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REVISION OF THE CALAPPIDAE

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SUMMARY

The brachyuran Calappidae *sensu* Balss (1957) is composed of three subfamilies, Calappinae, Matutinae and Orithyinae. However, an examination of the history of the comprehension of these three groups shows that they have been interpreted in various ways. From critical re-examination of Balss's diagnosis and from reconsideration of all available data, it can be concluded that because of the considerable differences in shape, structures and functions of adults and larvae, as well as their mode of life, these three groups, in spite of their several similarities, are not closely related, as believed before, and therefore their unity on a higher systematic level is questionable. The available data permits the conclusion that these three groups form separate well-delimited families, as originally stated by Ortmann (1892), i.e., Calappidae De Haan, 1833, Matutidae De Haan, 1833, and Orithyiidae Dana, 1852.

Introduction

As with all animal taxa, the brachyuran family Calappidae (*sensu* Balss, 1957), has been interpreted systematically in various ways. Comprehension of its status and position has varied from author to author. The group has been considered to be either a family or a superfamily, and it is interesting that for more than 140 years its sub-groups have been classified together, implying their close affinity. Because of increasing overall knowledge of crab biology, as well as theories of systematics and evolution, it is necessary from time to time to re-examine earlier concepts and test their conformity to modern views of science. Accordingly, I here present a solution of the problem posed by the calappids.

Balss (1957), in the last great monograph on decapod Crustacea, included in the family Calappidae Alcock, 1896 three subfamilies: Calappinae Alcock, 1896; Matutinae Alcock, 1896; Orithyinae Ihle, 1918. However, neither all previous authors, nor all subsequent ones, have invariably accepted such a classification, and so it is better at the outset to give a historical review of the knowledge of these groups from a systematic point of view.

The first classification of higher taxa that included calappids as such was that of de Haan (1833), who distinguished within the Oxystomata two relevant families, Calappidea and Matutoidea. Shortly after, H. Milne Edwards (1837) distinguished within the Oxystomata the tribe Calappiens comprising of the genera *Calappa*, *Platymera*, *Mursia*, *Orithyia*, *Matuta* and *Hepatus*. Macleay (1838) united the families Calappidae and Matutidae into one systematic unit—stirpe Calappina. Dana (1852) distinguished again within the subtribe Leucosoidea two relevant families, Matutidae and Calappidae, with two subfamilies within the latter, Calappinae and Orithyinae. Miers (1886) accepted the classification of Dana and further divided Matutidae into two subfamilies, Matutinae and Hepatinae. Ortmann (1892) established the subdivision Calappinea, composed of three families: Calappidae, Matutidae, and Orithyiidae. Alcock (1896) united all these groups into a single family Calappidae, with two subfamilies, Calappinae and Matutinae; the subfamilies of Miers thus were reduced to the status of alliances, i.e. Calappoida, Orithyoida, Matutoida and Hepatoida. Later, Ortmann (1901) subdivided the Calappidae into three subfamilies: Calappinae, Orithyinae and Matutinae. The latter classification was accepted by Borradaile (1907), Ihle (1918), and Balss (1957), as mentioned before. It is noteworthy that Ihle, after detailed morphological analysis, although accepting the latter classification, has expressed a doubt about the inclusion of *Orithyia* within Calappidae. Glaessner (1969) first used the category of superfamily, Calappoidea, for this group, but included in it only the family Calappidae, with two subfamilies, Calappinae and Matutinae. Recently Guinot (1978) has radically revised this group, excluding from it *Hepatus* and allied genera, and has included in the superfamily Calappoidea two families, Orithyiidae

and Calappidae, the latter composed of Calappinae and Matutinae. Most of the authors have placed these families in Oxystomata, either at the beginning or at the end of the brachyuran system. Only Guinot (1978) has rejected the Oxystomata as a taxon, and has established her own classification in which Calappoidea are placed in Heterotremata, and at the beginning of the phylogenetic scheme, following only Dorippoidea.

Having considered the historical development of the conceptions of the group, we can now pass to analysis of similarities and differences, and then set down a conclusion.

The unity of the groups considered is based on their common characters, which are as follows: front narrow; orbits incomplete; antennulae obliquely plicated; antennal basal article large; antennal flagella reduced in size; endostome elongated and epistome very much reduced; exostegal channel (formed by pterygostome and chelipeds) exists; inhalant respiratory openings in the front of the basis of the chelipeds; coxae of Mxp_3 enlarged on basis and placed on the entrance of inhalant opening; exhalant respiratory opening near and beneath the front; endopodite of first maxilliped forms the ventral floor of the exhalant channel; chelipeds pressed tightly against the anterolateral part of the carapace; male abdomen composed of 5 segments (3–5 fused), that of the female of 7 segments; sterno-abdominal cavity well developed; male sexual opening coxal; first pair of male pleopods with simple top; second pair of male pleopods long; female sexual opening sternal; 9 branchiae on each side.

Moreover, there are also similarities between the particular groups when considered in pairs:

Calappa–Matuta. (Pseudo)rostrum absent; orbital fissures present; supra-orbital tooth absent; antennulo-orbital septum present; antero-lateral spines absent (in some genera epibranchial spine present); longitudinal respiratory gutter on the endostome present; last part of the exhalant channel covered by the elongated endopodite of the third maxilliped; retaining mechanism of the abdomen present.

Matuta–Orithyia. Merus of third maxilliped elongated and acute; palp of the exopod of the third maxilliped absent; inhalant opening at the ocular cavity; last pair of walking legs paddle-like; sternum flat and rounded; episternites present; a part of 8th sternite visible from above.

Orithyia–Calappa. Third maxilliped does not cover completely the mouthparts; palp of third maxilliped not concealed by merus joint.

In order to better illuminate the similarities and differences between the three groups, we shall here adopt the method of considering some parts of the body as morphological-physiological and adaptive unities, since the shape of an organism depends, according to Hadži (1944), upon its organisation, (macro) habitat and mode of life. But at the outset it must be noted that although the mode of life of *Calappa* and *Matuta* is known to some degree, that of *Orithyia* is completely unknown. Concerning the habitat, all three groups occur mostly in shallow littoral waters, sometimes in tidal flats; exceptionally, some calappids enter deeper waters. They usually occur on sandy or sandy-muddy bottoms, with or without sea grass (Klunzinger, 1906; Thomassin, 1974; Mergner and Schumacher, 1974; Seidel, 1976; Hong, 1976; Basson et al., 1977).

Insofar as the mode of life includes the mode of locomotion, feeding, respiration, defence, reproduction, orientation and regulation (Štević, 1974), we shall be able to analyse only some of these, but the data should be sufficient to show the principal similarities and differences important for our considerations.

Respiration

The mode of respiration is very different in these groups.

Calappa

The respiration of *Calappa* was described in detail by Garstang (1897). The direction of respiratory currents is very complicated, and in the first (afferent) part is connected with the function of the chelipeds. The chelipeds are very heavily developed and flattened, and in flexion are pressed tightly against the pterygostomial region of the carapace, completely covering the mouthparts, leaving only a slit between the upper anterolateral margin of the carapace and the serrated crest of the upper margin of the chelipeds. The inner face of the propodus is smooth and slightly concave, and is closely apposed to the pterygostomial region, forming an accessory channel—the “exostegal channel” of Garstang (1898). The serrated upper margin forms a sieve for sand particles, and the hairs on the pterygostomial region aid in better filtration of the water. The inhalant apertures are in front of the chelipeds, and are protected by the bases of exopodites of the third maxillipeds, which are furnished with hairs. The exhalant part is formed on the endostome, which has two gutters separated by a septum, directing the exhalant water anteriorly.

The ventral floor of the gutter is the endopod of the first maxilliped, which is not covered by the third pair of maxillipeds; the other mouthparts are not covered completely by these maxillipeds either.

Matuta

The respiratory mechanism of this genus was also described by Garstang (1898). The respiratory water currents enter the orbital cavity, the margins of which are provided with hairs, thus forming a sieve. Afterwards, the water travels down and backwards through the orbital gutter. The first part of the gutter is furnished with long interlocked hairs, and the following portion is covered by the chelipeds, which are closely apposed to the pteryogostomial region. The latter is also covered by a carpet of hairs, as in *Calappa*, with the difference that the chelipeds do not cover all the mouthparts. The gutter becomes less defined in this region, and the water enters into an afferent aperture of the branchial chamber through an auxiliary channel formed by chelipeds and carapace. The exhalant part of the respiratory system is different from that of *Calappa*. The exhalant opening is underneath and near the front, and the endostomial gutter is not divided. Moreover, the endopod of the first maxilliped which forms the floor of the exhalant channel is completely covered by the third maxilliped—so completely that its palp is also concealed in the special groove. The flagellum of the exopod is also reduced.

Orithyia

As with *Matuta*, the inhalant water current enters the orbital cavity, which is furnished with marginal hairs. Subsequently, the current follows a different course from that in *Matuta*. The orbital gutter is situated between supra- and suborbital spines, and is covered by the usual hairs in this group. This first part is very short, and it is immediately covered by enlarged inner parts of the meri of the chelipeds, which are smooth, enlarged and flat. On the anterior part of this plate is a small groove. Many hairs on the outer margins of this plate enhance water filtration. The exhalant current is again different from those of the two previous species. The water passes through a tunnel, a special structure of the endostome, which opens near the front. The exhalant aperture is again protected by many long hairs. The first maxilliped is short, but serves also as the floor of the respiratory channel. The exhalant orifice is not covered by the third maxilliped, and the latter is not long and does not cover completely other mouthparts.

Locomotion

Calappa

All walking legs of this crab are unmodified and lack specialised structures. This means that they are used only for more or less sideways movements.

A special feature of this group, however, is the ability to bury in the substrate. The crab buries itself by means of the chelipeds (Schmiedlein, 1879; Schäfer, 1954), and remains partly buried so that only the anterior portion of the body protrudes from the sand bottom.

Matuta

This genus differs from all other crabs in having all legs modified into paddles or spades, especially the enlarged terminal articles of the second and fifth pairs. These crabs can swim, using all walking legs, but the second and the fifth pair are especially efficient in this mode of locomotion. Although all authors agree that they are able to swim, opinions differ on whether they can swim quickly or not. Some earlier authors such as Klunzinger (1906) cite others to the effect that they can swim very slowly, but later researchers, such as Seidel (1976) and Basson *et al.* (1977), claim that they can swim very rapidly. Moreover, these crabs have been observed swimming near the surface (Delsman and de Man, 1925). In Ras Burqa (Red Sea, near Eilat), however, I have observed *Matuta lunaris* swimming slowly in water only about several centimeters deep over the sand. The same observation has been made by Dr R.G. Wear in Hong Kong (pers. comm.). Additional observations on different *Matuta* species need to be performed in the field.

These crabs exhibit the ability to bury themselves backwards very quickly in the sand (Seidel, 1976; Basson *et al.*, 1977). For this they use the paddle-like legs. As with *Calappa*, they only partly embed in the substrate. It is interesting to note that Seidel (1976) and I observed *Matuta*, just as with *Calappa* (described by Schäfer, 1954), vigorously throwing out a jet of water mixed with sand immediately after digging in.

Orithyia

Locomotion in *Orithyia* is totally unknown.

Feeding*Calappa*

Those parts of the feeding complex (Štević, 1967) that have been analysed here include food, chelipeds and stomach structures. The feeding of *Calappa* has been described in detail by Shoup (1968). It feeds upon molluscs, and also upon hermit crabs protected in gastropod shells. This has been confirmed by Thomassin (1974). The claws of *Calappa* are somewhat different in size and have differing dentition on the occlusive surface. The right claw is usually the stronger one and is provided with a special crushing tooth (*Klöppelzahn* in Schäfer, 1954) that is used for destroying the shells of prey: it is the 'crusher claw'. The left claw is smaller, with more or less equal teeth; it is a 'cutter' or 'pincer'. Especially relevant stomach structures are the meso-cardiac (dorsal) teeth and a pair of lateral teeth of zygocardiac ossicles. The type of stomach structure is similar to that of the great majority of Oxystomata and Cyclometopa (Nauck, 1880), and is of a Platystilidea type, i.e. the dorsal tooth has no sharp ridges. The anterior (cusp) of the lateral tooth is very robust and strong. On the ventral part of the tooth there are many ridges, and on the ventral margin there are two ill-defined lobes.

Matuta

The manner of feeding of *Matuta* is poorly known, and the data are somewhat contradictory. Thomassin (1974) reported that the main food of *Matuta* is gastropod and bivalve molluscs, while Seidel (1976) observed that *Matuta lunaris* feeds on marine plants. However, my examination of the stomach contents of *Matuta lunaris* from the Red Sea (Ras Burqa) revealed the following components in eight specimens: sand (7); Polychaeta (5); undetermined organic matter (5); Decapoda: Natantia (4); Decapoda: Brachyura (4); vascular marine plants (2); Amphipoda (2); Gastropoda (2); Pagurida (1); Copepoda (1). From this, it is clear that *Matuta* is a very active predator within its surrounding area on the sand substrate. It is also an omnivorous species, with a preference for higher caloric animal food. Further knowledge will require continued observations on its food selection. The claws of *Matuta* species are symmetrical (i.e. monomorphic) and in this connection functionally identical, so that during feeding, the crabs use them alternately. It is interesting to note that all of my 12 male specimens from the Red Sea have chelipeds a little different in size. The teeth of the occlusive surface of the claws are very different in form and size, and likely have various functions, since crab claws, as established by Brown *et al.* (1979), are polyfunctional organs. The stomach ossicula are very similar to those of *Calappa*, although there are some differences. The tooth of the zygocardiac ossicula is not robust, but narrow and elongate, with a great number of sharp ridges. Two ventral lobes are only feebly developed.

Orithyia

The food of this crab is not known, but it will be useful to describe its chelipeds and stomach structure. The chelipeds in both sexes are different in size, the right chela being greater than the left one. On the bigger claw there are various types of teeth, and one tooth (crusher) is bigger than the others. The teeth of the big claw are not laterally compressed on the top; they are equally wide at base and top. On the smaller claw the teeth are unequal and are laterally compressed on the top. The stomach is generally similar to those of the crabs described earlier. The dorsal tooth (medio-cardiac) is relatively very robust. The lateral teeth also have well developed anterior cusps, the dorsal ridges are not numerous, and two ventral lobes are a little stronger and extend over all the ventral margin of the tooth. Altogether the teeth are all robust, and the food of this crab might be expected to be sturdy.

Defence

The main organs of defence (and attack), as in all other crabs, are the chelipeds. These are very efficient in *Calappa* (Schmiedlein, 1879) and in *Matuta* (pers. observation). Although in *Orithyia* there are no direct observations from the field, there is no doubt that they use the chelipeds in defence. Moreover, in order to protect themselves they are able to bury into the (sedimentary) bottom on which they occur. Doubtless, the bigger body size of adults of some *Calappa* species and of *Orithyia*, as well as lateral spines of *Acanthocarpus*, *Matuta*, and to some degree of *Orithyia*, contribute in their defence against potential predators. Concerning the colour in the genera mentioned, it is impossible to suggest without direct field observations of their habits in the natural habitats, whether or not it is cryptic.

Reproduction and development

The reproductive complex of these three groups is still insufficiently known. The reproductive behaviour of all of them is not yet known. There are only some data concerning larval development. In the older literature there are some data concerning the genus *Calappa* and one reference to *Mursia* (Raja Bai, 1959; Motoh, 1977). The zoeal stages of *Matuta* were first described by Raja Bai (1959). She pointed out some differences between the larvae of *Calappa lophos* and *Matuta lunaris*, but without making any systematic inferences. Recently, Hong (1976) described all three zoeal stages of *Orithyia sinica*. From the description it is clear that larvae of *Orithyia* are very different from those of the other crabs, especially in the shape of rostrum and telson. But the differences between *Matuta* and *Calappa*, although notable, are not as remarkable as with *Orithyia*. It is very difficult to evaluate these differences and derive systematic consequences, because only the larvae of some of the crabs are known, and the functional meaning and systematic value of some structures remains unclear.

General Discussion

From the above it can be seen that the mode of life, and many structures and functions, both of adults and of larvae, are insufficiently known or completely unknown, and therefore it is very difficult to assess completely their systematic status and phylogenetic importance. Subsequent examinations will doubtless reveal a number of similarities, but especially differences, as has already been seen in the work of Ihle (1918) and of Guinot (1979). However, even a non-specialist can see at first glance, that these three groups are basically different. *Calappa* and related genera (*Mursia*, *Acanthocarpus*, *Paracyclois*, *Cyclôes*, *Platymera*) are recognisable by means of their broadened carapace, specific shape and form and position of chelipeds; *Matuta* species by the fact that all walking legs are transformed into paddles; and *Orithyia* by the rounded carapace, fifth pair of walking legs transformed into paddles and specific form of cheliped. *Calappa* with related genera are adapted specifically to burying, *Matuta* to burying-swimming using all walking legs, and *Orithyia* can probably bury and maybe swim. Their shape and structures could be understood only in connection with these key adaptations, which are, as we have seen, different.

In the organisation of these three groups there are several structures whose function is not clear, e.g. flat and rounded thoracic sterna *Orithyia* and *Matuta*, the episternites, or postero-lateral vault-like expansion of the carapace over the walking legs of *Calappa* and others. Nevertheless, we can see that in all the vital functions we have considered there are differences.

Although at the beginning of the analysis of these groups some similarities were pointed out, a large number of them (e.g. position of genital openings, number of branchiae, incomplete orbits, etc.) are not specific to these three groups, but are well-known to be common among many groups of Heterotremata. Many similarities can be considered to be convergences arising from adaptation to similar mode of life (e.g. respiratory systems). The differences are also numerous. Most of them have been mentioned before in connection with analysis of their mode of life. Furthermore, a great number of differences occur in some structures analysed earlier by Ihle (1918) and by Guinot (1978) (front, orbits, anterolateral spines, retaining system of abdomen, thoracic sternum, female genital opening, etc.). These facts show that the differences are very numerous, especially between the *Orithyia* and the other two groups, and to a lesser degree between the *Matuta* and *Calappa* with related genera. It can be concluded that these three groups are morphologically, physiologically and ecologically so different that they should not be accommodated within a single family, and that they represent three quite distinct families: Calappidae de Haan, 1833; Matutidae de Haan, 1833; and Orithyidae Dana, 1852, as established by Ortmann (1892). Unity on a higher systematic level is somewhat questionable because their differences are very considerable.

Their evolution is very obscure, but there are some indirect indications of their evolutionary trends, seen for instance in their fossil records, geographical distribution, and diversity. Concerning the palaeontological evidence their fossils are not numerous, and those known need revision. They are, however, relatively old groups. The first Calappidae are known from Eocene, Orithyidae from Cretaceous (Albian, Turon), and Matutidae from the Miocene.

Their geographical distribution is rather limited. *Orithyia* is known only from Chinese waters, from Korea (Hong, 1976) to Hong Kong (A. J. Bruce, pers. comm.), and *Matuta* in tropical waters, chiefly of the Indo-Pacific region. Only calappids have a wide distribution in temperate and tropical waters of the Indo-Pacific, Eastern Pacific and Atlantic Oceans.

The number of subtaxa is very limited. Orithyiidae has only one species, Matutidae only one genus with about ten species, and Calappidae has six genera with about forty species.

These facts suggest that the evolution of these three groups has not been particularly successful, and that they have remained, in Mayr's (1969, p. 595) terms, only a limitedly successful 'evolutionary experiment', because after the occupation of the present adaptive zone, subsequent adaptive radiation has not occurred. For a better illustration of these terms, I would like to quote Mayr's statements that: "Each major shift of habitat is an evolutionary experiment" (p. 595) and later "However, not all such shifts are equally successful. No spectacular adaptive radiation has followed the invasion of the sand niche by a coelenterate. The shift of a carnivore (Giant Panda) to herbivorous diet has not led to a new phylogenetic breakthrough" (Mayr, 1960). The same could also be said for the three groups under consideration here in which each of them occupied its own "structural-functional and adaptive zone" (Simpson, 1963, p. 26) which is indeed, particular and peculiar, and therefore they occupy an isolated position in the system of the brachyuran crabs. Their "evolutionary experiments" to occupy new adaptive zones were also of limited success, as is evident from their limited diversity, distribution and also abundance and biomass. However, these three groups do not represent an isolated case in the brachyuran crabs. On the contrary, there are a great number of taxa with a very low number of subtaxa, for instance Dorippidae, Palicidae, Retroplumidae, Belliidae, Thiidae, Pirimelidae, Mimilambridae, Mictyridae, and others. On the other hand, some brachyuran taxa as Xanthidae, Majidae, Portunidae, Leucosiidae, Pinnotheridae, Potamidae, Grapsidae and Ocypodidae were extremely successful, having a great number of subtaxa, especially species, with high expressed biomass, abundance and distribution.

Conclusions

All available data show that the Calappidae *sensu* Balss (1957) are not a homogeneous, i.e. natural, group-taxon. *Calappa*, *Matuta* and *Orithyia* and their related genera form at least three separate families, as originally stated by Ortmann (1892). Future examination not only of these three groups, but also of all other crabs, with special attention to their habitat and way of life, will permit the reorganisation of brachyuran systematics and phylogenetic trees. This, however, must await future investigations.

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