NOTES ON THE IDENTIFICATION AND SPECIATION OF HETEROPODA (GASTROPODA)

by

S. VAN DER SPOEL
Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam

With 6 text-figures

Introduction

Specimens of Heteropoda, especially of Atlantidae, which are damaged by the nets and have lost their shells by the action of preservatives are usually considered to be hardly identifiable. Tokioka (1961) used the opercula as a new source of morphological information for the study of the shell-less Atlantidae. The laborious preparation of opercula enables only the identification of some species. The occurrence of groups of closely related taxa showing only slight morphological differences is responsible for other difficulties in identification. Recent expeditions, like the Cicar Expedition, the Eastropac Expeditions and the Acre project provided samples with large quantities of damaged heteropods, which induced me to look for a simple method to identify the damaged specimens with a high degree of certainty. The results of this attempt are given below together with a discussion on some problems in speciation of heteropods.

Acknowledgements

The author is very much indebted to Prof. Dr. L. D. Brongersma, who frequently made it possible for him and his co-workers to borrow material from the Rijksmuseum van Natuurlijke Historie, Leiden. That with the method discussed below certainly a large part of previously borrowed material can be identified is one of the reasons to regard it as an honour to dedicate this paper to Professor Brongersma. The staining method used for the heteropods has been developed by Mr. A. F. de Fluiter, to whom the author is very thankful.

Method

All specimens from a sample are stained at the same time and mounted, left side down, on microscopical slides. On the slides some species are recognizable without trouble, other species can be distinguished using meristic data. The size of the body whorls is taken because with only the soft parts left, the whorl formula developed by Tokioka (1955a, b; 1961) cannot be used. The formula described below expresses the increase of the soft parts in the first whorls. It can be considered a modification of Tokioka's method, probably it is a more accurate method especially when studying intact shells. The last whorls are more strongly influenced by the environment than the first ones, so that the latter will show smaller phenotypical variations. In the whorl formula the first whorl is indicated with I, the sum of the width of the first and second whorl with II, the sum of the width of the first, second and third with III, and so on. Figure 1 shows the method of

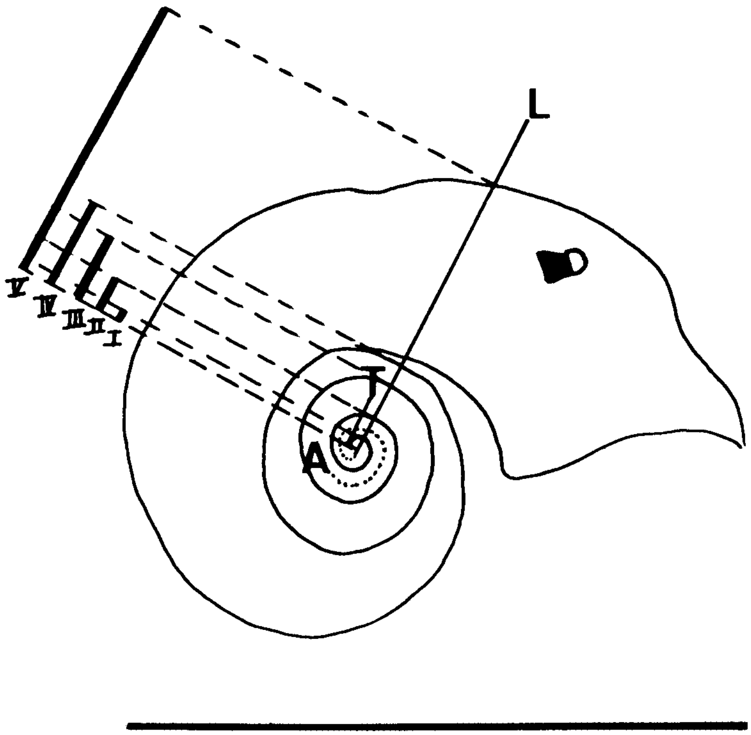

Fig. 1. Schematic drawing of body of *Atlanta* spec. seen from the right side to show system of measuring. For explanation see text on p. 546.

measuring the values as used in the formula. The line along which the sizes are measured (L) runs parallel to the last tangent (T) of the suture, and starts in the axis (A) of the first whorl. The section of the first whorl crossed by the line L is considered equal to one unit, thus I always is represented in the formula by 1, and all other sizes become independent of the absolute size of the whorls and the exact position of line L. The section of the first and second whorl crossed by line L represent the value II, and so on.

The second important point is the shape of the eyes. In the heteropods the eye is enclosed in the eye capsule, to which the tentacle is attached. Two separate sensory nerves run to the tentacle and the eye. The lens is supported by the pigmental zone and sometimes it is covered by a cornea. The pigmental zone, with a window at the dorsal surface, surrounds the retina. The six oculomotory muscles are attached to the right under surface and the left upper surface of the pigmental zone. In *Oxygyrus keraudreni* (Lesueur, 1817) the pigmental zone is very broad (fig. 2b), in *Atlanta* and *Protatlanta* the pigmental zone is narrower. *Atlanta helicinoides* Souleyet, 1852, and *Atlanta fusca* Souleyet, 1852, make an exception (fig. 2 e, f). In *A. helicinoides* the pigmental zone is broad and forms a wall around the lens, the same is visible in *A. fusca* though less distinctly expressed. The other species (fig. 2) show more slender eyes of rectangular or triangular shape; small differences of taxonomic value between these species are found in the eyes. In *A. inclinata* Souleyet, 1852, the upper horizontal band is very broadly triangular, in *A. turriculata* Souleyet, 1836, the opening between the pigmental area is strongly compressed. *A. peresi* Frontier, 1966, and *A. lesueuri* Souleyet, 1852, show nearly identical eyes with an almost rectangular pigmental zone, while in *A. inflata* Souleyet, 1852, the pigmental area is more or less cuboid and characterized by an opening between the left vertical and horizontal bands; this sometimes occurs in *A. peroni* also. The differences in eye-shape between some species is very small and the different orientation of the eyes on the slides sometimes disguises all differences.

The shape of the operculum is not visible in mounted specimens as it is usually found parallel to the direction of observation. However, in *Atlanta inflata* the dentation around the nucleus is clearly visible, as it projects from the surface to the operculum, and so is the punctation in *A. turriculata*.

The heteropods are prepared for staining by putting them for two minutes in destilled water to remove the preservatives, usually formalin. The staining procedure consists of the following steps:

1) Specimens are put in Toluidin Blue for five minutes.
2) Stain is replaced by alcohol 50% for about two minutes.
3) In alcohol 70% the specimens remain to obtain the correct degree of staining; the time is dependent on the size of the animal and the intensity of staining desired.
4) In alcohol 96% the specimens are kept for five minutes.
5) In Clove-oil (Oleum Caryophylli) Toluol mixture (6:4) the specimens are cleared in about 5 minutes.

After this treatment the specimens are mounted in Rhenohistol. To avoid crowding it is recommended to mount not more than 30 specimens on one slide, and to avoid a turn-over of smaller specimens, larger and smaller animals should be mounted on different slides. The stain is prepared by mixing 0.3 gram toluidin (G.T. Gurr Ltd.) in 75 cc destilled water, after which 5 cc acetic acid (conc. 97-100%) is added. The stain must be filtered before use, but it is recommended to store the solution for one week before filtering.

The soft parts become transparent in Clove-oil, and the pigmented eyes and other pigmented spots remain clearly visible. The sexual gland, the visceral organ, the buccal organs and the radula become visible through the tissues. Integument and glands in the skin are clearly stained.

Results

The genera of the Atlantidae are characterized by the tentacle size and the eye-shape. In *Oxygyrus*, with one species, *O. keraudreni* (Lesueur, 1817), the tentacles are very short and the pigmental zone in the eye is very broad. In *Protatlanta*, with one species, *P. souleyeti* (Smith, 1888), the tentacles are also short but the eyes are more slender and the head parts are usually proportionally large (fig. 3b). In *Atlanta* the tentacles are always long, nearly as long as the proboscis, while the eyes are never of the *Oxygyrus* type. Some species of *Atlanta* are recognized without any difficulties, e.g.:

A. inflata (with about 5½ whorls) is characterized by the dentation around the nucleus of the operculum.

A. turriculata (with about 5½ whorls) is marked by the strongly and loosely coiled spire, and by the tubercles around the nucleus of the operculum.

A. inclinata (with about 6½ whorls) is easily recognizable by the oblique spire. For the identification of the other species the whorl formula has to be used.

A. lesueuri (with 4 whorls) shows a large third whorl and a very large fourth, the formula is I=1 II=4-6 III=6-10 IV=14-40. All other species have lower values for III.

A. gaudichaudi (with 4 whorls) shows a large fourth whorl but a small third one: I=1 II=1½-3 III=3-5½ IV=6-18.

A peroni (with 5 whorls) is characterized by a small third and a small fourth whorl: I=1 II=2-4 III=3-5½ IV=5-8.

A. helicinoides and *A. fusca* (with 4½ up to 6 whorls) may be confused with the preceding species but the value for IV is usually more than 8, while V is always below 30. The depressed shape of the pigmental zone in

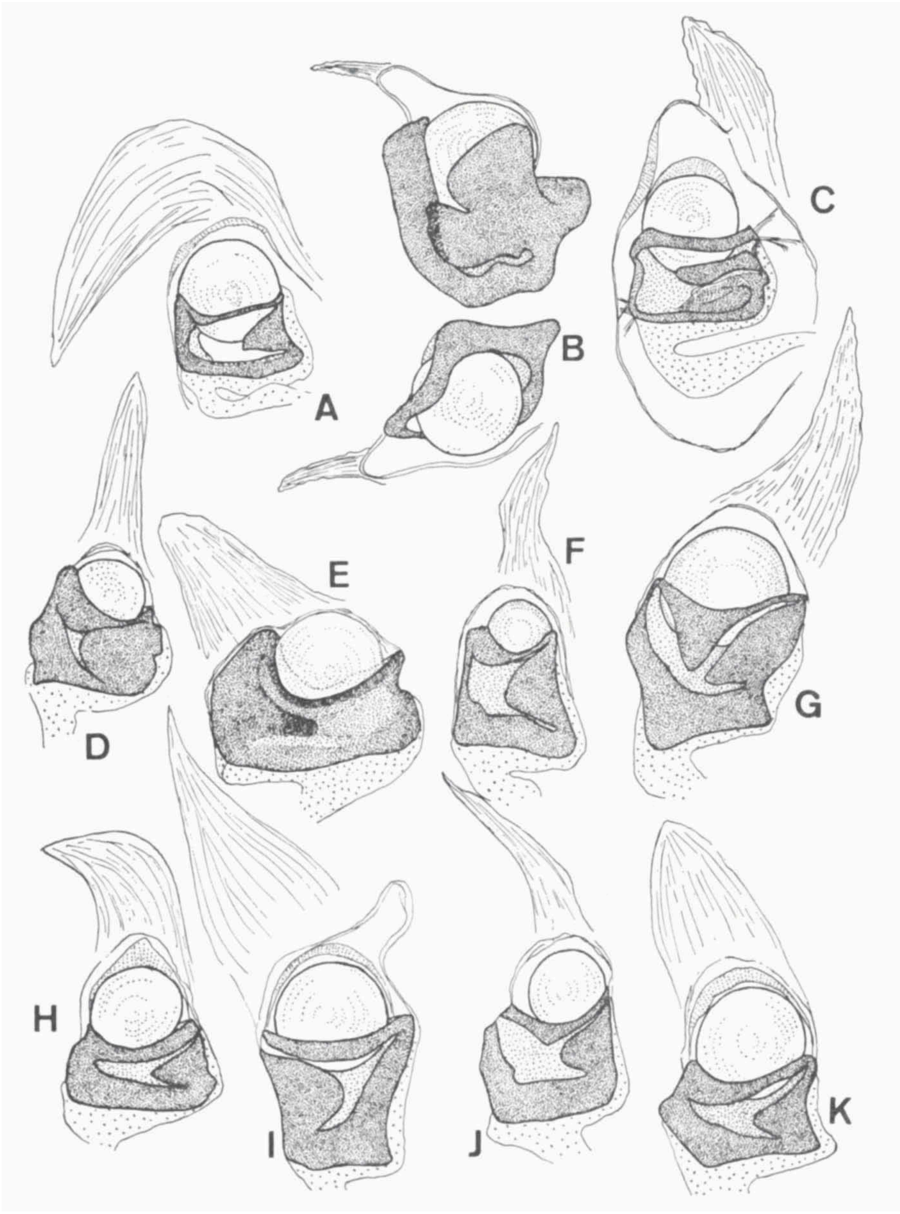

Fig. 2. Eyes of Atlantidae. A, *Atlanta lesueuri*; B, *Oxygyrus keraudreni* in lateral and cranial view; C, *Protatlanta souleyeti*; D, *A. turriculata*; E, *A. helicinoides*; F, *A. fusca*; G, *A. inclinata*; H, *A. gaudichaudi*; I, *A. peroni*; J, *A. inflata*; K, *A. peresi*.

A. helicinoides is, moreover, remarkable. *A. helicinoides* is larger than 1½ mm across, while *A. fusca* is smaller than 1½ mm across, moreover *A. helicinoides* always shows the wall of the pigmental zone enclosing the lens, which is only vaguely to be seen in *A. fusca.*

The above mentioned species form the group of the eight "classical" species. More difficult to recognize are the more recently described species: *A. peresi* Frontier, 1966, *A. pacifica* Tokioka, 1955, and the forms of *A. helicinoides* and *A. inclinata*. *A. peresi* most of all resembles *A. lesueuri*, but the whorls in the spire are growing more gradually than in the latter, which is also expressed in the whorl formulas. *A. peresi* (with about 3½ whorls) shows I=1 II=1-4 III=3-7 IV=6-20, while *A. lesueuri* shows II and III 4-6 and 6-10, respectively. *A pacifica* differs from its most strongly related species *A. gaudichaudi* by having a lower value for IV, while III and V are equal to those in *A. gaudichaudi*. The whorl formula of *A. pacifica* is I=1 II=1½-3 III=2½-5½ IV=4-10.

The two forms of *A. helicinoides* distinguished by Frontier (1966) can be correlated with two types of soft parts, viz., the one with a relatively large penultimate whorl, and the other with a relatively small penultimate whorl.

Of *A. inclinata* two forms have been described (Tokioka, 1955b; Frontier, 1966); they are distinguished by the relative size of the central parts with regard to the body whorl. *A. megalope* Richter, 1961, only differs in the size of the eyes from *A. inclinata*. "Mit Ausnahme der Augengrösse............ unterscheidet sich die Beschreibung in keinen Punkt von der die auf *Atlanta inclinata* zutrifft" (Richter, 1961: 232). The diameter of the eye lens in *A. megalope* is twice as large as in *A. inclinata*, but intermediate eye sizes are found. In *A. turriculata* two forms are found when studying the soft parts, these two forms differ in the same way as the forms of *A. inclinata*. In "*A. turriculata* forma A" the high spire consists of quickly increasing whorls. The tubercles on the operculum are sometimes absent, and this lack of punctation occurs usually in the "forma *B*". Up till now material has been too scanty to state definitely that the forma *B* always lacks the punctation. Tokioka (1961) remarked that the validity of *A. pacifica* is doubtful, because no differences between the opercula of this species and those of *A. gaudichaudi* are found. The soft parts of both species do not differ more than their shells. Like the different forms found in *A. inclinata* and *A. helicinoides* there may consequently be two forms in *A. gaudichaudi*.

The present method of staining makes it possible to detect specific differences in the shape and pigmentation of the salivary glands, intestine, gonads, and liver. Easily seen are also the differences between male and female specimens, as the gonads clearly show their contents. The hypothesis of

Fig. 3. Contours of the soft parts of Atlantidae (scale 1 mm). A, *Oxygyrus keraudreni*, adult and juvenile specimen; B, *Protatlanta souleyeti*, adult and juvenile specimen; C, *Atlanta inflata*; D, *A. inclinata* forma *inclinata*; E, *A. fusca*; F, *A. turriculata* forma *turriculata*; G, *A. helicinoides* forma *helicinoides*; H, *A. helicinoides* forma *B*; I, *A. lesueuri*; J, *A. peroni*; K, *A. gaudichaudi*; L, *A. lesueuri*, young specimen; M, *A. peresi*.

Tesch (1949) that spermatophores are formed by male Atlantidae proved to be correct. In all species I found one and sometimes two spermatophores in development in the accessory sexual glands. In some female specimens a spermatophore just accepted by the receptaculum was found. The spermatophores found attached to the shell as described by Tesch (1949) are identical to those found in the sexual organs. Fertilization by means of spermatophores is therefore normal in all Atlantidae. In *Carinaria* and *Firoloida* spermatophores are also found. For the species of the other genera, which are usually too large to prepare on slides, no records of spematophores exist.

The other heteropods present fewer difficulties with their identification, as they are usually recognized by the characters of the soft parts. The characters of the Carinariidae and Pterotracheidae are given below.

Carinaria shows a stalked visceral nucleus of triangular shape with gills directed ventrally; the body is cylindrical.

Pterosoma (with one species, *P. planum* Lesson, 1827) shows a stalked, rather triangular nucleus and the gills are directed dorsad but the body is flattened.

Cardiapoda shows a stalked, rounded visceral nucleus, the gills are directed dorsad.

Pterotrachea has the visceral nucleus at the end of the body without stalk, there is a distinct tail, but tentacles are always absent.

Firoloida (with one species, *F. desmaresti* Lesueur, 1817) shows tentacles in males, a tail is concealed behind the visceral nucleus, inserting on the body without stalk.

The species of the genera *Carinaria*, *Cardiapoda*, and *Pterotrachea* are chiefly distinguished by differences in the eye-shape, the shape of the visceral nucleus, the anatomy of the swimming fin, the tail, and the configuration of the integument. As this study is made to enable the identification of damaged material, attempts have been made also to identify fragments of animals. It is possible to identify fragments with eyes or with visceral nuclei. The eyes of the species are shown in figure 4, the visceral nuclei of the species are shown in figure 5. *Carinaria lamarcki* Péron & Lesueur, 1810 forma *lamarcki* Péron & Lesueur, 1810, is characterized by a depressed, triangular visceral nucleus, triangular eyes with broad base, and a tail without clasper. *Carinaria lamarcki* Péron & Lesueur, 1810 forma *challengeri* Bonnevie, 1920, shows a depressed triangular visceral nucleus, triangular eyes with broad base, and a tail with a distinct clasper (fig. 6). Young specimens of *Carinaria lamarcki* forma *challengeri* differ from young *Cardiapoda placenta* in having a relatively shorter tail and large first coils of the visceral

Fig. 4. Eyes of Carinariidae and Pterotracheidae. A, *Cardiapoda richardi*; B, *Pterosoma planum*; C, *Firoloida desmaresti;* D, *Carinaria lamarcki* forma *challengeri*; E, *C. galea*; F, *Pterotrachea minuta*; G, *P. hippocampus*; H, *Cardiapoda placenta*; I, *Pterotrachea scutata*; J, *P. coronata*; K, *Carinaria lamarcki* forma *lamarcki*.

mass. *Carinaria cristata* (Linnaeus, 1766) is distinguished by its elevated triangular visceral nucleus and its semi-circular dorsal crest with tapering prolongation at the end. *Carinaria japonica* Okutani, 1955, shows an elevated, triangular visceral nucleus, and an elevated triangular dorsal crest. *Carinaria galea* Benson, 1835, with triangular, narrow-based eyes, is characterized by the very high carina. Specimens without shells are only distinguishable from *C. lamarcki* by the relatively smaller, coiled portion of the visceral nucleus. *Carinaria cithara* Benson, 1835 forma *cithara* Benson, 1835, shows in contrast to the preceding species cylindrical eyes, while the visceral mass is highly erected with straight posterior margin. *C.c. procumbens* Tesch, 1949, is, in shell-less material, only recognizable by the posterior margin of the visceral nucleus, which curves anteriorly. *Cardiapoda placenta* (Lesson, 1830) is easily taken for *Carinaria lamarcki* forma *challengeri* when young specimens are concerned; the presence of tentacles, however, characterizes the first mentioned species. The eyes are broad-based, triangular, the shell is minute, the visceral mass is rounded and has a large number of gills along the whole upper border of the nucleus.

Cardiapoda richardi Vayssière, 1904, is provided with a rounded visceral nucleus with only about eight gill rays at the frontal pole of the nucleus. The eyes are typical, like in *O. keraudreni* a very voluminous pigmental band encloses the lens and retina. *Pterotrachea coronata* Forskål, 1775, with a slender visceral nucleus (4-5 times as long as broad) is distinct by the cylindrical eyes. *Pterotrachea hippocampus* Philippi, 1836, is distinguished by its broadly triangular eyes and by a not very slender visceral nucleus. *Pterotrachea scutata* Gegenbaur, 1855, is easily recognizable by the hyaline, gelatinous disk along the body between the eyes and visceral nucleus. The nucleus is thick and not distinctly acuminate. The eyes are elongated cylindrical. *Pterotrachea minuta* Bonnevie, 1920, shows a slender visceral nucleus (length 3 times its thickness), while the eyes are triangular with a broad base.

CLASSIFICATION

In *Atlanta* the remarkable feature of "pairs of taxa" occurs. *A. lesueuri* and *A. peresi*, the two forms of *A. helicinoides*, of *A. turriculata* and *A. inclinata*, and *A. peroni* and *A. gaudichaudi* form such pairs of closely related groups. These groups can be considered to be of species level or subspecies level. Only one species, *A. inflata*, is an isolated species without "relatives", while *A. fusca* and *A. pacifica* may be considered closely related to *A. helicinoides* and *A. peroni*, respectively. All these pairs consist of sympatric taxa. But distributional barriers in vertical sense are unknown, seasonal isolation has never been studied, while nothing is known concerning

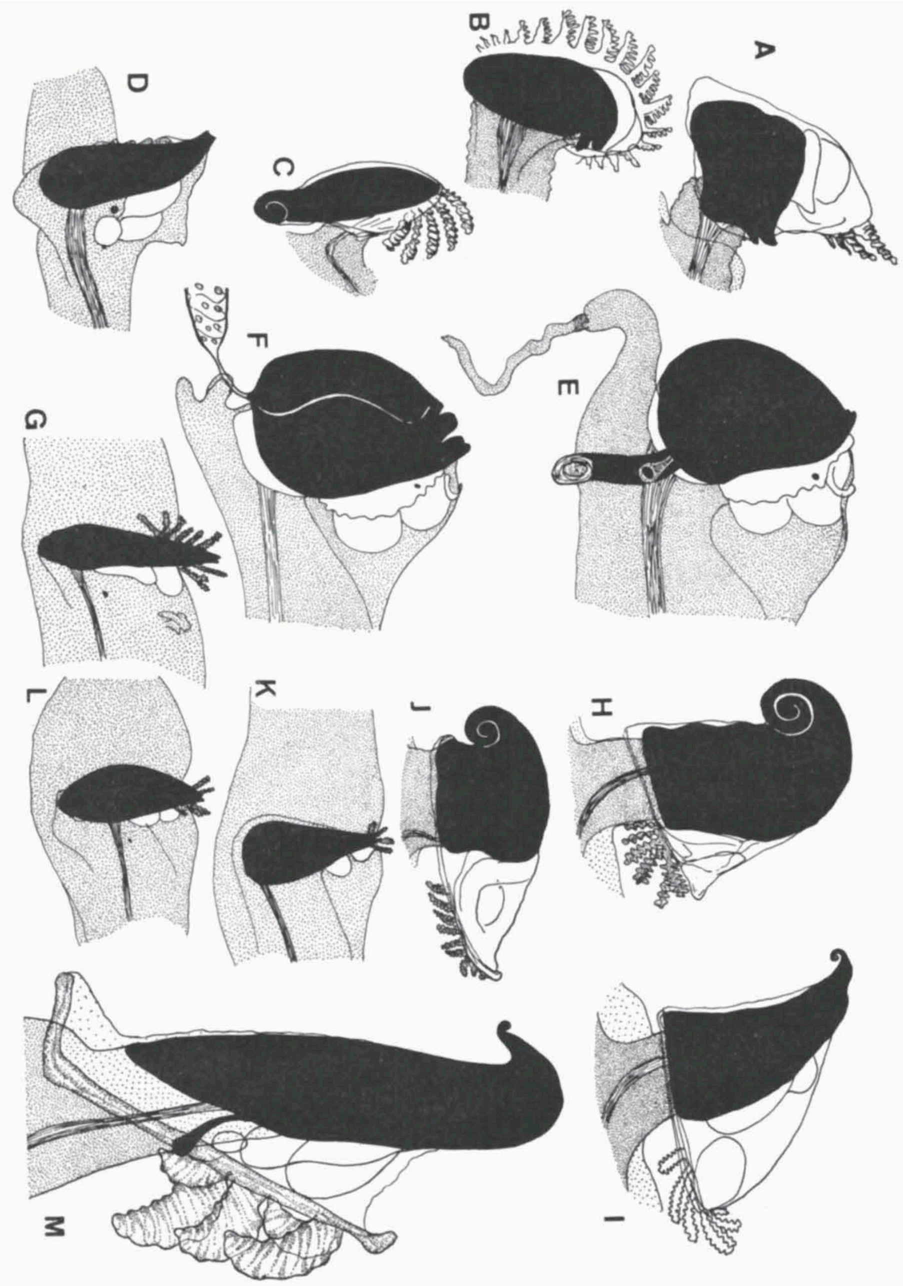

Fig. 5. Schematic drawing of visceral masses in Carinariidae and Pterotracheidae. A, *Cardiapoda placenta*; B, *C. richardi*; C, *Pterosoma planum*; D, *Pterotrachea minuta*; E, *Firoloida desmaresti* ♂; F, *F. desmaresti* ♀; G, *P. coronata*; H, *Carinaria galea*; I, *C. cristata*; J, *C. lamarcki*; K, *P. hippocampus*; L, *P. scutata*; M, *C. galea* juv.

interbreeding and intermediates between the taxa of one group. Two kinds of classification are possible at the moment, e.g., recognizing 14 species in *Atlanta*, or dividing the genus in only six species with, in total, 13 formae (or subspecies). For *Carinaria* the same is possible, e.g., six species or four species with in total six formae can be distinguished. The classification which, in my opinion, expresses the relationship of the taxa in the best way is given below.

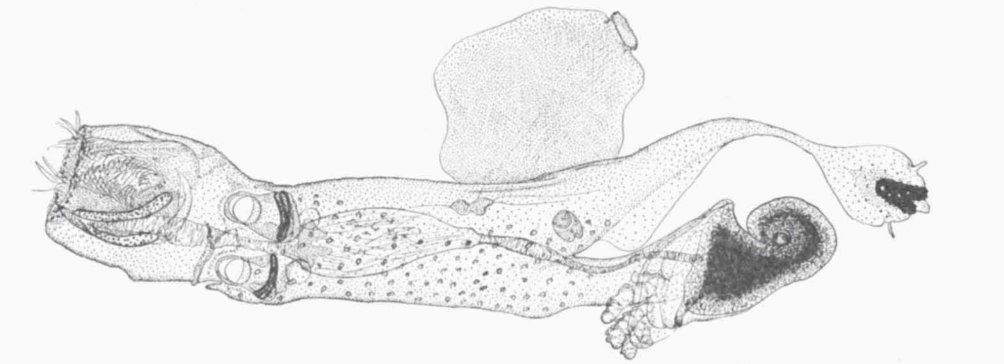

Fig. 6. *Carinaria lamarcki* forma *challengeri*, male specimen, length 10 mm.

ATLANTIDAE

Oxygyrus Benson, 1835	*O. keraudreni* (Lesueur, 1817)
Protatlanta Tesch, 1908	*P. souleyeti* (Smith, 1888)
Atlanta Lesueur, 1817	*A. inflata* Souleyet, 1852
	A. turriculata d'Orbigny, 1836 forma *turriculata* d'Orbigny, 1836
	A. turriculata d'Orbigny, 1836 forma *B*
	A. inclinata Souleyet, 1852 forma *inclinata* Souleyet, 1852
	A. inclinata Souleyet, 1852 forma *megalope* Richter, 1961
	A. inclinata Souleyet, 1852 forma *B* Tokioka, 1955
	A. helicinoides Souleyet, 1852 forma *helicinoides* Souleyet, 1852
	A. helicinoides Souleyet, 1852 forma *fusca* Souleyet, 1852
	A. helicinoides Souleyet, 1852 forma *B* Frontier, 1966
	A. peroni Lesueur, 1817 forma *peroni* Lesueur, 1817

	A. peroni Lesueur, 1817 forma *gaudichaudi* Souleyet, 1852
	A. peroni Lesueur, 1817 forma *pacifica* Tokioka, 1955
	A. lesueuri Souleyet, 1852 forma *lesueuri* Souleyet, 1852
	A. lesueuri Souleyet, 1852 forma *peresi* Frontier, 1966
CARINARIIDAE	
Carinaria Lamarck, 1801	*C. lamarcki* Péron & Lesueur, 1810 forma *lamarcki* Péron & Lesueur, 1810
	C. lamarcki Péron & Lesueur, 1810 forma *challengeri* Bonnevie, 1920
	C. cristata (Linnaeus, 1766) forma *cristata* (Linnaeus, 1766)
	C. cristata (Linnaeus, 1766) forma *japonica* Okutani, 1966
	C. cithara Benson, 1835 forma *cithara* Benson, 1835
	C. cithara Benson, 1835 forma *procumbens* Tesch, 1949
	C. galea Benson, 1835
Pterosoma Lesson, 1827	*P. planum* Lesson, 1827
Cardiapoda d'Orbigny, 1836	*C. placenta* (Lesson, 1830)
	C. richardi Vayssière, 1904
PTEROTRACHEIDAE	
Pterotrachea Forskål, 1775	*P. coronata* Forskål, 1775
	P. hippocampus Philippi, 1836
	P. scutata Gegenbaur, 1855
	P. minuta Bonnevie, 1920
Firoloida Lesueur, 1817	*F. desmaresti* Lesueur, 1817

The other heteropods do not show such problems. *Pterosoma* and *Firoloida* are represented each by a monotypic species. *Cardiapoda* consists of two, *Pterotrachea* of four species with restricted variability. The differences in diversity of the heteropod families may be explained by a special type of speciation in the groups.

Speciation

The speciation in heteropods is here chiefly compared with the speciation in pteropods, as both are groups of holoplanktonic molluscs. Heteropods and pteropods have in common that in both groups shell-bearing species and shell-less species are being found. The Atlantidae have normal shells in which the animal can completely retract. The Carinariidae have a reduced shell, in which the animal can never retract. The Pterotracheidae are completely shell-less. The percentage of shell-bearing species is strikingly identical in both groups. The Atlantidae constitute about 45% of the Heteropoda, the Euthecosomata and Peraclididae form about 45% of the Pteropoda. The percentage of species with reduced shells in heteropods is distinctly larger than in pteropods, viz., 30% and 13%, respectively.

The fact that there are relatively more species without shells in Pteropoda as a whole, indicates that this group is more adapted to the environment than the Heteropoda. In the distributional pattern of Pteropoda and Heteropoda there is another indication for the more specialized status of the Pteropoda. Heteropoda show a more restricted north-south range and a more limited penetration into the deeper layers of the oceans. The small north-south range of Heteropoda shows that they have not been — or could not have been — effected so intensively by the climatic changes during the Quarternary period and that speciation due to these influences does not occur. In pteropods the series of formae occurring from the Arctic to the Antarctic of, e.g., *Limacina helicina, Clio pyramidata* and *Clione limacina,* are considered to have developed under the influences of the ice ages. In heteropods such series of formae are not found and they are not expected to occur.

There are more different species of heteropods in the Indo-Pacific than in the Atlantic Ocean; in pteropods just the reverse is found. If the area with the greatest number of species is also the area where the group first developed, Heteropoda must originate from the Indo-Pacific area. The fact that there is a clear difference in Heteropoda found in the Atlantic and the Indo-Pacific is also related to their preference for warm-water masses. As a hypothesis one may state that Heteropoda are so thermophilous that they never can migrate from the Indian to the Atlantic Ocean through the waters south of Africa.

This theory can be reversed; in this case heteropods are not found in deeper layers, show a restricted north-south range, and are restricted to warmer waters as they did not speciate to occupy this biotope. Thus the biology of the Heteropoda itself prevents speciation. There are indeed indications of influences in the biology of Heteropoda which retard speciation, different from the influences found in Pteropoda.

An essential difference between heteropods and pteropods is that the former are gonochorists and the latter are not. Self fertilization and homosexual behaviour is impossible, and reduced geneflow as a result of hermaphroditism is excluded in Heteropoda. Mobility will be greater than in Pteropoda as the sexual partners have to move actively in search of each other. This mobility is also developed as an adaptation to their behaviour as animals of prey. Like the gymnosomatous pteropods, feeding likewise on zooplankton, the heteropods have to execute active swimming to catch their prey. The well developed eyes in this group indicate also that we are dealing with animals of prey detecting their victims by optical perception. For animals depending largely on optical stimuli, light is indispensable, which explains that heteropods are only found in the upper, photic layers of the ocean. Diurnal vertical migration, as occurring in pteropods, keeping the animals away from light, would be impractical in heteropods and strong vertical migration does not occur in these animals. Deep sea species are unknown in this group, which seems only logical. This makes the number of biotopes or water-masses available for heteropods rather small. This scarcity in biotopes makes geographic speciation in heteropods rather difficult and explains the small number of species. The mobility of the specimens at the other hand warrants gene transport through the populations and monomorphy throughout the species. Clinal variation and speciation in peripheral populations is thus expected to occur less frequently than in pteropods. The monotypic species in Gymnosomata and Heteropoda probably both are the result of the relatively important mobility of the specimens and their biology as animals of prey. It does not prove anything but it is striking that the less mobile Atlantidae are represented by more species and more polymorphic (-typic) species, than the mobile Carinariidae and Pterotracheidae.

With regard to the zoogeography of the heteropods only few data are available. Tesch (1949) distinguishes the "A group" of very abundant species (*Atlanta peroni, A. gaudichaudi, A. lesueuri, A. inclinata* and *Firoloida desmaresti*) consisting of the flatly coiled *Atlanta* species, and the "B group" of less abundant, more highly coiled species (*Atlanta inflata, A. fusca, A. helicinoides, A. turriculata*). These two groups have no great value as they give no more than a separation in ecologically and morphologically easily recognizable groups, without any relation to speciation.

As all heteropods in their distribution are restricted to warm water it is reasonable to suppose differences between the population of one species in Atlantic and Indo-Pacific regions. The separate conditions in the Atlantic are already proved by the distribution of *A. turriculata, Pterosoma planum, Carinaria galea, C. cristata* and *C. cithara.*

The occurrence of a greater diversity in *Atlanta* and *Carinaria* is consequently understandable; the occurrence of species always represented by two or sometimes three forms is, however, not clear. The forms of one species are sympatric, which implicates that geographic speciation does not apply. The separation between the formae can be a seasonal or vertical separation. Another possibility is that we are dealing with polymorphism.

Summary

A staining method for Heteropoda, especially for shell-less Atlantidae, is described. The identification of stained specimens is discussed. A classification of the heteropods is given, based on the idea that several taxa in *Atlanta* and *Carinaria* are more closely related than other species of these genera. Speciation is briefly discussed, comparing Heteropoda with Pteropoda, the other group of planktonic Mollusca.

Literature

FRONTIER, S., 1966. Notes morphologiques sur les Atlanta récoltés dans le plancton de Nosy-Bé (Madagascar). — Cah. O.R.S.T.O.M., sér. Océanogr., 4 (2): 131-139, figs. 1-36.

RICHTER, F., 1961. Die Radula der Atlantiden (Heteropoda, Prosobranchia) und ihre Bedeutung für die Systematik und Evolution der Familie. — Zeitschr. Morph. Ökol. Tiere, 50: 163-238, figs. 1-32.

TESCH, J. J., 1949. Heteropoda. — Dana Report (34): 1-53, figs. 1-44, pls. 1-5.

TOKIOKA, T., 1955a. On some plankton animals collected by the Syunkotu-Maru in May-June 1954. — Publ. Seto Mar. biol. Lab., 4 (2-3): 227-236, figs. 1-5, pls. 15-16.

——, 1955b. Shells of Atlantidae (Heteropoda) collected by the Sôyô-Maru in the southern waters of Japan. — Publ. Seto Mar. biol. Lab., 4 (2-3): 237-250, figs. 1-10, pls. 17-18.

——, 1961. The structure of the operculum of the species of Atlantidae (Gastropoda: Heteropoda) as a taxonomic criterion, with records of some pelagic mollusks in the North Pacific. — Publ. Seto Mar. biol. Lab., 9 (2): 267-332, figs. 1-42.