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# THE CARDIAC NOTCH IN DECAPODS

# Fenner A. Chace, Jr. and Brian Kensley

## ABSTRACT

The 1899 description and discussion by Henri Coutière of the cardiac notch on the posterior margin of the carapace in certain decapods is translated and reviewed, with special emphasis on the alpheids, in which it is usually present, and the otherwise similar hippolytids, in which it is almost invariably absent. The genus *Yagerocaris* Kensley, 1988, is transferred from the hippolytids to the alpheids. Similar notches in other decapod families are deemed not to be homologous, even though the practical importance of the structures described by Coutière continues to defy explanation.

#### GENESIS

The following passages are translated from one of the most remarkable and still only partly exploited doctoral dissertations of all time (Coutière, 1899: 104–106, 290–292) (for index, see Chace and Forest, 1970).

[Pages 104–106]. The carapace of all alpheids, without exception, displays on its posterior margin a detail of more immediate importance, which, until now, seems to have escaped the attention of all describers and is only very rarely illustrated. The character is a deep notch situated on each side of the cardiac region, which is thus precisely delimited.

The posterior margin of the carapace in all of the decapods is characterized by a prominent ridge extending more or less onto the branchiostegites, whose double contour is formed by two nearly parallel lines or only by *evaginations*. In all of the alpheids, without a single exception of which I am aware, the true posterior margin of the carapace shows, in the region where each branchiostegite is separated from the tergum and from the epimeral wall, a deep *invagination*, at the base of which the two contours of the posterior ridge come together (figs. 72, 81, V, as well as figures 326 [356], 327 [357], p. 291).

These notches appear at first to belong to the tergal region, the epimeral wall being reflected on the branchiostegite slightly below the ventral edge of the notch. In reality, the notch, itself, is entirely independent and should be considered as a narrow extension of the branchial chamber. One notes, in fact, a small mass, with a soft wall, directed upward from the carapace, which completely fills the notch on most of the specimens (fig. 326 [356]). It is the equivalent of the "glande péricardique" which Cuénot has shown to be constant in the decapods. Without prejudging the physiological functions attributed to it by that author, I can at least confirm his opinion on the position of this "glande." It is a projection from the body wall, homologous with a gill, and it assumes genuine importance in certain crustaceans.

The cardiac notch, I repeat, is not absent in any alpheid and constitutes almost the most constant feature of the family.

*Amphibetaeus* is one of the genera in which this detail attains its greatest development; it is present also in *Automate* (fig. 81).

Alope, Bythocaris, Caridion, Ogyris have no similar

notch; it is also wanting in all of the "*Natantia*" that I have examined. The only vestige that I have found is in *Hipp. gibberosus* (fig. 82) and *H. marmoratus*, M.-Edwards, where the cardiac notch is quite comparable to the one present in the larvae at the mysis stage of *Synalpheus neptunus* and *A. villosus*. It is worth noting that these hippolytid species show other points of resemblance with several alpheids in regard to the sixth abdominal somite.

This detail of the carapace offers a very reliable criterion for deciding whether or not a eucyphote belongs with the alpheids; moreover, it constitutes an important phylogenetic character. In fact, a similar notch, little modified in form and direction, is found in the schizopods such as *Euphausia (E. pellucida, E. superba, E. spinifera)* (fig. 85), *Thysanopoda (Th. obtusirostris)* (fig. 84), *Nyctiphanes (N. australis)*, forms for which Sars has described and illustrated this notch.

[Pages 290–292]. [Pleosomite 1] constitutes the posterior half of the thoraco-abdominal hinge; its tergum is covered by that of the carapace, while the pleura cover the branchiostegite. As a consequence of this disposition, the tergum of pleosomite I comprises two distinct parts: the larger, in the form of a partial sphere, never bears protrusions and slides easily under the posterior margin of the carapace. The latter is delimited by the cardiac notches that I have described above as very characteristic of the alpheids (figs. 72, 358, 359).

The posterior part of the tergum is reduced to a narrow band that widens progressively on the flanks in passing to the pleura and that is perfectly distinct from the smooth anterior part over its entire extent, thereby giving the illusion of two fused somites. The narrow strip by which this portion of the somite encroaches on the first, instead of being a regular curve as in the other eucyphotes, forms a slight anterior convexity that corresponds to the cardiac notch on the same side and partially covers it (fig. 358).

It is also below this sinuosity that the anterior portion of the somite, in the form of a spherical segment, joins the rest of the tergum. This juncture is covered by the strip in question and is consequently invisible exteriorly; when it is uncovered, it is noted that it is extended as a strong point or conical tooth, directed forward and slightly outward. This tooth marks one end of the double-jointed thoraco-abdominal articulation; it still has a very curious function in the aforementioned joint.

One notes in fact that, in the angular space between it and the tergal wall (fig. 358-359), the posterior margin of each branchiostegite just fits, regularly curving posteroventrally from the base of the cardiac notch.

The angular tergal space of the first abdominal somite, "riding horseback" on this posterior margin, is able to slide over it as on a cam with circular margin, guiding the abdomen to which it belongs. The anteriormost point of the arc described in a similar displacement will also be the most elevated; the posteriormost point will be at the same time the lowest, and all lateral displacement of the abdomen in this movement from low to high and from back to front will be prevented, thanks to the conical tergal teeth that guide the course of pleosomite I.

The thoraco-abdominal articulation is therefore not a gynglyme [? = "ginglyme" (English: "ginglymus"), hingelike joint (teste L. B. Holthuis, in correspondence)] with a single transverse axis; it should include two such axes: the first fixed, situated on the thorax, the other mobile, passing by the conical tergal teeth and displaced with respect to the first, like one of the "génératrices" of a cylinder with respect to its axis, in describing the curve of the posterior margin of the carapace. This is, in fact, what happens, and, as one can see, the extremities of the fixed thoracic axis and the parallelly displaced abdominal axis are joined by a straight line. That is, in the alpheids and the other eucyphotes, a nearly straight and even calcified bar (fig. 359, rax). Huxley has described it in the crayfish under the name of "pièce en L." In that reptant crustacean, the reduction of pleosomite I makes the disposition quite different, the tergal tooth is no longer present, and it is the rudimentary pleuron that fills the role. Likewise, the thoracic axis is more complex, and Huxley interposed "pièces triangulaires," articulating them in turn with "pièces en L." In the eucyphotes, the transverse axis is marked from end to end by the extremity of the sternum of the fifth pair of legs, prolonged very far upward and fused without doubt to an indistinct episternal piece.

To our knowledge, the cardiac notch, which Coutière (1899: 104) noted as "un détail d'une importance plus immédiate, qui semble jusqu'à présent avoir échappé a tous les descripteurs et n'est que très rarement figuré [sic]," has been similarly ignored during most of the century following his disclosure of it. Very possibly our familiarity with the 20th century literature is deficient, but we have been able to find only three subsequent references to the cardiac notch. Balss (1940: 93) mentioned the peculiar hinge between the carapace and the first abdominal somite as described by Coutière in the Alpheidae. Armstrong (1949: 13) stated that one of the four distinctive differences displayed by his proposed alpheid genus Thunor is "the absence of the cardiac notch, well developed in all the other genera of the family." Most significantly, in a discussion of the phylogenetic relationships of the families and genera of caridean shrimps, Christoffersen (1987: 361, fig. 5) used the cardiac notch as one (character 110) of three synapomorphies characterizing the Alpheidae.

Coutière's study has been reviewed with the help of material in the Smithsonian collections. At least one sample of each of 113 decapod families included in, but not limited to, the classification by Bowman and Abele (1982: 21–25) has been examined with particular reference to the juncture of the posterior margin of the carapace and the anterior somite of the abdomen. Whenever possible, type species—indicated by asterisks (\*)—were selected for examination.

### Alpheidae

Inasmuch as the cardiac notch is especially distinctive of the alpheids, a representative of each of the genera of that family available to us has been studied and illustrated (Fig. 1). Six of the 29 currently recognized alpheid genera are not represented in the Smithsonian collections: *Amphibetaeus* Coutière, 1897; *Athanopsis* Coutière, 1897; *Metabetaeus* Borradaile, 1899; *Parabetaeus* Coutière, 1897; *Parathanas* Bate, 1888; and *Pterocaris* Heller, 1862.

Of the remaining 23 genera, one (*Yagerocaris*) is transferred to the Alpheidae from the Hippolytidae. That genus not only displays a distinct cardiac notch, but it bears both an appendix interna and an appendix masculina on the second pleopod in both sexes (Kensley, 1988: 697), as in the possibly related genus *Salmoneus* (see Carvacho, 1989).

It may be apparent from Fig. 1 that most alpheids display a very distinct pair of cardiac notches at the juncture of the posterior margin of the tergum of the carapace and the branchiostegite. They are less distinct, however, in \*Salmoneus serratidigitus (Fig. 1s), \*Pomagnathus corallinus (Fig. 1p), \*Synalpheus comatularum (Fig. 1t), and especially in \*Racilius compressus (Fig. 1p) and \*Thunor rathbunae (Fig. 1u).

Of the genera not available to us, Coutière (1899: 105) noted that *Amphibetaeus* displays a greatly developed notch, *Parabetaeus* may prove to be a senior synonym of *Neoalpheopsis*, and *Parathanas* is known only from a larval stage. It would be interesting to know whether *Pterocaris* has any semblance of a cardiac notch that might



Fig. 1. Right posterodorsal margin of carapace in genera of the Alpheidae: *a, Alpheopsis aequalis* Coutière, 1896 (USNM 63454); *b, Alpheus strenuus* Dana, 1852 (USNM 180013); *c, \*Aretopsis amabilis* de Man, 1910 (USNM 180026); *d, \*Athanas nitescens* (Leach, 1814) (USNM 152107); *e, \*Automate dolichognatha* de Man, 1888 (USNM 173778); *f, \*Batella parvimanus* (Bate, 1888) (USNM 252095); *g, \*Betaeopsis aequimanus* (Dana, 1852) (USNM 107347); *h, \*Betaeus truncatus* Dana, 1852 (USNM 229978); *i, \*Fenneralpheus chacei* Felder and Manning, 1986 (USNM 228053); *j, \*Leptalpheus forceps* Williams, 1965 (USNM 181657); *k, \*Metalpheus rostratipes* (Pocock, 1890) (USNM 134718); *l, \*Mohocaris bayeri* Holthuis, 1973 (USNM 140276); *m, Nennalpheus* sp. near \*N. sibogae (de Man, 1910) (USNM 222982); *n, \*Neoalpheopsis euryone* (de Man, 1910) (USNM 216071); *o, \*Notalpheus imarpe* Mendez and Wicksten, 1982 (USNM 244250); *p, \*Pomagnathus corallinus* Chace, 1937 (USNM 237026); *q, \*Potamalpheops pylorus* Powell, 1979 (USNM 17463); *r, \*Racilius compressus* Paulson, 1875 (USNM 222981); *s, \*Salmoneus serratidigitus* (Coutière, 1897) (USNM 244262); *t, \*Synalpheus comatularum* (Haswell, 1882) (USNM 41737); *u, \*Thunor rathbunae* (Schmitt, 1924) (USNM 211467). (Type species indicated by asterisk (\*).)

strengthen its qualification for inclusion among the alpheids.

### HIPPOLYTIDAE

Inasmuch as knowledge of the presence or absence of the cardiac notch contributes substantially to the greater ease of separating the alpheids from the hippolytids, we have been grateful that all 38 hippolytid genera here recognized are represented in the Smithsonian collections, 32 of them by their type species. Examination of these specimens discloses that 37 of them differ little from \**Hippolyte varians* (Fig. 2*d*), the type species of the family, in lacking any trace of a cardiac notch. The only exception is \**Saron marmoratus* (Fig. 2*e*), which displays a shallow sinus at the tergal-branchiostegal juncture of the posterior margin of the carapace almost identical with the one in \**Synalpheus comatularum* (Fig. 1*t*). Coutière (1899: 106) mentioned this exception under the names *Hippolyte marmoratus* and its synonym *H. gibberosus* H. Milne Edwards, 1837.

Coutière also called attention, on the same



Fig. 2. Right posterodorsal margin of carapace in some decapod families other than the Alpheidae: *a*, Sergestidae; \*Sergestes arcticus Krøyer, 1855 (USNM 8088); *b*, Luciferidae: \*Lucifer typus H. Milne Edwards, 1837 (USNM 119418); *c*, Ogyrididae: Ogyrides alphaerostris (Kingsley, 1880) (USNM 96679); *d*, Hippolytidae: \*Hippolyte varians Leach, 1814 (USNM 9066); *e*, Hippolytidae; \*Saron marmoratus (Olivier, 1811) (USNM 105999); *f*, Crangonidae: \*Crangon crangon (Linnaeus, 1758) (USNM 205845); *g*, Glyphocrangonidae: \*Glyphocrangon spinicauda A. Milne Edwards, 1881 (USNM 134935); *h*, Thaumastochelidae: \*Thaumastocheles zaleucus (Thomson, 1873) (USNM 170683); *i*, Axiidae: \*Axius stirhynchus Leach, 1815 (USNM 6539); *j*, Callianassidae: \*Callianassa subterranea (Montagu, 1808) (USNM 252394); *k*, Callianideidae: \*Callianidea typa H. Milne Edwards, 1873 (USNM-Bikini Atoll); *l*, Thalassinidae: \*Thalassina anomala (Herbst, 1804) (USNM-Balayan Bay, Philippines); *m*, Polychelidae: \*Polycheles typhops Heller, 1862 (USNM 99455); *n*, Albuneidae: \*Albunea symnysta (Linnaeus, 1758) (USNM 68613); *o*, Hexapodidae: Hexapus sp. near \*H. sexpes Fabricius, 1798 (USNM 120729). (Type species indicated by asterisk (\*).)

page, to the fact that Ogyris—here represented by Ogyrides alphaerostris (Fig. 2c)—agrees with the hippolytids in lacking any vestige of a cardiac notch.

### SPURIA?

The only other occurrences of an invagination of any kind in the posterior margin of the carapace—probably none of them homologous with the true cardiac notch—were observed in the following: The sergestid \*Sergestes arcticus (Fig. 2a) and the luciferid \*Lucifer typus (Fig. 2b) display a broadly rounded, indiscrete sinus where the tergalbranchiostegal juncture might be. The crangonid \**Crangon crangon* (Fig. 2*f*) has the tergal and branchiostegal margins meeting at a widely obtuse angle. In the glyphocrangonid \**Glyphocrangon spinicauda* (Fig. 2*g*), the first abdominal pleuron slightly overlaps the branchiostegal margin and is locked in place by an internal submarginal elevation of the abdominal somite set into a submarginal pit on the branchiostegite. Nearly all of the axiids and calocarids have a notch, but with the lower margin produced into a restraining lobe. The axiid \**Axius stirhynchus* (Fig. 2*i*) has the tergal-branchiostegal juncture deeply indented, quite unlike the smoothly curved margin in the thaumastochelid \*Thaumastocheles zaleucus (Fig. 2h). The callianassid \*Callianassa subterranea (Fig. 2*i*) has an inconspicuous notch at the posterior end of the *linea thalassinica*. In the callianideid \*Callianidea typa (Fig. 2k) a shallow sinus is present in the dorsal part of the posterior margin of the carapace. The thalassinid \*Thalassina anomala, with its many adaptations for burrowing, has the posterior margin of the carapace deeply concave, armed with a strong, slightly submarginal median tooth impinging on a quadrate dorsal plate of the first abdominal somite and the latter produced laterally to overlap the margin of the carapace. In the polychelid \*Polycheles typhlops (Fig. 2m), the posterior margin of the branchiostegite has a distinct notch flanked by flattened, semicircular lobes to receive a sturdy, distally rounded projection from the first abdominal pleuron, apparently as a means of restricting the posteriad extension of the branchiostegite. The albuneid \*Albunea symnysta (Fig. 2n) is shallowly incised at the posterolateral angle of the carapace at its juncture with the side wall. The only brachyuran observed with a sinus in the posterior margin of the carapace was the hexapodid Hexapus sp. near \*H. sexpes (Fig. 2o), in which there is a somewhat obscure depressed notch opposite a lobe projecting from the lateral end of the anterior margin of the first abdominal somite.

### **FUNCTION**

The utility of the paired cardiac notches is not clear from the study of preserved specimens. The availability of the notches as a means of extending the first abdominal pleuron farther over the branchiostegite might enhance the protection of the branchial cavity in often cryptic animals like alpheids, but the anterior margin of the first abdominal somite is by no means always accommodated in the notches in preserved material with flexed abdomens. Furthermore, the branchiostegite is truncate posteriorly and overlapped but little by the first abdominal pleuron in \*Automate dolichognatha, which has a distinct cardiac notch, but that relationship pertains as well in \*Pomagnathus corallinus and \*Racilius compressus, in both of which the cardiac notch is barely discernible.

A cursory collateral study of representatives of 54 "macruran" decapod families revealed that the branchiostegite is usually overlapped to a variable extent by the first abdominal somite but that the branchiostegites and the integument of the first abdominal somite are more or less widely separated in representatives of the Sergestidae, Luciferidae, Stenopodidae, Axianassidae, Axiidae, Callianassidae, and Upogebiidae, and virtually so in the Polychelidae and Synaxidae. An unexpected and almost certainly coincidental revelation was that a small, almost identically shaped, subrectangular tooth on the anterodorsal margin of the first abdominal somite overlies the posterior limit of the branchiostegite in both the penaeoid shrimp *Benthesicymus altus* Bate, 1881, and the lobster Nephrops norvegicus (Linnaeus, 1758).

## **Epilogue**

The revival herein of carcinological information that has lain virtually dormant in the literature for nearly a century relates in a significant way to the quick-fix proposal to stabilize nomenclature that seemed to mesmerize the 1990 meeting of the International Commission on Zoological Nomenclature. Any list of "approved names" even if accompanied by a complete enumeration of synonyms, as would be mandatory if the names were to serve their primary purpose as keys to the literaturewould unavoidedly cast some doubt on the assurance that "historically valuable earlier taxonomic literature would continue to serve as a source of biological information and earlier hypotheses" (Ride, 1991: 121). The terminal clause of that sentence, "... but it would have no impact on nomenclature," is negated by the example proposed herein to transfer Yagerocaris from the Hippolytidae to the Alpheidae. As long as binominal nomenclature endures, there will continue to be far more challenges to a stable nomenclature from category transfers and from splitting and lumping than from the rare chance that a forgotten name might take precedence over a name in common usage, especially among the poorly known invertebrates. As Mayr (1969: 300) so appropriately noted in discussing the emendation of the International Code of Zoological Nomenclature: "An unresolved difficulty is posed by the drastically different needs of different taxonomic groups. The needs that exist in popular groups like birds and mammals, in which a limited number of species are referred to by their scientific names hundreds or thousands of times annually, are very different from the needs in an obscure group of arthropods attended to by a single specialist, with many species not mentioned in the literature more frequently than once every 30 or 50 years ... Dissension and controversy will inevitably result if specialists in one group of organisms are oblivious to the needs of specialists in other groups."

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