Plate III

Xanthocalanus alvinae n. sp., female (continued)

Figure 41.   Dorsal
Figure 42.   Mandible palpus
Figure 43.   Mandible blade
Figure 44.   Maxillule
Figure 45.   Maxilla
Figure 46.   Maxilliped
Figure 47.   First leg
Figure 48.   Second leg
Figure 49.   Third leg, exopod broken off
Figure 50.   Third leg, exopod of another specimen
Figure 51.   Fourth leg, exopod and endopod broken off
Figure 52.   Fourth leg, second and third endopodal segments of another specimen
Figure 53.   Fifth leg
Figure 54.   Fifth leg, another specimen

Xanthocalanus distinctus n. sp., male

Figure 55.   Lateral
Figure 56.   Dorsal
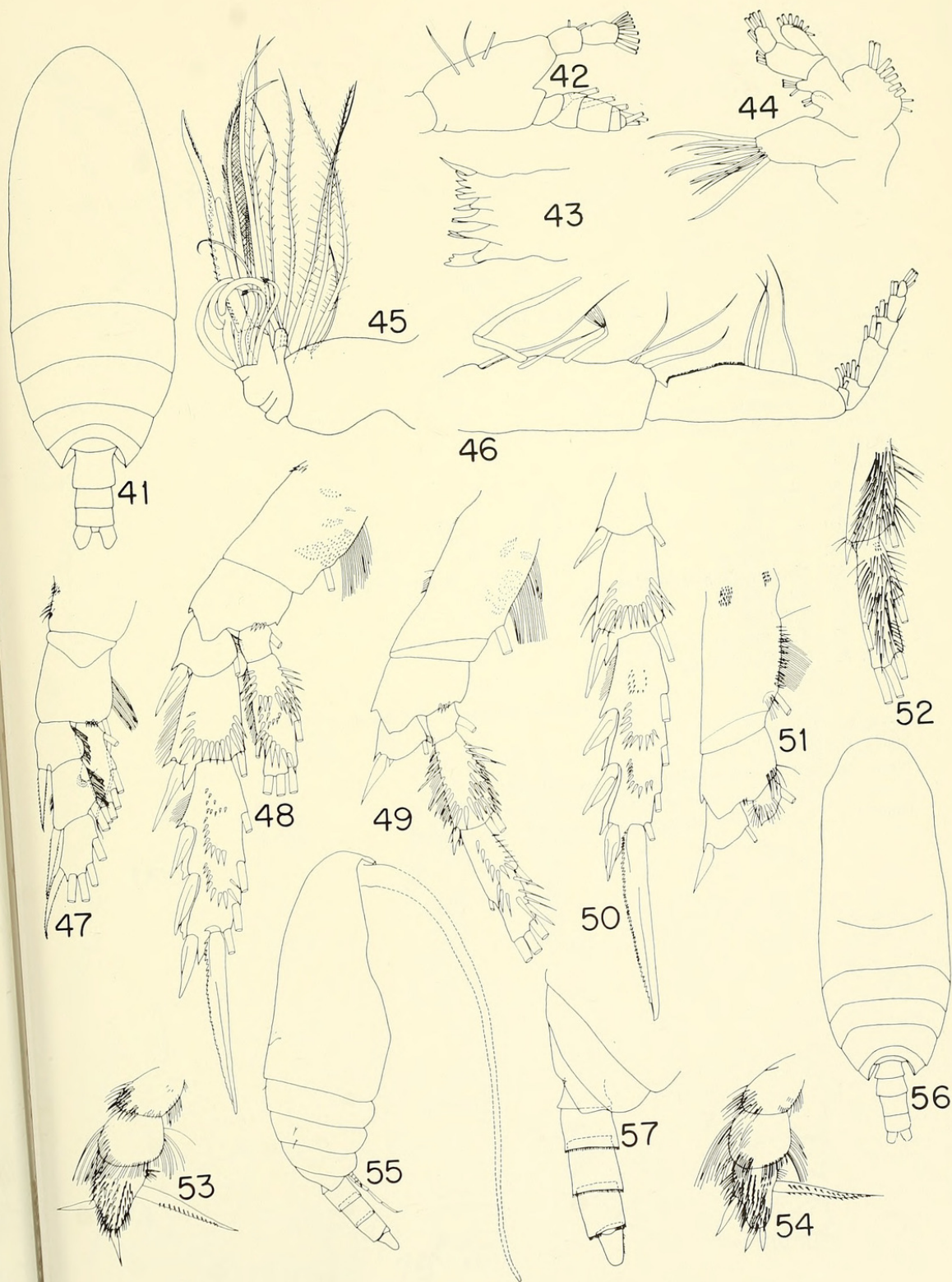Figure 57.   Fourth and fifth thoracic segments and abdomen, lateral

Plate IV

Xanthocalanus distinctus n. sp., male (continued)

Figure 58.   Anterior portion of head
Figure 59.   Left antennule, lateral
Figure 60.   Antenna
Figure 61.   Mandible palpus
Figure 62.   Mandible blade
Figure 63.   Maxillule
Figure 64.   Maxilla
Figure 65.   Maxilliped
Figure 66.   First leg
Figure 67.   Second leg
Figure 68.   Third leg
Figure 69.   Terminal spine of third leg
Figure 70.   Fourth leg
Figure 71.   Fifth legs
Figure 72.   Right fifth leg, posterior side
Figure 73.   Tip of left fifth leg

Xanthocalanus elongatus n. sp., female

Figure 74.   Lateral
Figure 75.   Dorsal
Figure 76.   Fifth thoracic segment and abdomen, lateral
Figure 77.   Fifth thoracic segment and abdomen, dorsal
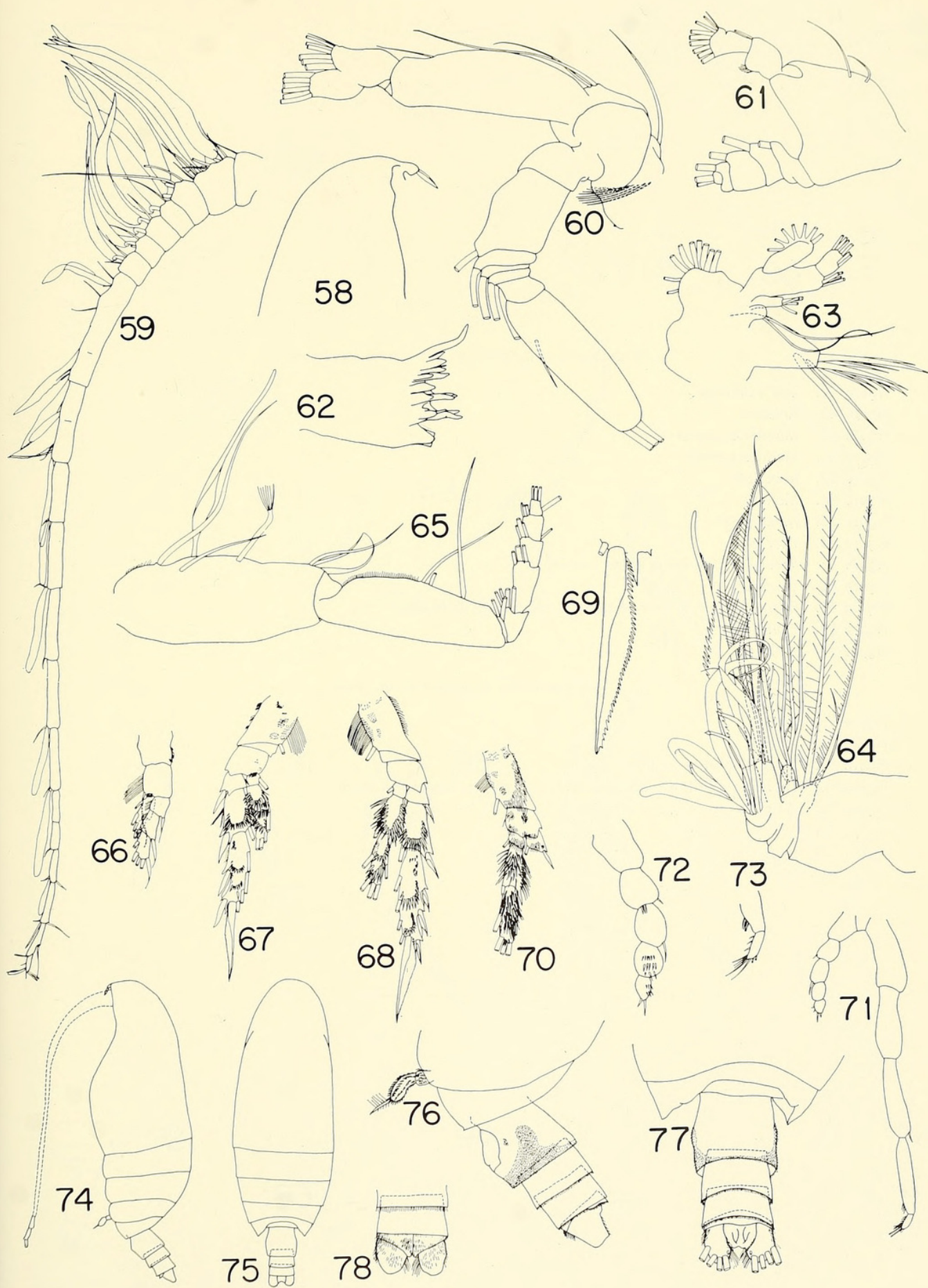Figure 78.   Fourth and fifth abdominal segments and furca, ventral

Plate V

Xanthocalanus elongatus n. sp., female (continued)
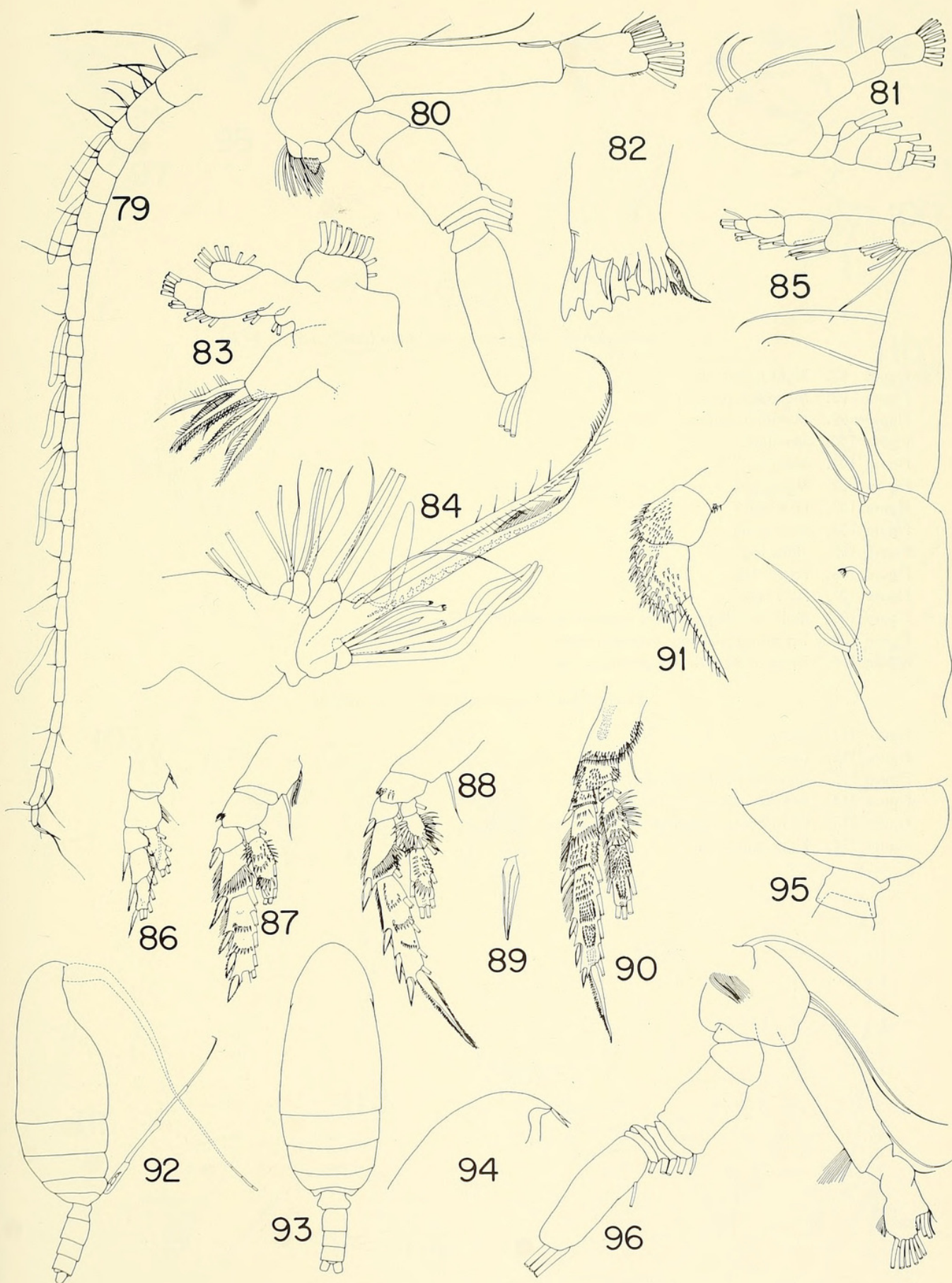
Xanthocalanus elongatus n. sp., male

Plate VI

Xanthocalanus elongatus n. sp., male (continued)

Figure 97.   Right antennule
Figure 98.   Mandible palpus
Figure 99.   Mandible blade
Figure 100.   Maxillule
Figure 101.   Maxilla
Figure 102.   Maxilliped
Figure 103.   First leg
Figure 104.   Second leg
Figure 105.   Third leg
Figure 106.   Fourth leg
Figure 107.   Fifth legs
Figure 108.   Right fifth leg and first segment of left fifth leg
Figure 109.   Tip of left fifth leg, posterior side
Figure 110.   Tip of right fifth leg, anterior side

Xanthocalanus macrocephalon n. sp., female

Figure 111.   Lateral
Figure 112.   Dorsal
Figure 113.   Anterior portion of head, lateral
Figure 114.   Anterior portion of head, ventral
Figure 115.   Fifth thoracic segment and abdomen, lateral
Figure 116.   Right antennule
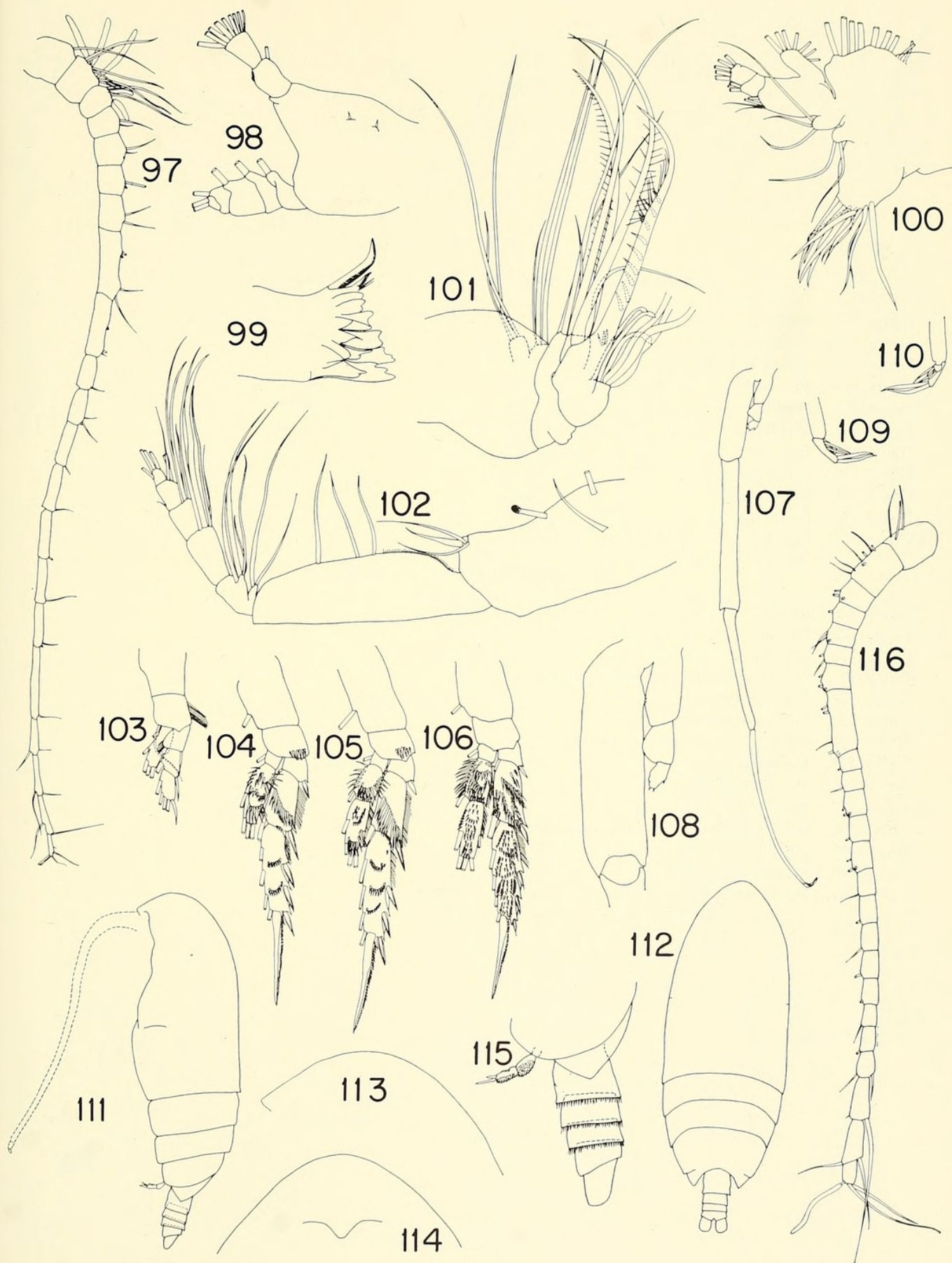
Plate VII

Xanthocalanus macrocephalon n. sp., female (continued)

Figure 117.   Antenna
Figure 118.   Mandible palpus
Figure 119.   Mandible blade
Figure 120.   Maxillule
Figure 121.   Maxilla
Figure 122.   Maxilliped
Figure 123.   First leg
Figure 124.   Second leg
Figure 125.   Third leg
Figure 126.   Fourth leg
Figure 127.   Fifth leg

Amallophora macilenta n. sp., male

Figure 128.   Dorsal
Figure 129.   Lateral
Figure 130.   Rostrum
Figure 131.   Portion of genital segment, enlarged
Figure 132.   Right antennule
Figure 133.   Exopod of antenna
Figure 134.   Endopod and basipod of antenna
Figure 135.   Mandible palpus
Figure 136.   Mandible blade
Figure 137.   Maxillule
Figure 138.   Modified spine of first inner lobe of maxillule
Figure 139.   Maxilla
Figure 140.   Maxilla, other side
Figure 141.   Maxilliped
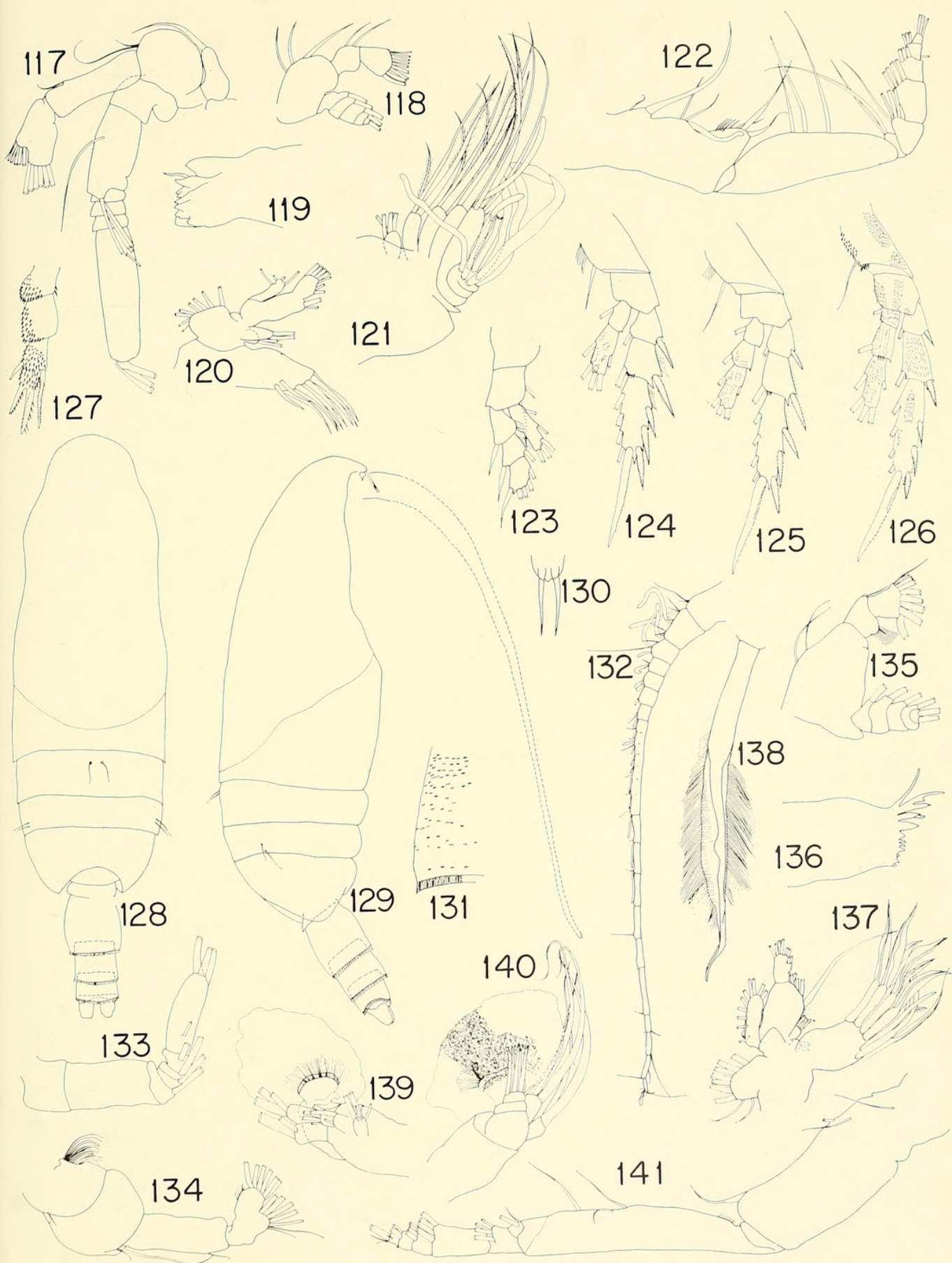
Plate VIII

Amallophora macilenta n. sp., male (continued)

Figure 142.   First leg
Figure 143.   Second leg, exopod broken off
Figure 144.   Third leg, exopod broken off
Figure 145.   Fourth leg
Figure 146.   Fifth legs
Figure 147.   Endopod of left fifth leg
Figure 148.   Tip of left fifth leg, posterior side
Figure 149.   Tip of left fifth leg, anterior side

Amallophora rotunda n. sp., male

Figure 150.   Lateral
Figure 151.   Dorsal
Figure 152.   Ventral margin of second and third thoracic segments
Figure 153.   Anterior portion of head, lateral
Figure 154.   Anterior portion of head, ventral
Figure 155.   Right antennule
Figure 156.   Antenna
Figure 157.   Mandible palpus
Figure 158.   Mandible blade
Figure 159.   Maxillule
Figure 160.   Modified spine of first inner lobe of maxillule
Figure 161.   Maxilla
Figure 162.   Maxilliped
Figure 163.   Right maxilliped, slightly turned outward
Figure 164.   First leg, posterior
Figure 165.   Endopod of first leg, anterior
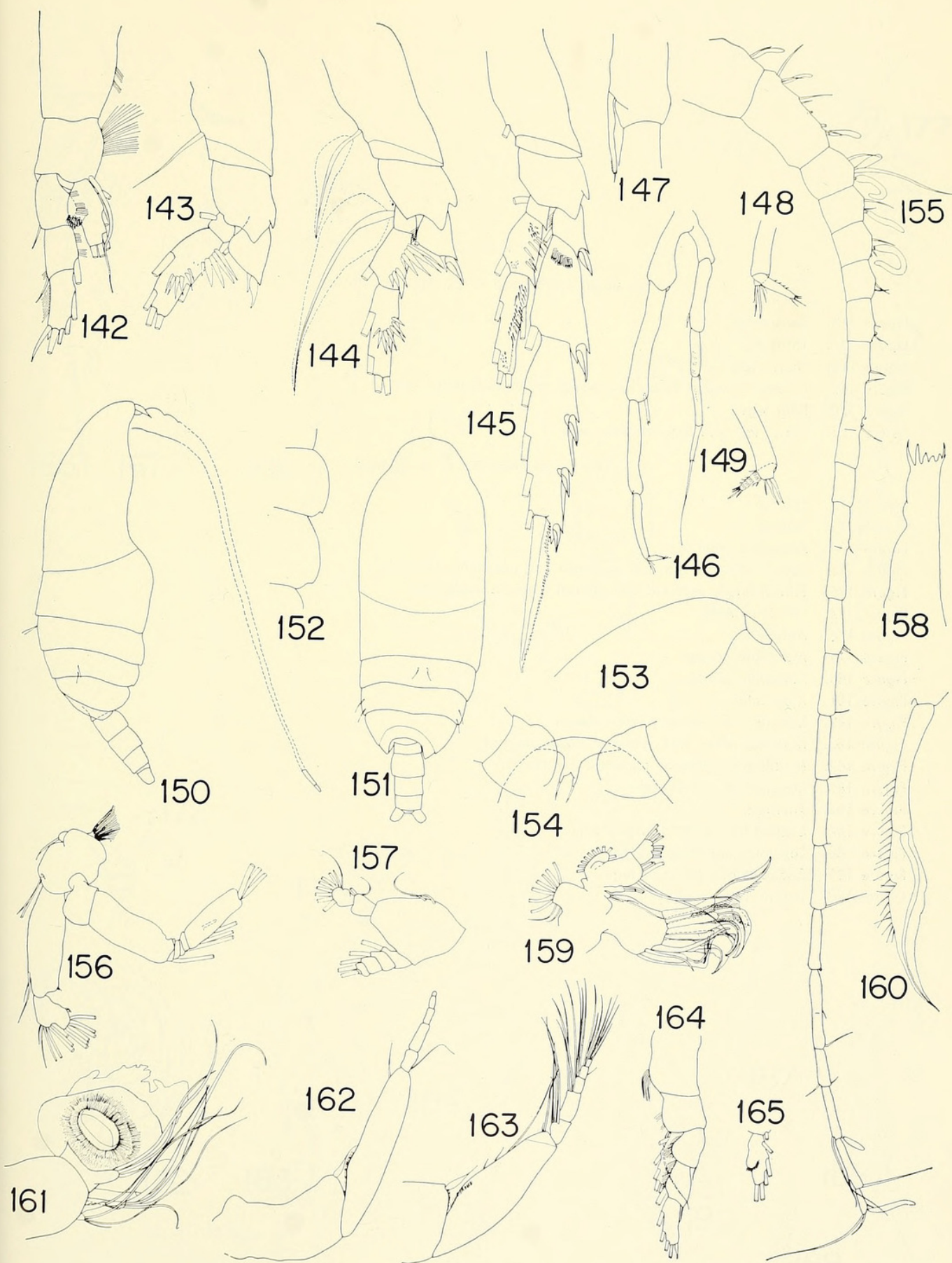
Plate IX

Amallophora rotunda n. sp., male (continued)

Figure 166.   Second leg
Figure 167.   Third leg
Figure 168.   Fourth leg
Figure 169.   External spine of second exopodal segment of fourth leg
Figure 170.   Fifth legs
Figure 171.   Tip of left fifth leg, posterior side

Diaixis asymmetrica, n. sp., female

Figure 172.   Lateral
Figure 173.   Dorsal
Figure 174.   Abdomen, ventral
Figure 175.   Fourth and fifth thoracic segments and abdomen, left side
Figure 176.   Fifth thoracic segment and genital segment, right side
Figure 177.   Left antennule
Figure 178.   Antenna
Figure 179.   Mandible palpus
Figure 180.   Mandible blade
Figure 181.   Maxillule
Figure 182.   Maxilla, only sensory setae shown
Figure 183.   Maxilla, other side, sensory setae omitted
Figure 184.   Maxilliped, setae on endopod omitted
Figure 185.   Endopod of maxilliped
Figure 186.   First leg
Figure 187.   Second leg, exopod broken off
Figure 188.   Left third leg, endopod broken off
Figure 189.   Endopod of right third leg
Figure 190.   Fourth legs, incomplete
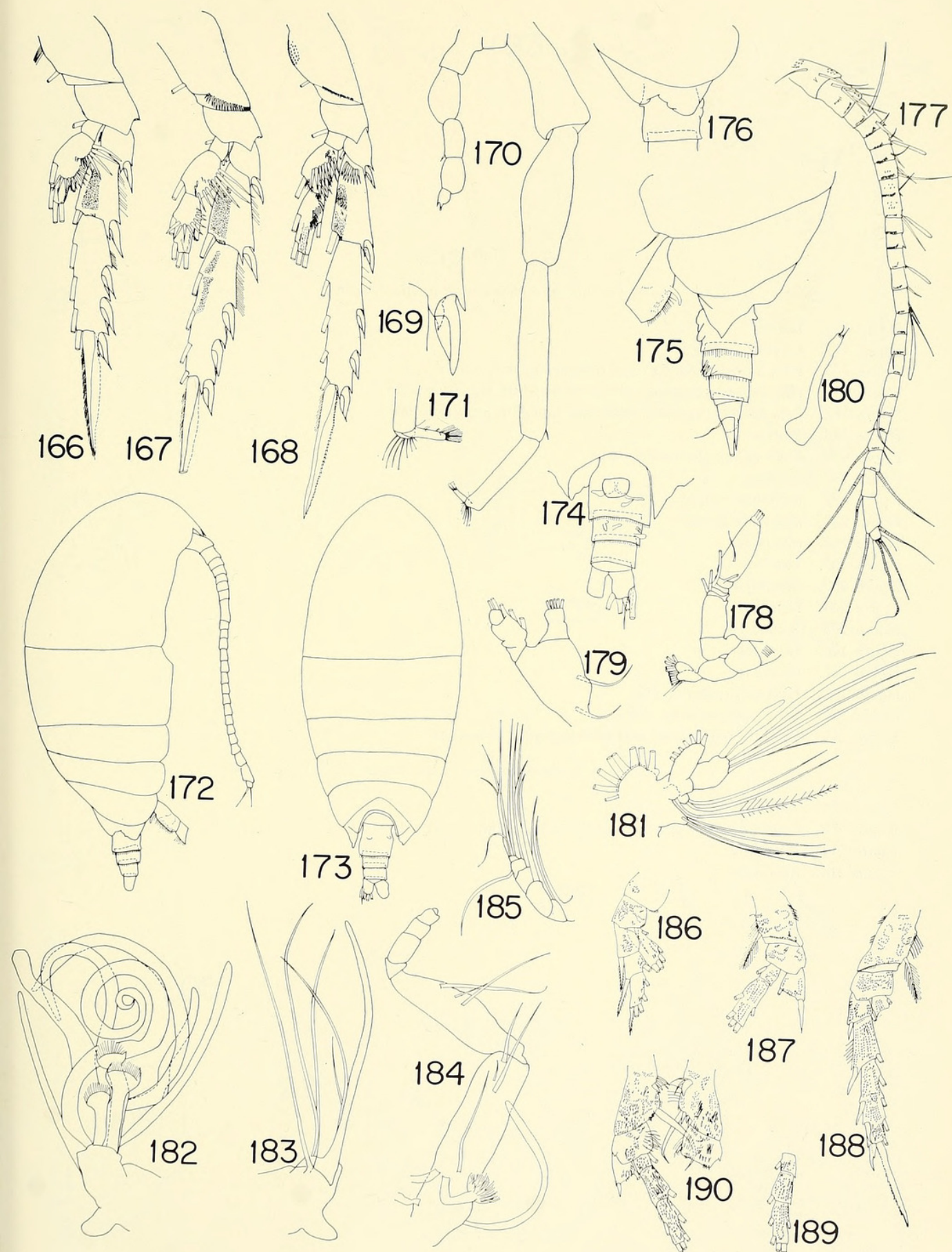
Plate X

Parundinella emarginata n. sp., female

Figure 191.   Dorsal
Figure 192.   Lateral
Figure 193.   Fifth thoracic segment and genital segment, dorsal
Figure 194.   Fifth thoracic segment, abdomen and fifth leg, right side
Figure 195.   Fifth thoracic segment, abdomen and fifth leg, left side
Figure 196.   Rostrum
Figure 197.   Right antennule, broken short
Figure 198.   Antenna
Figure 199.   Mandible palpus
Figure 200.   Mandible blade
Figure 201.   Maxillule
Figure 202.   Maxilla
Figure 203.   Maxilliped
Figure 204.   First leg
Figure 205.   Second leg
Figure 206.   Third leg
Figure 207.   Fourth leg
Figure 208.   Fifth legs, anterior side
Figure 209.   Fifth legs, posterior side
Figure 210.   Left fifth leg, second and third segments of exopod

Undinella altera n. sp., male

Figure 211.   Antenna
Figure 212.   Fourth and fifth thoracic segments and genital segment
Figure 213.   Mandible
Figure 214.   Maxillule
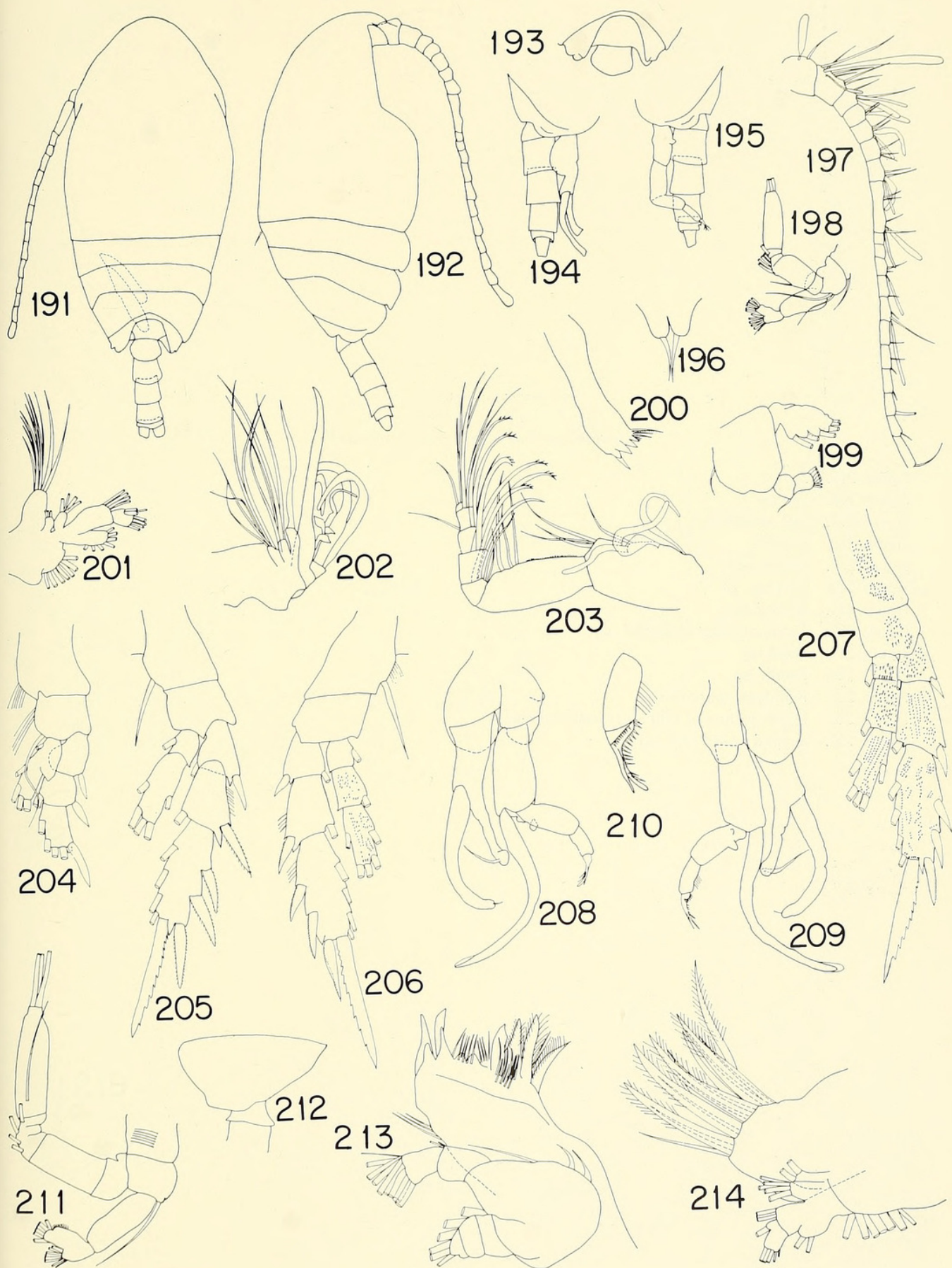
Plate XI

Undinella altera n. sp., male (continued)

Figure 215.   Dorsal
Figure 216.   Lateral
Figure 217.   Left antennule
Figure 218.   Maxilla
Figure 219.   Maxilliped
Figure 220.   First leg
Figure 221.   Second leg
Figure 222.   Terminal spine of second leg
Figure 223.   Third leg
Figure 224.   Fourth leg
Figure 225.   Fifth legs, anterior side
Figure 226.   Distal portion of fifth legs, posterior side
Figure 227.   Exopod of left fifth leg
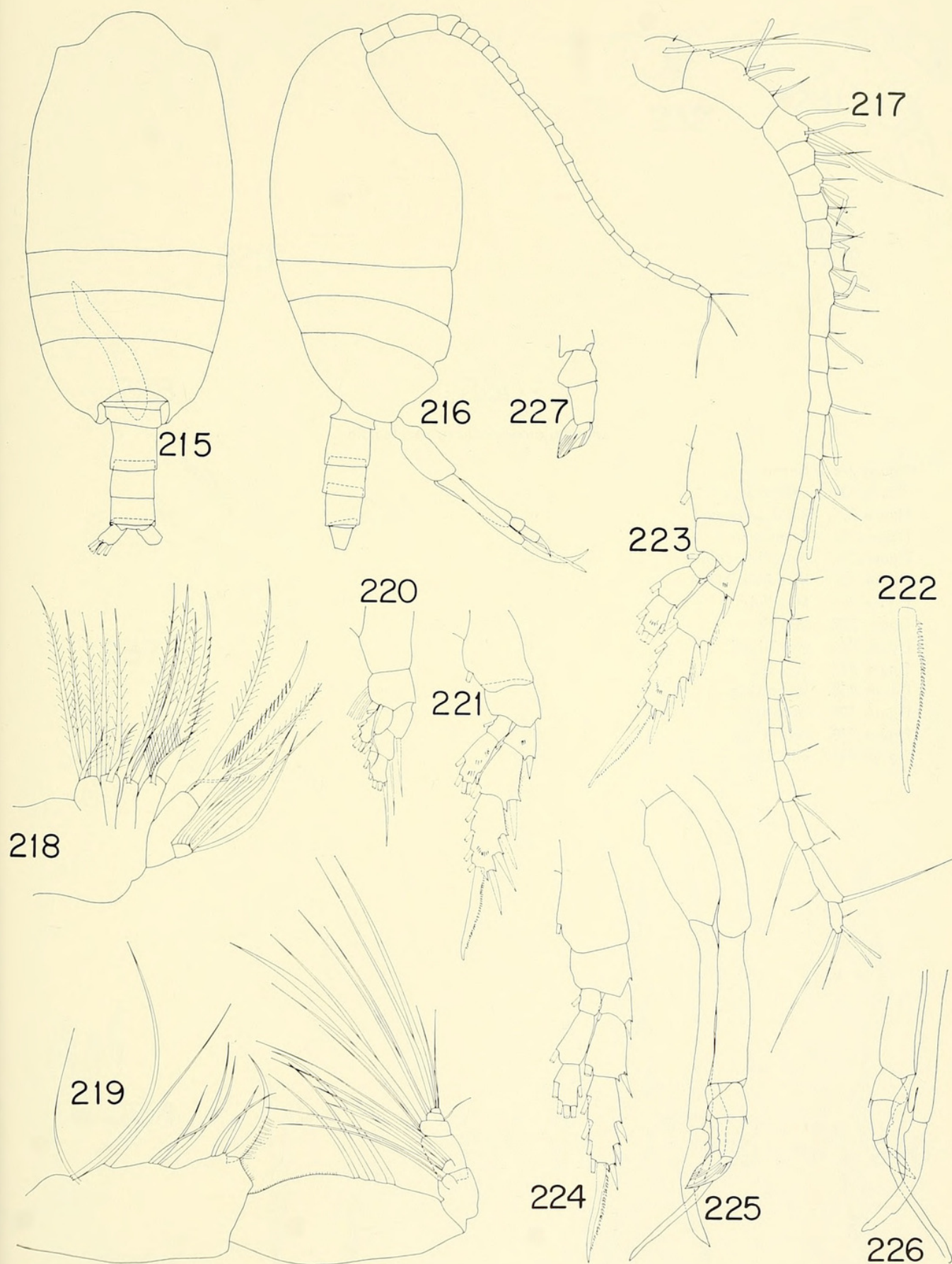
Plate XII

Undinella compacta n. sp., female

Figure 228.   Dorsal
Figure 229.   Lateral
Figure 230.   Right antennule
Figure 231.   Antenna
Figure 232.   Mandible palpus
Figure 233.   Mandible blade
Figure 234.   Maxillule
Figure 235.   Maxilla
Figure 236.   Maxilliped
Figure 237.   First leg
Figure 238.   Second leg
Figure 239.   Third leg
Figure 240.   Fourth leg
Figure 241.   Fifth legs

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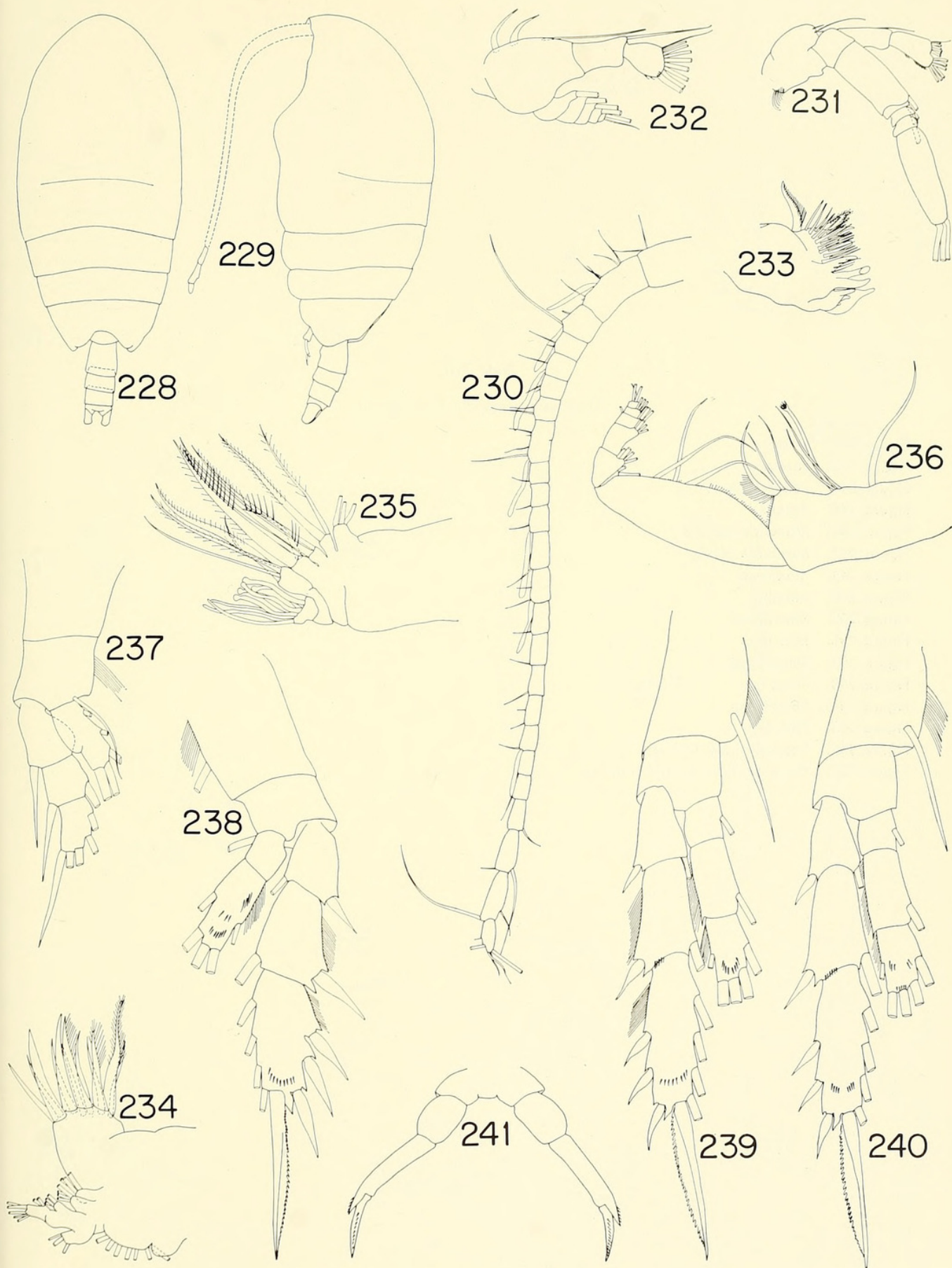
Plate XIII

Undinella compacta n. sp., male
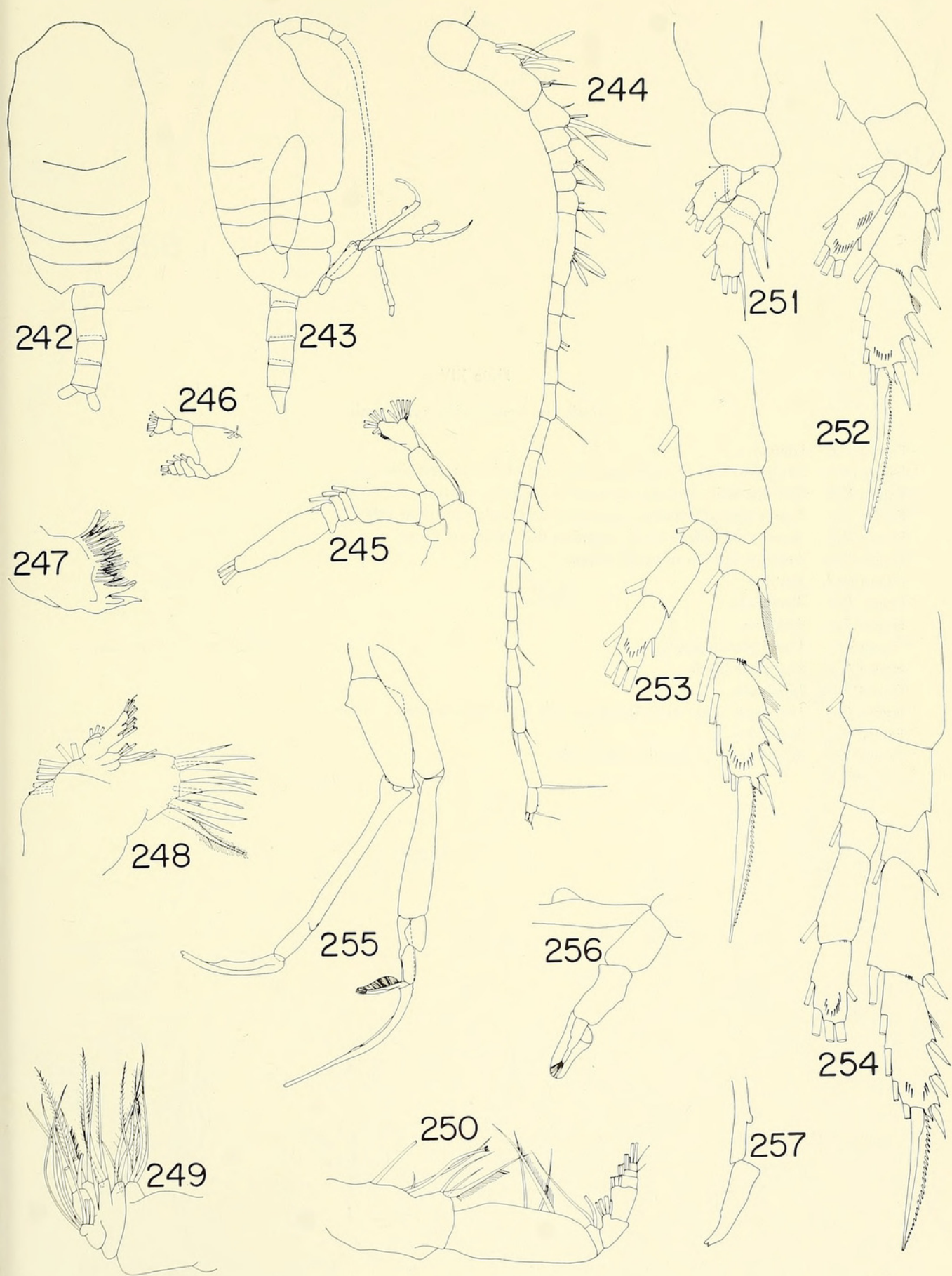
Plate XIV

Undinelia hampsoni n. sp., female

Figure 258.   Lateral
Figure 259.   Second to fifth thoracic segments and abdomen, left side
Figure 260.   Fifth thoracic segment and genital segment, ventral
Figure 261.   Fourth and fifth thoracic segments and abdomen, right side
Figure 262.   Fourth and fifth thoracic segments and abdomen dorsal
Figure 263.   Anterior portion of head, lateral
Figure 264.   Rostrum
Figure 265.   Antennule
Figure 266.   Antenna
Figure 267.   Mandible palpus
Figure 268.   Mandible blade
Figure 269.   Maxillule
Figure 270.   Maxillule, other side, spines on first inner lobe omitted
Figure 271.   Maxilla
Figure 272.   Fourth lobe of maxilla, other side

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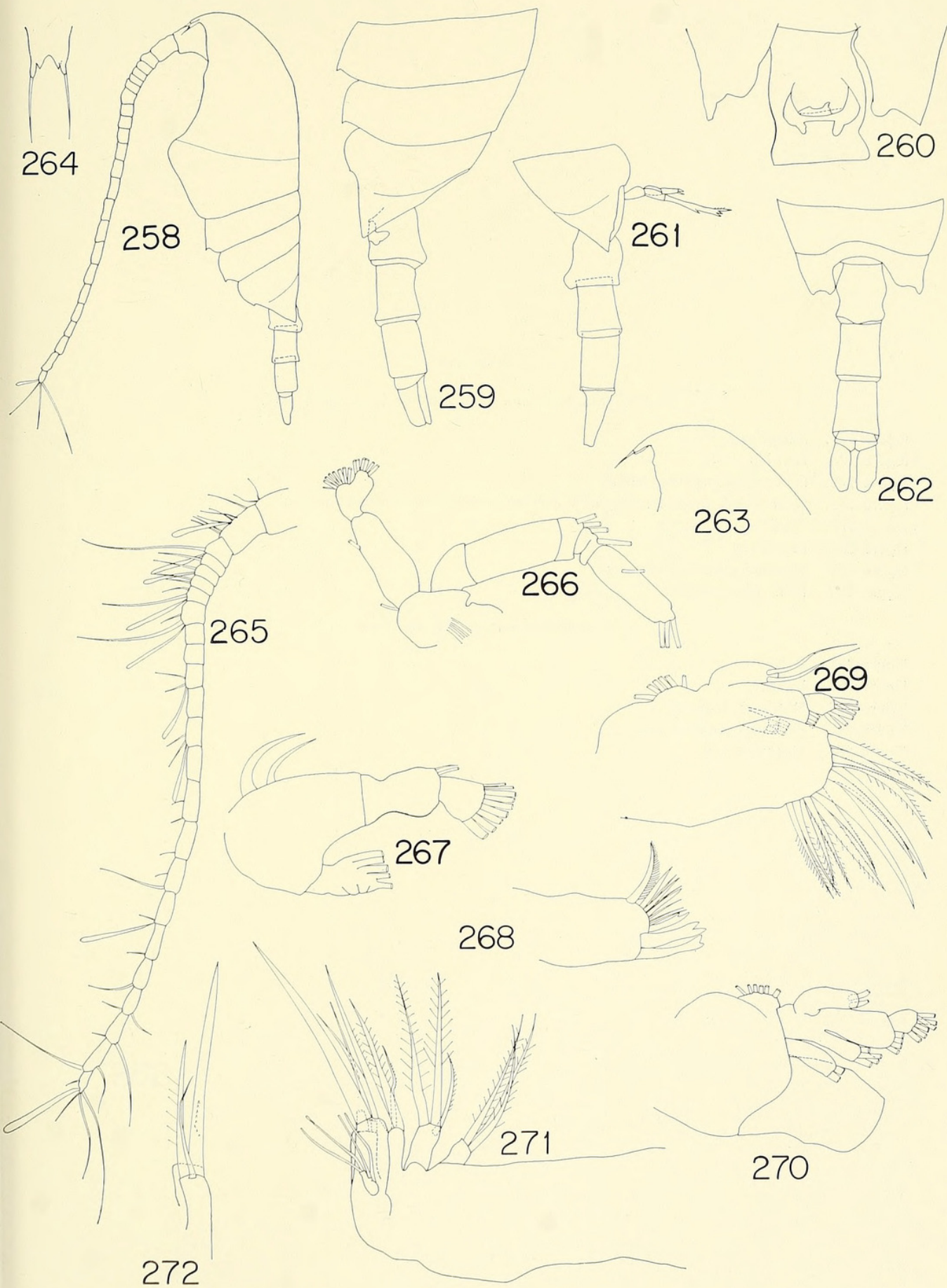
Plate XV

Undinella hampsoni n. sp., female (continued)

Figure 273. Maxilliped
Figure 274. First leg
Figure 275. Endopod of first leg, anterior
Figure 276. Second legs, anterior, exopod of left leg omitted, one endopod normal
Figure 277. Third leg
Figure 278. Fourth leg
Figure 279. Terminal spine of fourth leg
Figure 280. Fifth legs, posterior

Undinella hampsoni n. sp., male

Figure 281. Dorsal
Figure 282. Lateral
Figure 283. Fifth legs, from left
Figure 284. Fifth legs, another view
Figure 285. Right fifth leg

The Proterosuchia and the Early Evolution
of the Archosaurs; an Essay About the
Origin of a Major Taxon

OSVALDO A. REIG

THE PROTEROSUCHIA AND THE EARLY EVOLUTION OF THE ARCHOSAURS; AN ESSAY ABOUT THE ORIGIN OF A MAJOR TAXON

OSVALDO A. REIG[1]

CONTENTS

ABSTRACT

After comments on several methodological and theoretical questions connected with the classification and the origin of major taxa, various hypotheses on archosaurian origins are discussed. A comparative survey of the characters of the early archosaurs, the proterosuchian thecodonts, shows that they are probably derived from the ophiacodont-varanopsid group of pelycosaurian synapsids. As the synapsids are known to have separated very early from the captorhinomorphs, and as the milleretids and younginids, which are captorhinomorph derivatives, are considered closely related to the origin of modern lepidosaurian orders, it is concluded that the two groups of diapsid reptiles, lepidosaurians and archosaurs, have quite different origins. A survey is also made of the present state of knowledge of the origin of the various archosaurian groups. The conclusion is that the final establishment of archosaurian orders as the dominant reptiles of the Jurassic and Cretaceous was the outcome of a gradual process, one which had an exploratory phase during the Middle and Upper Triassic. During this phase, various archosaurian lines of evolution developed, competing among themselves and with the therapsids in the exploitation of two basic food resources: green plants and animals. In the Upper Permian, the roles of plant-eaters and carnivores were mainly played by synapsids; from the uppermost Triassic to the end of the Cretaceous, they were mainly played by archosaurs. The origin

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of a major taxon is thus thought of as a long process involving several adaptive phases within the frame of the exploitation of food resources and of ecological competition. This process does not necessarily claim either the presence of special evolutionary processes or the acceleration of the rates of evolution in the transitional zone.

INTRODUCTION

The emergence and the rapid diversification of the archosaurian reptiles is one of the major events in the history of the vertebrates. During about 110 million years the terrestrial faunas of the world were dominated by the different dinosaur groups, which actually replaced, during Jurassic and Cretaceous times, most of the previously existing tetrapods in the exploitation of the varied terrestrial niches. During the same time another archosaurian group, the crocodiles, successfully occupied the freshwater, semi-aquatic, predaceous niche. Moreover, the Jurassic witnessed the first appearances of new major adaptive types among vertebrates: animals able to overcome the gravity barrier, the archosaurian order Pterosauria and the first birds, the latter being the most successful archosaurian derivatives surviving to the present time.

Disregarding the peculiar phenomenon of human evolution, we have to agree that the triumph of the dinosaurs and their relatives has been the major accomplishment in land vertebrate evolution, if we take as a criterion of evaluation the attainment of the greatest biomass by a single vertebrate group during the longest span of geological time. In this sense, the archosaurs have not been surpassed by any other vertebrate groups occupying the terrestrial environment. (The higher bony fishes in the seas have obviously surpassed the archosaurian achievement on land, but this does not matter in the present context.)

Many problems are posed by this empirical statement. The aim of science is to give causal explanations to observed phenomena, and we are far from being able to do this in the present case. However, we are at least able to draw the outlines of the framework within which such an explanation can eventually be attained. First of all, any metaphysical or pseudoscientific concept, such as "internal drive" or "phyletic senescence," must be excluded. Concepts of this kind are outside of scientific discourse, as they are untestable and do not sustain any kind of public demonstration of their existence. Instead, the phenomenon of archosaurian expansion and dominance may be thought of as part of a vaster and more complex phenomenon of life expansion within an entire ecosystem, since the rise of a land vertebrate biomass requires an even greater expansion of the biomass within the first trophic level, that of the green plants. However, one of the more important requirements for understanding such a phenomenon is a thorough and accurate knowledge, at the descriptive level, of the events leading to the dominance of archosaurs during the different phases of their evolution. In this sense, the first steps of archosaurian evolution and, indeed, the very emergence of the group are of paramount importance.

The first steps in archosaurian evolution took place during Triassic time, and the group attained dominance during the early Jurassic. The fossil record shows that the Triassic witnessed a major overturn in the distribution of roles in the food-web relationships: the roles of herbivores and carnivores during Permian and early Triassic times were mainly filled by synapsids, whereas during Jurassic and Cretaceous times, these roles were filled by archosaurs.

The Triassic, then, was the period during which the archosaurs became dominant. Once having achieved their dominance, they held it during two entire geological periods. However, the rise of the archosaurian orders was actually accomplished at the very end of the Triassic, and was a step-wise process, in which several lines

evolved and became extinct. The principal archosaurian roles were played during these first steps by taxa currently included in the order Thecodontia. One can say that the archosaurians had a first, exploratory radiation before their main one, a radiation that took place within this order of the thecodonts.

The very beginning of this exploratory radiation was developed during early Triassic times by a very primitive and atypical archosaur group, the Proterosuchia, usually grouped as a suborder of the Thecodontia. The proterosuchians are hence the stem archosaurs, the stock from which most of the later archosaur groups took their origin. An adequate understanding of them is thus essential for a good interpretation of all the further events of archosaurian evolution.

Knowledge of the Proterosuchia has been very unsatisfactory until recently. Fortunately, during the last ten years (and especially during the very last part of this period), descriptions of new materials and thought-provoking revisions have shed new light, thus helping us to reach a better understanding of the group. As usual in scientific progress, new knowledge leads to new problems, and our progress in the understanding of these primitive thecodonts poses several new questions. The general outlines of archosaurian evolution are now in need of a thorough revision, and the whole problem of the origin of this subclass must be approached in a new way because of the improvement of our knowledge of the Proterosuchia. Nevertheless, neither of these goals can be adequately achieved before a good assessment of the bearing of proterosuchian peculiarities on archosaurian evolution is available. The assessment of these peculiarities also poses a problem in classification. The aim of this paper is to stress the general evolutionary significance of the characters of this group of primitive thecodonts and to stress some methodological points that arise

in our attempt to place them in an evolutionary classification.

As the stem group of a major taxon, the Proterosuchia set forth some interesting classification problems for the theory of evolutionary systematics, which will also be discussed in the following pages.

ACKNOWLEDGMENTS

FOUNDATIONS

Some theoretical points are worth stating before discussing our topic. Authors frequently disagree for the simple reason that the one is not aware of the underlying concepts of the other. This is especially true when the concepts are controversial in nature. As most of our argument deals with supraspecific taxa, it will be convenient to assess the sense we give to this concept.

A supraspecific taxon is not here thought

of as a mere artifact created to fulfill the aims of taxonomic practice. It is considered a natural group, a historico-spatial entity formed by various subordinate taxa connected among themselves by special evolutionary relationships: common origin, links of descent, and a common evolutionary role. The origin of a supraspecific taxon is not here assumed to be the outcome of special evolutionary processes. We take for granted that the known short-term processes of evolution at the species level are also the causal agents responsible for the establishment of major taxa over long-term evolutionary processes. But as the scale of the latter processes allows and requires more general descriptive concepts, we can also say that, in the emergence of supraspecific taxa, anagenesis, cladogenesis, and extinction are involved. The type of anagenesis here operating is the "open anagenesis" (Waddington, 1960) or arogenesis (Reig, 1963b). Arogenesis is associated with the acquisition of a new "basic general adaptive complex" (Simpson, 1959: 270). Other authors name these kinds of acquisitions "Erfindungen" (Rensch, 1947) or "key innovations" (Bock, 1965). It is commonly supposed that the emergence of these novelties is responsible for opening the possibility of exploiting new adaptive areas to the new taxon, thus promoting its splitting to fill up new ecological niches and situations (cladogenesis). We want to emphasize that the extinction of the groups previously exploiting the same ecological niches may be a triggering factor for the emergence of the new taxon. This extinction may also be thought of, however, as provoked by the rapidly evolving, and better adapted, emerging new taxon.

Another attribute of a supraspecific taxon is monophyly. As this concept is rather controversial, we will enunciate the two extreme possibilities for the fulfillment of this condition: a monophyletic group may be considered as either a group originating from a single ancestral species or,

at the least, a group originating in a taxon of the same rank.

Supraspecific taxa originate by the differentiation from an original group of a new group showing new characteristics (Sharov, 1965). It has been generally assumed that in this process of the differentiation of a new group the shift of the evolving organisms into a new adaptive zone is a necessary condition. Such a shift would then involve a threshold effect, and the rate of evolution would be accelerated in the transitional area. Simpson (1953) named this supposed phenomenon "quantum evolution," pointing out that the period of rapid transition involved in such a process may serve to establish comparatively nonarbitrary divisions among major taxa (Simpson, 1961). Gisin (1966), in developing the same ideas, emphasizes that the "evolutionary quantum" affords the main criterion for the definition of taxonomic groups. As far as the theory of classification is concerned, he defines the concept of evolutionary quantum as follows: "Un quantum n'est pas la somme de toutes les différences, mais celle des caractères clefs développés lors de l'évolution quantique du groupe, autrement dit, les caractères sont pesés en fonction de leur signification évolutive" (Gisin, 1966: 4). Gisin refers to these ideas as a "quantum theory of taxonomy," a development of his former "synthetische Theorie der Systematik" (Gisin, 1964). It seems obvious to the present author that all these concepts are better considered as part of the approach already named "evolutionary taxonomy" (see Mayr, 1965).

We believe that these principles give a sound basis for the assumption that natural groups have (or had, in the case of extinct groups) a real existence in nature as objective, historico-spatial collective entities, their unitary character being given by evolutionary relationships linking their different subordinate constituents. Nevertheless, these natural groups (having existence in the ontic level; see Bunge, 1959) are not

to be confused with the taxon-concepts we construct about them (existing in the cognitive or conceptual level). Systematists hypothesize that a given set of species belongs to a supraspecific taxon, that a constructed taxon-concept matches a natural taxon. When we say that a given number of species of Lower Triassic thecodonts are to be placed together in the suborder Proterosuchia, we are dealing with a taxon-concept (the suborder Proterosuchia) that we construct for a taxon we believe to have existed in nature. In this sense, the construction of a taxon-concept is equivalent to the statement of a hypothesis (Reig, 1968).

It must be stressed that, as with any scientific hypothesis, these evolutionary-taxonomic hypotheses may never be claimed to have reached a status of certainty after having been "proved." These hypotheses may be stronger or weaker, more or less well founded, but they can never be transformed into a fully certain piece of knowledge, certainty not being at the core of the scientific way of thinking. Nevertheless, this assessment does not obviate the necessity of trying to make our hypotheses match as closely as possible the events for which they are erected. The likelihood that an hypothesis closely approximates natural events will be greater if it is able to support testing procedures, if it has a high explanatory value, and if its predictions are infalsifiable (see Popper, 1959; Wilson, 1965). If the hypothesis fails to fulfill these requirements, clearly it must be rejected as a tool for understanding natural events.

By the very nature of paleontological evidence and of taxonomic-phylogenetic inference, we must admit from the start that fully satisfactory testing procedures for this kind of hypothesis have not yet been developed (for an interesting and thought-provoking discussion of this topic see Goudge, 1961). In most cases, in order to accept it, we must take refuge in its heuristic value or in such attributes as its internal coherence or accordance with available scientific knowledge. This means that the foundations of our argument could be very weak if we are not careful to clarify our taxonomic concepts as far as the available evidence and theory permit.

As with any concept, the taxon-concepts have intension (connotation) and extension (denotation). The intension of a taxon-concept is the set of peculiarities that determine its own nature, that is, the set of characters that distinguishes it from others. Its extension is the set of subordinate taxa that belong to it.

The taxon-concepts are polythetic concepts, as defined by Beckner (1959; Beckner named these kinds of concepts "polytypic concepts," and the name "polythetic" was introduced later by Sneath, 1962). For a better understanding of the nature of polythetic concepts, see also Sokal and Sneath (1963). Membership in a polythetic group is not decided by the complete sharing of a set of sufficient and necessary features. Sufficient and necessary properties are useful for classifying static entities, but not evolving organisms. In other words, any taxon-concept, for the very reason that it is intended to approximate an evolving entity, must be defined by reference to a set of characters that are assumed to be evolving in the frame of the taxon itself. Thus no claim is to be made that any member of the taxon must present all the relevant characters in the defined state, nor that any form must necessarily belong to it because it possesses one or a few of the stated characters.

Acceptance of these points makes it possible to understand why the Proterosuchia are to be considered archosaurs in spite of the fact that they lack many of the relevant archosaurian peculiarities, such as the full development of an otic notch or the habitually upright stance, and why the euparkeriids need not necessarily be considered proterosuchians, although they share with them some primitive characters.

Yet a taxon-concept cannot be a full polythetic class in the sense of the third

condition pointed out by Beckner, a condition asserting that membership in a particular aggregate does not of necessity require the possession of a given character. Actually, the intension of a taxon-concept must include one character or a limited number of characters, the possession of which is necessary for membership in the said concept. Otherwise, our theoretical assumption that a taxon evolves through the acquisition of defined "key innovations" is not fulfilled.

These foundations may be considered the theoretical and formal tools for approaching our topic within the framework of evolutionary systematics. We think the approach of evolutionary systematics has greater depth, is far more explanatory in nature, and accords better with modern evolutionary thought than do others, such as the cladistic approach (e.g., Hennig's "phylogenetisches Systematik") or the neo-Adansonian phenetic one.

THE EXTENSION OF THE PROTEROSUCHIA-CONCEPT

The first point to make clear in our attempt to elucidate the taxon-concept involved in the name "Proterosuchia" is the assessment of its extension. Though some sort of circular reasoning is unavoidable, it seems evident that the inferential process that leads to the construction of a taxon-concept begins with the failure to assign certain taxa to existing taxa of higher rank, thus revealing the existence of a previously unknown taxon. The concept of this taxon is now constructed on the basis of a need for a group to contain certain definite subordinate constituents. Needless to say, it is the peculiarities of the subordinate members that fail to find a place in existing taxa that indicate that these members need to be referred to a new taxon. However the intension of the latter can only be fully assessed after it is clear which are its members.

Charig and Reig (in press) have made an extensive survey of the genera to be included within the Proterosuchia and have discussed Hughes's broad conception and interpretation of this taxon (1963). It is unnecessary to repeat here the arguments developed in that paper, but a summary of the conclusions and further discussion of some points are relevant to the present topic: that Proterosuchia include only, so far as is presently known, one Upper Permian and several Lower Triassic genera. Most Lower Triassic archosaurs are proterosuchians, the only exceptions being *Mesorhinosuchus*, *Euparkeria* (including *Browniella*), and the doubtful *Wangisuchus* and *Fenhosuchus*. Some Middle and Upper Triassic archosaurs occasionally referred to the Proterosuchia, such as *Rauisuchus*, *Dasygnathoides*, *Hoplitosuchus*, *Saurosuchus* and *Stagonosuchus*, are well enough known to be excluded from this group (Reig, 1961; Charig and Reig, in press).

All the known proterosuchian genera seem clearly to fall into two distinct subordinate taxa of family rank, for which it is advisable to use the names Proterosuchidae and Erythrosuchidae. The former is the older, more primitive, and more aquatic group. The latter family is almost surely derived from the proterosuchids, appears later in the fossil record, is more advanced, and seems to have been composed of largely terrestrial carnivores.

The Proterosuchidae include the following genera: *Archosaurus* (1 species, from the Upper Permian Russian Zone IV); *Chasmatosuchus* (2 or 3 species, from the Russian Zone V, lowermost Triassic); *Chasmatosaurus* (Figs. 1, 3, 5) (3 or 4 species: one in the *Lystrosaurus* Zone, lowermost Triassic, South Africa, another in beds of the same age in Sinkiang, China, another in the Chinese Ermaying Series, late early Triassic, and a probable fourth unnamed species in the Panchet Series of Bengal); *Proterosuchus* (1 species, probably from the *Procolophon* Zone, middle
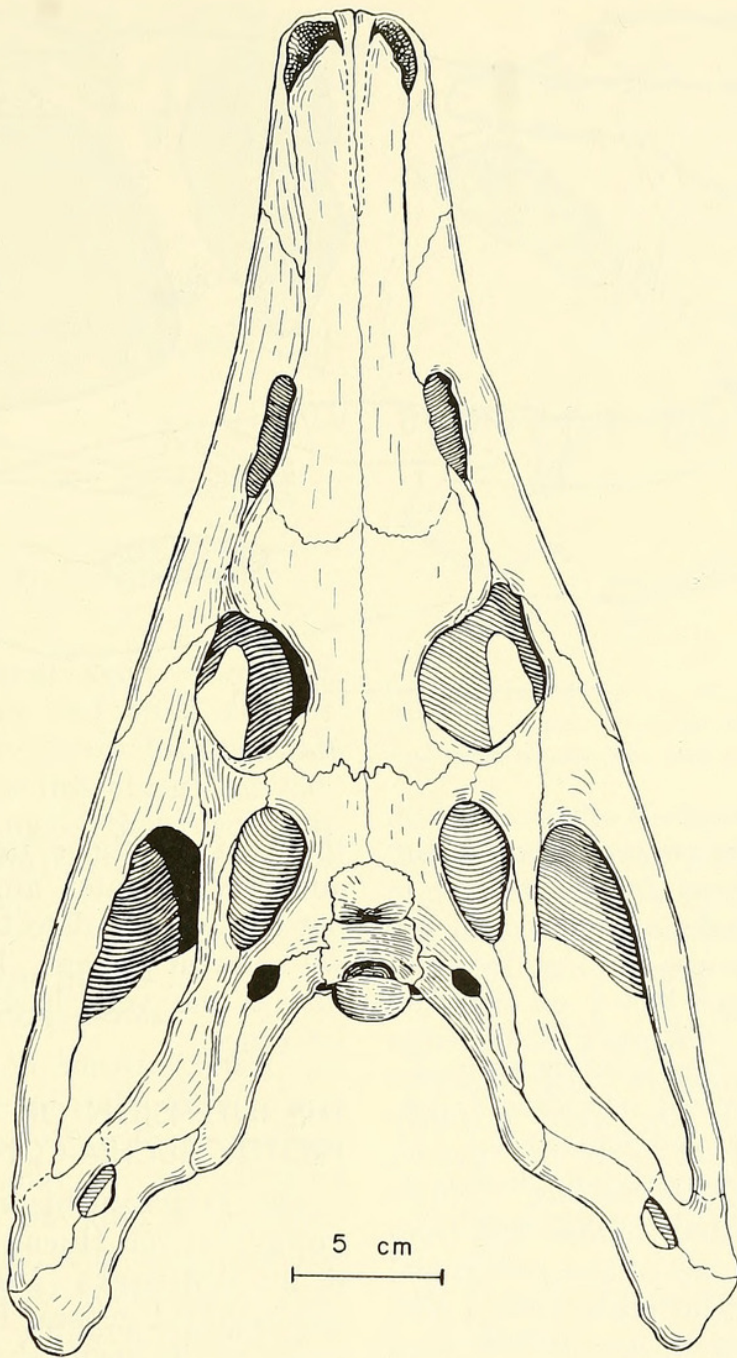
Figure 1.   Dorsal view of the skull of *Chasmatosaurus vanhoepeni* Haughton.   (From Broili and Schröder.)

Lower Triassic of South Africa); and *Elaphrosuchus* (1 species, from the *Lystrosaurus* Zone, South Africa).

The Erythrosuchidae includes the following genera: *Garjainia* (Fig. 2) (1 species, from the Russian Zone V, lowermost Triassic); *Erythrosuchus* (1 species, from the *Cynognathus* Zone, late early Triassic, South Africa); *Vjushkovia* (Fig. 4) (1 species, from the Russian Zone VI, late early Triassic); and *Shansisuchus* (1

or 2 species, from the Chinese Ermaying Series, late early Triassic).

Cuyosuchus (1 species, Cacheuta beds, Lower Triassic, Argentina) must be considered as Proterosuchia *incertae sedis*, as the material is not sufficient for family allocation. *Ankistrodon*, *Arizonasaurus*, *Dongusia*, *Seemania*, and *Ocoyuntaia* are generic names applied to material that may prove to be referable to the Proterosuchia, but which must be considered
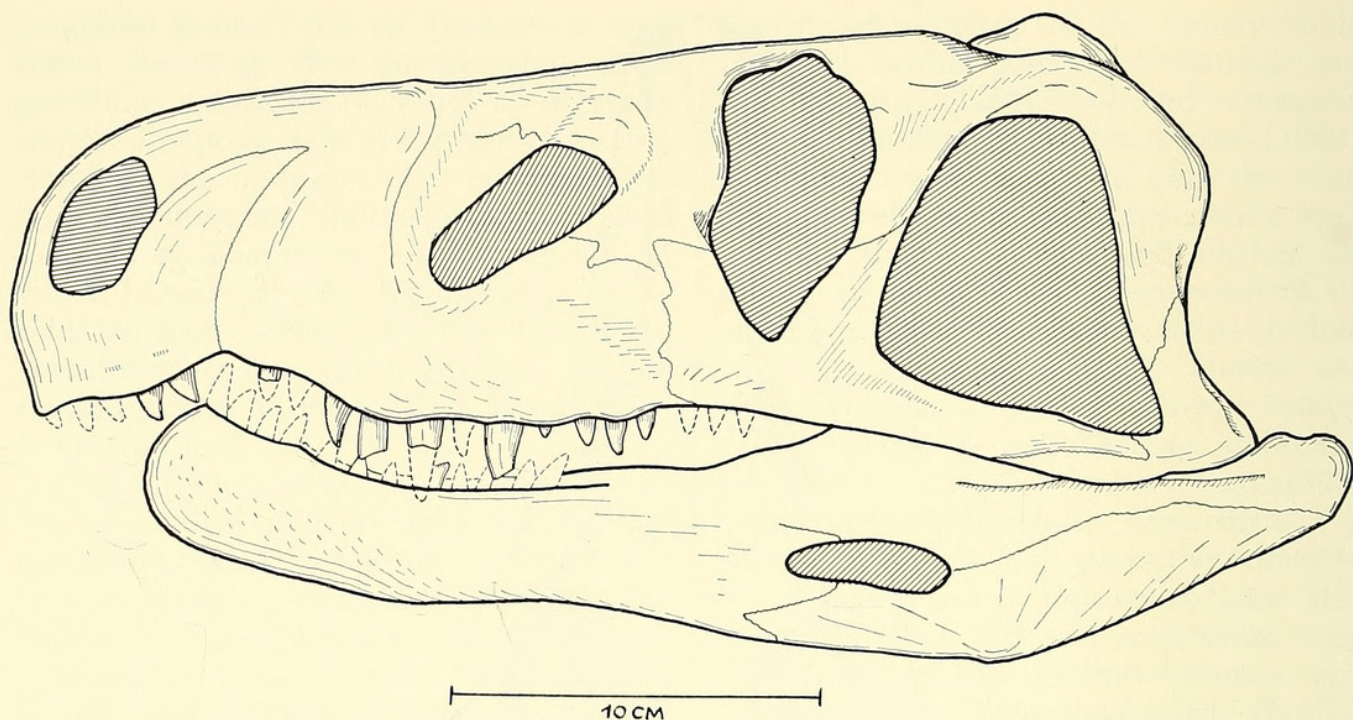
Figure 2. Lateral view of the skull of *Garjainia prima* Ochev. (From Ochev.)

nomina dubia for the present because the specimens are extremely fragmentary.

As these last remarks imply, not all the above-mentioned genera are really well known, and some are based on material too incomplete for adequate knowledge of all relevant characters. All evidence considered, however, we have a fairly good knowledge of at least the genera *Chasmatosaurus, Erythrosuchus, Vjushkovia, Shansisuchus,* and *Cuyosuchus,* from all of which a good part of the postcranial skeleton is known. The other genera that permit family allocation are known from less complete material. They are very useful, however, either to infer phylogenetic conclusions, as in the case of *Elaphrosuchus* and *Garjainia,* or to improve knowledge of the temporal and geographical distribution of the groups concerned.

Nevertheless, we must admit that we know only a very small part of the actual proterosuchian array, and this must be carefully kept in mind when discussing early archosaur evolution. It must be taken for granted that many proterosuchians existed that are at present unknown, and

that among them might lie the direct ancestors of later archosaurs, which are not easily to be detected among the forms we know at present. This kind of assumption is the very basis of paleontological inference.

THE INTENSION OF THE PROTEROSUCHIA-CONCEPT

The Proterosuchia are such a puzzling group that von Huene was inclined, in one of his first works (1911), to place one of the included genera, *Erythrosuchus,* in an order of its own, sharing pseudosuchian and pelycosaurian features. As stressed by Hughes (1963), they combine some truly archosaurian peculiarities in the skull and other parts, with primitive, non-archosaurian characteristics in the limbs and girdles. As we shall see below, some non-archosaurian features are also present in the skull structures.

Hughes made a careful analysis of the peculiarities of the Proterosuchia, but he emphasized primarily postcranial morphology. Romer (1956, 1967), on the other hand, pointed out the significance of very
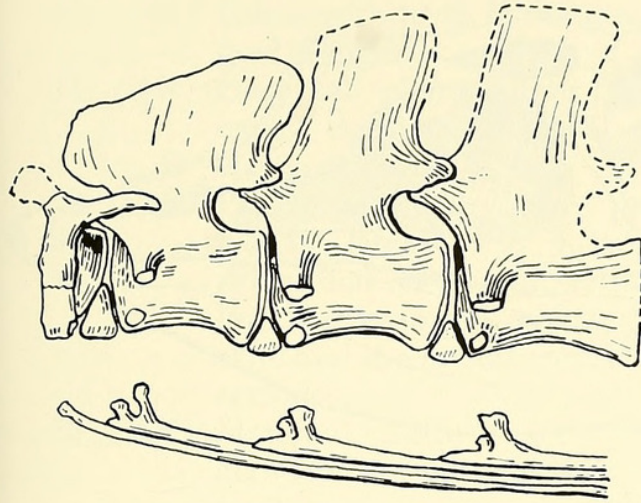
Figure 3. Cervical vertebrae and ribs of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

peculiar proterosuchian skull characters, neglected by Hughes and other authors. Charig and Reig (in press) list the state of many characters in this taxon, but they do not discuss thoroughly their evolutionary significance. A further analysis, therefore, seems necessary.

Statement and analysis of the proterosuchian character-states

Following Sokal and Sneath (1963), we shall use the character-state terminology in our present analysis. For these authors, a character is a variable that can occur in different states from one kind of organism to another. These character-states are the relevant features that taxonomists deal with in comparing different taxa. For instance, "dermal ossifications" is a character, and "dermal ossifications absent" is a character-state.

Since they belong to a taxon of higher rank, the subclass Archosauria, the Proterosuchia have a set of character-states shared by all archosaurs. We shall refer to this set of character-states as the "All-Archosaurian set of character-states" (*AA*). This *AA* set represents the intension of the taxon-concept Archosauria, and should not afford a relevant basis for elucidating the concept of Proterosuchia, though its assessment is very important to support the
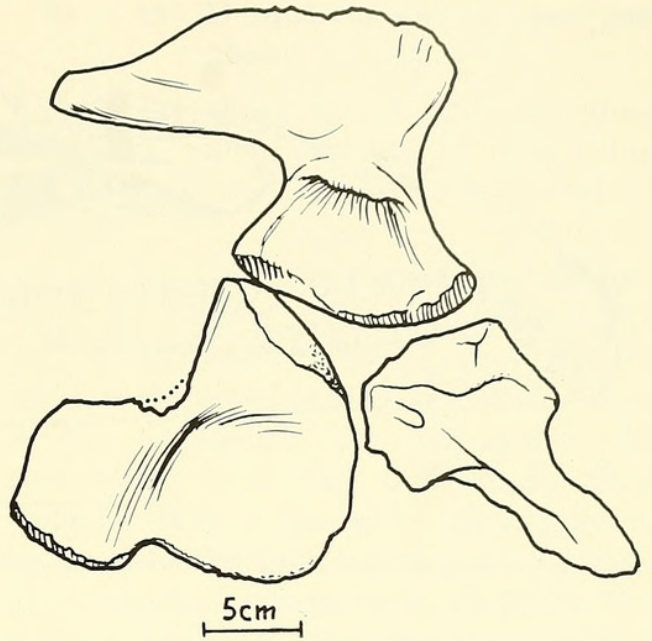
Figure 4. Lateral view of the pelvis of *Vjushkovia triplicostata* von Huene. (From von Huene.)

inclusion of the Proterosuchia in the Archosauria and for an enquiry regarding the origin of the whole subclass. The following list includes the character-states that we consider as belonging to this set:

  i) Two-arched skull (diapsid condition)
 ii) Antorbital fenestra present
iii) Mandibular fenestra present
 iv) Laterosphenoid ossified
  v) Skull metakinetic
 vi) Quadrate-squamosal articulation moveable
vii) Supratemporal and tabular bones absent
viii) Posttemporal fenestrae small
 ix) Vertebrae not notochordal
  x) Ribs with capitulum and tuberculum
 xi) Rib facets of dorsal vertebrae on transverse processes, becoming closer to a complete fusion posterad
xii) Capitular facets for cervical ribs situated well anteriorly and ventrally on the centrum; tubercular facets for the same ribs at the tip of transverse process
xiii) Posterior limbs longer than anterior (limb disparity)
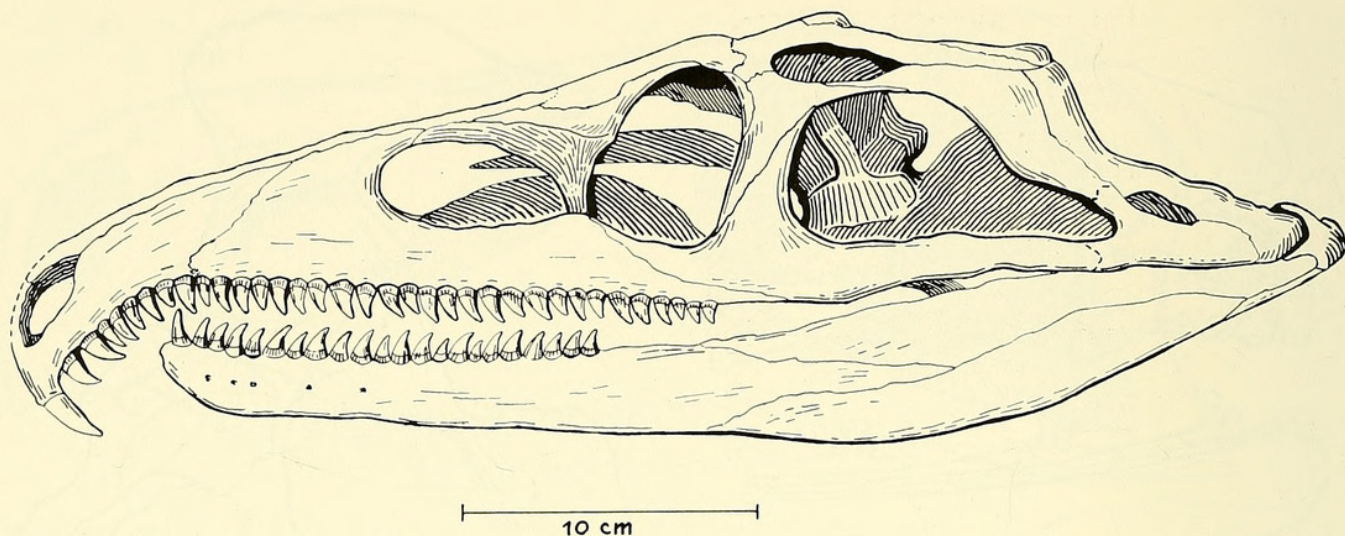
Figure 5.   Lateral view of the skull of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

Some allegedly characteristic archosaurian character-states, such as upright stance and bipedalism, are not included in this list. As has been suggested by Charig (1965), they are neither characteristic nor widespread archosaurian features.

The core of our discussion should be connected with those character-states that would help to define the Proterosuchia as distinct from other taxa included in the Archosauria. These character-states may be grouped in four different classes: (a) the All-proterosuchian-No-other-archosaurian set of character states (*AN*), which includes peculiarities shared only by the proterosuchians, absent in any other archosaurian taxon; (b) the Some-proterosuchian-No-other-archosaurian set (*SN*), comprising characters that are present in the described state only in some of the proterosuchians, while present in a different state in other proterosuchians and in all the other archosaurs; (c) the All-proterosuchian-and-Some-other-archosaurian set (*AS*), including character-states shared by all the members of the extension of the Proterosuchia, but also present in some other non-proterosuchian archosaurs; (d) the Some-proterosuchian-and-Some-other-archosaurian set (*SS*), referring to those character-states shared by some, but not all the members of the Proterosuchia, and

also by some, but not all, archosaurian groups not belonging to the Proterosuchia.

The following list attempts to synthesize the relevant character-states of the Proterosuchia. The letters preceding each statement refer to the above-defined sets.

1. (*AS*) A single median postparietal bone present
2. (*AS*) Small postfrontal bones present
3. (*SN*) A small pineal foramen present
4. (*AN*) A typical otic notch not present
5. (*AN*) The posterior border of the infratemporal fenestra nearly straight (without the V-shaped contour characteristic of most archosaurs)
6. (*AS*) The jaw articulation well behind the level of the occiput
7. (*AS*) Antorbital fenestra of moderate size, not opening as a part of a more extended, basin-like depression
8. (*AS*) Nares of moderate size, subterminal, fairly well separated from the antorbital fenestra
9. (*AS*) Pterygoids not meeting in the midline, bordering a long and narrow interpterygoid vacuity extending forward between the vomers

10. (SS) Palate with teeth in the pterygoid flanges

11. (AN) Occipital plane rather concave, slanting forward towards the skull table

12. (AS) Prefrontal bones large, projecting laterally to form a ridge that makes an abrupt limit between the roof of the skull and the lateral antorbital region

13. (AN) Marginal teeth isodont and acrodont or subthecodont in implantation

14. (SS) Intercentra usually present behind the axis, more commonly between the cervical vertebrae

15. (AS) Gait quadrupedal

16. (AN) Propodials horizontal in position (sprawled stance)

17. (AN) Posterior limbs moderately longer than the front ones (primitive limb disparity)

18. (AN) Femur bearing a large internal trochanter

19. (AN) Intertrochanteric fossa of the femur present

20. (SS) Humerus with wide and twisted ends

21. (AN) Pes with mesotarsal ankle joint (proximal tarsals without specializations)

22. (AS) Iliac blade with anterior spine absent or only moderately developed

23. (AS) Posterior expansion of the iliac blade narrow and long

24. (AS) Acetabula completely closed, only moderately excavated, and relatively far apart one from the other

25. (AS) Pubis and ischium comparatively short

26. (AS) Coracoids large

27. (SN) Scapulae broad and short

28. (AS) Dermal elements of the pectoral girdle well developed

29. (AS) Dermal armor of any sort absent

From the above list of character-states, interesting conclusions can be drawn, but it is first necessary to make a brief analysis of them.

(1) The possession of postparietal bones (Fig. 1) (interparietal, dermosupraoccipital) is a primitive condition for reptiles, and is widespread in such primitive groups as the cotylosaurs, the pelycosaurs, the eosuchians, and the millerettids. This character-state is shared by all the genera assigned to the proterosuchia, in the form of an unpaired postparietal. However, this is not an exclusive proterosuchian condition among the archosaurs, as a postparietal is also present in the pseudosuchian thecodont *Euparkeria*.

(2) Postfrontal bones (Fig. 1) are also present in most primitive reptile groups and in all the proterosuchians so far known. As in the former case, other non-proterosuchian archosaurs retain this primitive state, as postfrontals are present not only in *Euparkeria* but also in the phytosaurs, the stagonolepidid pseudosuchians, and the rhamphorhynchoid pterosaurs.

(3) A pineal foramen is, as far as is known, present only in all the known specimens of the erythrosuchid genus *Erythrosuchus*, in the primitive erythrosuchid *Garjainia* (see Tatarinov, 1961: 121), and in one of three known skulls of *Chasmatosaurus*. Other proterosuchian genera either have been reported as not possessing this character, or cannot be checked due to the nature of the material. Among other non-proterosuchian archosaurs, this character is absent, save in one doubtful genus, *Mesorhinosuchus* (=*Mesorhinus* auct.), currently considered the only Lower Triassic phytosaur. We are also dealing here with a very primitive state of a character, present as such in the earliest reptilian groups.

(4) Romer pointed out (1956, 1967) the absence of a typical otic notch in the Proterosuchia. He based his statement on the genera *Chasmatosaurus* (Fig. 5) and *Erythrosuchus. Garjainia* (Fig. 2), *Shansisuchus,* and *Vjushkovia* give support to the same view. The latter genus has indeed been reconstructed by von Huene (1960) as having a well-developed otic notch, but this reconstruction is purely hypothetical and is not supported by the morphology of the surrounding parts. Tatarinov (1961) has indicated that the posterior border of the infratemporal opening was straight in *Vjushkovia,* as in *Erythrosuchus,* a feature correlated, in other proterosuchian genera, with the absence of a defined otic notch. In all proterosuchian skulls, therefore, the construction of the otic region is very primitive. This recalls the pelycosaurian and captorhinomorph condition and differs from all remaining archosaurs and from lepidosaurs (including millerettids and eosuchians, in which a distinct lepidosaurian otic notch is clearly present). In all non-proterosuchian archosaurs the otic notch is clearly defined by a curved posterior border of the quadrate and by a projection of the squamosal, which extends posteriorly above the head of the quadrate to form the dorsum of the notch. The character-state "absence of the otic notch" hence belongs obviously to the *AN* set.

(5) Linked with the otic notch is the shape of the posterior border of the infratemporal fenestra. The V-shaped contour of this border, with the apex of the V facing forward, is common to all the non-proterosuchian archosaurian genera (save those with secondary modifications from a primitive V-shaped condition). In connection with the posterior position of the mandibular articulation, the quadrate of the proterosuchians slants sharply backwards. The ascending ramus of the quadratojugal and the descending ramus of the squamosal follow the quadrate in this position. In more advanced archosaurs, the jaw articulation moved forward, apparently in connection with the development of a more efficient biting mechanism (Ewer, 1965), and the quadrate acquired a more vertical position. In this position of the quadrate, the V-shape of the quadratojugal and squamosal arms is obligatory, and, consequently, room is developed for an otic notch, further enlarged by the backward projection of the squamosal. The proterosuchian condition of this character is again a primitive one, as this is the state shown by the pelycosaurs, especially by the varanopsid pelycosaurs. The assumption that this condition is shared by all the proterosuchians is safe, and the same is valid for character-state 4, as it is present both in primitive (*Chasmatosaurus*) and advanced genera in which the skull is known (*Erythrosuchus, Shansisuchus*). Therefore, this is to be considered an *AN* character-state.

(6) As far as the position of the jaw articulation is concerned, this character obviously belongs to the same cluster as the two previously described. All the proterosuchian skulls so far known show a backward position of the suspensorium (Figs. 1, 2, 5), the articular condyles for the mandible lying in a line well posterior to the line of the occipital condyle. This condition is distinctly different in the non-proterosuchian archosaurs, save the primitive crocodile *Proterochampsa* and, in a lesser degree, some phytosaurs. Character-state 6 belongs therefore to the *AS* class. Romer (1967) pointed out that this long-jawed condition is characteristic of very primitive reptiles and is reminiscent of the captorhinomorph skull architecture. In primitive pelycosaurs of the ophiacodont-varanopsid group this character-state is even more pronounced, but both the millerettids and the eosuchians are more progressive in this respect.

(7) The presence of an antorbital fenestra is a characteristic archosaur character-state. It is safe to consider the

condition of the character in the protero-
suchians as primitive, as in them the fe-
nestra does not reach a large size and,
especially, as it does not lie in a depression
with sharp borders, as is the case in
most other thecodonts and other archo-
saurs. Though the function of this fenestra
is not completely clear (Ewer, 1965;
Walker, 1961), it is obvious that whatever
its function may have been, its increase
in size, and the development of a basin-like
structure to contain it are to be considered
as an intensification of the function; the
structure was not fully developed in the
proterosuchian level of archosaurian evo-
lution. The described proterosuchian state
of this character seems to be shared by
all the known skulls (Figs. 2, 5) referred
to this taxon, with *Shansisuchus* as an
atypical example, since this genus has
the peculiarity (also present in some
saurischian dinosaurs) of having an ad-
ditional opening, though not a basin-like
depression. *Vjushkovia* has been restored
by von Huene with a great antorbital open-
ing, but again this seems clearly to be a
quite tentative reconstruction, as most of
the borders of the fenestra are not pre-
served in the known specimens. The fact
is that other, non-proterosuchian, archo-
saurs share this state of the character, as
is shown in the primitive crocodile *Protero-
champsa*, in the peculiar pseudosuchian
Rhadinosuchus (=*Cerritosaurus*), in *Cla-
renceia*, and in the phytosaurs. This char-
acter-state is therefore to be considered
as belonging to the AS class. It is indeed
very suggestive that an antorbital fenestra,
elsewhere only an archosaurian character-
state, is present in the varanopsid pely-
cosaurs (Olson, 1965, and see also below).

(8) The described state of the external
nares is shared by all the proterosuchian
genera (Figs. 1, 2, 5). More advanced
thecodonts usually have the external nares
larger and nearer to the antorbital vacuity,
or else posterior in position (phytosaurs).
Subterminal, small nares well separated

from the antorbital opening are also present
in *Rhadinosuchus* and *Clarenceia*, and the
situation in *Euparkeria* is best considered
reminiscent of the proterosuchian state.
This character-state must therefore be
grouped in the AS category.

(9) This character-state is inferred from
the condition in *Chasmatosaurus*, the only
proterosuchian in which the palate is well
known. Inasmuch as the same condition
is shared in such a probable erythrosuchid-
derivative as *Euparkeria*, it is safe to con-
clude that this state was widespread among
the proterosuchians. Among other archo-
saurs, it is shared not only by *Euparkeria*,
but also by *Proterochampsa*, so that the
character-state must tentatively be con-
sidered as belonging to the AS class.

(10) The presence of palatal teeth in
the pterygoid flanges has been verified in
Chasmatosaurus and *Proterosuchus* among
the proterosuchids, but no erythrosuchid
has given any evidence of them. Palatal
teeth are known among archosaurs, other
than proterosuchians only in *Euparkeria*
and in *Proterochampsa* (Sill, 1967). This
state of the character is obviously a primi-
tive one, as palatal teeth are present in
millerettids, younginids, procolophonids,
pelycosaurs, and captorhinomorphs among
the primitive groups. It must hence be
placed, so far as present knowledge allows,
in the SS class.

(11) This is a peculiar, primitive, and
pelycosaur-like state of the occipital region.
All the proterosuchian genera in which the
character can be checked show this state
clearly; it is especially evident in *Chasma-
tosaurus*. No other archosaur shows a
similar condition, so that this feature is to
be allocated to the AN class.

(12) This state of the prefrontal is not
a proterosuchian peculiarity, as it is also
characteristic of many thecodonts that are
not proterosuchians and of some saurischi-
ans. The condition is also shared by some
non-archosaurian reptiles, such as the

ophiacodont and varanopsid pelycosaurs. This fact suggests that we are confronting a primitive character-state that evolved slowly within the archosaurs. As it is shared by all the proterosuchians so far known, it must be placed in the AS class.

(13) In all proterosuchians so far known, the marginal teeth are isodont and either acrodont (proterosuchids) or subthecodont (erythrosuchids); true heterodonty and thecodonty are not clearly developed in either group. All non-proterosuchian archosaurs are definitely thecodont in tooth implantation, and their teeth are primitively heterodont or subheterodont. The proterosuchian condition is also a primitive one, widespread among the earliest reptiles and their first derivatives. This character-state must hence be placed in the AN class.

(14) Another primitive condition reminiscent of the seymouriamorph, captorhinomorph, pelycosaurian, and early lepidosaurian condition, is the presence of intercentra. This has been clearly demonstrated in the neck vertebrae of *Chasmatosaurus vanhoepi* (Fig. 3), and Young (1963) has described the same situation in the trunk vertebrae of *Chasmatosaurus yuani*. Neck intercentra have been reported in *Erythrosuchus*, but seem not to be present in *Shansisuchus*, *Garjainia*, *Vjushkovia*, and *Cuyosuchus*. In later archosaurs, intercentra have not been reported in any genus save *Euparkeria*, where they seem to be present all along the presacral region of the column. Another (abnormal) exception is the rauisuchid *Ticinosuchus*, which is alleged to have had an intercentrum associated with one of the caudal vertebrae (Krebs, 1965). We are dealing therefore with a feature of the SS class.

(15) The quadrupedal gait is, of course, a character-state shared by all the known proterosuchians, but obviously common, too, in many non-proterosuchian archosaurs, such as the euparkeriids, the rauisuchids and the stagonolepidids among the thecodonts, the crocodiles and phytosaurs, and many groups of saurischians and ornithischians. This is obviously a primitive reptilian feature, and must hence be placed in the AS class.

(16) The position of the propodials has been inferred by Hughes (1963) to be horizontal in the known proterosuchians. Nevertheless, Young's (1964) reconstruction of the skeleton of *Shansisuchus* shows the propodials in a vertical position, which is probably also reasonable. Completely sprawled legs would not have allowed large terrestrial animals such as the erythrosuchids to be successful predators, and the evidence seems to indicate that they had a time of success during the Lower Triassic. It is probable that all the proterosuchians had a sprawled stance most of the time, as indicated by the anatomical data, but that at least the advanced erythrosuchids could proceed in a largely upright stance for short distances. In any case, it is obvious that the proterosuchians sprawled more than any later archosaur, and that this state was shared by all the genera that afford relevant evidence in the girdle and limb skeletons. As stated by Ewer (1965), *Euparkeria* also seems to have had a sprawled stance, but this genus seems to have been far more advanced than the proterosuchians as far as locomotion is concerned. This feature can therefore safely be considered to be in the class of the AN character-state.

(17) This character-state is a typical archosaur one, though it has been exaggeratedly associated with bipedalism, which is not only not a widespread condition in archosaurs, but is not even a primitive archosaurian characteristic (Charig, 1965). Charig has named this condition limb-disparity, and though characteristically archosaurian, it must be noticed that this is also present in the ophiacodontid and varanopsid pelycosaurs. Limb disparity may be considered a preadaptation for

bipedalism, but is less marked in the Proterosuchia than in more advanced archosaurs. In the known cases, for instance, the humerus/femur ratio is never lower than 77.7 in the proterosuchians, and is always lower than 67 in the non-proterosuchian thecodonts. This might be therefore considered an *AN* character-state.

(18), (19) The possession of an internal trochanter and of an intertrochanteric fossa is alleged by Hughes (1963) to be a full indication of the sprawled position of the legs. As far as is known, all proterosuchian femora share in the possession of these characters. The pelycosaurs and captorhinomorphs share the same character-state, but none of the known non-proterosuchian archosaurs have either an internal trochanter or an intertrochanteric fossa. Hughes assumed that the Argentinian rauisuchid *Saurosuchus* shared the proterosuchian state of these characters, but this is a misinterpretation of the illustrations given by Reig (1961), as Charig and Reig (in press) have already made clear. These character-states hence belong to the *AN* class.

(20) The structure of the humerus is well known in *Chasmatosaurus* (Young, 1963), *Erythrosuchus*, *Shansisuchus*, *Vjushkovia*, and *Cuyosuchus* (Rusconi, 1961, wrongly described this bone in *Cuyosuchus* as the femur of the labyrinthodont *Chigutisaurus*). In all these genera the ends are twisted, but in the last they are not typically wide, as is the case in the other four genera. Humeri with wide and twisted ends are also present in the rauisuchid *Stagonosuchus* (von Huene, 1938; Boonstra, 1953) and in the problematic Argentinian Middle Triassic genus *Argentinosuchus* (Casamiquela, 1961). This may be considered a primitive character-state, as it is also present in the pelycosaurs and captorhinomorphs. In any case, the exception of *Cuyosuchus* and the presence of the same state in other non-proterosuchian

thecodonts, indicate that it is convenient to place this feature in the SS class.

(21) The structure of the feet in the proterosuchians has been elucidated by Hughes (1963) with the help of new material. Work by Ewer (1965) and Krebs (1963, 1965) on *Euparkeria* and *Ticinosuchus* respectively, offers additional support to Hughes's conclusions. In the proterosuchians the foot anatomy is only known to an appropriate degree in *Chasmatosaurus* and *Erythrosuchus*, but it seems safe to infer that the condition in these genera was widespread among all the proterosuchians. The state is that of a tarsus without "crocodiloid" or "dinosaurian" specializations in the proximal tarsals (astragalus and calcaneum), and with a primitive, mesotarsal ankle joint. All other archosaurs show some type of tarsal modifications from this primitive condition, which is, by the way, like that in primitive lepidosaurians, such as *Youngina*, and in captorhinomorphs and pelycosaurs. All evidence indicates the convenience of placing this character-state in the *AN* class.

(22) The shape of the anterior spine of the iliac blade (Fig. 4) varies among the different proterosuchian genera from almost obsolete in *Chasmatosaurus* to moderately developed in genera like *Cuyosuchus*, but it is never highly developed, as it is in some pseudosuchians and "dinosaurs." The proterosuchian type of anterior spine of the ilium is very similar to that of the varanopsid pelycosaurs. At the same time, this same feature is also present in some non-proterosuchians, as is the case in *Euparkeria* and the rauisuchids, and for this reason it must be considered an *AS* character-state.

(23) The posterior spine of the iliac blade is long and narrow in all the known proterosuchian genera that afford evidence in this regard. Among the non-proterosuchian thecodonts, *Euparkeria* and the rauisuchids share the same condition, so

that this is also a character-state of the AS class.

(24) The fully closed condition of the acetabula is a proterosuchian character, associated with the amount of space between them; both conditions are related to the generally sprawled position of the posterior propodials. All the thecodonts show a closed acetabulum, and in most of them these are relatively far apart. Open and more closely approximated acetabula were developed in the saurischian and ornithischian dinosaurs in connection with the advanced bipedal stance. This is also an AS character-state.

(25) The relative length of the ventral pelvic bones varies within narrow limits in the proterosuchians, never reaching the development shown in more advanced archosaurs with triradiate pelves (Fig. 4). In the primitive forms the triradiate trend is only incipient, although it is more obvious in terminal forms like *Erythrosuchus*. In forms like *Chasmatosaurus* and *Cuyosuchus*, features of the very primitive puboischiadic plate can also be observed. *Euparkeria* shows in this respect a condition more proterosuchian than typically pseudosuchian, and *Ticinosuchus* seems to be transitional in this regard. This character-state must thus be considered to be in the AS class.

(26) Coracoids are known in *Chasmatosaurus*, *Cuyosuchus*, *Erythrosuchus*, *Shansisuchus* and *Vjushkovia*. In the first two they are obviously larger and more primitive than in the latter, but in any case, the proterosuchian coracoids are to be considered as large in comparison with those of most later archosaurs. Among the Pseudosuchia, large coracoids are present in *Euparkeria*, the rauisuchids *Ticinosuchus* and *Proterosuchus*, and the stagonolepidids. We must hence place this character-state in the AS class.

(27) The scapular blade is short and broad, and primitive in general shape, in both *Chasmatosaurus* and *Cuyosuchus* (Fig. 1). In the genera *Erythrosuchus*, *Shansisuchus*, and *Vjushkovia* it is higher and narrower, with both ends more expanded than the median "shaft." Short and broad scapulae are to be considered as primitive, and the shape of this bone in the erythrosuchids is obviously an improvement, which becomes more fully developed in pseudosuchians and later archosaurs. This character-state is to be placed in the SN set.

(28) The presence of dermal elements of the pectoral girdle is now known in *Chasmatosaurus*, *Shansisuchus*, *Erythrosuchus*, *Vjushkovia*, and *Cuyosuchus*. The first had been assumed to have a clavicle and interclavicle because of the presence of these bones in more advanced thecodonts (Hughes, 1963), but Young (1963) actually found a clavicle associated with other bones of *Chasmatosaurus yuani*. It is safe to conclude that dermal bones of the shoulder girdle were present in all the members of the Proterosuchia. At the same time, this primitive feature is also shared by many pseudosuchians, such as the rauisuchids, the stagonolepidids, *Euparkeria*, and even *Ornithosuchus* (see Walker, 1964: 110). We are dealing therefore, with a character-state of the AS class.

(29) As far as dermal armor is concerned, the Proterosuchia, in lacking any indication of it, are clearly different from all other thecodonts (Charig and Reig, in press). The only doubtful case in this respect is *Cuyosuchus*, as among the original material some atypical scutes were found. Since these could belong to the labyrinthodont found associated with the Argentinian proterosuchian, it is better not to consider this case as an actual exception. Crocodiles, phytosaurs, and ornithischians have osteoderms, but they are missing in saurischian dinosaurs (see below) and pterosaurs, so that the present condition must also be considered as an AS character-state.

Evolutionary and taxonomic significance of the proterosuchian character-states

The foregoing analysis indicates that the Proterosuchia-concept is not a fully polythetic one, as only five among twenty-nine peculiarities are not shared by all the members of its extension. But, by the same token, it is not a monothetic concept. More significant is the fact that eighteen of the twenty-nine character-states are shared by non-proterosuchian archosaurs. A completely phenetic classification, based on overall similarity, would indeed include some other taxa in the extension of the Proterosuchia-concept, a procedure that we believe would be misleading from the evolutionary point of view.

This analysis supports the inference that characters evolved at different rates in the early evolution of archosaurs. Some characters changed in state within the group Proterosuchia itself, as reflected by all characters in the SN set. In both cases of SN character-states, we are dealing with very primitive reptilian heritages, hardly to be considered of positive selective value at the archosaurian level of evolution, and their persistence should have been disadvantageous for the changes that the proterosuchians developed in skull architecture and locomotor improvements. Other characters changed only little beyond the proterosuchian threshold; they are our AS set. As in the former case, these are also primitive characters, most of which are maintained in some families of primitive pseudosuchians, in the first crocodiles, or in the phytosaurs, and only exceptionally in more advanced archosaurs. They seem to indicate that the achievement of a progressive archosaurian stage was, for more than half of the characters involved, a process of gradual evolutionary change. There are also those characters of our SS set that changed both within the proterosuchians and beyond them. They have the combined meaning of both the previous cases, and indicate that some proterosuchians evolved beyond the level reached by some of their first derivatives. These characters are useful, indeed, to infer phylogenies: no proterosuchian descendant can be supposed to have evolved from a proterosuchian ancestor that had evolved a different state in a character belonging to the SS class, if it maintains the same character in the state described in that class. There remains, finally, a set of characters that show little or no change within the Proterosuchia, but that behave differently beyond the proterosuchian threshold (the AN class). Nine of the twenty-nine analyzed belong to this group. In most of the cases, the change in these characters in proterosuchian descendants may be interpreted as improvements linked with the emergence of new evolutionary possibilities, as we will attempt to demonstrate below.

The general pattern of character-state changes within and beyond the proterosuchians is obviously indicative of the process known as mosaic evolution (de Beer, 1954), heterobathmy of characters (Takhtajian, 1959), or stepwise evolution (Bock, 1965 presents an illuminating analysis of the process).

As a matter of fact, characters involved in mosaic evolution do not afford any basis for a clear-cut distinction of a taxon from its close descendent relatives. In our case, this is especially obvious for the characters belonging to the SN, AS, and SS sets of character-states. On the other hand, character-states of the AN class actually do afford a clear-cut distinction of the Proterosuchia from the Pseudosuchia, the Crocodilia, the Parasuchia, and the other more advanced archosaurian groups. An Aristotelian-minded taxonomist would very easily find the clue for what in the context of his philosophy should be a mere pseudo-problem: he would choose only the AN character-states as the sufficient and necessary features that determine the "essence" of the Proterosuchia. This procedure will not satisfy the purposes of evolutionary taxonomy, as in this universe of discourse

we are not trying to grasp the essence of any static entity, but to discover how to evaluate evolving characters in order to define evolving entities.

As far as the characters belonging to the SN, AS, and SS classes are concerned, the question could be raised whether they are not better excluded from the definition of the intension of the Proterosuchia-concept, as they are either shared by other non-proterosuchian archosaurs or not shared by all the proterosuchians. It could also be questioned whether the very existence of this kind of character-state is not an indication that the proterosuchian-concept is an artificial construct without any real referent in the objective world. We think that the answer to both questions must be negative, but in any case, it is true that we are facing a common and one of the most difficult of taxonomic problems: namely that of tracing borderlines (needed because of the requirements of taxonomy, but also, alas, because the human brain does not seem to be capable of functioning without categorizing) in ancestor-descendant series that evolve gradually from one state to the other. From the point of view of the logic of the system, an analysis of the "core" and the "fringe" of the taxonomic set represented by the proterosuchian-concept (as these terms have been defined and used by J. H. Woodger, 1952) would indeed help very much in a full elucidation of this problem. Such a sophisticated formal treatment is, however, beyond the aim of the present essay. We must keep in mind only that a fringe of vagueness seems to be unavoidable in any concept having evolving entities as referents; the peculiarities involved in such a vagueness are not to be excluded from the definition of this concept, if they are relevant for an adequate understanding of the evolutionary meaning of the entity we are dealing with. The polythetic nature of the proterosuchian-concept, with its fringe of vagueness, must be considered, on the contrary, an inherent quality of the con-

cept, one which affords plenty of information for a better understanding of the features of early archosaurian evolution, a point which we will attempt to stress in the following part of this article.

But we must first refer to the following point: we have already said that Simpson and Gisin stressed the importance of alleged discontinuities arising during the process of detachment of a new taxon (as it shifts into a new adaptive zone) for the task of establishing non-arbitrary limits between major taxa. In Gisin's terms: "Um auch hier 'natürliche' Einheiten zu erhalten, müssen deren Grenzen den in der Natur objektiv gegebenen Diskontinuitäten, und diese einer bestimmten Qualität entsprechen" (Gisin, 1964: 9). These discontinuities given objectively in nature are believed to be the result of the threshold transition arising from a faster evolution between two major adaptive zones, a situation in which selective pressures act upon one character or a set of characters very strongly, making them evolve at a faster speed (the quantum effect). Should the explanation be correct, we would have a clue with which to trace borderlines between a series of ancestor-descendant major taxa, provided that we are able to discover which are the relevant characters involved in such a threshold effect, i.e., the "key innovations" responsible for the emergence of a new taxon. Whatever the relativity of the discontinuity, it should be possible to discover these characters if we have a complete enough fossil record.

The situation is perhaps less simple, however. Bock (1965) has contended that to postulate that in the origin of a major taxon (and hence in its delimitation) the operating process is a single-phase change, involving a switch from one major adaptive zone to another, implies an oversimplification not supported by any positive evidence. For him, the process is better thought of as a stepwise one, through which minor radiations occurred in the transitional adaptive zone. Key innovations

and preadaptations are involved in this process, but there is no special reason to assume that evolution is greatly speeded up in the intermediate area. The stepwise character of the transition between major taxa is exemplified for Bock by the mosaic pattern of character changes occurring in the known cases of the emergence of major taxonomic groups. This view seems to discourage any attempt to look for natural boundaries between major taxa and, hence, to get an accurate assessment of the intension of their concepts.

It should be very interesting, therefore, to investigate just how the evidence from early archosaur evolution does match each of these views. But such an investigation will require, first of all, a new evaluation of the evidence, for the assessment we have made of the proterosuchian character-states will have new consequences for the explanation of the origin and early evolution of archosaurs. However, before discussing our main topic, we must refer to the origin of the proterosuchians, and to the proterosuchian descendants.

THE ORIGIN OF THE PROTEROSUCHIA

Obviously, if the Proterosuchia are the first and the most primitive archosaurs, the problem of the origin of the Proterosuchia is to be identified with the problem of the origin of the Archosauria. The latter has been considered a difficult matter and has been generally approached in a very broad context, usually in connection with the discussion of the alleged early split of the reptiles into two main branches, the Sauropsida and the Theropsida. A special account of this general question is beyond our present aim and we must restrict ourselves to the points more closely connected with archosaur ancestry [for a general survey of the whole matter, see Vaughn (1955), Watson (1954, 1957), Parrington (1958), Tatarinov (1959), Olson (1962)].

The fact that archosaurs and lepidosaurs have two-arched skulls led to their being grouped in one single taxon, the Diapsida, in early classifications. This taxon-concept has been generally abandoned since Romer (1956) advanced the current classification. But the general idea of a close relationship between archosaurs and lepidosaurs survives, and the concept of Diapsida is frequently used in phylogenetic discourse, although devoid of any explicit taxonomic intention. How close this relationship is is a matter of the disagreement, but little doubt has been cast upon the assumption that the two groups had a common origin, or that archosaurs are derived from early lepidosaurians.

The critical groups for the enquiry into archosaurian ancestry usually have been considered to be: the younginid eosuchians, the millerettiforms, and the captorhinomorph cotylosaurs. As far as the different possible hypotheses of archosaurian ancestry are connected with these three groups, we can speak of the younginid hypothesis, the millerettiform hypothesis, and the captorhinomorph hypothesis.

In a recent paper (Reig, 1967), I have briefly discussed these different hypotheses, pointing out that the proterosuchian character-states make it necessary to rule out both the younginid and the milleretti-form hypotheses. Each of these groups is more advanced than the first archosaurs (the proterosuchians) in relevant character-states.

The younginid hypothesis was first advanced by Broom (1914, 1922, 1924a, 1946) and has been subsequently adopted by such authors as Camp (1945), Piveteau (1955) and von Huene (1956). This hypothesis maintains that the archosaurs, the rhynchocephalians, and the squamates took their origin from the younginids, represented by the small South African *Cistecephalus* Zone reptiles *Youngina*, *Youngoides*, and *Youngopsis*, known mostly from skull material. The family Younginidae forms the central group of the suborder Younginiformes of the Lepidosauria in Romer's (1956) classification, the other

families of the same suborder being Paliguanidae, Prolacertidae, and Tangasauridae. The younginids have both the diapsidan temporal opening fully developed (character-state i of our *AA* class) and the typical lepidosaurian otic notch, formed by a curved posterior border of the quadrate and defined above by a small spur of the squamosal (in disagreement with our proterosuchian character-state 4). At the same time, the suspensorium is nearly at the same level with the occipital region (contradicting our character-state 6), and the quadrate is attached by suture with the squamosal in a monimostylic way (in contrast with character-state vi of our *AA* class).

It is now generally accepted that the younginids can be considered as the stem group of the Rhynchocephalia and that the origin of the Squamata is better sought in the Prolacertidae (Camp, 1945; Parrington 1935; Kuhn-Schnyder, 1954, 1962). As far as the archosaurs are concerned, the younginid ancestry has been seriously questioned by Romer (1946, 1956). And apart from the arguments of this author, it is clear that the younginids cannot be considered ancestors of the proterosuchians because of the structure of the quadrate, as even the first proterosuchians (i.e., *Chasmatosaurus*, Brink, 1955) show a movable quadrate, articulated with the squamosal through a head, a condition which has been established in the millerettids (Watson, 1957). But in addition, the lack of any sort of otic notch and the very backward position of the mandibular articulation of the quadrate (shown already in the most primitive proterosuchians) definitely preclude the idea of any kind of younginiform ancestry for them. The proterosuchian character-states 4 and 6 constitute a serious objection to the younginid hypothesis, and this is better abandoned.

The core of the Millerettiformes (also a suborder of the Eosuchia of the Lepidosauria in Romer's classification of 1956) is formed by several genera described by Broom (1938, 1940, 1948) from the same *Cistecephalus* beds of South Africa and placed in the family Millerettidae. Earlier genera of the same group are usually referred to different families. The whole taxon has been carefully surveyed by Watson (1957) who maintained that these are sauropsid reptiles possessing very primitive qualities, though not having already developed the two-arched condition. He suggested (1957: 388) that the thecodonts could have come direct from the Millerettiformes (called by him Millerosauria), and, in the chart of figure 23 of the same work, he derives the Pseudosuchia plus later archosaurs and the "Erythrosuchia" (= Proterosuchia), as a separate branch, from the "millerosaurs." The implication is that the proterosuchians do not belong in the ancestry of later archosaurs (a contention not expressed in his text), but that both pseudosuchians and proterosuchians evolved independently from "millerosaurs." As we shall make more evident below, no relevant evidence exists ruling out the proterosuchians from the ancestry of the pseudosuchians and, on the contrary, the presence of such intermediate forms as *Euparkeria* suggests that proterosuchians actually were the ancestors of the pseudosuchians.

As far as proterosuchian origin from the millerettids is concerned, it is highly improbable that at least any of the small genera of the *Cistecephalus* Zone could be in the line of proterosuchians. All of them have an otic notch already developed, and the quadrate in an upright position, with the mandibular articulation close to the occipital plane. These are character-states that are not expected to be found in any proterosuchian ancestor. It is true that the millerettids are more plausible archosaur ancestors than are the younginids, because the former have a movable quadrate-squamosal articulation, but, at the same time, the millerettids had not reached the diapsid condition already developed in the young-

inids. Furthermore, the millerettids could hardly be considered as adequate fore-runners of the contemporaneous *Archo-saurus* from the Russian Upper Permian Zone IV. This genus indicates that, at the time the millerettids thrived, the protero-suchids were fairly large animals which had already developed their typical char-acter-states.

However, discarding the millerettids as direct proterosuchian ancestors is not the same as discarding the millerettiform hypothesis, since the group is not restricted to millerettids of the South African *Ciste-cephalus* Zone. The older *Tapinocephalus* Zone of the Karroo succession has yielded *Broomia*, a genus tentatively placed in a family of its own, and the still older strata of the Mesen River in Russia (Upper Ka-zanian, Zone II of the Russian Permian) afforded *Mesenosaurus*, a genus considered of pelycosaur affinity by Efremov (1938) and by Romer and Price (1940), but more correctly placed in the Millerettiformes as the type of a family of its own (Watson, 1957; Romer, 1956; Tatarinov, 1964). Romer (1967) has stressed the phylo-genetic importance of the Millerettiformes. They are likely to have been a widespread group, both in time and in space. Can it be supposed, therefore, that the Protero-suchia evolved from some early milleretti-form population? This is hardly probable, as such an early member of this taxon as *Mesenosaurus* had already acquired, ac-cording to published descriptions, a perfect otic notch. The Millerettiformes are better considered as forerunners of the Lepido-sauria, not as a group having direct relationships with the archosaurs.

Romer (1956: 519) suggested that the archosaurs might have arisen independently from cotylosaur ancestors. It is obvious that the captorhinomorphs are here im-plied, as he did not consider other cotylosaur groups as being close to the archosaurs. The two-arched temporal re-gion of archosaurs and lepidosaurs would in this view be another case of parallelism,

which, by the way, might also be the case if one advocated a millerettiform ancestry.

The first adequately known captorhino-morph, and also the earliest adequately known reptile, comes from the Lower Penn-sylvanian (Westphalian A) of the Port Hood formation in Nova Scotia. This is the genus *Romeriscus*, a limnoscelid re-cently reported by Baird and Carroll (1967). Remains of two romeriid capto-rhinomorphs and one pelycosaur have also been described from the Joggins of Nova Scotia, a slightly higher level in the Lower Pennsylvanian (Westphalian B) (Carroll, 1964). Romeriids are represented also by dubious remains from the Middle Penn-sylvanian, and they are better known through their last representatives in the Lower Permian (*Romeria, Protorothyris*). The other captorhinomorph family, namely the captorhinids, has its first members in the Lower Permian Leonardian stage (see Table I), with *Captorhinus* as a well-known representative. Members of this family are, moreover, the latest captorhinomorphs, reaching the early Guadalupean and early Kazanian (*Rothia, Kahneria*, etc.). The limnoscelids departed very early from the main line of reptilian evolution (Baird and Carroll, 1967), so that only romeriids and captorhinids could be relevant in the dis-cussion of archosaur ancestry.

It is clear that both romeriids and capto-rhinids would make better archosaur an-cestors than younginids, prolacertids, or millerettids, in the sense that they do not contradict the requirement of the absence of an otic notch as demanded by the pro-terosuchians. They are, however, very archaic, fully anapsid, and with the sus-pensorium not primarily posterior in position. The form and the relationships of the quadrate, moreover, are more archo-saur-like in the millerettids than in the captorhinomorphs. However, Parrington (1958) has demonstrated that the mil-lerettid condition of the quadrate is easily derived from that of *Captorhinus*. But, as the same arguments used by Parrington
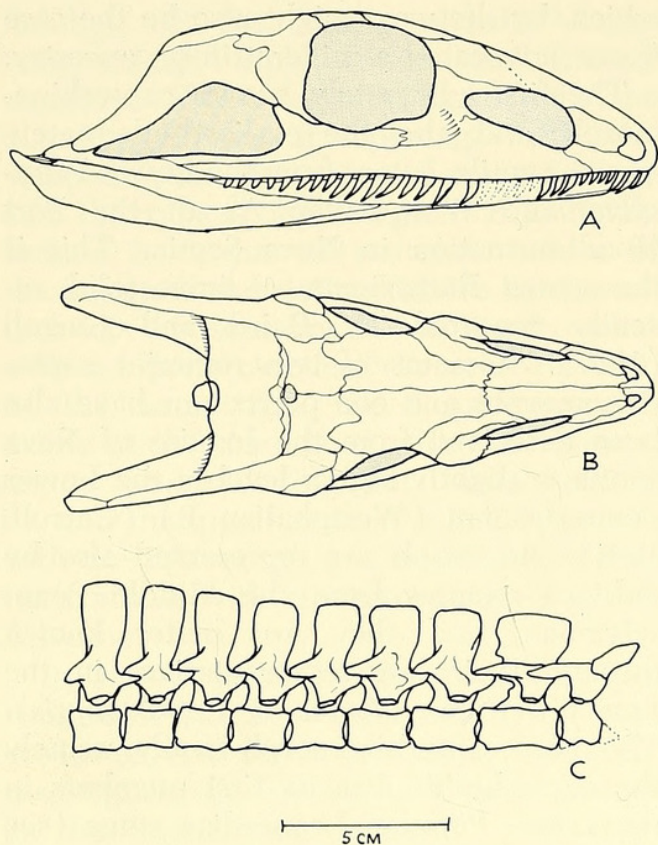
Figure 6. *Varanodon agilis* Olson. A, lateral view of the skull; B, dorsal view of the skull; C, series of cervical vertebrae. (From Olson.)

could be applied to derive the archosaurian condition of the quadrate from that of the captorhinids, this does not run counter to the possibility of captorhinomorph derivation of the archosaurian skull. In fact, no theoretical objection can be raised against the contention that the proterosuchian skull, diapsid, without otic notch, and with a very posterior suspensorium could be derived from a romeriid or captorhinid skull. Furthermore, the postcranial skeleton is so primitive in these cotylosaurs that practically every proterosuchian character-state of that part of the body could easily be thought of as having evolved from a captorhinomorph state.

But it is clear that too large a morphological gap exists between even the more primitive proterosuchians and the more advanced captorhinomorphs, and neither romeriids nor captorhinids show any definite trend towards some of the peculiar

archosaurian character-states. Even if intermediate forms should be discovered between captorhinomorphs and early archosaurs, the amount of difference between the ancestor and the descendent groups would necessarily be so great that the linking group might better be considered as a major taxon of its own. In this case, the captorhinomorph hypothesis should be transformed into one arguing for ancestry from this intermediate taxon.

Another objection to the captorhinomorph hypothesis is the lack of explanatory value, as it can be agreed that many reptilian groups could eventually have stemmed from captorhinids or romeriids. Moreover, it becomes clear that this hypothesis should be abandoned if another reptilian group more closely related to the first archosaurs exists. As I have already proposed (Reig, 1967), I believe that a strong case exists for assigning this role to a definite group of pelycosaurs; this makes it necessary to put forward a new hypothesis, namely the pelycosaurian hypothesis.

This idea is not completely new. The notion of pelycosaur and archosaur relationships was first expressed by von Huene (1911), when he discussed the position of *Erythrosuchus*. He found that this genus shared with pelycosaurs so many features in skull and postcranial morphology, that he created for it an order of its own, Pelycosimia, a name coined with the evident purpose of expressing the idea of pelycosaur relationships. He later abandoned the idea of the Pelycosimia as a separate order, and the name has been used in its original spelling, or as Pelycosimioidea, as an equivalent of Proterosuchia, or Proterosuchoidea, and, hence, as a taxon subordinated in the Thecodontia.

More recently, Rozhdestvenskii (1964: 204) suggested plainly the pelycosaur origin of the archosaurs, when he said: "The mammal-like reptiles, and particularly the pelycosaurs, are also to be considered as archosaur ancestors. The earliest archosaurs, the Triassic thecodonts, are

MAJOR DIVISIONS	STANDARD AMERICAN SCALE	NORTH-CENTRAL TEXAS	STANDARD RUSSIAN STAGES	RUSSIAN CONTINENTAL ZONES	KARROO SYSTEM IN SOUTH AFRICA	POSITION OF GENERA RELEVANT TO THE PROBLEM OF THE ANCESTRY OF ARCHOSAURS
PERMIAN — UPPER PERMIAN	OCHOAN SERIES		?	IV	CISTECEPHALUS B — LOWER BEAUFORT STAGE	ARCHOSAURUS; HOMODONTOSAURUS; YOUNGINA YOUNGOPSIS YOUNGOIDES; MILLERETTIDS
	GUADALUPIAN SERIES — CAPITAN	WHITE HORSE GROUP	TATARIAN	IV / III	CISTECEPHALUS A	"PROBLEMATIC REPTILE" OF PARRINGTON
	GUADALUPIAN SERIES — WORD	PEASE RIVER GROUP — DOG CREEK, BLAINE, FLOWERPOT SHALE, SAN ANGELO	KAZANIAN / UFIMIAN	III / II	ENDOTHIODON; TAPINOCEPHALUS	BROOMIA ELLIOTSMITHIA, ANNINGIA; MESENOSAURUS VARANODON ROTHIA, KAHNERIA
PERMIAN — LOWER PERMIAN	LEONARDIAN SERIES	CLEAR FORK GROUP — CHOZA, VALE, ARROYO, LUEDERS, CLYDE, BELLE PLAINS	KUNGURIAN / ARTINSKIAN	I	ECCA SERIES	VARANOSAURUS VARANOPS; AEROSAURUS, SCOLIOMUS; OPHIACODON
	WOLFCAMPIAN SERIES	WICHITA GROUP — ADMIRAL, PUTNAM, MORAN, PUEBLO	SAKMARIAN	O	DWYKA SERIES	VARANOSAURUS; OPHIACODON

TABLE I. CORRELATION CHART OF THE VARIOUS DIVISIONS OF THE PERMIAN IN U.S.A., SOUTH AFRICA, AND RUSSIA. (MAINLY FROM DUNBAR AND FROM OLSON.)

significantly similar to the pelycosaurs, both in general features and in details."

The pelycosaurs are, however, a large group including several specialized subordinate taxa that are surely not connected with the archosaurs. The more generalized members of this order are to be sought in the Ophiacodontia and in the Varanopsidae among the Sphenacodontia. Even though some ophiacodontids show several notable resemblances to the more primitive proterosuchians, this is not the group most likely to include the archosaur ancestors. It is the varanopsids that have features that strongly suggest proterosuchian relationships, and that have developed some character-states that are found elsewhere only in the archosaurs among the reptiles. Olson (1965) has recently described *Varanodon agilis* (Fig. 6), an advanced varanopsid

from the Guadalupean of Oklahoma, which strongly suggests a theoretical proterosuchid ancestor in skull and postcranial structure. It is thus desirable to consider the composition of this family.

The best known genus of the Varanopsidae is *Varanops*, from the Clear Fork beds of Texas (Leonardian, Lower Permian: see Table I to visualize the Permian successions), carefully described by Romer and Price (1940). These authors referred to the same family the genera *Aerosaurus* and *Scoliomus*, from the largely equivalent Abo beds of New Mexico, the South African *Elliotsmithia* and *Anningia* (= *Galesphyrus*) from the *Tapinocephalus* Zone of the Upper Permian, and the Russian *Mesenosaurus*, which, as has already been said, is now better placed in the Millerettiformes. *Homodontosaurus* of the South African *Cistecephalus* Zone has also been included in the same family. However, the position of the South African and New Mexican genera is doubtful. Watson (1957) suggested that *Elliotsmithia* and *Anningia* might be considered to be millerettids; *Aerosaurus* and *Scoliomus* are known from material too fragmentary to permit an accurate family allocation. *Homodontosaurus*, a pelycosaur according to Broom (1949), is considered a therapsid by Brink (1950), and the nature of the material suggests that it is better considered as a synapsid *incertae sedis*. Olson (1965) maintains that *Varanops* and his new genus *Varanodon* (Fig. 6) are the only genera to be considered as certainly belonging to this family, and, as far as the other genera are concerned, in his view *Elliotsmithia* is the only one for which a convincing case can be made.

Extending from the lowest Vale (*Varanops*) to the *Tapinocephalus* Zone, the family Varanopsidae would be a long-lived one during Permian times, and its extension in time matches very well that which would be expected for a group ancestral to the archosaurs.

The skulls of varanopsids and ophiaco-

donts share a number of characters with the proterosuchians. First of all, the absence of an otic notch, the presence of a lateral temporal fenestra, and the posteriorly situated suspensorium with the quadrate strongly slanting backwards, constitute an assemblage of characters that we have not found associated in any of the other groups alleged to be connected with archosaur ancestry; by themselves these make a strong case for suggesting relationships. Besides this, there is the common possession of postparietal and postfrontal bones and of a pineal foramen, conditions that even though not indicative of special relationships, for the same character-states are shared by other primitive reptiles, do not contradict our hypothesis. Far more important is the fact that so typical an archosaur character-state as the presence of an antorbital fenestra has been described in *Varanodon* and is apparently also present in *Varanops* (Olson, 1965). At the same time, the characteristic archosaur mandibular fenestra is found well developed in *Ophiacodon* (Romer and Price, 1940) and apparently also in *Varanops* (a detailed account of the mandible of *Varanodon* has not yet been reported). Moreover, ophiacodontids and varanopsids share with the proterosuchians an elongated antorbital region, an occipital plane that is concave and slants forward towards the skull table (as in most pelycosaurs), and large prefrontal bones that project laterally and form a ridge, making an abrupt limit between the roof of the skull in front of the orbits and the lateral antorbital region. The palate is not adequately known in the Varanopsidae, but typical proterosuchian character-states, such as pterygoid flanges, teeth on these flanges, and long and narrow interpterygoid vacuities, are observable in *Ophiacodon*. Pelycosaurs also have in common with the proterosuchians and some later archosaurs the presence of epipterygoids and the small size of the posttemporal fenestra, and in both groups the prootics are extensive. A peculiar condition of the

pelycosaurs is the presence of a prominent *dorsum sellae* formed mainly by the prootics, rather than by the basisphenoid (Romer and Price, 1940; Romer, 1956). This condition is not known in the proterosuchians, but the fact that in the phytosaurs the *dorsum sellae* is partly formed by the median union of the prootics (Camp, 1930), suggests that participation of the prootics in the *dorsum sellae* is to be expected in proterosuchians.

The proterosuchian skull is metakinetic (Versluys, 1910: 197), and this seems also to be the original condition of the pelycosaurs (Versluys, 1912: 661). As far as skull kinetism is concerned, however, an important difference between the pelycosaurs as a whole and the proterosuchians is the nature of the quadrate, which is completely monimostylic in the former and streptostylic in the latter. It is clear, nevertheless, that more research is needed in order to know which is the primitive condition of this character. We have already mentioned that the movable quadrate of the millerettids seems to be easily derivable from the rigid condition of *Captorhinus* (Parrington, 1958).

Additional differences are shown in the fact that all pelycosaurs lack the upper temporal fenestra and that they retain the tabular and supratemporal bones and have not developed laterosphenoid ossifications. All these character-states are, however, to be expected in proterosuchian ancestors, the different state in the first archosaurs being obviously an evolution from a primitive condition like that seen in the pelycosaurs or romeriid captorhinomorphs. Romer and Price (1940: 194–195) argued that the diapsid condition of the archosaurian skull is hardly derivable from the synapsid condition of the pelycosaurs. Their arguments, however, do not seem to the present author very convincing, and there seems to be no serious doubt that, as Kuhn-Schnyder recently advocated (1962), the development of the lower temporal fenestra is the first step towards the

realization of the two-arched, diapsid condition. The size and position of the temporal fenestra in the Varanopsidae make it clear that this fenestra is homologous with the diapsidan lower temporal fenestra. Another point against pelycosaur-archosaur relationships in the Romer and Price argument, the morphology of the pelycosaur occiput, is contested by present knowledge of occipital structure in the proterosuchians.

Another distinction refers to the anterior extensions of the lacrimals that in ophiacodontids and varanopsids contribute to the borders of the external nares. This feature is not shown by any proterosuchian, but the fact that the same condition is observed in other primitive groups, such as millerettids, diadectids, gephyrostegids, and captorhinomorphs, suggests that this is a primitive reptilian heritage; it is not surprising to find it in proterosuchian ancestors.

Taking into account the combined group of the ophiacodonts and varanopsids, it is highly suggestive that they share four of the eight character-states of *AA* class (2, 3, 5, 8) that refer to skull characters, and that in one other (1) they are intermediate. Even more suggestive is the fact that they share all the thirteen skull character-states of the proterosuchians (character-states 1–13 of our list). In short, the data of skull anatomy seem to indicate that the primitive pelycosaurs of the ophiacodontid-varanopsid group make better proterosuchian (and archosaur) ancestors than any other reptilian group. Among these, the Varanopsidae show character-states suggesting that they are close to the group from which the proterosuchians may have arisen, as they have already developed the otherwise characteristically archosaurian antorbital fenestra and have a very large lateral temporal opening and strongly backward-oriented suspensorium.

The same conclusion is supported by the axial skeleton. The pelycosaurian vertebral column is of course more primitive

than the proterosuchian one, as the vertebrae have persistently notochordal centra, intercentra commonly present in all the presacral vertebrae, and a presacral number of twenty-seven. The vertebral morphology, however, does not preclude archosaur ancestry in any way. On the contrary, proterosuchian vertebrae show character-states such as the presence of lamellae connecting the apophyses for the rib heads (present also in ophiacodonts, at least) that seem to be reminiscent of the primitive pelycosaur condition. The atlas-axis complex is closely comparable in *Chasmatosaurus* and the ophiacodonts, as Broili and Schroeder have already pointed out (1934), and the Varanopsidae (Fig. 6c) add to the general picture the fact that they have, as in the primitive proterosuchians, elongated cervical centra (Romer and Price, 1940: 274; Olson, 1965: 53) and a tendency for the dorsal rib facets to become more closely approximated from the front backwards. The similarity in sacral vertebrae is also striking, as von Huene (1911: 36) noted, and this similarity becomes more evident when primitive pelycosaurs are considered, as both ophiacodontids and varanopsids have only two sacral ribs. Mention should also be made here of the few vertebrae associated with portions of humerus and ulna and other fragments that Parrington (1956) described from the Upper Permian (*Endothiodon* Zone) of Tanganyika. The vertebrae of this "problematic reptile" are suggestive of a transitional type between pelycosaur and archosaur vertebrae; they are pelycosaurian in the retention of the notochordal canal, and archosaurian in the form and position of rib articulations. It is of interest to note that these remains come from a level in the Upper Permian immediately following the *Tapinocephalus* Zone, which yielded the specimens of the supposed last varanopsid, *Elliotsmithia*.

Of prime interest for the pelycosaur hypothesis are the striking resemblances that exist in the morphology of the appendicular skeleton between proterosuchians, on the one hand, and ophiacodontids and varanopsids, on the other. Members of both these pelycosaurian families show the primitive reptilian feature of sprawled legs, as in the proterosuchians (character-state 16), and both are, of course, quadrupedal (character-state 15). But, at the same time, ophiacodontids and varanopsids present the characteristic archosaurian limb disparity (character-state xiii of the AA class) in just the stage of development shown by the proterosuchians (character-state 17). The girdles and the limbs show striking points of affinity, even in details. The scapular blade in *Chasmatosaurus* and *Cuyosuchus* is closely comparable to that in *Ophiacodon* and *Varanops*: short and broad by archosaurian standards, with a supraglenoid buttress and a supraglenoid foramen (at least in *Cuyosuchus*) (Fig. 7). This character-state (27) is not shared by all proterosuchians, as has already been said, and it is interesting that such a feature of the SN class should be shared by varanopsids and ophiacodontids. As far as the coracoids are concerned, pelycosaurs differ strongly from archosaurs in the possession of two coracoidal ossifications, a point that has been stressed by Romer and Price (1940: 194) in discarding the possibility of pelycosaur-archosaur relationships. But it is now commonly agreed that the single archosaur coracoid represents the synapsid precoracoid, and the presence of two coracoids in various primitive reptiles (such as pelycosaurs, captorhinids, procolophonoids, and pareiasaurs) proves that two coracoidal ossifications are an early acquisition in the first reptiles, and that this condition has been lost in later stages of reptilian evolution, the synapsids being the only group in which it survived. From this assumption, it is logical to conclude that in the ancestors of archosaurs a trend towards the reduction or disappearance of the posterior "true" coracoid occurred. It is therefore highly significant that among the Varanopsidae, which show
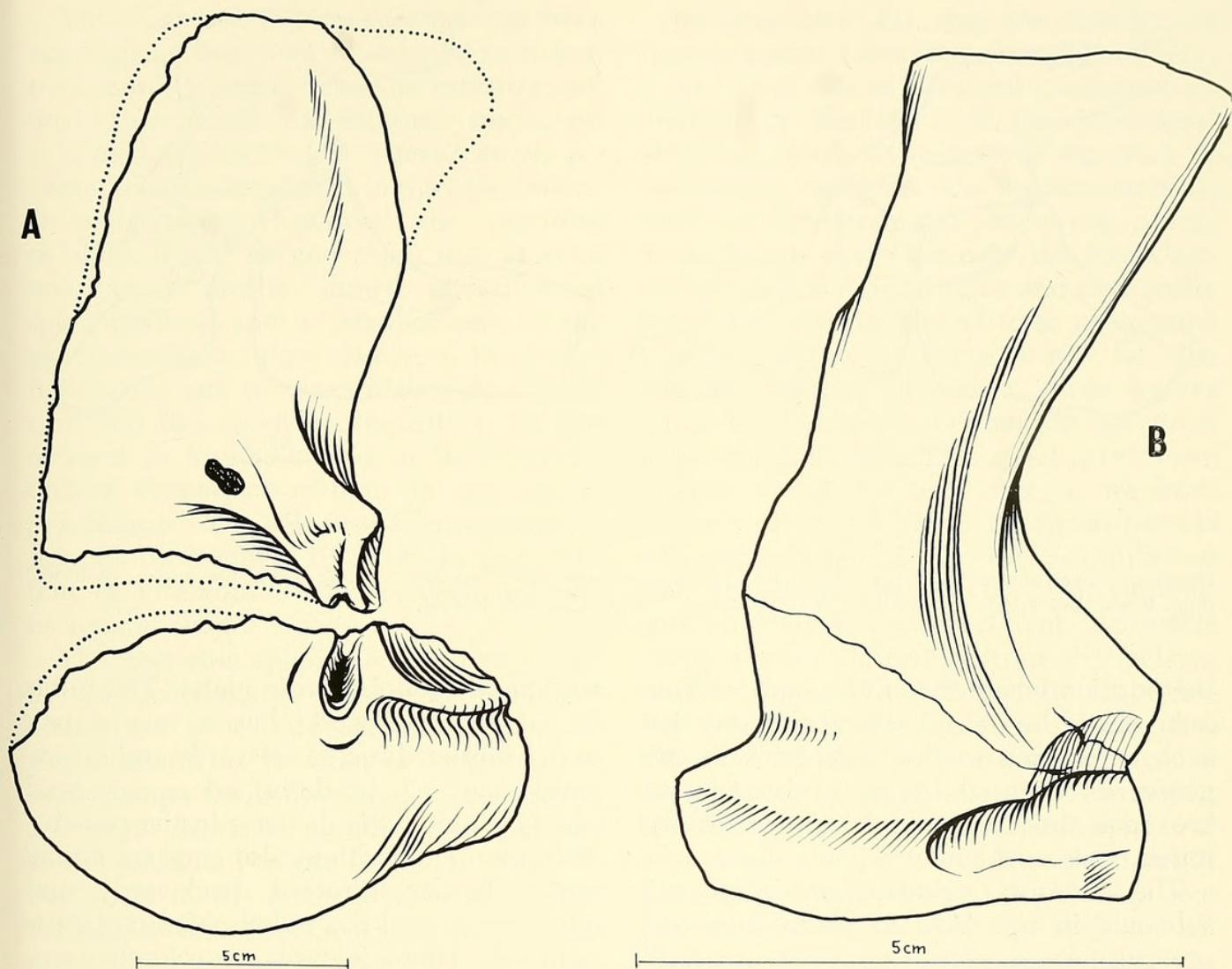
Figure 7. Scapula and coracoid of one proterosuchian and one varanopsid pelycosaur. A, *Cuyosuchus huenei* Reig; B, *Varanops brevirostris* (Williston). (A, from original specimen; B, from Romer and Price.)

so many similarities to the proterosuchians, *Varanops* (Fig. 7) is unique among pelycosaurs in lacking a posterior coracoidal ossification (Williston, 1914)—a feature that has been interpreted by Romer and Price (1940: 274) as a lag in ossification; this lag has been reported by the same authors (1940: 263) as a characteristic feature in sphenacodonts. The situation in other typical varanopsids is not clear in this respect, and the ophiacodonts exhibit the characteristic double condition of the pelycosaurian coracoids.

In pelycosaurs, the humerus is characterized by the expanded and twisted ends, the distinct shaft region, the presence of a large entepicondylar foramen, and a well-developed deltopectoral crest. The known humeri of proterosuchians, with the exception of *Cuyosuchus*, also possess expanded and twisted ends (character-state 20), a strong deltopectoral crest, and distinct shaft. They look very different from the humeri of most of the pseudosuchians and are very close to the pelycosaurian ones, but they do not show the entepicondylar foramen characteristic of the latter. However, it must be noted that the humerus of *Chasmatosaurus* recently figured by Young (1963) is not only closely comparable with that of *Varanops*, but also shows a discontinuity in the entepicondylar border in
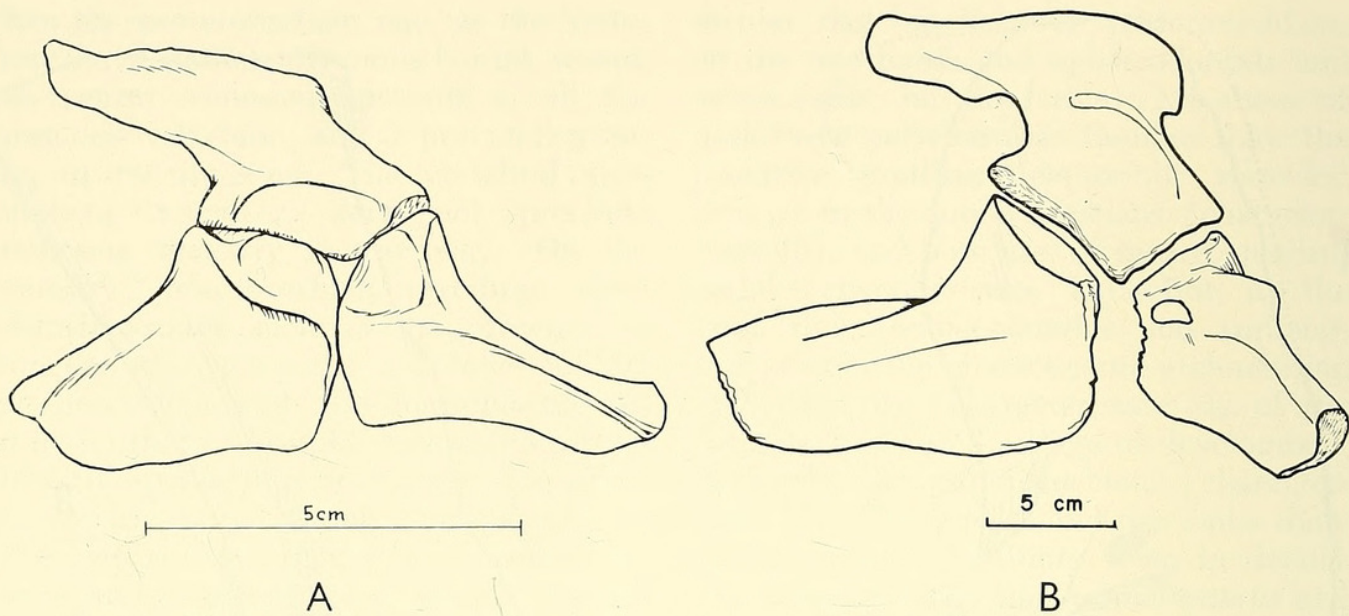
Figure 8. Pelves of one varanopsid pelycosaur and one proterosuchian thecodont. A, *Varanops brevirostris* (Williston) (from Romer and Price); B, *Vjushkovia triplicostata* von Huene (from von Huene).

the position where the entepicondylar foramen should be placed, which suggests that such a foramen might be present in this genus, its external bridge of bone being broken in the specimen. An ectepicondylar notch is also evident.

The anterior epipodials are short and subequal in size both in pelycosaurs and proterosuchians. The former have a well-developed olecranon on the ulna, which is apparently lacking in the proterosuchians. But, as Romer and Price have indicated (1940: 46), the extreme lag in ossification of the olecranon during ontogeny makes this character untrustworthy in problems of phylogeny. It is suggestive that the ulna of *Varanops* looks very much like that of *Chasmatosaurus* described and figured by Young (1936), especially as regards the proximal end, which in both is massive and has a relatively weakly developed olecranon area.

We have already said that the pelvic girdle of the primitive proterosuchians may be better described as incipiently triradiate, the triradiate condition being more evident in such advanced forms as *Erythrosuchus.* Earlier forms retain many primitive characteristics, such as a reduced but fairly

continuous puboischiadic plate. The pubis in *Varanops* (Fig. 8) has a very strong upper border directed forwards and downwards, and can be described as a twisted plate of bone, as is the case in the proterosuchians. The ischium also shows a strong upper border directed backwards and downwards, and the puboischiadic plate is reduced. These features are closely comparable to those in primitive proterosuchians and suggests that the archosaurian trend toward a triradiate pelvis was beginning to develop in *Varanops*-like pelycosaurs. This corresponds to our proterosuchian character-state 25. As far as the other pelvic characters are concerned, the ilia of *Chasmatosaurus* and *Shansisuchus* are very like that of *Varanops* in that the anterior process of the blade is very weakly developed (character-state 22). This process is absent in the ophiacodonts, but is very well developed in later sphenacodonts and edaphosaurs. The posterior spine of the blade is long and narrow in ophiacodonts and more proterosuchian-like in *Varanops.* In short, the ilia of varanopsids and proterosuchians are very similar, which is not the case in more advanced pelycosaurs.

The femur of proterosuchians has been reported as being very primitive in that it possesses a terminal head, an intertrochanteric fossa, and an internal trochanter (character-states 18, 19). These features are characteristically present in the pelycosaurs. In pelycosaurs, however, the posterior condyle is far larger than the anterior one, as is clearly shown in advanced sphenacodonts and in edaphosaurs. In the proterosuchians, this characteristic is not noticeable, and it is again strongly significant that this condylar disparity is far less marked in *Varanops* and in the ophiacodontid *Varanosaurus* than in the typical pelycosaurs. The femur of *Chasmatosaurus* figured by Young (1963) looks very like that of *Varanops* in this respect and also in general shape.

The posterior epipodials are generalized in both pelycosaurs and proterosuchians, and do not afford any evidence of relationships. As far as the foot is concerned, in both groups the astragalus and calcaneum are large elements, closely appressed one to the other and to the fibula and tibia, so that most of the ankle joint is mesotarsal (character-state 21). In addition, the metatarsals of *Chasmatosaurus* (Young, 1936, fig. 12) are very like those of *Varanosaurus* and *Varanops* in general shape and proportions. In the three genera, the fourth metatarsal is the largest, and the size progression is the same: 1<2<5<3<4. The phalangeal formula of *Chasmatosaurus*, as restored by Young, is, as in pelycosaurs, the primitive reptilian one, with the improbable exception of the three phalanges of the first toe, which is almost surely a faulty reconstruction.

We should finally mention that an additional point of resemblance is afforded by the dichocephalous type of ribs, a characteristic archosaur feature (character-state x of our *AA* class) that is shared by ophiacodontids, varanopsids, and most of the other pelycosaurian groups, and that pelycosaurs also agree with the proterosuchians in the presence of a dermal pectoral girdle

(character-state 28) and the absence of dermal armor (character-state 29).

As in the case of the skull characters, an analysis of the traits of the postcranial skeleton affords an overwhelming array of similarities between the proterosuchians and the ophiacodontid-varanopsid group. Both groups share three of the five character-states of our *AA* class and practically the whole set of the sixteen postcranial character-states we have listed for the proterosuchians. Obviously, these figures could be misleading, as they do not cover important dissimilarities that we have pointed out in the text. But, as we have already discussed, these dissimilarities do not preclude in any case the possibility of the pelycosaur hypothesis, the proterosuchian state of the pertinent characters being readily derivable from the pelycosaurian state. What they indicate is that the group of pelycosaurs in question has not reached the proterosuchian stage of evolution in several relevant features, a conclusion that does not contradict our hypothesis, since it is not here intended to demonstrate that these pelycosaurs *are* proterosuchians, but only that they include the taxon from which the proterosuchians could have taken their origin.

As in the case of the skull characters, we have also observed that within the ophiacodontid-varanopsid group of pelycosaurs, the Varanopsidae seem to be plainly in the line of archosaur ancestry, as they have already developed, or begun to exhibit, relevant trends toward the first archosaurs, such as the single nature of the coracoid, the general shape of the pelvis, the elongated cervical centra, and the pattern of the rib facet displacement in the dorsal vertebrae. None of these trends is developed in more advanced pelycosaurs, and when we also recall that the archosaurian features already developed in the varanopsid skull, such as the antorbital fenestra, the large lower temporal opening, the probable presence of a mandibular fenestra and the backward displacement of
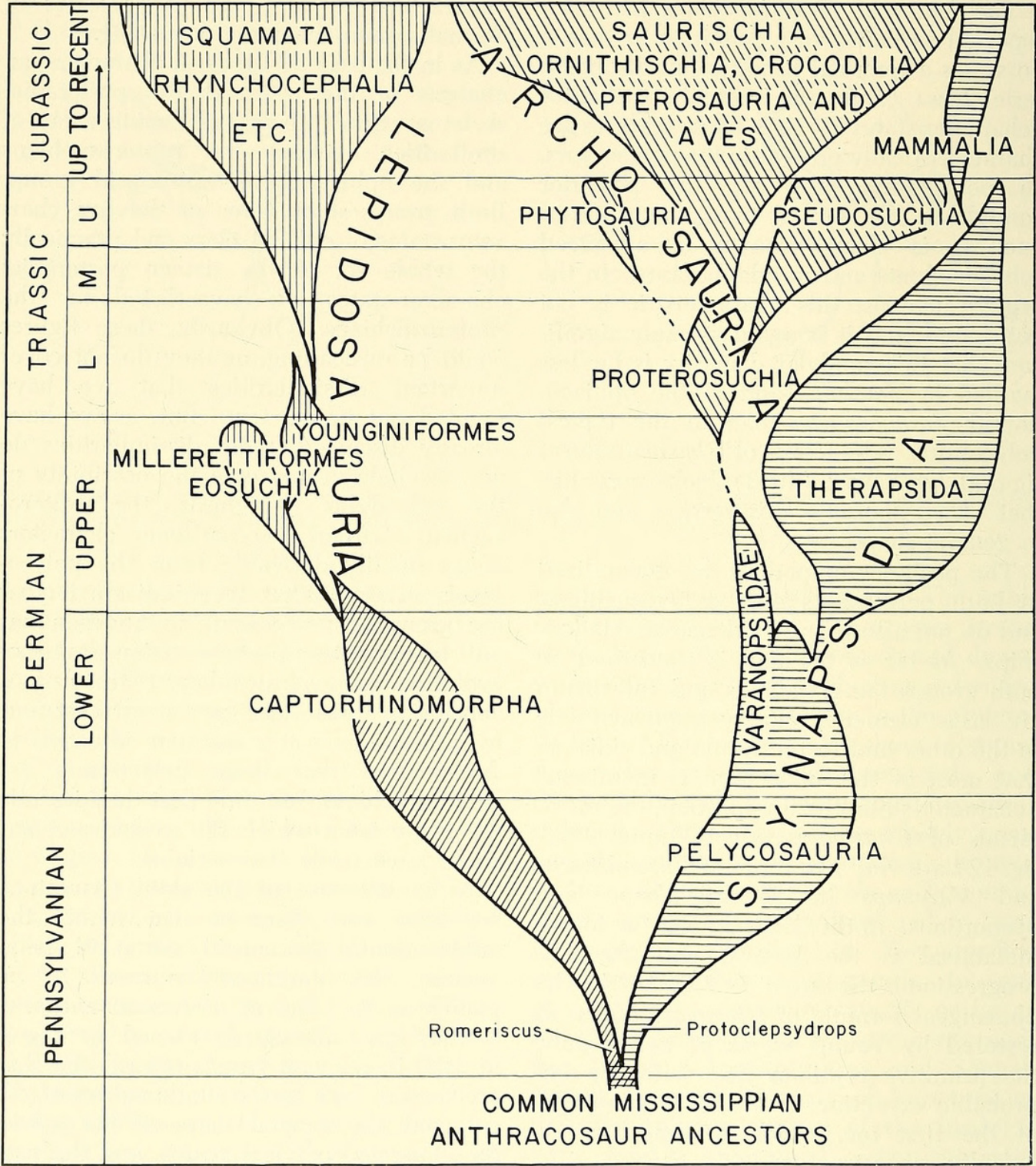
Figure 9. Phylogenetic diagram of the suggested ancestry of the Archosauria and the probable relationships among captorhinomorphs, synapsids, lepidosaurs and archosaurs. (Modified from Reig, 1967.)

the mandibular articulation, are not developed in the more advanced pelycosaurs, we can agree with Olson's suggestion that the Varanopsidae have departed from the main lines of pelycosaur evolution (Olson, 1965). Romer and Price (1940), however, maintained that the Varanopsidae are ancestral sphenacodontians, a contention that does not seem to be supported by the specialized, archosaur-like features shown by the known members of this family. The occurrence of true sphenacodonts as early

as the Lower Pennsylvanian (Carroll, 1964; Baird and Carroll, 1967) clearly indicates, moreover, that the hypothesis of derivation of sphenacodontids from varanopsids should be at least submitted to a critical reappraisal. In our present state of knowledge, I think it is more reasonable to place the Varanopsidae in the Ophiacodontia, as a family in which at least the known members separated from the main direction of synapsid evolution to follow their own evolutionary course, a course that eventually led to their transformation into the proterosuchians. The possibility should not be discarded, however, that very early, unknown varanopsids could be the common ancestors of both sphenacodontians and proterosuchians.

Mention must also be made here of the problematic late Pennsylvanian reptile *Petrolacosaurus* (Peabody, 1952). On the basis of strong similarities in the palatal structure with the eosuchian *Youngoides* and rather less relevant postcranial features, Peabody interpreted this genus as being a primitive eosuchian and proposed a diapsid reconstruction of its skull. This reconstruction is obviously quite hypothetical, but the material seems to suggest, at least, that it possessed a lower temporal opening. Analyzing the quadrate region of the skull and other cranial features, Watson (1954) contended that *Petrolacosaurus* is to be considered a theropsid reptile, a contention that Vaughn (1955) is inclined to accept. In agreement with these views, Romer (1966b) places *Petrolacosaurus* as a probable member of the primitive edaphosaurian family Nitosauridae. It seems to me highly probable that this genus belongs to the Pelycosauria, the data afforded by Peabody giving strong support to this interpretation. If this is the case, it must be noted that the structure of the palate and the elongated cervical centra shown by *Petrolacosaurus* are character-states suggestive of archosaurian ancestry. But in other respects, this genus is so primitive that it cannot successfully contend with the known varanopsids as a proterosuchian ancestor, the geological occurrence of the varanopsids being also more consistent with the idea that they make better forebears of the archosaurs.

I believe that the body of evidence supporting the pelycosaurian hypothesis (Fig. 9) is stronger by far than that supporting any alternative view, and I have not been able to find any serious evidence against it. Apart from its empirical foundations, it can also be said that the hypothesis is also supported by such attributes as explanatory value and simplicity. It is able both to explain the until now obscure question of archosaurian origin in a simple way, and also to explain the reasons for seemingly aberrant features of the late Varanopsidae and the peculiar characteristics of the proterosuchians. It is also rich in suggestions that explain the ecological factors underlying early archosaurian evolution, and is in agreement with other cases of emergence of major groups, namely a pattern of steady development of features of the evolving group.

ECOLOGICAL AND EVOLUTIONARY FEATURES WITHIN THE PROTEROSUCHIA

We have already suggested in the introduction that the proterosuchians represent the first step in an exploratory radiation performed by the thecodonts before the complete dominance of the archosaurs at the end of the Triassic. Now, it will be of prime interest to investigate what conclusions can be drawn about the pattern followed by early archosaurian evolution during this first phase. For this, knowledge of the ways of life and the ecological roles of the proterosuchians can afford important data.

Not much doubt can be cast upon the conclusion that the proterosuchids were mostly aquatic, predaceous reptiles living in ponds, lakes, and rivers, using swimming as their main form of locomotion, and preying upon other vertebrates. This con-

clusion is based on the similarity that they display in body form and proportions to modern crocodiles and in the characteristics of the skull and the dentition. Tatarinov (1961: 130) suggested that big forms like *Chasmatosaurus* fed upon fishes, and that the small forms like *Chasmatosuchus* might have been invertebrate eaters (how far invertebrates contributed to the diet of the proterosuchids is not clear). Moreover, the fact that proterosuchids have been found associated with unquestionable water dwellers, gives additional support to this conclusion. Hughes (1963: 221) affirms that in South Africa "bones of *Lystrosaurus* and *Chasmatosaurus* may be found side by side," and although Robinson (*fide* Hughes, 1963, same reference) cast doubts about the association of these two genera in the Panchet beds of India, this association, with the presence of labyrinthodonts as an additional element, has recently been reported by Satsangi (1964) in the Raniganj coal field. Moreover, Young (1936) reported the same fact in China. It must be recalled that *Lystrosaurus* is a dicynodont very specialized for an aquatic way of living, as indicated by the dorsally placed nostrils, the orbits projecting above the level of the roof of the skull, and the features of the carpus and tarsus. *Lystrosaurus* seems to have been an herbivorous animal not unlike the modern hippopotamus in habits, and its frequent association with the carnivorous *Chasmatosaurus* can be interpreted as an indication of food chain relationships between the two genera, the former playing the food role of a primary consumer fed upon by the latter, which played the role of a secondary consumer in the freshwater communities in which they lived. The pattern would, of course, be more complicated, since fishes and labyrinthodonts probably provided an additional food supply for the maintenance of the *Chasmatosaurus* populations, and since *Lystrosaurus* could have provided food for other pond predators, such as the big rhinesuchids that have been

recorded in the *Lystrosaurus* Zone (see Watson, 1962). But the widespread occurrence of the *Lystrosaurus-Chasmatosaurus* association and the relative abundance of the former in the deposits are to be considered as good indications that the relationships of both these genera represented the dominant channel of energy flow in the food web of the communities to which they belonged.

Garjainia has been found in the deposits of the Russian Zone V, which is considered equivalent to the *Lystrosaurus* Zone. It is, in our belief, the first known erythrosuchid, and its position in the fossil record agrees with its possession of several intermediate features between proterosuchids and erythrosuchids (Charig and Reig, *in press*). The dentition is more carnivorous, and the skull shows modifications for a more efficient biting mechanism. The postcranial skeleton is unfortunately very little known. The skull characteristics of this genus are better developed in later erythrosuchids.

The way of life of more advanced erythrosuchids may be inferred from the skeletal morphology of the upper Lower Triassic genera (*Erythrosuchus, Shansisuchus, Vjushkovia*). Von Huene (1911: 20) pointed out that *Erythrosuchus* should be considered a mainly aquatic predator ("ein sich viel im Wasser aufhaltendes Raubtier"), maintaining that its enormous head can hardly be supposed to belong to an entirely terrestrial animal and that the same conclusion is supported by the structure of the remainder of the body ("Der plump Körper, der kräftige, aber relativ nicht lange Schwanz und namentlich der des grossen Schädels wegen aussergewöhnlich kurze Hals unterstützen die Annahme, das *Erythrosuchus* sich meist im Wasser aufhielt [Flüsse oder Tümpel]."). Tatarinov (1961: 131), on his part, although accepting that "the general proportions of its body, with a relatively huge head and short legs" indicate that erythrosuchids were tied to the water, seems inclined to believe that

they were relatively more terrestrial than the proterosuchids, and stressed the carnivorous specializations of these animals, saying: "The main difference of the erythrosuchids with respect to the proterosuchids is related to the passage to an active carnivorous way of life" (Tatarinov, 1961: 130). We doubt that bulky and clumsy animals like *Erythrosuchus* or *Shansisuchus* should be considered very active animals, a point that has been emphasized by Young (1964: 146). It is more likely that they were inhabitants of swamp marshes, able to prey upon big, slow herbivorous vertebrates, inhabiting the same environments, which could be caught by a relatively slow and heavily built predator. In this connection, we may explore the question of what animals were the prey of the erythrosuchids.

Although evidence of certain association is not abundant, it is meaningful that the erythrosuchids can be considered animals that belonged to the same communities inhabited by the big, upper Lower Triassic dicynodonts of the families Kannemeyeriidae and Shansiodontidae (for a modern survey of these dicynodonts, see Cox, 1965). The most reliable association data are probably those coming from the deposits of the Ermaying Formation in China (Young, 1964; Sun, 1963). In several localities of this formation, bones of *Shansisuchus* and of *Erythrosuchus* were found, although not in actual association. Pearson (1924: 851) maintains that *Kannemeyeria* was a terrestrial animal that probably used its well-developed paws for digging or scraping in order to obtain its food, and she reported that Watson supposed that *Dicynodon* and *Kannemeyeria* lived on dry land. The origin of the giant dicynodonts of the Kannemeyeriidae is not well known but, as Cox (1965) has stated, the dicynodonts are hardly derivable from the aquatic and specialized lystrosaurids of the earlier level of the Lower Triassic. More probably they originated from some member of the vast array of

Upper Permian dicynodontids, which are commonly considered herbivorous reptiles well adapted to living in terrestrial environments (see Watson, 1960: 201). The Middle Triassic representatives of the same group (kannemeyeriids and stahleckeriids) provide good evidence of association with terrestrial reptiles.

It can be argued that if the giant kannemeyeriids are derivable from the terrestrial herbivorous dicynodonts of the Upper Permian, the Lower Triassic Kannemeyeriids and shansiodontids should be also considered as upland dwellers. We believe, however, that this conclusion is not necessarily valid, and that the heavily-built and big-headed kannemeyeriids may be better thought of as inhabitants of shallow waters.

Moreover, there is no reason why, if the Upper Permian terrestrial dicynodontids should have been able to evolve into the fully aquatic lystrosaurids, they could not also have been the ancestors of semiaquatic marsh dwellers. Therefore, Pearson's interpretation of the habits of *Kannemeyeria* cannot be taken as conclusive.

If this reasoning is correct, proterosuchian evolution during Lower Triassic times can be interpreted as a shift from the aquatic and swimming predaceous way of life as represented by the proterosuchids, towards a shallow-water predaceous way of life, the shallow-water predators being adapted for slow walking in swamps. In the first case the main prey was the aquatic lystrosaurids, in the second case, the giant marsh-dwelling herbivorous kannemeyeriids.

In support of this conclusion, it is meaningful that the high point of the proterosuchids occurs in the *Lystrosaurus* Zone and equivalent levels of the lowermost Triassic, and that the erythrosuchids began to be abundant once *Lystrosaurus* itself became extinct. This seems to indicate that the shift in proterosuchian evolution from an aquatic towards a lowland marsh environment was necessitated by the extinction

of the main source of food of the protero-
suchid populations: the aquatic lystro-
saurids. Once these became extinct, the
originally aquatic proterosuchians were
forced to look for their prey in the large
herbivorous dicynodonts inhabiting the
lowland marsh regions. This triggered the
development of improvements for a walk-
ing locomotion and for large animal pre-
dation, both of which are characteristics
of erythrosuchids. The sprawled condition
of the legs is less efficient than the upright
stance in a walking animal, but the latter
is not completely necessary for slow
animals hunting in shallow water environ-
ments for sluggish herbivores. This may
explain how the erythrosuchids were suc-
cessful animals in spite of the fact that they
were sprawled and not very active pred-
ators and, at the same time, why they
developed improvements for a walking
locomotion as compared with the protero-
suchids. In this sense, the changes in
appendicular skeleton shown by the
erythrosuchids, which do not reach a full de-
gree of fitness for a terrestrial active loco-
motion, can be satisfactorily explained as an
adaptive level suitable for a marsh dweller,
and as a prospective adaptation (or a "pre-
adaptation") for future terrestrial loco-
motion.

The fossil record also indicates that the
proterosuchids did not become completely
extinct after the *Lystrosaurus* zone and
the extinction of the lystrosaurids, as one
species of *Chasmatosaurus* has been re-
ported in beds equivalent in age to the
Cynognathus Zone (Young, 1964). Seem-
ingly, the proterosuchids remained in their
old environment as such, but were reduced
in number and variety and played a second-
ary role in the aquatic communities. These
aquatic proterosuchids from the upper part
of the Lower Triassic, surviving after the
detachment of the erythrosuchids, may
well be the source of the other aquatic
groups of archosaurs present in the record
at later levels in the Triassic period.

The erythrosuchids seem to have become
extinct by the end of the Lower Triassic.
From the very beginning of the Middle
Triassic other large predaceous archosaurs
have been found in different parts of the
world, representing a more terrestrial type;
most of these belong to the family Rau-
isuchidae of the pseudosuchian thecodonts.
At the same time, the evidence seems to
indicate that at least some kannemeyeriids
shifted towards a more terrestrial life in
middle Triassic times, as their remains
have been found associated with typical
upland reptiles. The extinction of the
erythrosuchids, however, and their replace-
ment by more terrestrial thecodonts better
adapted for upland and active locomotion
could also be explained by a change in
habitat of the animals representing the
main source of food for carnivorous archo-
saurs. But in this case, the replacing group
is not derivable from the replaced one, as
the rauisuchids seem to have evolved from
another group of Lower Triassic theco-
donts, the pseudosuchians of the family
Euparkeriidae. It will be of interest now,
to review our knowledge of the protero-
suchian descendants.

PROTEROSUCHIAN DESCENDANTS

It is here maintained that the Protero-
suchia may be considered the stem archo-
saurian group, in which most of the
subsequent evolution of archosaurs is
rooted. The ways in which descent took
place remain, however, rather obscure.

The taxa which seem most likely to have
been derived directly from the protero-
suchians are the Pseudosuchia and the
Crocodilia. Saurischians and phytosaurs are
also likely to be direct derivatives of the
proterosuchians, but the evidence is far
from being conclusive. The Ornithischia
and the Pterodactyla are better thought of
as descendants of the Pseudosuchia, but
we are lacking the relevant data to advance
any more secure opinions about them.

This theory does not agree with the
classical view, which considers the pseu-
dosuchian thecodonts as the ancestral