ON THE POSTEMBRYONIC OCCURRENCE OF THE MEDIAN "DORSAL ORGAN" IN CRUSTACEA MALACOSTRACA

I. Introductory Remarks.

In a paper on Sergestes (Proc. Zool. Soc. London 1896) the present author wrote in the description of the youngest Mastigopus-stage of S. arcticus Kr.: "just is front of the gastro-hepatic groove is observed a short protuberance in the median line". - In his valuable paper: Zur Kenntnis der Metamorphose von Sergestes arcticus Kr. (Zool. Anz. Bd. XXXIII, 1908) E. Wasserloos writes (p. 318) in the description of the second Protozoëa-stage: "In der Mittellinie des Cephalothorax bemerkt man über dem Gehirn und dem Naupliusauge eine linsenartige Hervorwölbung des Chitins die bisher bei keiner Sergestes-Larve ausser bei einigen Mastigopen von Sergestes arcticus von Hansen beschrieben worden ist..... An Schnitten habe ich ausser der Chitinbucht und der darunter liegenden, allerdings undeutliche Matrix nichts wahrgenommen.... Eine genaue Beschreibung und genaue Angaben über die erwähnte Hervorstülpung kann ich nicht geben, doch möchte ich eine Vermutung aussprechen: Die Lage des Organs über dem Naupliusauge und der Umstand, dass es mit der Zurückbildung des Naupliusauges ebenfalls verschwindet, lassen es als wahrscheinlich erkennen, dass die Protuberanz als Sammellinse für das Naupliusauge dient". His suggestion on the function of the protuberance is certainly erroneous.

While working out the rich collection of Sergestidæ collected by the Prince of Monaco, I observed the dorsal protuberance in

The "dorsal organ" in Crustacea Malacostraca.

Acanthosoma-stages of five species and in young Mastigopusspecimens of several species, furthermore a rudiment of the same organ in adult specimens. The idea struck me that it must be the so-called "dorsal organ" known in embryos of Crustacea of most orders, but unknown in almost all adult Malacostraca and in larvæ of the same sub-class. In examining adults of a good number of species belonging to all orders of Malacostraca, I was surprised that the dorsal organ, though frequently looking only as a rudiment, exists in some or several representatives of most orders. It is found on the surface most frequently nearly vertically above the mandibles or their base.

II. On our earlier Knowledge.

Nearly all original observations on the dorsal organ are scattered in papers very different in contents, though the majority deal with embryology or development. In 1904 W. T. Calman's excellent hand-book on Crustacea was published; in 1913 W. Giesbrecht's part on Crustacea in Lang's Handbuch der Morphologie was edited. These careful authors had written "records" on the Carcinology during a number of years and were uncommonly well versed in the vast literature; the statements of both authors together in the books mentioned on the occurrence of the dorsal organ may therefore be considered nearly sufficient, and an extract is given here.

On Anaspides (the order Anaspidacea) Calman writes (p. 164): "On the dorsal surface [of the head], in front of the cervical groove, is a pigmented area with a circular central spot surrounded by four minute pits. The significance of this structure is quite unknown, but it may be comparable to an obscure "dorsal organ" apparently glandular in nature, occupying a similar position in certain other Malacostraca". It may be pointed out, that Calman in his treatment of the other orders of Malacostraca does not mention the occurrence of a "dorsal

67

5*

organ" in the adult of any other form, but possibly he refers in the lines quoted to the organ found in embryos of other orders. - On the Tanaidacea he says (p. 194): "A paired "dorsal organ" is present" in the embryo; on p. 213: "A "dorsal organ" is present in many Isopod embryos, and assumes very different forms", which are mentioned. On the Amphipoda (p. 237): "A "dorsal organ" is early developed as a median thickening of the ectoderm " — On the embryo in Mysidæ (p. 179—80): "A pair of lateral thickenings of the epiblast appear very early and, approaching each other on the dorsal side, fuse to form an invaginated "dorsal organ"." But I may remark that Nusbaum und W. Schreiber in 1898 (Biolog. Centralbl. Bd. 18, p. 742) figured a transverse section of an embryo of Mysis Lamornæ showing the unpaired dorsal organ and a pair of dorso-lateral organs, and all three organs have already begun to degenerate. - At the Nebaliacea, Cumacea, Euphausiacea, Decapoda, and Stomatopoda Calman does not mention any dorsal organ.

Giesbrecht writes (p. 156—57) that not only in Cladocera but in "vielen anderen Crustacea ein anderes Organ von meist drüsiger Struktur, ebenfalls in der Dorsalwand des Kopfes, das aber nur transitorisch (bei Embryonen, seltener Larven) auftritt und sich meistens schon früh zurückbildet; das ist die Nackendrüse (Nackenorgan, Nackenschild, Dorsalorgan...)". Among the Malacostraca it is found early in the embryo in Arthrostraca (consequently Tanaidacea, Isopoda, and Amphipoda), in Cumacea, Mysidacea, perhaps also some Decapoda; "bei Leptostraken scheint es eine unpaarige Leiste zu bilden"; finally "als Nackendrüse aufgefasst wird auch eine dorsale Drüsenscheibe in the Maxillargegend von jungen und adulten Euphausien etc.". I have been unable to find in the special literature on the Euphausiacea any statement on the organ.

In a small paper published in Journ. Linn. Soc. Lond. vol. XXIX (1903) the present writer pointed out an organ on the surface of the head near the posterior margin in the Isopod *Bathynomus giganteus*; the organ — which shall be mentioned later on — was briefly described, figured and compared with the organ discovered by Calman (1896) in *Anaspides tasmaniæ*; it was added, that I had found a vestige of the organ in the allied form *Cirolana borealis.* — The statements in the literature on the organ in larvæ of *Sergestes arcticus* are quoted above.

Let us sum up. The median dorsal organ has been found in embryos of representatives of the following orders of Malacostraca: Nebaliacea, Mysidacea, Cumacea, Tanaidacea, Isopoda, Amphipoda and perhaps some Decapoda. The Embryologists tell us that it, at least generally, is of glandular nature and disappears early; on its function nothing is known, besides it is unknown in the embryo of Stomatopoda. — In adult forms it has been found in *Anaspides* of the order Anaspidacea; in *Bathynomus* and a species of *Cirolana* of the order Isopoda; finally, according to the quotation from Giesbrecht, in young and adult forms of the order Euphausiacea. In larval stages it is only known in *Sergestes arcticus*.

III. The "dorsal organ" in adult Malacostraca and some larvæ.

It has not been my intention to inspect every genus available, but types of families or genera have been selected and examined with a good pocket-lens; it was found that within the same family, sometimes even within the same genus, an organ could not infrequently be discovered in a large species, but not with any certainty in small forms. The following enumeration shows that the organ has a much wider occurrence than might have been supposed.

1. Nebaliacea.

Nebalia bipes O. Fabr. — In turning the animal a little to and fro so that the light changes on the smooth, shining dorsal surface of the head it is generally possible to perceive a faint vestige of a median protuberance situated not inconsiderably behind the base of the movable rostral plate.

2. Anaspidacea.

Anaspides tasmaniæ G. Thoms. — Calman described and figured a very conspicuous dorsal organ (Trans. Roy. Soc. Edinburgh, XXXVIII, 1896). Nothing is to be added.

Paranaspides lacustris Geoff. Smith. — The organ is more reduced than in *Anaspides*, as there is no pigmentation; the very small pits are irregularly arranged, and their number in three specimens varies from 3 to 5.

3. Mysidacea.

Gnathophausia. — In a gigantic specimen of G. ingens Dohrn a part of the dorsal keel a little in front of its base and about 15 mm. long is flattened above and behind the middle distinctly thickened, this narrow area has a pair of very conspicuous, very oblique, convex spots marked off all around by an depression, and the spots look almost as scars. In G. $zo\bar{e}a$ Will.-Suhm about one mm. of the dorsal keel above the mandibles is, seen from above, rather considerably thickened but not flat; seen from the side with the light transmitted the dorsal chitine of this part is thin and the contents opaque, indicating that the tissue is of another quality than in the surroundings.

Eucopia. — In one specimen of *E. sculpticauda* Faxon a nearly circular, somewhat shallow depression situated above the mandibles somewhat in front of the anterior transverse furrow; the depression has a minute, dark point as if a scar after a prick with a needle. In another specimen the depression is wanting, but the dark point exists; in a third specimen nothing could be seen with certainty. In specimens of *E. unguiculata* Will.-Suhm nothing was found.

Lophogaster. — In L. typicus M. Sars no vestige is discoverable.

Boreomysis. — B. scyphops G. O. S. has somewhat in front of the gastric groove a moderately large and rather shallow depression, at the middle of which is seen a somewhat low, a little oval, rounded and very distinct protuberance with one to three minute pits. — B. nobilis G. O. S. has very near the gastric groove a small but rather high, a little oval protuberance without visible pits. — B. microps G. O. S. has a little in front of the gastric groove a conspicuous, nearly semiglobular, smooth protuberance.

Of the subfamily Mysinæ two moderately large forms, viz. *Mysideis grandis* Goës and *Mysis mixta* Lilljeb., have been inspected, but no vestige of any organ was found.

4. Cumacea.

Some few larger forms have been examined, but nothing could be found.

5. Tanaidacea.

Some large specimens of *Apseudes* and *Alaotanais*, thus representatives for both families of the order, have been inspected with negative result.

6. Isopoda.

Idothea. — In I. balthica Pall. is frequently found near the posterior margin of the head a very small area a little broader than long, and with a few tiny pits or, in one specimen, with impressed transverse lines; the area is generally a little or somewhat depressed, but in one specimen it is larger than usual, raised and shining. In a well-sized specimen from Iceland the area is uncommonly conspicuous, moderately large, very slightly depressed, shining, with a large, oblong pit in the middle, and

around this 8 or 9 extremely minute, oblong pits. — In I, emarginata F. and I. ungulata Pallas organs somewhat similar to those in I. balthica are found.

Among other animals belonging to the sub-order Valvifera Mesidothea sibirica Bir., M. Sabini Kr., and Arcturus Baffini Sab. have been inspected, but with negative result.

Serolis. — S. paradoxa Fabr. has a very distinct though somewhat small, a little oblong, depressed area near the posterior margin of the head; the area has several tiny pits, especially near the masgin. — S. Schythei Ltk. has a similar nearly circular area.

Bathynomus. — In B. giganteus A. M.-Edw. an organ was discovered, briefly described and figured by me in 1903 (see p. 68). I have examined a large immature female. Near the posterior margin of the head it has a most conspicuous, whitish spot, which does not show the numerous, irregularly impressed points on the surrounding brownish chitine. The spot is as a whole a little arched but depressed along the middle; each half has a small group of 6 or 7 minute pits; the median part has a very oblong area well marked off by an depressed line and with a linear depression in the median line; somewhat behind each group of pits is found a shallow excavation which has a number of oblique, parallel, impressed striæ; at the front end of the area is seen a group of some nearly rudimentary pits.

Cirolana. — In C. borealis Lilljeb. a very small group of three to six tiny pits is found near the posterior margin of the head; they are sometimes situated in a very shallow or very distinct depression. — A specimen of C. Rossii Miers has some irregularly scattered minute pits.

 \mathcal{E} ga psora L. and specimens of Rocinela, Anilocra and Cymothoa have been inspected with negative result.

Among the sub-order Asellota Asellus aquaticus L., Munnopsis typica M. Sars and Munnopsurus giganteus G. O. Sars,

72

among the Oniscoidea *Ligia oceanica* L. and the gigantic *Tylos* granulatus Krauss have been examined without finding any vestige of the dorsal organ.

7. Amphipoda.

Large specimens of genera comprising forms of very considerable size, as *Anonyx*, *Stegocephalus*, *Gammarus*, *Maera*, have been inspected, but the result was absolute negative.

8. Euphausiacea.

Thysanopoda. — In T. egregia H. J. H. the gastric keel between the front margin and the gastric groove — has somewhat behind the middle a short part raised rather considerably; this part is cut off horizontally so that its upper surface is flattened, and this surface shows an aspect different from that of the surrounding integument. (The raised part is shown in fig. 21 in my paper on Schizopoda in Bull. Mus. Océan. Monaco, no. 30, 1905, p. 23) — T. cornuta Illig shows a similar structure. — In T.æqualis H. J. H. nothing could be perceived. — T. microphthalma G. O. S. has a feeble vestige on the gastric keel which on its highest part is a little flattened above.

In *Bentheuphausia amblyops* G. O. S. a vestige is scarcely perceptible.

In *Meganyctiphanes norvegica* M. Sars the gastric keel has a somewhat high and rather short part thickened upwards with the dorsal surface distinctly flattened; seen from the side with transmitted light the contents of the raised part is generally lighter than the surrounding tissue.

Euphausia. — In *E. superba* Dana the median keel is at some distance in front of the gastric groove more or less distinctly raised and thickened, and at each side of this part the surface of the carapace is distinctly excavated, but the keel itself is rounded above without vestige of any special structure.

In E. Krohnii Brandt no vestige.

In Nematobrachion boopis Calm. and Nematoscelis megalops G. O. Sars the gastric crest is at its highest point slightly angular and shows a vestige of the organ; seen from the side with transmitted light the contents of that part of the keel is lighter than the surrounding tissue.

Larvæ. — Some larvæ belonging to the genus *Euphausia* have been examined, but it was not possible to discover any rudiment of a dorsal organ. At a future occasion I will have to examine the vast material of larval forms secured together with adults in the North Atlantic by the Prince of Monaco, and then there will be a good opportunity to look for the dorsal organ in representatives of almost all genera.

9. Decapoda.

The dorsal organ is found in the adults of most species of the Penæidæ inspected by me, and in all genera and species of the Sergestidæ excepting *Lucifer*. Furthermore it was detected in several genera of the Caridea. Besides it was discovered in certain larval stages of the genus *Sergestes* and in a few larvæ of Penæidæ. In the following an account shall be given, but as to the genus *Sergestes* a brief abstract may be sufficient, because in a monograph of the North-Atlantic species secured by the Prince of Monaco and now in composition a more detailed report will be embodied. — In vain I have looked for the organ in a species of the genus *Cambarus*, and it is scarcely to be found in Astacidæ, Palinuridæ, Galatheidæ, etc. or in the crabs.

A. Penæidæ.

Aristeus. — A. Edwardsianus Johns. has a little behind the first dorsal spine the median keel thickened with its upper surface expanded; in the middle of this part is found a somewhat oblong area well marked off by a depression; this area has slightly before the middle an oblong, dark-brown spot sharply defined and with at least one minute pit. — In A. semidentatus Bate is found a moderately small but uncommonly deep depression a little behind the first dorsal spine; the depression has a small, circular, somewhat convex area behind the middle.

Solenocera Agassizii Fax. — A little behind the first dorsal spine an oblong, rather depressed area with a small knot at the middle.

Penæus. — P. setiferus L. has considerably behind the first dorsal spine a proportionately somewhat long part of the median keel thickened and flattened above or even longitudinally a little excavated; the broadest part of that area has in one specimen an oblong pit, in another specimen nothing. It must be remarked that the area in question is situated more backwards than in any other genus of the Malacostraca. — In P. caramote Risso nothing could be discovered.

Larvæ. — In a gigantic larva in the *Mysis*-stage, measuring 20.5 mm. from the tip of rostrum to the end of telson and captured in the Pacific, a small, oblong and rather low protuberance is easily seen a little behind the origin of the rostral keel. — In a larva in an older *Mysis*-stage, belonging to a quite different, somewhat small type, an oblong and somewhat high protuberance is found a little in front of the gastro-hepatic groove; seen from the side the protuberance is directed upwards and forwards; the larva is from lat. $4^2/a^\circ N$., long. $107^{1/2} \circ E$.

B. Sergestidæ.

Sergestes. — The organ has been found in adult specimens of everyone of the 15 species hitherto captured north of equator, but it could not be seen in every specimen of some of the smaller species, as S. mollis Smith, S. arcticus Kr., S. atlanticus M. Edw., S. vigilax Stimps., and S. Edwardsii Kr. The organ is situated a little or somewhat in front of the gastro-hepatic groove. It is a small or very small area, in most cases distinctly or considerably raised as a rounded, nearly circular or transverse-oval protuberance, sometimes, but far from always, marked off by an depressed line; in a few cases the whole area is depressed. Frequently the area has a very distinct granule or raised point in front of the middle, in other cases a few tiny pits or no pit could be made out. In a few cases the area is brown, but generally of the same colour as its surroundings. There is also some individual variation in the area as to its height or the depth of its surrounding impression.

Petalidium. — In one specimen of P. obesum Kr. is found a moderately small, a little oblong and feebly elevated area with a tiny and more raised point in front. In some specimens an area was not discoverable with certainty, but the quality of the integument makes the investigation difficult and uncertain.

Sicyonella. — In one specimen of S. maldivensis Borr. a distinct, small group of five minute pits close behind the dorsal crest; in another specimen the group has nearly vanished.

Acetes. — In one specimen of A. vulgaris H. J. H. a group of six minute pits close together and somewhat in front of the rudimentary gastro-hepatic groove; in another specimen a rudimentary protuberance with vestiges of a few pits.

Lucifer. - No trace of any organ.

Larvæ of Sergestes. — As mentioned above (p. 66) Wasserloos discovered the dorsal organ — but did not interpret it as such — in the second Protozoëa-stage and the Acanthosomastages of S. arcticus Kr.; the present writer had found the protuberance in question in the youngest Mastigopus of the same species. The dorsal organ is an erect or distinctly procurved, rounded protuberance in the Atlantic Acanthosoma-stages known to me and belonging to S. arcticus Kr., S. tenuiremis Kr., S. robustus Smith, S. corniculum Kr., and S. vigilax Stimps.; the protuberance is generally easily seen from the side. It is also

The "dorsal organ" in Crustacea Malacostraca.

found in the younger Mastigopus-stages of several and probably all species, but it differs sometimes considerably in aspect, as in S. pectinatus Sund it is shaped as a thick, short spine directed obliquely forwards. In the older larval stages it has apparently disappeared, but yet it exists in all probability, because it is found in adult specimens, though its aspect is quite different; I have not undertaken the certainly difficult investigation of the dorsal integument in front of the gastrohepatic groove in older larvæ or very young specimens with black eyes.

Larvæ of Lucifer. — In the youngest Mysis-stage without pleopods — of L. Faxonii Borr. a rather large and considerably vaulted dorsal protuberance is found above the base of the mandibles; it is not marked off in any way from the surrounding integument, and I am unable to decide whether it is homologous with the very characteristic protuberance in the Acanthosoma — or Mysis-stages — of Sergestes. In older stages, with pleopods, the protuberance is proportionately smaller.

C. Caridea.

Acanthephyra multispina Cout. — A little behind the first dorsal spine the median line has a small, circular depression surrounding a more or less distinct protuberance.

In *Nematocarcinus exilis* Bate a very small organ close at the base of the first dorsal spine.

In *Ephyrina* sp. from the North Atlantic the anterior crest of the carapace is somewhat from its base flattened above with a small but very distinct, circular, rounded protuberance, the surface of which has two or three pits so tiny that they could not be counted with certainty.

Pasiphaë. — In P. principalis Sund the dorsal keel is distinctly thickened considerably behind the rostrum, but a protuberance is wanting and no pit could be discovered. — A young P. sivado

Risso about 13 mm. long has a just perceptible, rudimentary protuberance considerably behind the rostrum.

In Spirontocaris microceros Kr. an area marked off by a circular depression very near the base of the first dorsal spine.

In Bythocaris leucopis G.O.S. a distinct rudiment in the keel a little behind the first spine.

In *Alpheus avarus* F. a small, but well developed depression a little or slightly behind the median keel.

Palæmon brasiliensis Hell., Pandalus Bonnieri Caull. and Pontonia sp. have been inspected with negative result.

10. Stomatopoda.

To begin with it may be remarked that moderately large to very large specimens of the present order have frequently the surface of the median part of the carapace more or less rubbed and are consequently badly fit for the investigation, as in such cases the dorsal organ is frequently difficult or impossible to point out with certainty.

The dorsal organ has been mentioned in descriptions — and besides shown in figures — of some species of the genus Squillaby at least two able Zoologists, viz. Stanley Kemp in his excellent memoir on the Indo-Pacific forms of the order (1913) and by Calman (1917). They name it the "dorsal pit", which is only a descriptive term, as they did not recognize what this pit really is. — It may also be pointed out that Giesbrecht in his useful, extremely élaborate, long-winded and as to literature not always very fair monograph of the Mediterranean Stomatopoda (1910) has not observed the "dorsal pit", though it is conspicuous in the common Squilla mantis I., at least sometimes not difficult to see in S. Desmarestii Risso, and ought at least to have been indicated on his large figures of the carapace of these two species.

78

The "dorsal organ" in Crustacea Malacostraca.

Squilla. — In S. mantis L. the median keel is considerably widened and flattened above somewhat behind the bifurcation and far in front of the mandible; the widened, rather short part has a very oblong depression, the bottom of which is a little convex and looks as pricked feebly with a needle. — In S. raphidea F. the organ is conspicuous and nearly as in S. mantis. — In S. Desmarestii Risso was found in two of four specimens examined a small, circular, low depression with a rudimentary median pit; the depression is situated considerably in front of the mandibles. — In S. gibba Nobili the median carina is flattened and much widened a little behind the middle and has there a small, a little oblong, convex area surrounded by a rather deeply depressed ring, and placed a little in front of the mandibles.

Lysiosquilla. — In a rather large specimen of L. cusebia Risso a very small and feeble depression a little in front of the middle of the carapace above the mandibles; in another rather large specimen and in small specimens nothing could be observed. — In L. maculata F. no vestige was found.

Pseudosquilla ciliata F. — In two specimens a nearly circular, very conspicuous and somewhat deep depression with two or three tiny pits on the flat or a little convex bottom, situated a little in front of the middle of the carapace and somewhat in front of the mandibles. In a third specimen the depression is small and shallow, in a fourth quite rudimentary.

Odontodactylus scyllarus L. — Slightly behind the middle of the carapace a rather large, moderately shallow depression, in the middle of which a small, circular, somewhat convex area.

Gonodactylus Oerstedii H. J. H. — A deeper or more shallow, small, circular, depressed area a little behind the middle of the carapace and above the mandibles. In young specimens the depression is either considerably more feebly developed or not discernible. Larvæ. — Specimens of Alima, Pseuderichthus and Lysierichthus, also the first stage, have been inspected, and the result was always negative.

IV. Summary.

The preceding chapter shows that the "dorsal organ" can be observed on the posterior part of the dorsal surface of the head or on the carapace in adults of some or several genera of all orders of Malacostraca, excepting in Cumacea, Tanaidacea and Amphipoda. Whether it sometimes or frequently or even generally has a special function must be made out by a student, who has a good material either of living animals or of specimens especially preserved for histological research, for cutting by microtome. As the organ has such wide occurrence, it is no very probable that it has no function in the adult. And this supposition is strenghtened by the fact that it exists in many and probably in most adult Stomatopoda, but seems to be wanting in their larvæ; that it should exist in the embryos of this order - on which nothing is known - then be absent in the larvæ. but reappear in the adults, is highly improbable. We are in reality completely ignorant on the significance of the dorsal organ both in embryos, in larvæ and in adults, so ignorant that it seems scarcely possible to produce even a hypothesis. Perhaps experiments on living animals similar to those carried out by some authors in order to investigate the excretory system might yield some result.

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STUDIES ON ARTHROPODA

by Dr. H. J. HANSEN

WITH FOUR COPPER-PLATES

AT THE EXPENSE OF THE RASK-ØRSTED FUND

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1921

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