THE IDENTITY OF *HIPPA CAERULEA* RISSO, 1816: AN ISOPOD IN MOLE CRAB'S DISGUISE

BY

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Until now, the identity of the Mediterranean crustacean described by Risso (1816) as *Hippa caerulea* has never been adequately ascertained. The only conclusion appears to be that it is not a hippid crab (Decapoda, Anomura, Hippoidea, Hippidae), as no revision of hippid crabs has included this species (Miers, 1878; De Man, 1896), and no species of *Hippa* has ever been subsequently recorded from the Mediterranean. The only published suggestion as to its true identity was made by Holthuis (1977), who placed it in synonymy with *Albunea carabus* (Linnaeus, 1758) (Hippoidea, Albuneidae). In doing so, Holthuis (1977: 62) admitted that Risso's species "has several aspects which do not agree with [*A. carabus*]". In fact, an examination of the descriptions of Risso (1816, 1827) shows that *H. caerulea* substantially differs from *A. carabus* in color, morphology, size, habitat and behavior and, as such, cannot be considered conspecific with that taxon. However, many of the characters of *H. caerulea* agree with those of female isopods of the genus *Gnathia* Leach, 1813. A comparison of the components of Risso's (1816) description of *H. caerulea* to gnathiid isopods is given below in support of this hypothesis.

Risso (1816: 50-51) described *Hippa caerulea* as follows (also in translation from the French):

> "Il n'est point d'espèces de paguriens sur lesquelles un certain luxe de couleur ne se fasse plus ou moins remarquer. Cette hippe diffère de celles qui sont connues, par la forme alongée de son corps, par sa couleur jaunâtre sur son pourtour, et d'un beau bleu d'outre-mer au milieu. Son têt est ovale, oblong, échancré sur le devant. Les yeux sont placés sur des pédicules courts. Les antennes extérieures sont grosses, les intérieures courtes. La bouche est entourée de petits palpes soyeux. L'abdomen est glâbre. La première paire de pattes a ses articles un peu plus larges que ceux des autres paires, lesquelles sont dépourvues de crochets. Les écailles natatoires qui sont au bout de la queue sont terminées par une pointe recourbée en-dessous. La femelle m'est inconnue.

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A mesure que les naturalistes français soumettent à l'observation les êtres qui vivent autour d'eux, on voit s'accroître le nombre des espèces des divers genres que la nature sembloit avoir rélégués dans les contrées les plus reculées de l'Europe. la hippe que j'ai trouvée dans nos mers ne vit point en parasite sur les huîtres de nos rochers, mais elle se cache seulement dans les trous extérieurs de ces bivalves. Ayant mis plusieurs fois des hippes à la surface de l'eau, j'observai qu'elles descendoient promptement au fond, et qu'aussitôt qu'elles touchoient la coquille, elles la parcouroient en tout sens avec une vélocité extraordinaire. Quand je les irritois avec une paille, loin de s'échapper, elles venoient au contraire audevant, l'entouroient de leurs bras, et la pressoient fortement. Actifs, voraces et courageux, ces petits crustacés conservent toutes ces qualités, même quand il y a long-temps qu'ils ont été retirés de leur élément."

[There are no pagurid [sic] species on which a certain abundance of color is not more or less noticeable. This hippa differs from those that are known by the elongated form of its body, by its yellowish color on its periphery, and a beautiful ultra-marine blue in the middle. Its shell is oval, oblong, crescent-shaped on the front. The eyes are placed on short peduncles. The external antennae are large, the interior short. The mouth is surrounded by small setose palps. The abdomen is smooth. The first pair of legs has its articles a bit broader than those of the other pairs, which are deprived of hooks. The swimming scales [uropods] that are at the end of the tail are ended by a ventrally recurved point. The female is unknown to me.

As fast as French naturalists have observed creatures that live around them, one sees the number of species increase of the various genera that nature appears to have relegated to the most distant regions of Europe. The hippa that I have found in our seas does not live at all parasitic on the oysters of our boulders, but only hides in external holes of these bivalves. Having put several times these hippas to the surface of the water, I observed that they descend promptly to the bottom, and that as soon as they touched the shells, they ran around it in all directions with an extraordinary speed. When I irritated them with a straw, far from escaping, to the contrary they came ahead, surrounding it with their arms, and squeezed strongly. Active, voracious and courageous, these small crustaceans have all these qualities, even when they have been pulled out of their element for a long time.]

The color of these animals is the first characteristic noted by Risso (1816) and, indeed, it is one of the four characters he gives ("in medio caerulea") to diagnose the species. This color pattern is certainly not that of a hippid crab, as species in that family are invariably either uniform in color, or possess a banded, mottled appearance (Boyko, unpubl.), but are never blue. Holthuis (1977) suggested that this color "fit rather well for *Albunea carabus*", but in point of fact, that species is a dark purplish-brown color which is evenly distributed across the carapace (Rubió & Holthuis, 1976). However, note the similarity between the color given by Risso (1816) for *H. caerulea* and the following description by Bate (1858: 171) of a pre-ovigerous female gnathiid isopod:

"I . . . perceived, after a few days, that the blue mass, which first appeared to fill and distend the large segment of the pereion, gradually diminished, apparently deteriorating. It recedes first from the margin. In so doing it displays a series of layers, placed one before the other, lying across the animal."

And this from Bate & Westwood (1868: 184), also regarding a gnathiid:

> "In the earlier period of its parasitic life, the female takes a green color, which at a later stage deepens into a bright blue."

When taken together, these descriptions match with a surprising degree of accuracy the color description of *H. caerulea* by Risso (1816). But what of the other characteristics of *H. caerulea*?

The morphological description of Risso (1816) is limited at best. The shape of the carapace ("oval") fits species of *Hippa* well (fig. 1A), but not *Albunea*, as those species are invariably subquadrate in appearance (Boyko, in prep.). Male gnathiid isopods are in no way oval in appearance, but females (fig. 1B-D) can be extremely ovate, sometimes elongate, and remarkably *Hippa*-like in overall shape for an isopod. Risso's (1816) description of the eyes as "on short peduncles" does not fit a *Hippa*, nor an *Albunea*, but might well fit a female gnathiid if the pronounced lateral bulge of the eyes was described with improper terminology. The morphological features which most clearly excludes *H. caerulea* from either *Hippa* or *Albunea* are the antennae and antennules. Risso (1816) described them as being large externally (antennae) and short interiorly (antennules). The exact opposite is found in both *Hippa* and *Albunea*, where the antennules are elongated and, in *Albunea* at least, used as a breathing tube in the sandy habitats which they favor. Additionally, the antennae and antennules of *Hippa* and *Albunea* are not morphologically similar and likely to be confused; they are also placed relatively

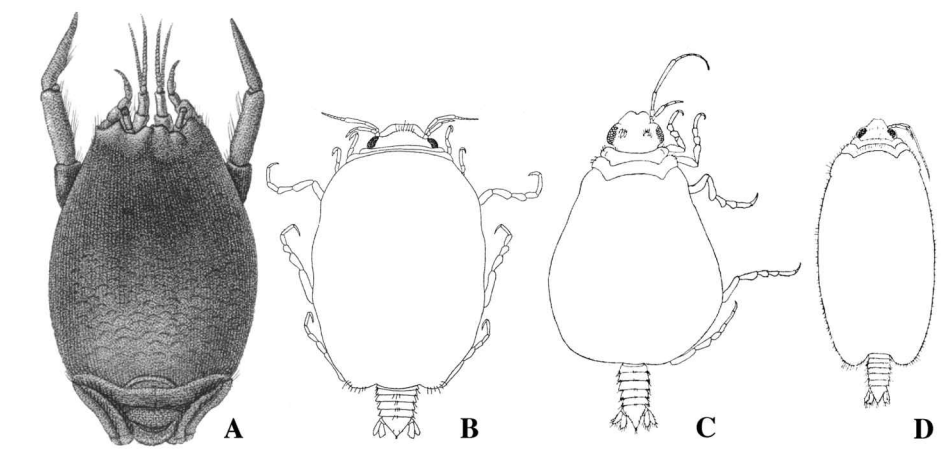

Fig. 1. A, *Hippa adactyla* Fabricius, 1787 (from H. Milne Edwards, 1837, pl. 21 fig. 14); B, *Gnathia maxillaris* (Montagu, 1804), female (after Monod, 1926, fig. 235); C, *Gnathia phallonajopsis* Monod, 1925, female (from Monod, 1926, fig. 197A); D, *Gnathia phallonajopsis* Monod, 1925, female (from Monod, 1926, fig. 198A). Note: figures not to scale.

far apart on the front of the animal. Gnathiid isopods have longer antennules and shorter antennae also, but they are quite similar, other than in length, and placed close together. This may have lead Risso (1816) to a misinterpretation of which structure was external. Risso's (1816) description of the mouthparts and abdomen could apply to many crustaceans, and fits hippids, albuneids, and gnathiids equally well. The first periopods, described by Risso (1816) as with broader articles and lacking claws, agree with the genus *Hippa*, but not *Albunea*, which has subchelate first periopods. Gnathiid isopods have simple dactyli as well, but their "first" legs (actually the second pair as the first pair are modified into an opercular mouthpart) are not markedly larger than the other pairs. However, the third pair of legs is slightly longer than the others in female gnathiid isopods, and often appears longest in dorsal view. It is of interest to note that gnathiids have only five pairs of locomotory appendages, whereas most isopods have seven. This, as will be expanded on later, may be part of the reason that Risso (1816) grouped his species *caerulea* with decapods rather than isopods. The final morphological detail given by Risso (1816) concerned the "swimming scales" (= uropods). In *H. caerulea* they are described as ending in an "ventrally recurved point", which does not agree with the uropods of *Hippa* or *Albunea* which are entirely smooth at the margins. However, gnathiid isopod uropods are often serrate in appearance, although not curved down nor pointed. This discrepancy may again be the result of Risso's (1816) poor use of descriptive terminology. The size given for *H. caerulea* ("long. 0,012 larg. 0,004" or 12 × 4 mm) is also far too small for an adult hippid or albuneid, but is well within the size range for female gnathiid isopods.

The habitats for *H. caerulea* given by Risso (1816) are also anomalous for a hippid or albuneid crab. Hippid and albuneid crabs are always found in sandy bottom habitats, where they burrow backwards using their hind legs. As their legs are so strongly modified for digging, they are poor swimmers. Risso's (1816) species lived in the crevices between bivalve mollusks, probably *Spondylus gaederopus* Linnaeus, 1758 (Risso MS, fide Holthuis, 1977). In contrast to hippoids, gnathiid isopods are often found "in crevices of rocks" (Bate & Westwood, 1868).

Perhaps the most decisive element in determining the correct identity of *H. caerulea* is found by noting where the species was placed in the classification of Crustacea by Risso (1816). Risso (1816) listed this species as one of only two in his "Troisieme [sic] famille. Paguriens. I. Mains adactyles" without providing any diagnostic features for any of these categories. The other taxon in the "Mains adactyles", *Anceus forficularius* Risso, 1816, is clearly a gnathiid isopod as illustrated by Risso (1816, pl. 2 fig. 10). The genus *Anceus* Risso, 1816, is a synonym of *Gnathia* Leach, 1813, and *A. forficularius* has been considered one of the gnathiid "espèces Méditerranéennes indéterminables" (Monod, 1926),

due to Risso's (1816) exceedingly poor description. If Risso (1816) thought that *H. caerulea* and *A. forficularius* were related, this would explain his statements "la femelle m'est inconnue" [the female is unknown to me] and "la hippe que j'ai trouvée dans nos mers ne vit point en parasite sur les huîtres de nos rochers" [the hippa that I have found in our seas does not live at all parasitic on the oysters of our boulders]. It is not likely that he would make this mention unless he was aware of some type of secondary sexual dimorphism in this group, much the same as is found in gnathiid isopods. Secondary sexual dimorphism is hippids was not appreciated until much later (e.g., MacGinitie, 1938; Efford, 1967), and is not strongly developed in the genus *Hippa* itself. Secondary sexual dimorphism has not been well-documented in the Albuneidae, although it occurs there as well, albeit not as dramatically as in some hippids (Boyko, in prep.). In contrast, the marked sexual dimorphism of gnathiids has been known since the mid-1800s. Risso (1816) also remarked that his species was not parasitic in the local "oysters", but rather hiding in holes externally. This indicates his awareness of a typically parasitic lifestyle for these animals elsewhere. Gnathiid isopods have both strong sexual dimorphism and parasitic juvenile stages (praniza larvae) and it would be logical for Risso (1816) to comment on the lack of females in his material if he thought he was dealing with this type of crustacean. Hippid and albuneid crabs are, of course, all free-living species. The clinging behavior of the animals noted by Risso (1816) would also be in keeping with a species with an exoparasitic lifestyle and one adapted to cling to passing larger objects in search of hosts.

Careful examination of the morphological, behavioral, and habitat characteristics of *H. caerulea*, as described by Risso (1816), in conjunction with Risso's (1816) close association of this taxon alongside *Anceus*, a known gnathiid, suggests that Risso (1816) was dealing with the male and female forms of *Gnathia.* Risso later (1844) also used the name *Praniza* Latreille, 1817, for larval gnathiids, as clearly shown by his then-unpublished figures (see Monod, 1931). Risso (1816) was not the only author to apply different generic names to the males, female, and larval stages of gnathiid isopods. Montagu (1804) described a male gnathiid as *Cancer maxillaris* and later (1813) described the female of the same species as *Oniscus caeruleatus* (see also Monod, 1926). Note from the specific name of Montagu's (1813) species that Risso (1816) was obviously not the first author to remark on the striking color of these animals.

Clearly, Risso (1816) identified the male gnathiids as one species (*A. forficularius*) and the females as another (*Hippa caerulea*), thinking them two related but generically distinct taxa, as did most other authors of the early-to-mid 1800s (e.g., Bate, 1858). The females he had were not ovigerous, as they had the blue color of the pre-ovigerous condition (Bate & Westwood, 1868). The lack of eggs is undoubtedly another reason why Risso (1816) thought he had no females.

But why, if *caerulea* is a gnathiid isopod, did Risso (1816) place it in the genus *Hippa*? All evidence indicates that Risso (1816) severely misinterpreted the generic definition of *Hippa* Fabricius, 1787. There were few published illustrations of hippid crabs in 1816, and none identified as being *Hippa*, so Risso (1816) had nothing to compare his material to except the brief Latin description of Fabricius (1787). The genus *Hippa* is typified by the species *adactyla* Fabricius, 1787, by subsequent designation of Rathbun (1900). That Risso (1816) should misinterpret the genus *Hippa* in some fashion is not surprising, given that most 19th century authors used the generic name *Remipes* Latreille, 1806, for this genus and incorrectly used *Hippa* for those mole crabs now correctly called *Emerita* Scopoli, 1777. What is suprising is that *Hippa* could be so extensively misinterpreted that it was thought to belong in the Isopoda, regardless of the vaguely hippoid appearance of the female gnathiids and their possession of five pairs of legs.

Later authors (Risso, 1827, 1844; Hope, 1851) merely repeated the citation of Risso (1816), and made no comments on the identity of *H. caerulea*. Risso (1827) placed this taxon correctly (for a *Hippa*) in the first section of the "famille décapodes macroures", while placing four *Praniza* species father back in "fourth" [actually, the ninth] section of his book. However, given Risso's history of mistakes and inaccuracies, it is not improbable that he merely moved the species to the section where the genus *Hippa* was correctly and unambiguously placed by other authors (e.g., Latreille, 1817), and that this change of placement involved no critical analysis of the identity of the taxon in question. Risso (1844) still placed the gnathiid isopods with the Decapoda, presumably due to their shared possession of five pairs of legs. Hope (1851) included all of the species of Risso (1816, 1827, 1844) in his list of Mediterranean taxa, including the seven nomina nuda species of *Praniza* first introduced by Risso (1844). Hope (1851) also considered the males and females of gnathiids to belong to different genera (*Anceus* and *Praniza*), but correctly recognized that both were isopods. The aberrant habitat of *H. caerulea* cited by Risso (1816) led Hope (1851) to include this taxon in the Paguridae under the heading "Malacosomata Conchophila". Holthuis (1977) correctly concluded that Risso's (1816) species could not be a hippid crab, but was mislead by Risso's (1816) generic placement into thinking that it was a crab at all, and placed *H. caerulea* in synonymy with *Albunea carabus*.

So, in the same way that other early authors used *Gnathia* for the male isopods and *Praniza* for the females (see Monod, 1926), so Risso (1816) used *Anceus* for the males and *Hippa* for the females. Although it is clear that Risso (1816) was dealing with a female gnathiid isopod, it is not possible to identify the species of gnathiid he had, due to the poor nature of his description. Unless type material becomes available, which is unlikely, I suggest that *Hippa caerulea* Risso, 1816, be considered a synonym of *Gnathia* sp. cf. *phallonajopsis* Monod, 1925.

Although *Gnathia maxillaris* (fig. 1B) is a European species which is also known to have a bright blue pre-ovigerous coloration in females (Bate & Westwood, 1868), it has not often been recorded from the Mediterranean (Monod, 1926) and is considerably smaller (cf. 4 × 2 mm) than the size given by Risso (1816) for *H. caerulea*. Of the eight known Mediterreanean gnathiid taxa (see Monod, 1925), the one which matches the morphological description of *H. caerulea* best, and is closest in size (cf. 7.5 × 3 mm) to Risso's (1816) given measurements for females, is *G. phallonajopsis* Monod, 1925 (fig. 1C, D). An abbreviated synonymy of *G.* sp. cf. *phallonajopsis* is given below (see also Monod, 1926).

Gnathia sp. cf. **phallonajopsis** Monod, 1925

cf. *Gnathia phallonajopsis* Monod, 1925: 5-6.
Hippa caerulea Risso, 1816: 50-51. — Desmarest, 1825: 424. — Risso, 1827: 36-37.
Hippa coerulea [sic]: Risso, 1844: 94.
Hippa coerulea [sic]: Hope, 1851: 12.
cf. *Gnathia phallonajopsis*: Monod, 1926: 463-470, figs. 195-199 (synonymy).
Albunea carabus: Holthuis, 1977: 61-62 (not *Albunea carabus* (Linnaeus, 1758)).

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