THE MAIN FEATURES OF BRACHYURAN EVOLUTION

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Abstract

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The identity of the ancestors of the Brachyura remains uncertain. Nevertheless, it seems obvious that the Brachyura have reached the highest organizational level found among the decapod Crustacea. The genesis of the new organization—brachyurization—involves changes in shape and structure accompanied by maximal diversification or organs and of their functions. This new level of organization has led to great biological improvement as manifested by taxonomic diversity, wide distribution and the ability to leave the primary (littoral) environment. The brachyuran organization is very plastic and has undergone many secondary modifications in connection with further changes of habits and habitats. [Brachyura; Crustacea; evolution.]

INTRODUCTION

The abundance of very different phylogenetic systems that have been proposed for the crabs (Brachyura) reflects the many diametrically opposed ideas about brachyuran evolution that have been held by students of this group of animals. The main reason for the disparity prevailing among these systems is a methodological one. The evolution of crabs has usually been studied from just one point of view at a time (e.g., comparative morphology, ontogeny, paleontology) with concommitant overreliance on some evidence and neglect of the remainder. Thus, in the course of time, the various hypothesis have not approached one another; but, on the contrary, they have become more and more divergent and the "gap" between them has widened.

As we might expect, the majority of investigations have involved morphological aspects of evolution, as these are generally the most readily available. Investigations of ontogeny have also clarified some important evolutionary problems; though, unfortunately, neither the relationship between ontogenetic and phylogenetic development of crabs, nor the laws of development of larval structures and their habits are well known. Paleontological evidence has also frequently proven invaluable to understanding the origins and evolutionary trends and tempo of brachyuran groups. Phylogenetic interpretations based solely on paleontology have, however, foundered because critical fossil forms, especially the oldest ones, are very rare and often incomplete. Additionally, though the overall shape of a given fossil organism and the form of some structures (orbits, dorsal furrows, appendages, etc.) can frequently be estimated, full reconstruction and phylogenetic use of the fossils must rely on knowledge of structuro-functional laws (Gesetzmassigkeiten) as derived from recent forms. Other aspects of brachyuran evolution (e.g., those primarily involving ecology or ethology) have been, to date, rarely involved in studies of crab phylogeny.

It stands to reason that the synthesis of all available evidence is most likely to lead to a satisfactory conclusion to any phylogenetic investigation. Unfortunately, very few

carcinologists have availed themselves of all of the accessible facts (Ortmann, 1896, 1901; Bouvier, 1896, 1940; Balss, 1940–61), and their deductions are now outdated or suffer (Balss) from uncritical use of the available evidence.

In order to meaningfully strengthen our concepts of brachyuran phylogeny it is necessary that several basic and general problems be worked out in detail. Among the most urgent of these are the following: the origin of the group, the genesis of its organization, and the identification of the end products of brachyuran evolution.

THE ORIGIN OF THE BRACHYURA

A most difficult and still unsolved problem concerns the origin of this group. The true ancestors of the crabs are unknown; the oldest demonstrably applicable fossil forms (*Eocarcinus, Prosopon*) being true crabs. All present hypotheses, no matter what evidence they rely on, cannot, without raising grave objections, explain the principal biological properties of the brachyuran ancestors. Three major groups of such hypotheses which attempt to attribute, respectively, macrouran, anomuran or pemphicoid characters to the crab ancestors, now enjoy their own ardent partisans.

The first and the oldest hypothesis ("macrouran") dates from Huxley (1878), who considered that the Brachyura had orginated from the Astacidae. A similar interpretation was that of Bouvier (1896, 1940) who, in his comprehensive and splendid essay, used not only comparative morphological evidence, but also all of the paleontological and ontogenetic facts of that period. This author derived the Brachyura from the Nephropsidea (Homaridea).

A quite different hypothesis is that of Boas (1880) who regarded the Brachyura as having risen from forms related to the genus *Axius* of the Thalassinidea. Ortmann (1892, 1896) derived the Brachyura from the Anomura, specifically from a form intermediate between the Paguridea and the Galatheidea and considered the Dromiacea as either the most developed Anomura or

the most primitive Brachyura. Based on examination of larval stages, Gurney (1942) and Burkenroad (1963) considered the Thalassinidea to have been ancestral to the Dromiacea. They placed the Dromiacea in the Anomura. Recently Pike and Williamson (1960) derived the Dromiacea from a form intermediate between the Nephropsidea and the Thalassinidea.

Finally, the third hypothesis is that of van Straelen (1928) who postulated, from paleontological evidence, that the ancestors of the Brachyura are to be found among the Triassic Pemphicoidea. This opininon has been supported and supplemented by Beurlen (1930), Glaessner (1930, 1960) and Förster (1967).

Which, if any, of these hypotheses is correct? For the reconstruction of the first transition stages ("missing links") between the Brachyura and their ancestors it would be necessary to know the laws of specific evolutionary development not only of the crabs, but of all the decapod Crustacea. Unfortunately, such knowledge is, at present, largely lacking. Among these basic laws it would be most important to know the relationship between morpho-physiological changes and changes in mode of life and habitat. The importance of such relationships is exemplified by two examples elucidated by Schäfer (1954). He established that typical (crab-like) forms (e.g., *Xantho* or *Eriphia*) have chelipeds folded against the anterolateral margin of the carapace. In this case, the chelae are commonly heterochelic and heterodont. These crabs have sternites arranged in parallel and move sideways. Such forms live primarily in places of strong current or wave action and their condensed body is an adaptation to these environmental conditions. However the triangle-shaped or deltoid-shaped forms (e.g., Spider Crabs) lack chelipeds folded against the carapace, and the chelae are neither heterochelic nor heterodont. Their sternites are radially arranged and therefore the animals can move in all directions relative to the longitudinal axis of the body. These forms live

in the places where motion of water is reduced because of roughness of the bottom. Citing another example, Števčić (1967, 1968) has "linked" environmental factors (bottom, food, etc.) to the chemical composition of the body and to the behavior of the Spinous Spider Crab (*Maja squinado* Herbst). It is obvious that knowledge of these and similar relationships provides a key to the understanding of the process of brachyuran evolution.

With regards to the origin of crabs, a further question intrudes: Are the Brachyura indeed a monophyletic group? As we have seen before, there have been some attempts to consider Dromiacea as Anomura (Ortmann, 1892, 1896; Gurney, 1942). Bourne (1922) from his wide investigations on the Raninidae, argued that this group originated from the Astacidae independently of other crabs. Lately Pichod Viale (1966) separated the Homolidea as being more primitive than the Brachyura. However, today the predominate opinion holds that the Brachyura are a homogeneous, monophyletic group (Glaessner, 1930, 1960; Bouvier, 1940; Abrahamczik-Scanzoni, 1942; Balss, 1940–61) discrete from the other decapods. The following are considered as general characteristics of the Brachyura: the abdomen is very much reduced and folded under the cephalothorax; the last thoracic segment is fused with the cephalothorax; the epistome is fused with the carapace; the movable finger of the chelae (*digitus mobilis, dactylus*) is posed externally; the females have a *receptaculum seminis*; the first two pleopods of males are transformed into copulatory organs (gonopods) and the other pleopods are reduced; the males have a penis; the inhalant opening lies primarily before the base of the cheliped. Other properties vary in connection with the grade of organization and with adaptation to specific conditions of existence.

At present the question of the origin of crabs is still enigmatic and must be considered open.

BRACHYURIZATION

One of the most important problems regarding the evolution of the Brachyura is the genesis of their organization. Borradaile (1916) was among the first to comprehend the meaning of this process, calling it carcinization. However, it would be better to use the term brachyurization because it is more general and relevant to all crabs as a whole, without regard to shape and organizational level. Since we do not know the true brachyuran ancestors, we can follow the genesis of their organization only partially, i.e., on the forms which are already crabs. Further, the most primitive crabs are deep-sea inhabitants and are aberrant, so that it is very difficult to distinguish between adaptive peculiarities and ancestral features in these forms. Nevertheless, by using all available evidence, we can make many important deductions about the development of the new organization.

In order to make our understanding of the new organization and its successful advances easier, we should firstly acquaint ourselves with "typical" representatives, such as the crabs, *Portunus* and *Xantho*. Their shape is normally crab-like, i.e., the carapace is usually transverse, depressed, wide in front with the anterolateral margins regularly arched. Their head is condensed, i.e., the occular segment is invaginated into the antennulary one (Pichod Viale, 1966). The antennulae are transversally folded. The antennae are fused with the epistome. The eyes can be protected by complex orbits. The maxillipeds are depressed, and their third pair covers the others as the operculum. The chelipeds are folded against anterolateral margins and are, thus, heterochelic and heterodont. In females the first pleopod is absent. The branchiostegites close the gill chamber (branchial cavity). The gills are phylobranches (usually 9 on each side). The endoskeleton is very highly developed (Abrahamczik-Scanzoni, 1942), continuous (Drach, 1950) and the sternites are arranged in parallel (Schäfer, 1954). The

zoea is typically brachyuran, i.e., with dorsal spine, and lacks both the nauplius eye and the frontal organ (Eloffson, 1963).

In fossil and recent crabs it is possible to follow the gradual improvement of organization from the very primitive to the most advanced forms. Among the most primitive recent crabs are the Homolodromiidae, which are characterized by a great number of ancestral features: the cephalothorax is cylindrical, the epistome and the front are not quite fused, the head is not condensed, orbits are lacking, and the antennae are not fused with the epistome. The antennal thorn and traces of uropods remain. The gills are trichobranches in great number on each side (21). On this organizational level are the fossil Eocarcinidae and Prosoponidae. A higher degree has been reached by the Homolidae and the Latreillidae, in which the number of ancestral properties is diminished but they have not quite condensed the head and the continuous endoskeleton. The next step of organization is evident in the Dromiidae and Dynomenidae, which have still more advanced properties; the general shape is crab-like, the chelipeds are folded against the carapace, the head is condensed and the endoskeleton is well developed. This level of organization has been attained by the Raninidae and Tymolidae. All the above mentioned groups have some primitive and specific properties, however, by which they differ from all the other Brachyura: the abdomen is not quite pressed against the sternum; the sternum is narrow; all of them have the primitive spermatheca (Gordon, 1950); and they possess sternal furrows (excluding the Homolidae and Raninidae) as well as the coxal sexual opening. Additionally, females retain the first pair of pleopods (excluding the Tymolidae and Raninidae); the antennae are normally parallel and longitudinally posed; the larvae (zoeas) lack the typical brachyuran shape and structures; and the last one or two pairs of pereiopods are abnormal and posed dorsally (excluding the Latreillidae and some Prosoponidae).

The majority of the crabs possess the more or less typical brachyuran properties described above. The highest morphofunctional level has been reached by the semiterrestrial and terrestrial forms such as the Ocypodidae, Mictyridae, Grapsidae, Gecarcinidae and some species of Potamonidae.

The first step in the process of brachyurization can be followed indirectly in some "pseudobrachyurans" i.e., in the crab-like Anomura, where numerous brachyuran-like shapes and structures, are attained without reaching the level of brachyuran organization. These properties can be found in the families Lomisidae, Porcellanidae, Lithodidae, and partially in the family Hippidae and in several genera of the Paguridae, namely: *Ostraconotus, Porcellanopagurus, Tylaspis* (Borradaile, 1916). These forms (excluding the Hippidae) have a depressed and broadened cephalothorax and the abdomen folded partially under the cephalothorax (*Porcellana* can still swim by means of the abdomen). The rostrum is often reduced with a broad front (*Porcellana*). *Lithodes* has the anterolateral margin well developed. Some of these forms have reduced the first pair of pleopods in the females and the last pleopods in the males (Lomisidae, Porcellanidae). The endoskeleton may be continuous (Lithodidae, Porcellanidae) and the sternum broad (Porcellanidae) permitting sideways locomotion. Gills are phyllobranches. The uropods are often reduced (Lithodidae, Lomisidae). These are specialized forms for specific environmental conditions, and are often aberrant (Lithodidae, Hippidae). These groups have reached the level of organization at which Brachyura presumably began their evolutionary development.

It is very probable that folding of the abdomen was the first and perhaps decisive act making it possible for either macruran or anomuran ancestors to achieve a higher grade of organization. Even in recent Scyllaridae and Galatheidae the abdomen may be flexed under the cephalothorax, protecting the tender ventral parts

of the abdomen from damage. A similar phenomenon, where animals flex the abdomen or fold the body in a ball, is well known in many animals such as the trilobites, some isopods, the hedgehogs, armadillos and others. The long abdomen in benthonic Reptantia progressively lost its locomotor function and grew weaker and more folded under the cephalothorax, as natural selection preferred forms with a reduced abdomen and stronger ambulatory legs. Simultaneously with the reduction and folding of the abdomen occurred the process of gradual depression and broadening of the cephalothorax. It is very probable that this process commenced in littoral waters, which agrees with Beurlen's (1931) point of view, who considered crabs primarily littoral inhabitants. As mentioned above, the depressed form may be especially advantageous in such habitat, where wave action may be unusually strong. Consequent to the development of locomotion by means of pereiopods was the development of stronger muscles. These are attached to the endoskeleton, which itself became stronger through fusion of the sternites into the rigid sternal plastron. The broadening of the cephalothorax and modification of the sternites brought with them the peculiar characteristic of the crabs, their sideways locomotion. This process began in the Jurassic and by the Cretaceous had resulted in the organization of the true Brachyura.

In the process of brachyurization two diametrically opposed processes can be distinguished: differentiation and integration. The segments, especially their appendages, are strongly differentiated in relation to those of the other decapod Crustacea. This differentiation is connected with the maximum division of labour reached among the decapods. Some segments with reinforced functions such as the thoracic ones, are intensified, but segments with diminished function, such as the abdominal ones, are reduced. An especially great amount of differentiation occurred in the frontal region (antennae, antennulae, orbits and maxillipeds). Concomitantly with appendicular specialization there occurred modification and specialization of the inner organs and organ systems, (muscular and circulatory systems, endoskeleton, stomach and others).

Simultaneously with this differentiation, structural and functional integration (Franz, 1924; Schäfer, 1954) occurred. In part, integration was realized by concentration of segments, resulting from the shortening and compressing (*Stauchung*) of the thoracic segments. Integration is also manifested through the fusion of the particular parts of the body as, for instance, the epistome with the carapace and all the thoracic sterna into the thoracic plastron. The proximal segments of the antennae are fused with each other and with the epistome. In all the pairs of pereiopods the basis and ischium are fused. The concentration is especially manifested in the central nervous system, where the ventral ganglia are fused into a great ventral ganglionic mass. The integration of the central nervous system has presumably resulted in increased coordination of movements and in complex behaviour, especially in the amphibious and terrestrial forms.

These processes allowed considerable biological progress (in the sense of Sewertzoff, 1931) which is manifested not only by taxonomic diversity (the number of species and individuals) but also in the diversity of habitats occupied by the Brachyura and the means by which they exploit their environment. Thus 4450 of 8300 species of the decapods (after Waterman and Chace, 1960) belong to the crabs; an unusually high number of species for a taxon which is of only infraordinal rank (Waterman and Chace, 1960; Glaessner, 1960, 1969). In comparison, the order Isopoda comprises 4000 species, while the Amphipoda contains 3600. Although the majority of crabs live in shallow water (especially in tropical seas) some exist on land and others live at depths as great as about 5000 metres. Because of their great quantity (biomass) and abundance they

represent a very conspicuous link in the chain of nourishment of inhabited biotopes. This evidence indirectly confirms the efficiency and importance of the new brachyuran organization.

THE END-PRODUCTS OF BRACHYURAN EVOLUTION

From the aforementioned evidence it is obvious that the process of brachyurization led to higher organization and to general improvement relative to ancestral forms. The process involved increasing the complexity of organization, which enabled better exploitation of environmental factors and expansion into new habitats (deep-sea, fresh water, land as well as new niches in the littoral zone). The Brachyura in comparison with other decapod groups were more plastic and adapted to life in various environments. In the Brachyura, the chelae, for example, vary markedly in connection with their function, such as alimentation, so that the crabs as a group use a much greater variety of food than did their ancestors. The increased mobility of various types (involving, variously, running, swimming, burrowing or climbing) enabled the crabs to achieve great hunting or foraging efficiency and speed; particularly quick are the terrestrial forms, and in water some portunids are even able to capture mackerels. Brachyura vary in size to where some forms inhabit the phytal zone (algae), the coral reefs and even the mantle cavities of molluscs and the tubes of worms.

Having attained this new level of organization, the crabs began a large adaptive radiation. The majority continued to live in the littoral zone (most members of the families Xanthidae, Portunidae and Majidae). The remainder inhabited the intertidal zone and the land (Ocypodidae, Grapsidae and Gecarcinidae) and fresh water (Potamonidae), modifying their structure according to the conditions of the environment. However, these modifications were not dramatic and the organization remained on more or less the same level.

Some organs were further developed concomitant with reduction of others; thus, in terrestrial forms the importance of the "lungs" is increased and that of the gills decreased; chemical receptors are weaker, and the role of vision (and the eyes) is increased. Despite such modifications members of these groups are all of basically the same crab-like form in which appear the greatest number of subfamilies, genera, species and individuals.

Among the remainder of the crabs there are a considerable number of aberrant forms, in which shape and structure have deviated considerably from that of the typical brachyuran, sometimes to the point of their being difficult to identify as crabs. Such organisms have undergone especially far-reaching modifications of the ectosomatic organs (chelipeds, walking legs, eyes, antennae, and mouth parts) in response to specialization to a particular mode of life in more or less strongly limited surroundings. Such modifications have appeared in deep-sea, burrowing and commensal forms, and must certainly represent an evolutionary two-edged sword, as, after all, does every specialization. Better exploitation of a limited range of environmental conditions has been attained but, presumably, at the expense of evolutionary plasticity. Such conspicuous specialization has occurred in the Homolodromiidae, Homolidae, Latreillidae, Cymopoliidae (deep-sea forms), Corystidae, Atelecyclidae, Calappidae, Leucosiidae, Raninidae (burrowing forms), Pinnotheridae and Trapeziinae (commensals). Additionally, there are a few species of other families (Majidae, Xanthidae, Portunidae, and others) which have become deep-sea inhabitants (Doflein, 1904). Since the conditions under which these crabs live are simpler and more uniform than those of typical crabs, there has been a gradual decrease of their vital activity. In some forms there can be seen signs of regressive evolution (in the morphophysiological sense) such as unrolling of the abdomen (Raninidae, Tymolidae, Dorippidae, Corystidae), the reduction of the

sensory organs (especially the eyes) and weakening of the locomotor system. In considering the phylogenetic development of these aberrant forms it is necessary to take into account the fact that many of these properties are secondary and that they have originated from typical littoral forms.

Finally, far-reaching transformation has occurred in the Hapalocarcinidae, which are so changed that such students of crab systematics as Balss (1940–61) and others consider them a separate superfamily. Hapalocarcinids are obligate, life-long inhabitants of coral-galls; they are microphagous (Potts, 1915) and have experienced striking regression of their locomotory (walking legs, muscles, endoskeleton) alimentary (chelae, mouth parts, gastric-mill) and sensory (eyes) organs.

These have been the main results of brachyuran evolution. It goes without saying that because of the enormous diversity of the crabs it is impossible always to establish the pathway by which a given brachyuran group has evolved. The Geryonidae, for example, being deep-sea forms, have some specific regressive characters, but on the other hand, are very active and raptorial crabs. Finally, it is worth reemphasizing that our difficulty in determining the pathways of evolution within the Brachyura is a consequence not only of the diversity of crabs but also, and more critically, of the dearth of knowledge about the mode of life of the majority of crabs.

DISCUSSION

I have presented only the most general outline of the principal features and problems of brachyuran evolution. From the foregoing pages, the extent of the difficulty and complexity of the problem of the origin and subsequent development of the crabs may be seen. I have focussed on these general problems first, so that it will be easier to subsequently solve specific cases of the evolutionary development of various smaller groups.

In work on brachyuran systematics up to the present a common pitfall has been the differentiation of primary or ancestral characters from those which are secondary or adaptive. For example, most authors have considered a dorsal position for the 4th and 5th pairs of pereiopods (*Homola, Dorippe*), an elongated and cylindrical body (*Homolodromia, Ranina, Corystes*), elongated mouth parts (*Homolodromia, Calappa, Corystes*), reduced orbits (*Homola, Uca, Mictyris*), and so on as primary (ancestral) features. Such an interpretation represents an oversimplification of the matter. It is true that the primitive forms such as the lower Dromiacea have an elongated body, elongated mouth parts and incomplete orbits, but other crabs have secondarily acquired these properties. The elongation of the body and mouth parts can be associated with a burrowing mode of life. The reduction of the orbits is correlated with the movability of the eyestalks (Pichod Viale, 1966) and is often found in terrestrial animals. The dorsal position of the legs is also a secondary feature and according to Dollo's law of the irreversibility of evolutionary process, it is impossible to return them into the 'normal' position of typical crabs. Additionally, previous workers have generally failed to recognize the widespread occurrence of convergence among crabs. Where several groups of various levels of organization have migrated into the same habitat or acquired the same mode of life (deep-sea, burrowing, etc.) they have assumed similar shapes, structures and habits (*Tymolus-Dorippe, Matuta-Portunus, Ranina-Corystes*). Thus, there exist assemblages of convergent forms which, at first sight, seem to be monophyletic as for instance the Oxystomata. The majority of carcinologists believe that this group is a homogeneous and monophyletic one because it possesses many linking properties such as similar mouth parts, buccal cavern and respiratory system (course of water currents). Likewise the Oxystomata is maintained as a primitive group because its members possess elongate mouth parts,

and, in the Dorippidae, the last two pairs of pereiopods are positioned dorsally. These conclusions are without any real foundation because, as we have seen before, these properties may be adaptive (i.e., secondary) ones. Probably all these characters, excluding the dorsal leg position, are really primitive only in the Homolodromiidae, which possess the lowest overall organizational level among the crabs. Only a few carcinologists have doubted that the Oxystomata are a monophyletic group (Boas, 1880; Gurney, 1942; Williamson, 1965; Pichod Viale, 1966; Gordon, 1966). The same situation pertains with the Catometopa. It is very probable that the families in this group are uniform only superficially (Pichod Viale, 1966). Lately Guinot (1966) has cited several examples of genera being quite erroneously classified on the basis of outward similarity.

The evolution of crabs has thus been intimately associated with changes in mode of life and environment; brachyuran subgroups have, in short, been formed through adaptive radiation. The principal supporter of this point of view is Glaessner (1930, 1957, 1960); others, such as Beurlen (1930, 1933) and Russell (1962) have considered that adaptive radiation is not the only and indispensable mode of evolutionary change, believing that because new forms arose rapidly ("explosively") their evolution was not necessarily adaptive. These students were followers of the theory of orthogenesis, and their theories are not susceptible to any form of objective proof. It is true, that in the evolution of crabs there are, as we have seen, many unsolved questions, but our insufficient knowledge or complete ignorance of some evidence gives us no right to base explanations or hypotheses which are justified solely on the basis of random premises. In addition, it is interesting to note that Beurlen (1929, 1931) unintentionally demonstrated facts that were in opposition to his basic thesis. He stated that the evolution of the crabs was connected with changes occurring on the earth's surface. He established that new types arose in times of transgression of the sea, and that during regression several forms invaded the land and fresh water while others moved into the deep-sea. He believed that this process was repeated several times. Therefore it is not necessary to postulate the existence of an autonomous, undefined inner force for the explanation of the evolution of this group.

Undoubtedly the organization of the Brachyura represents an advance over that of the other decapod Crustacea. However, this assertion is true for the Brachyura as a whole, but not for all of the sub-groups. Complete morpho-physiological and general biological progress has been attained only by several groups of higher crabs (Brachygnatha) in which there are many genera and species (figures from Chace, 1951): Majidae 145 genera with 673 species, Portunidae 38 genera with 297 species, Xanthidae 133 genera with 928 species, and Grapsidae 40 genera with 333 species. Several specialized groups have a lesser number of genera and species: Homolodromiidae 4 genera with 6 species, Latreillidae 3 genera with 9 species, Cymopoliidae 3 genera with 29 species, Dynomenidae 2 genera with 13 species. Exceptionally, somewhat more plastic, though relatively specialized, groups have more genera and species: Leucosiidae 40 genera with 338 species, Pinnotheridae 26 genera with 222 species. Several groups show, in every way, a maximal progressive development, for example, the terrestrial and semiterrestrial forms; by contrast some groups showed a total regressive development to the point of dying out: Eocarcinidae, Prosoponidae, Dacoticancridae (the most primitive groups) and Lobocarcinidae.

SUMMARY

1. In order to study the evolutionary development of any group it is necessary to use all the available evidence within the framework of the general laws of evolution. Most previous research on brachyuran evolution considered only a single suite

(usually external morphology) of characters and was frequently undertaken outside the context of a contemporary theory of evolution.

2. Brachyuran ancestors and forms transitional between the Brachyura and other groups of decapods have not been identified with certitude and the origin of the group remains uncertain.

3. The genesis of the new organization (brachyurization) has involved a great advance over the other decapods. This process is connected with increasing differentiation of the segments and their appendages and with maximal integration caused by the concentration of the segments. The result of these changes is an improvement of organization to a higher level. The process started with the flexion of the abdomen under the cephalothorax, and proceeded with shortening, broadening and depressing of the cephalothorax. The associated changes of the organs and the organ systems caused far-reaching structuro-functional modifications and the entire organization rose to a higher grade.

4. The attainment of this new organization enabled a large adaptive radiation connected with the occupation of new habitats and associated modifications of shape, structure and habits. The majority of the crabs evolved in typical brachyuran fashion, while a minority more or less specialized on limited environments, becoming aberrant and, in some cases, underwent regressive evolution.

5. All the aforementioned modifications are connected with changes in the biotope and mode of life. The existence of orthogenesis cannot be confirmed.

6. These investigations were necessary to clarify the most elementary processes, establishing the limits reached by crab evolution. Consideration of the principal features of brachyuran evolution is a necessary prerequisite to studying the phylogeny of single sub-groups.

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