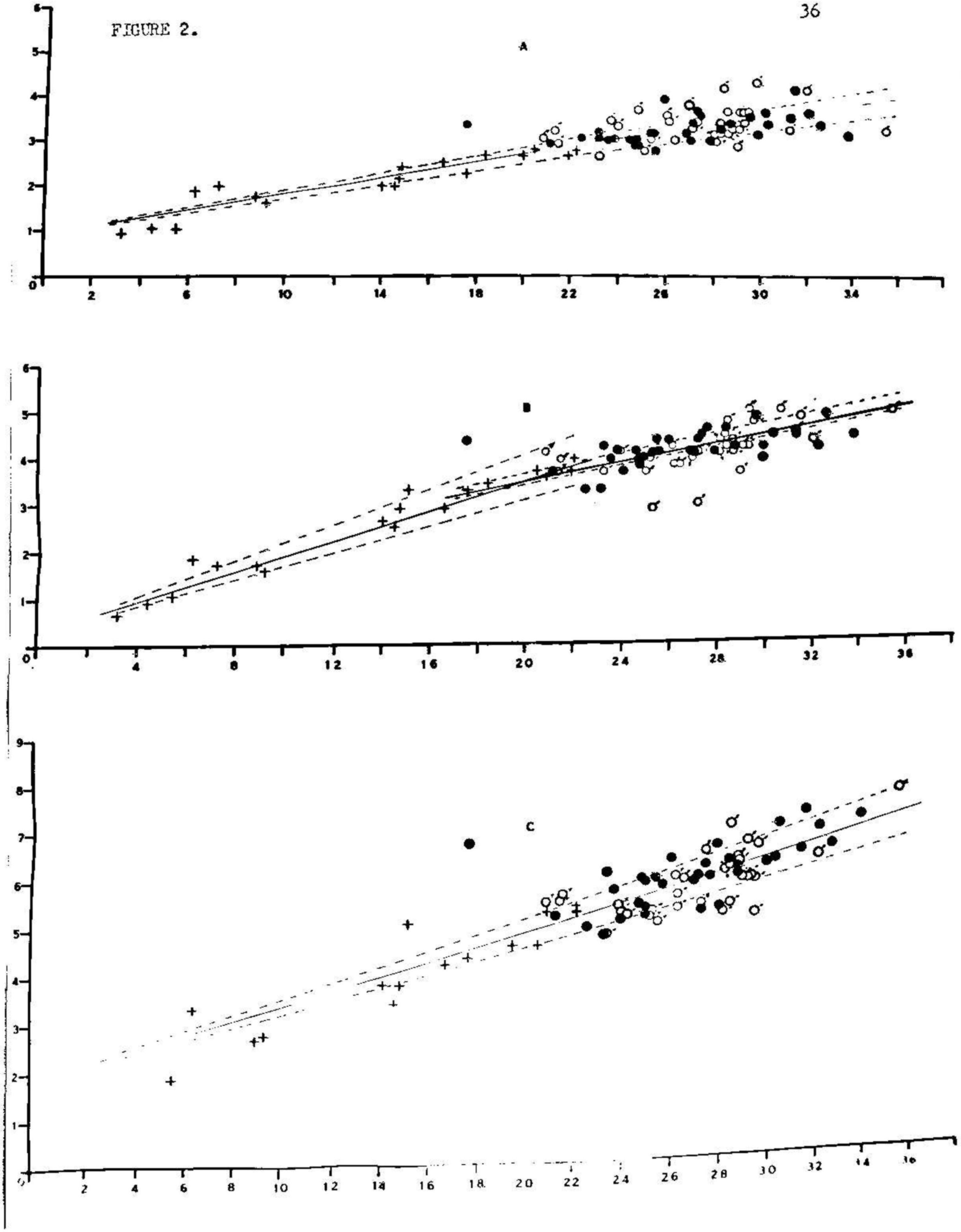


FIGURE 1.

FIGURE 2.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32
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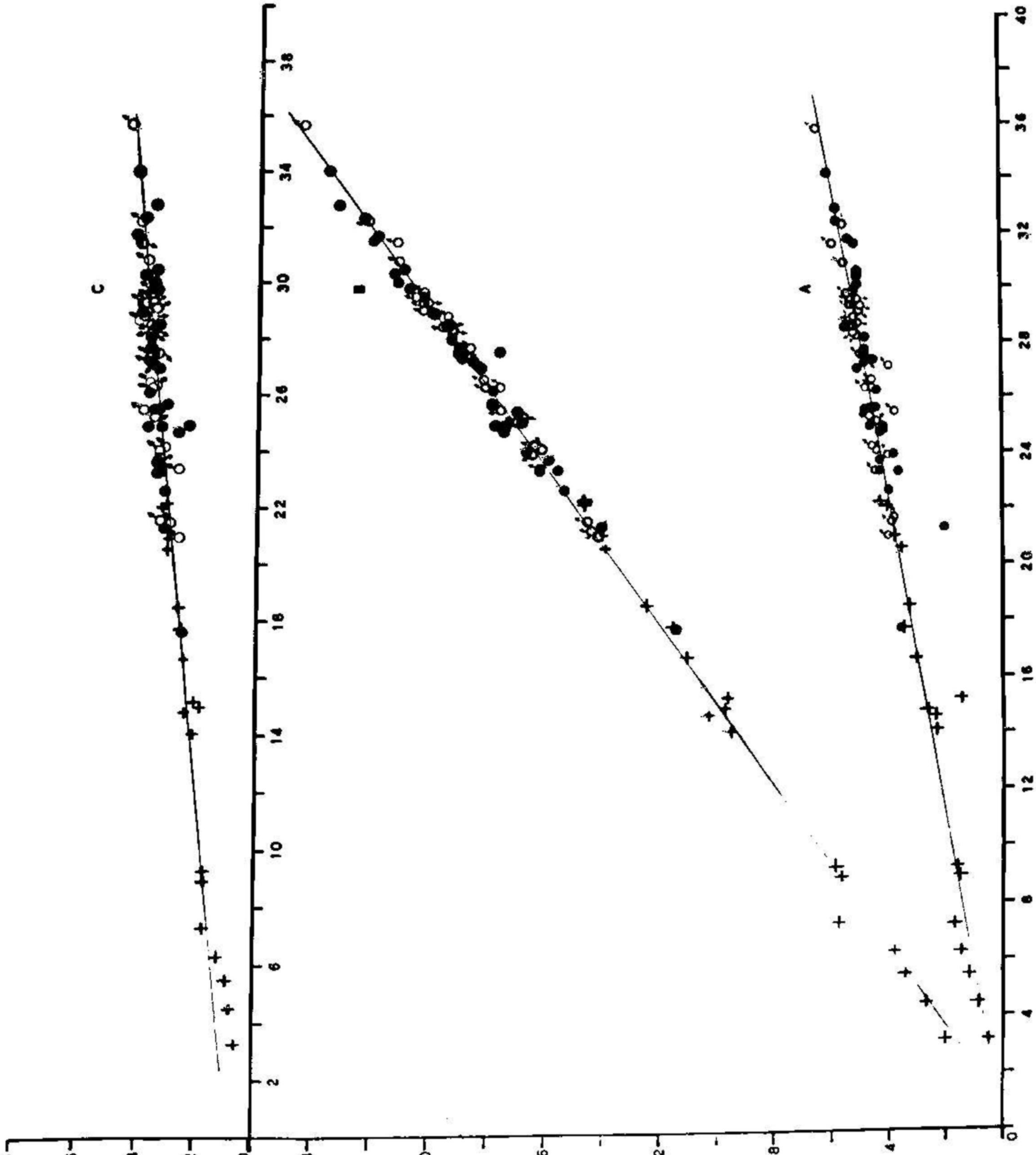
FIGURE 3.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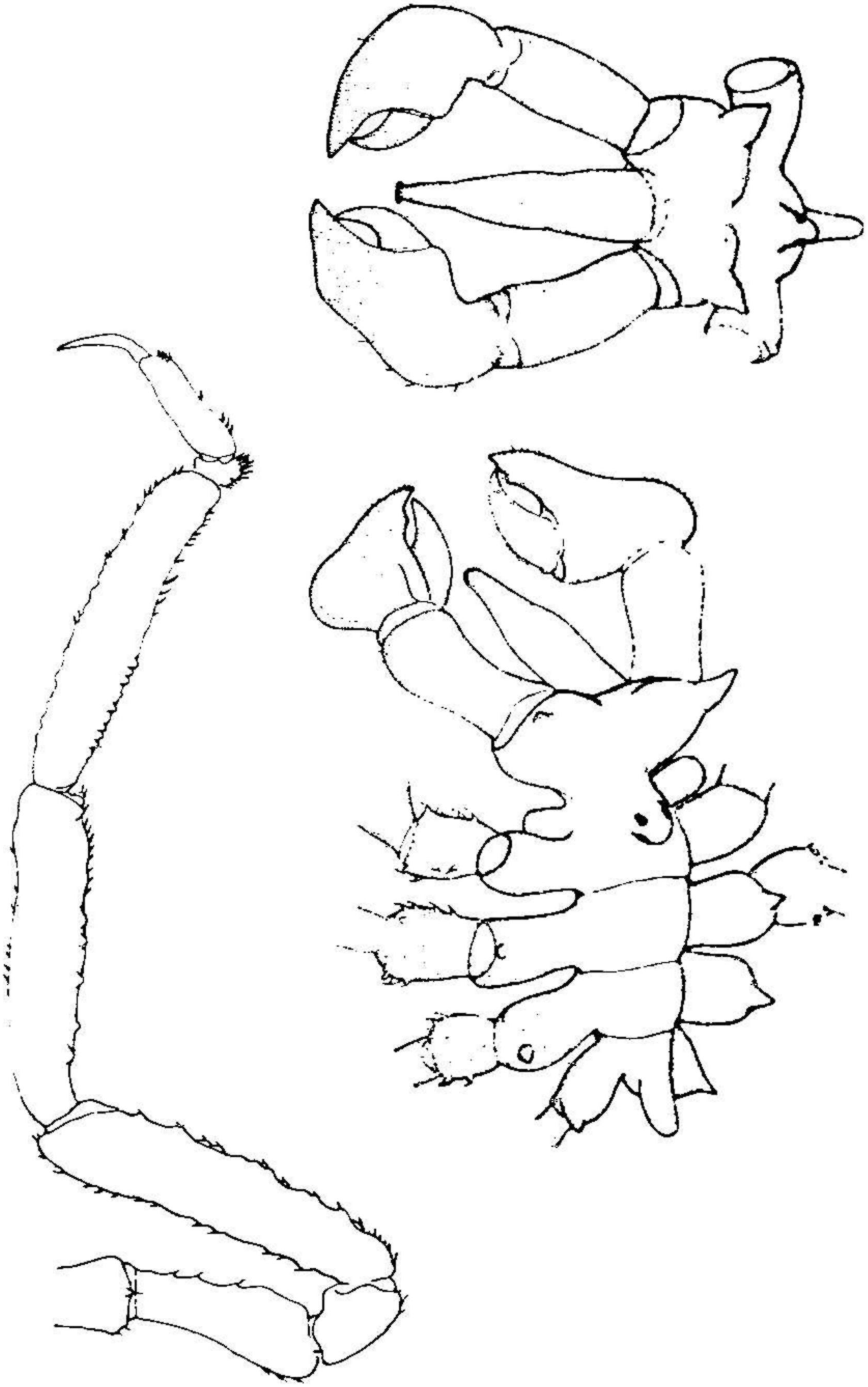

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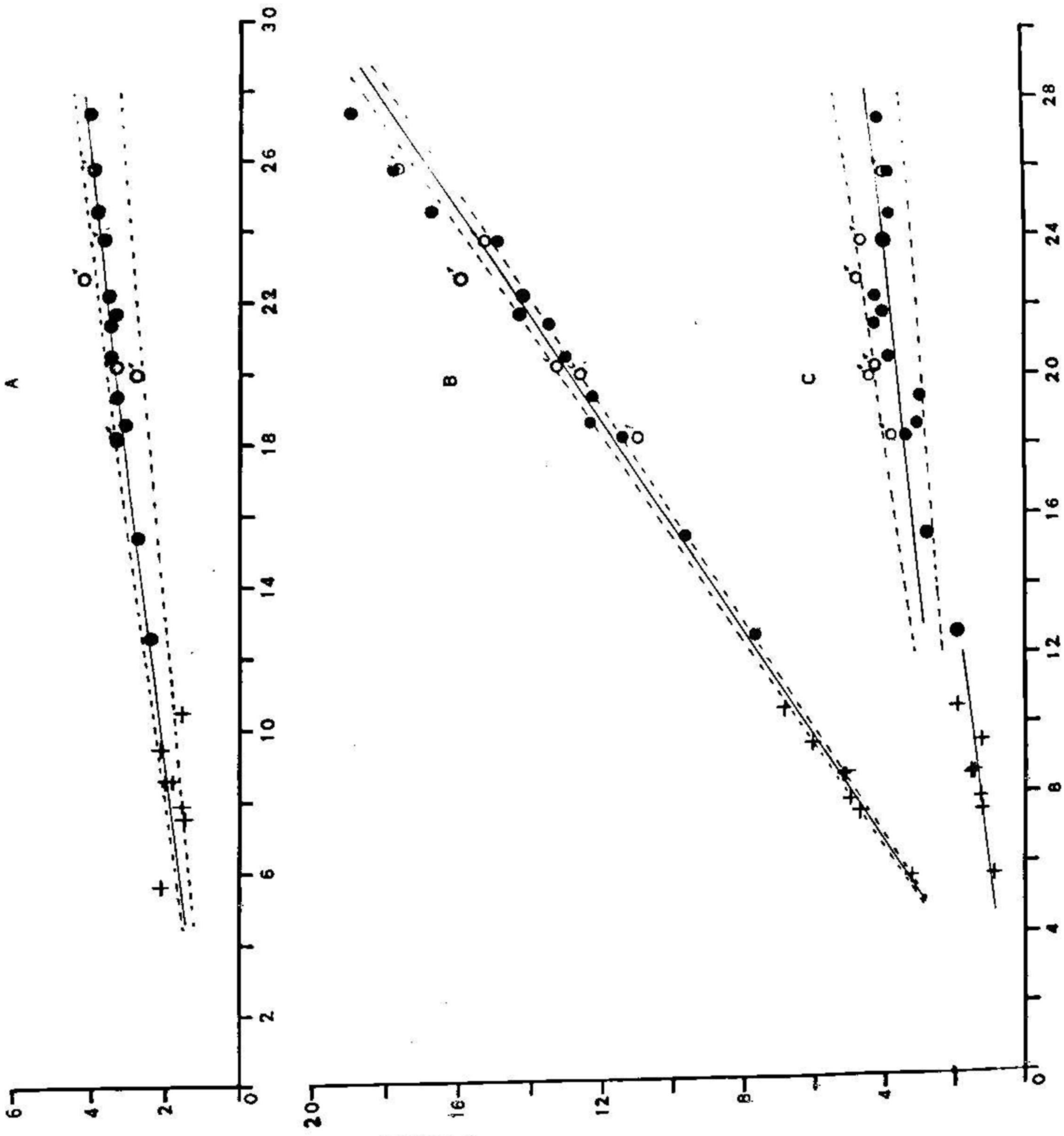

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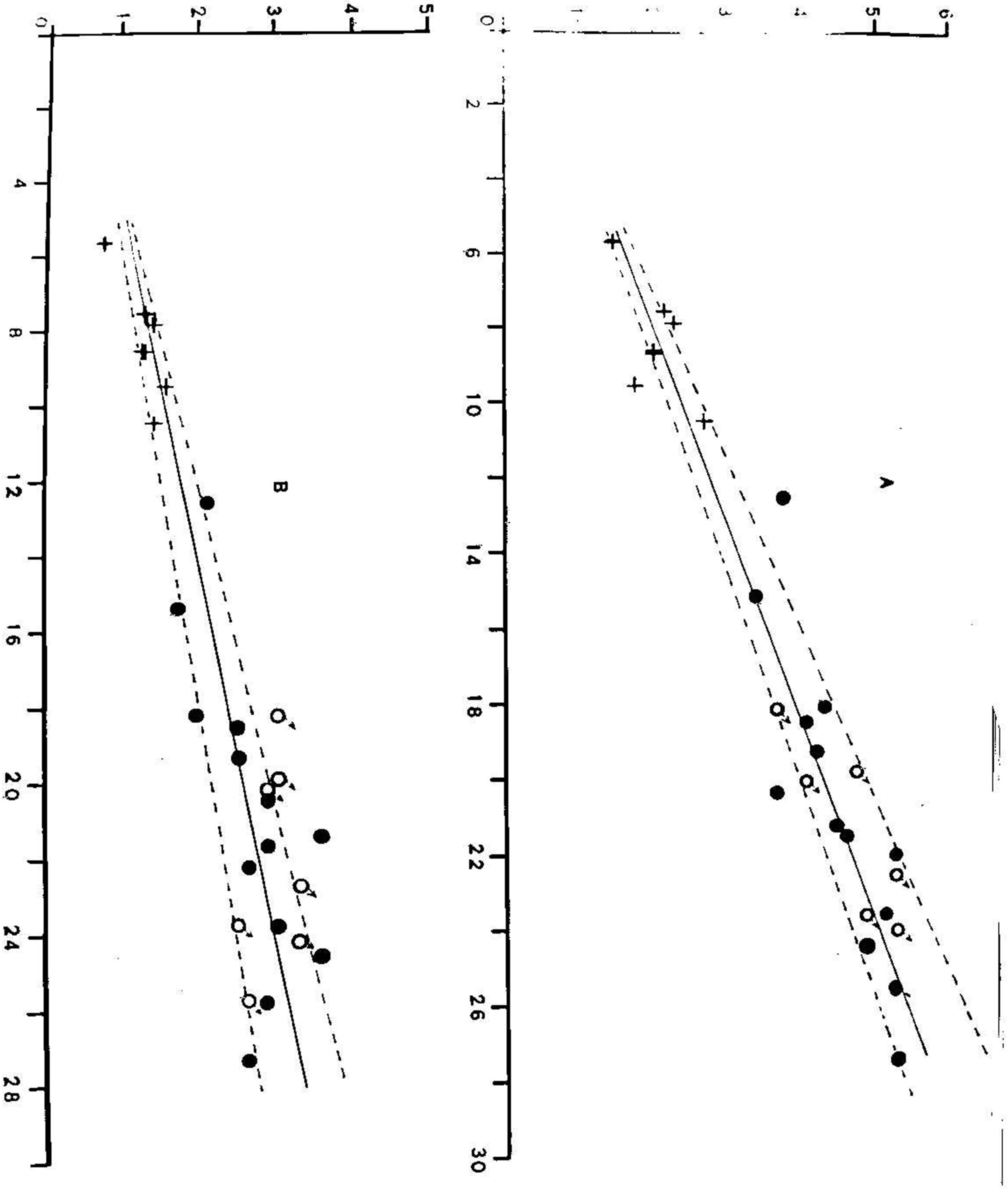

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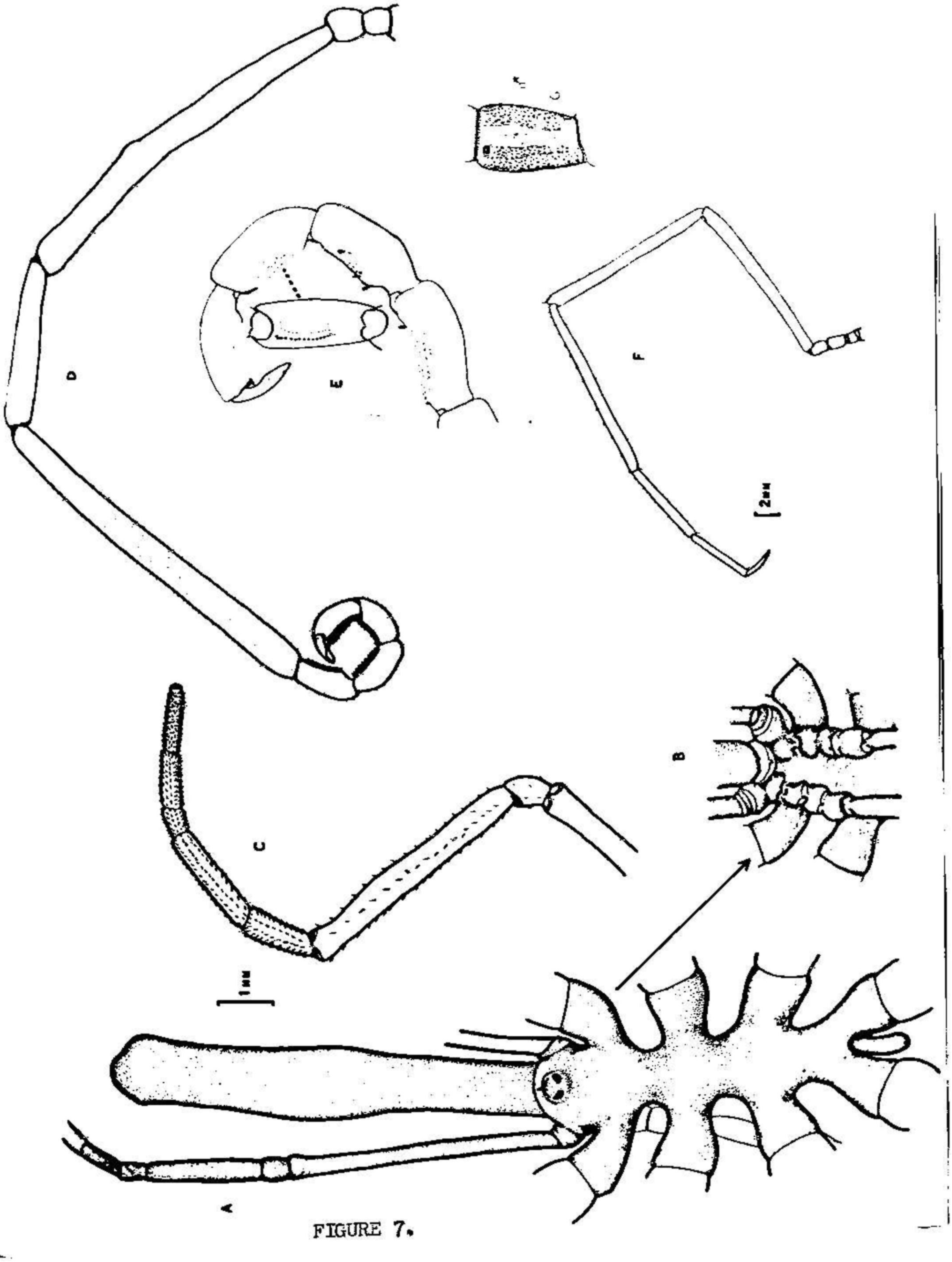

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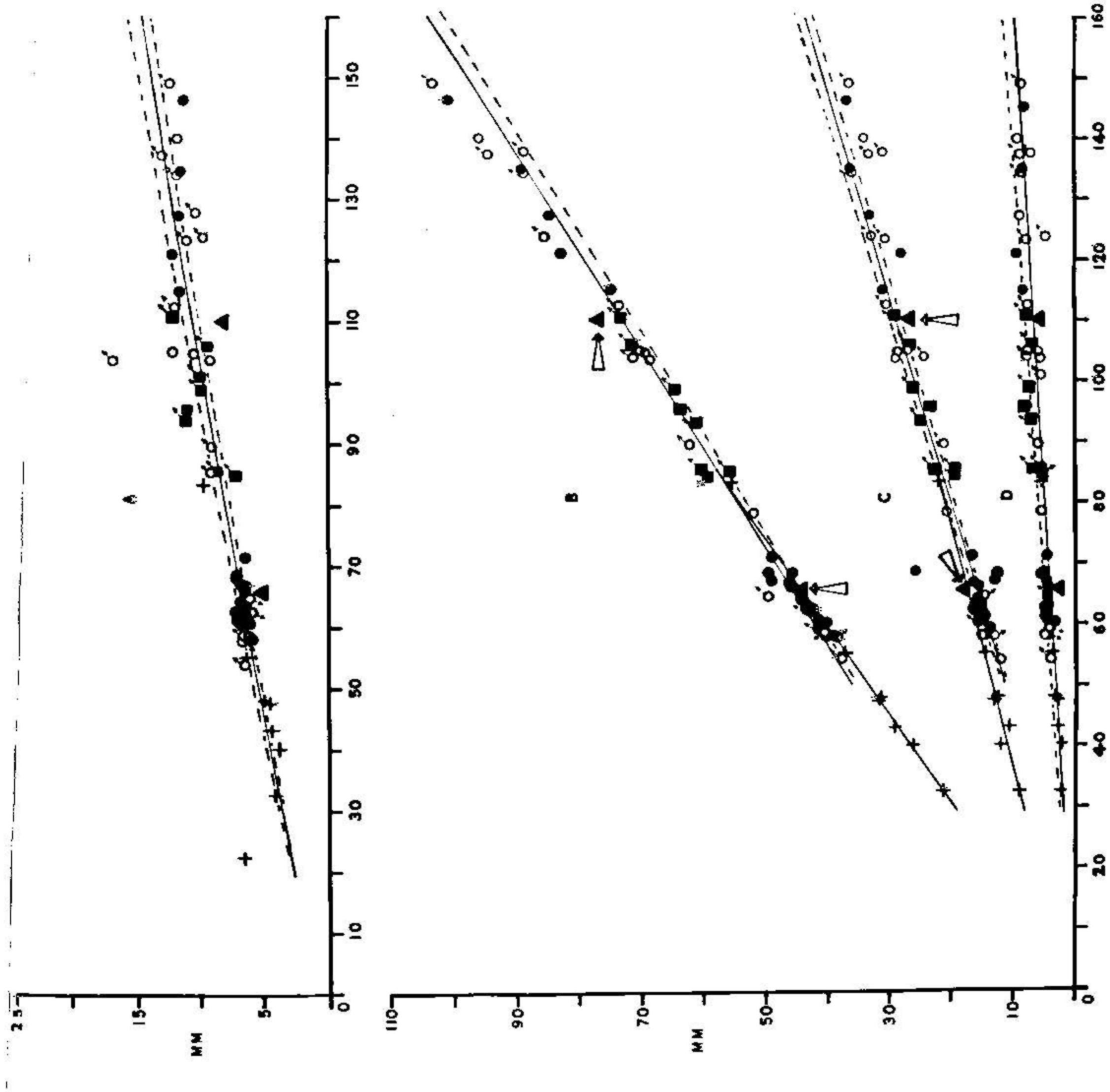
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FIGURE 8.

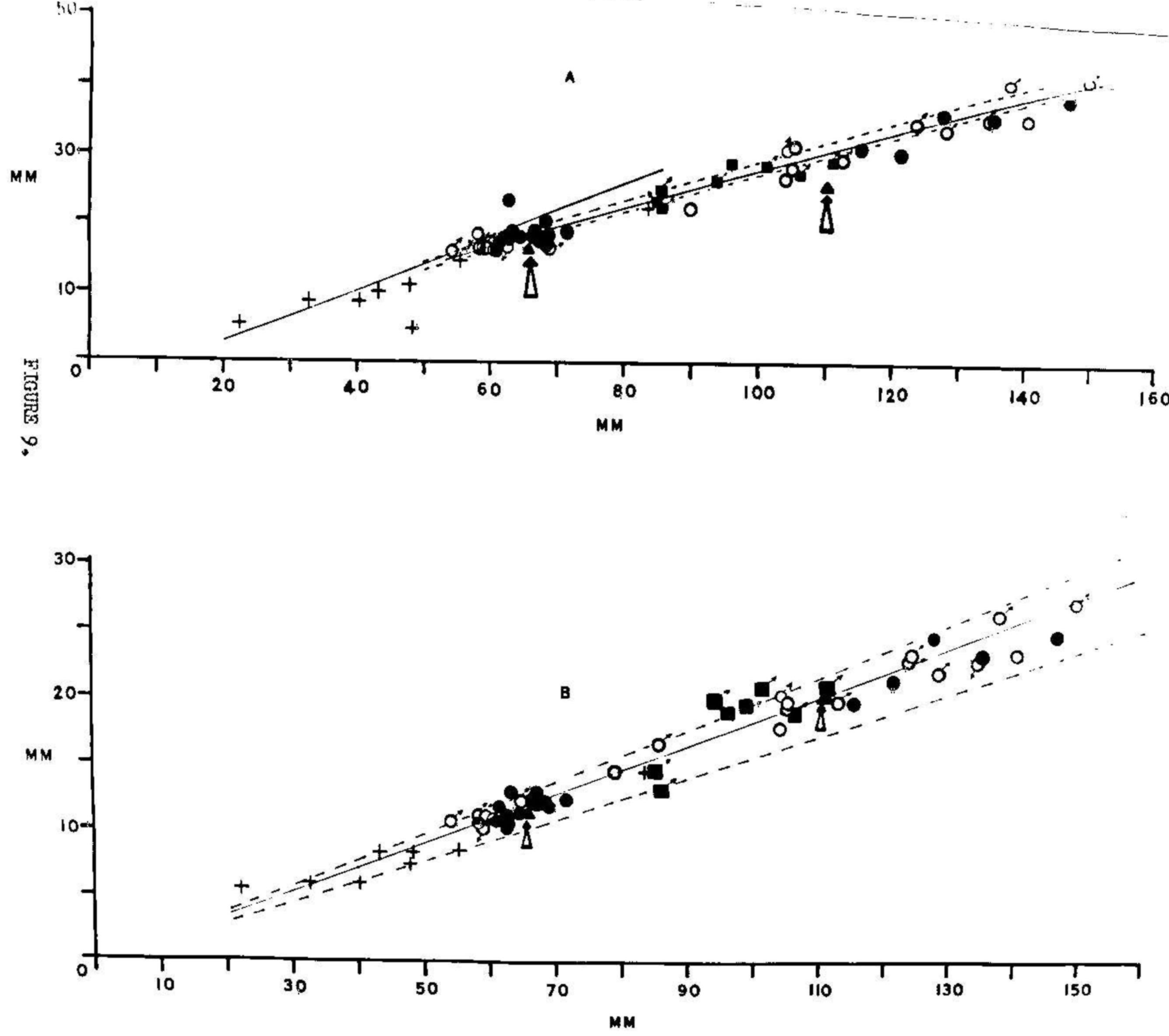
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FIGURE 9.