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HETEROPODA*

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INTRODUCTION

The heteropods are transparent planktonic animals, whose systematic position has undergone considerable reappraisal since the last century. It was Lamarck who, in 1812, created the order Heteropoda, which he placed between the Cephalopoda and the fishes, and brought together the genera *Carinaria*, *Firola* and *Phyllirhoë*. Later, Cuvier (1829) added to these the genus *Atlanta*.

Although several authors attempted to place the heteropods close to the pteropods, it was Milne-Edwards (1842) who finally showed that without doubt the heteropods should be placed among the Gastropoda. More recently Thiele (1929–1935) placed the heteropods within the Mesogastropoda, between the Strombacea and the Naticacea. In recent classifications Taylor and Sohl (1962) no longer use the term 'heteropod' but place the superfamily 'Atlantacea' between the Cypraeacea and Naticacea while Franc (1968), similarly, refers to the Atlantoidea. Nevertheless, the term 'heteropod' is used currently in scientific literature and it seems timely to suggest that the name should be preserved in nomenclature as the superfamily Heteropoda, rather than the Atlantoidea, within the order Mesogastropoda.

Since Forskål (1775), who erected the genus *Pterotrachea*, a great many species have been described: see, Lamarck (1801), Péron and Lesueur (1810), Lesueur (1817a,b), Blainville (1825), Lesson (1830), Quoy and Gaimard (1832), Benson (1835), D'Orbigny (1836), Gray (1821), Souleyet (1852), Gegenbaur (1855a), MacDonald (1862), Smith (1888), Oberwimmer (1898), Vayssière (1904, 1927), Schiemenz (1911), Issel (1911, 1915), Bonnevie (1920). Tesch (1906, 1908, 1910, 1949) has endeavoured to clarify the systematics of the group, believing that the multiplicity of described species could be explained by the distortion that occurs following fixation and, furthermore, that almost all the descriptions were useless. Tesch (1949) also criticized the importance given to the radula by Vayssière (1904, 1927) and Bonnevie (1920) as a criterion of specific determination, regarding it of value only in the determination of genera. In 1949 Tesch, after examining material from the Dana expedition, gave corrected descriptions of 22 species of heteropods which he recognized as valid following a concensus of 107 species. Since then three new species have been described (Tokioka, 1955; Richter, 1961; Frontier, 1966a), while descriptions of certain species originally described by

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Tesch (1949) have been made more precise by Franc (1949a), Dales (1957), Furnestin (1961), Richter (1961, 1968), Frontier (1966a), and Tokioka (1955, 1961) who define new criteria of shell form and dimensions for the species of the family Atlantidae.

LIST OF SPECIES

(Synonomy is given in Tesch, 1949, and Tokioka, 1955).

The superfamily Heteropoda comprises three families; namely, the Atlantidae characterized by a calcareous transparent shell which can contain the entire animal and a laterally flattened fin-like foot with an operculum and a sucker; Carinariidae with shell very much smaller than the animal in which the foot, is transformed into a fin, carries a sucker but not an operculum; and the Pterotracheidae without a shell and in which the foot is flattened and elongate, without an operculum while a sucker is present only in the male.

The principal characters of the known species are given below and have been compiled from Tesch (1949), from workers since that date, and from my personal observations on the Atlantidae.

ATLANTIDAE

Oxygyrus keraudreni (Lesueur, 1817a)

Adult shell plano-spiral and surrounded by a carena, double at its base, cartilaginous, reaching from the mouth to half way around the circumference where it terminates abruptly; sinuous longitudinal striae at the origin of the spire, development varies according to the age of the animal; more or less light brown in colour; massive proboscis and short tentacles.

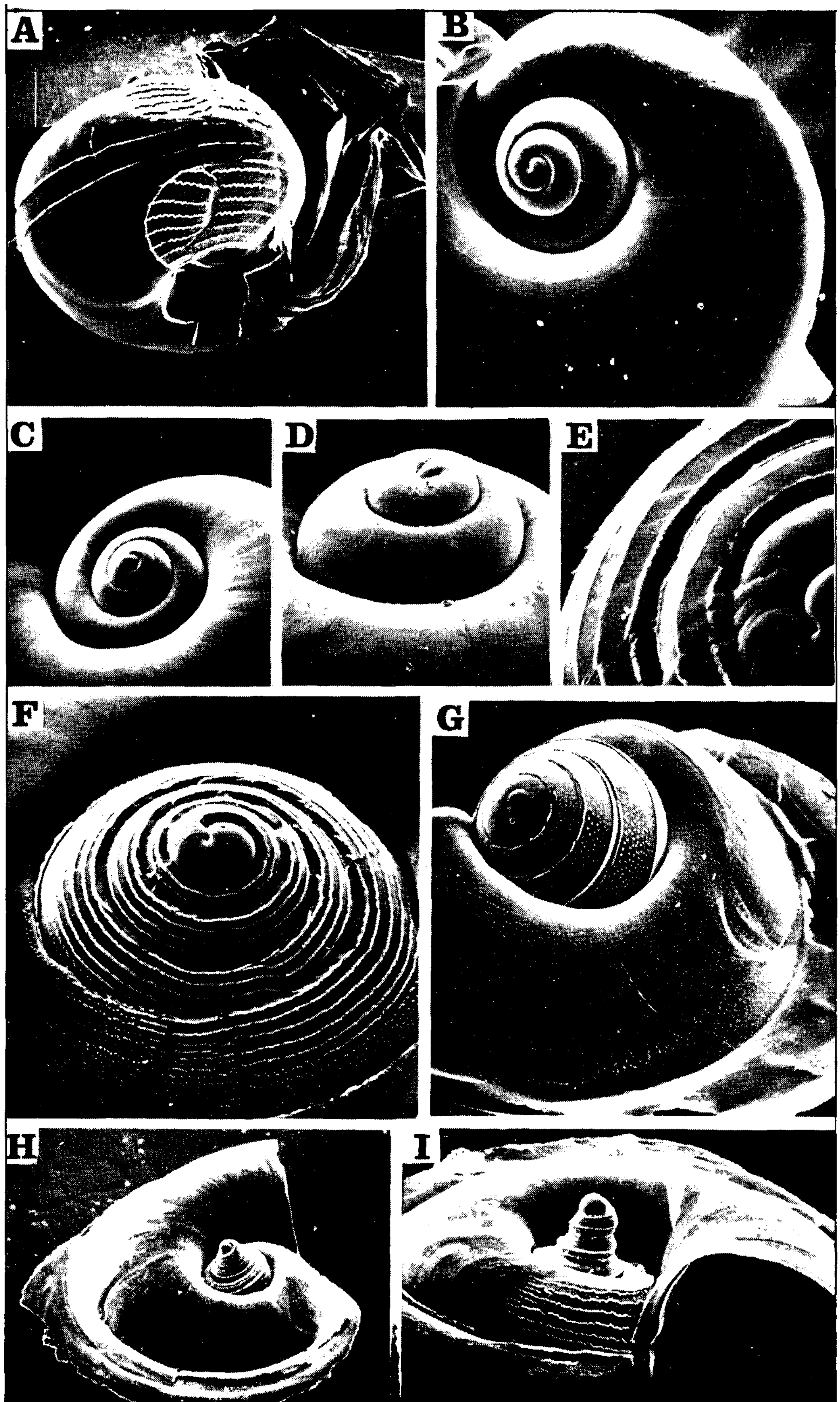
Proatlanta souleyeti (Smith, 1888)

Calcareous shell, transparent and smooth with a cartilaginous carina that is particularly translucent and which encircles approximately half the shell; older individuals have 3½ turns in the spire, which has a slightly convex, but regular profile; the first turns of the spire are a fawn/beige colour; massive buccal region.

Atlanta peroni Lesueur, 1817a

Shell smooth and flat, except for the first turns of the spire which are in slight relief; spire with 5 turns in older specimens (diameter 10–11 mm); carena surrounds the entire external circumference and penetrates between the turns in old specimens; the first contoured spires are pink, while the base of the carena is a diffuse brown colour; elongate buccal region, tentacles long. As shown by Frontier (1966a) there is a fine stria parallel to the outline of the spire.

Fig. 1.—Scanning electron micrographs of shells of Atlantidae: A, *Oxygyrus keraudreni* (juvenile specimen) × 45, note the limit between larval shell and juvenile shell; B, *Proatlanta souleyeti*, × 100, note the beginning of the keel (arrow); C, *Atlanta peroni* (apex) × 65; D, *A. lesueuri* (apex) × 200; E, *A. inflata* (detail of whorls) × 580; F, *A. helicinoides* (apex) × 190; G, *A. inclinata* (juvenile) × 95; H, *A. fusca* × 39; I, *A. turriculata* × 62.


A
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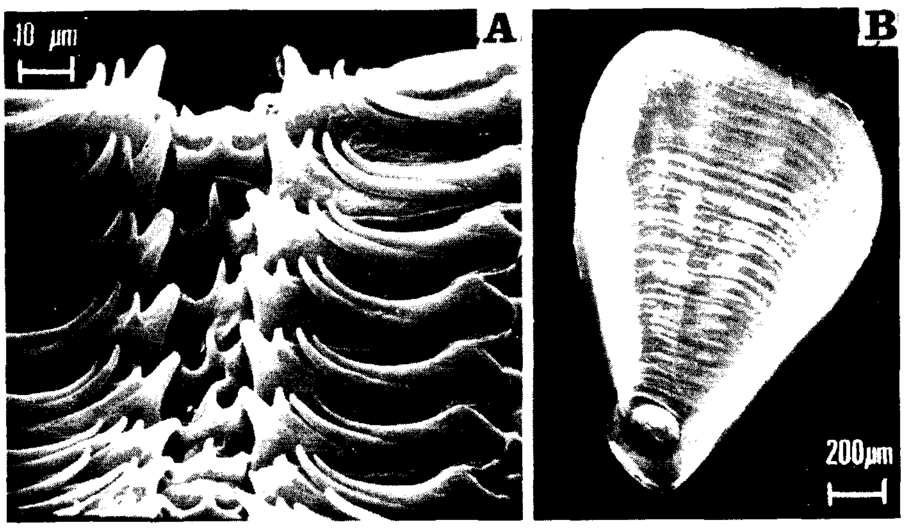


Fig. 2.—Scanning electron photomicrographs of *Atlanta peroni:* A, anterior part of the taenioglossan radula; B, operculum.

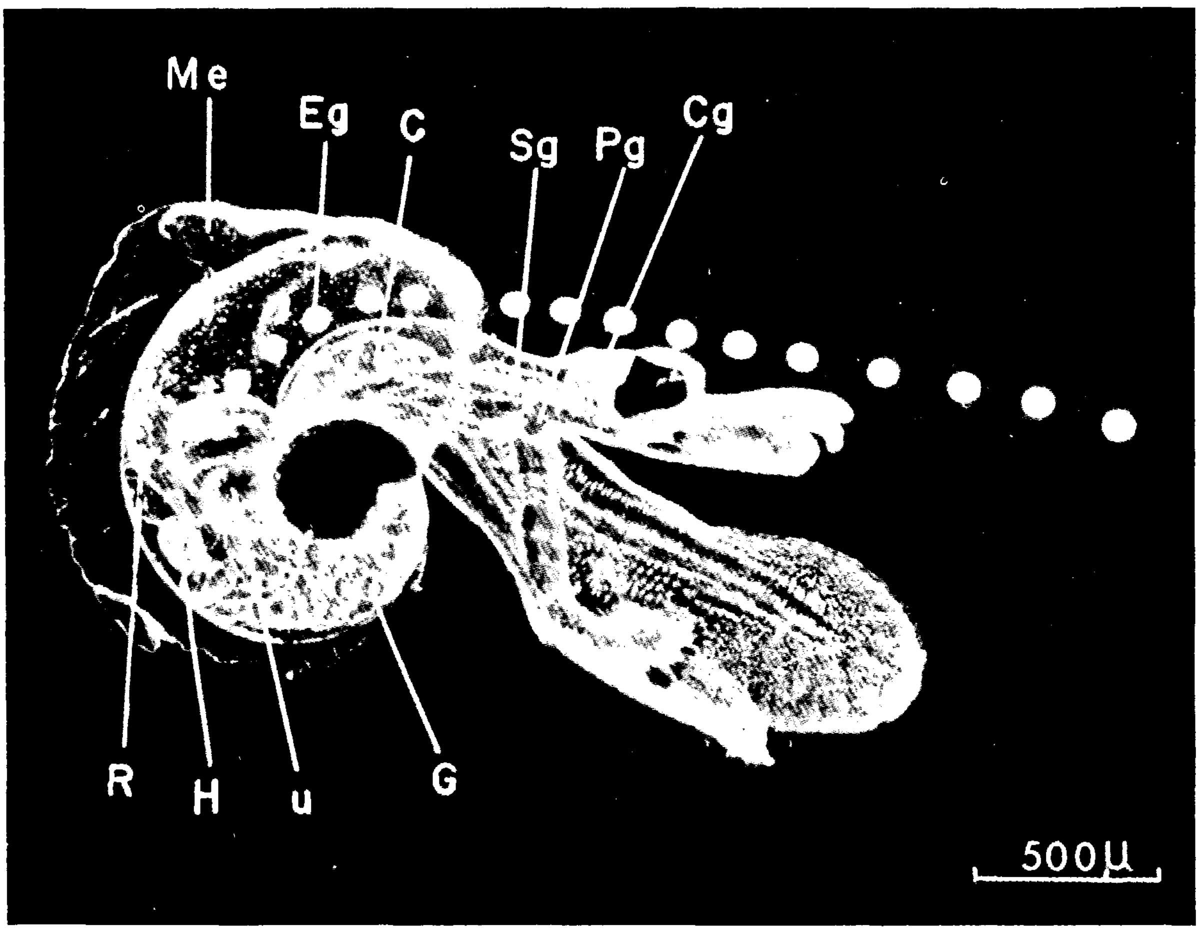


Fig. 3(a).—Adult of *Atlanta inflata* (after Thiriot-Quiévreux, 1969b; photograph by C. Lecomte N. R. S.). 1, female. C, crop; Cg, cerebral ganglion; G, gonad; H, heart; Eg, egg; Me, mantle edge; Pg, pedal ganglion; R, rectum; Sg, salivary gland; u, uterus.

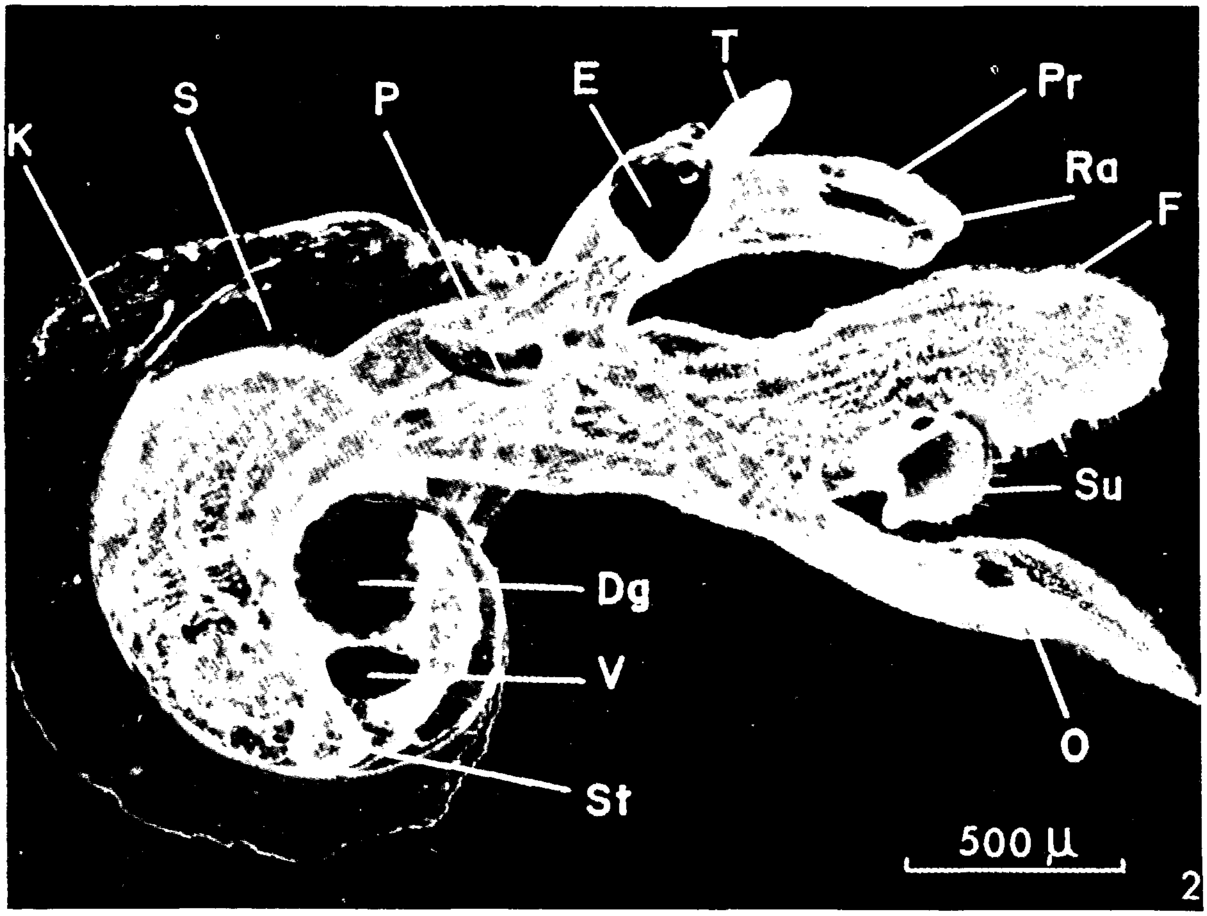


Fig. 3(b).—Adult of *Atlanta inflata* (after Thiriot-Quiévreux, 1969b; photograph by C. N. R. S. Lecomte). 2, male. Dg, digestive gland; E, eye; F, fin; P, penis; Pr, proboscis; K, keel; Ra, radula; S, shell; St, stomach; Su, sucker; T, tentacle; V, vesicula seminalis; O, opercular lobe.

Atlanta gaudichaudi Souleyet, 1852

Very similar to the preceding species; shell smooth, with up to 4 turns of the spire, the diameter of the mouth of the shell larger than that of the preceding species; base of the carena a red/brown colour and the carena penetrating between the first, rose coloured, turns. As shown by Frontier (1966b), the shell is ornamented at the edge by a large number of fine longitudinal striae which are sometimes lost after being kept for some time in formalin. Tesch (1949) suggested that this was but a variety of *A. peroni*, although Richter (1968) and Frontier (1966a) both maintain that it is a distinct species.

Atlanta lesueuri Souleyet, 1852

Shell flat and smooth with 2½–3 turns in the spire, the width of the shell aperture attaining half the diameter of the shell; animal transparent with little colour except for spots of beige/pink on the sucker at the centre of the lower side of the operculum and on the penis; digestive gland colourless.

Atlanta inclinata Souleyet, 1852

Shell smooth, spire with numerous (5) turns, the axis of the first turn forms an acute angle with the plane of the last turn, the angle of inclination varying with the age of the animal; spire sometimes ornamented with fine spiral lines which are formed by microscopic punctae.

Atlanta megalope Richter, 1961

This species is close to *A. inclinata*, shell smooth, hyaline or white, 6–7 turns to a spire, 6 mm in diameter, eyes particularly large (2–3 times the size of the preceding species).

Atlanta pacifica Tokioka, 1955

This species is close to *A. gaudichaudi;* shell with 4–4½ turns to the spire, small parts of the carena are inserted between the first turns of the spire; the turns, in profile, are a little more prominent than in *A. gaudichaudi;* colour of spire purple (shell whitish in some specimens), the base of the carena sometimes brownish in colour.

Atlanta peresi Frontier, 1966a

Shell smooth, with 3½ turns to the spire in a specimen 2·69 mm diameter; colour milk-white; dimensions, from the criteria given by Tokioka (1955), intermediate between *A. lesueuri* and *A. peroni.*

Atlanta inflata Souleyet, 1852

Shell, in profile, relatively flat, 4–5 turns to the spire, carena penetrates between the first turns either little or not at all; fine longitudinal striae on the second and third turns, and sometimes at the beginning of the fourth, striae may become worn with age or with state of preservation of the shell; small species, the suture of the carena a purple or a brownish colour, first turns of the spire dark purple, violet/purple spots on the sucker, on the lower side of the operculum and on the penis; denticulations on three quarters of the length of the operculum (Tokioka, 1961).

Atlanta helicinoides Souleyet, 1852

This is similar to the previous species, the suture is a little less strongly coloured and the colouration in general is more yellowish; longitudinal striae more numerous (7–8 instead of 3–4). Frontier (1966a) distinguishes two groups, one with a thick spire and very pronounced ornamentation, the other with a flattened shell and almost effaced ornamentation.

Atlanta fusca Souleyet, 1852

Shell, brown in colour; in profile, and in relation to the last turn, the first turns of the spire can be clearly seen in relief; ornamentation consists of longitudinal striae, which are particularly obvious on the first turns but which become less obvious during growth; body deeply pigmented.

Atlanta turriculata D'Orbigny, 1836

Shell brownish or pink in colour, the first turns of the spire form an attenuate forwardly inclined turret; spiral striae are present on the first turns of juveniles and on the convex part close to the aperture in older individuals.

If certain species show clear cut specific characters (e.g., *Oxygyrus keraudreni*, *Proatlanta souleyeti*, *Atlanta lesueuri*, *A. fusca*), others are most difficult to differentiate, for example, *A. gaudichaudi* and *A. peroni*. Tesch (1949) made the same observation and considered that *A. gaudichaudi*, *A. peroni*, and *A. inclinata* might be varieties of the same species. The numbers of turns of the spire and the existence and arrangement of striae, being a function of the age of the animal, are variable criteria and it must be emphasized that the degree of ornamentation may be affected by the method of preservation. The systematics of the Atlantidae needs revision using both living and fixed animals.

Richter (1961) studied the evolution of the radula during the course of the ontogeny of the Atlantidae and established two phylogenetic lines starting from a common ancestor, *A. fusca*, which is characterized by two cuspids on the intermediate teeth, the intermediate teeth being present in all the juvenile individuals of all the species he examined: these are (1) *A. fusca*, *A. helicinoides*, *A. inflata*, *Proatlanta* and *Oxygyrus;* and (2) *Atlanta fusca*, *A. gaudichaudi*, *A. peroni*, *A. inclinata*, *A. lesueuri*, and *A. megalope*. The first series tends towards the simplification of the intermediate teeth and species listed after *A. helicinoides* have only one cuspid, while the loss of the second cuspid is later in the second series.

CARINARIIDAE

Carinaria lamarcki Péron and Lesueur, 1810

Body long (25 cm maximum), transparent, with a thick epidermis which bears conical papillae; head with a proboscis and two tentacles; visceral region situated at the middle of the animal, level with the fin; shell flattened, thin and transparent, transversely furrowed; carena straight, the length of the upper base greater than the height.

Carinaria galea Benson, 1835

Animal much smaller than the preceding species (5 cm); body without tubercles; shell much higher than the preceding species.

Carinaria cristata Linné, 1766

Animal may attain 46 cm, body with epidermal tubercles and with a crest on the tail; shell is identical to that of *C. galea* but the carina is low.

Carinaria cithara Benson, 1835

Animal is small (5 cm), with some tubercles on the body but the tail without a crest; shell rectangular in form with the striae nearly straight; right tentacle absent.*

Pterosoma planum Lesson, 1827 (Crosse, 1896, *emend.*)

Body flattened, very transparent ending in a narrow tail; shell flat, traversed by a double axial line; embryonic shell with transverse striae on the first turn.

Cardiopoda placenta (Lesson, 1830)

Viscera (or 'nucleus') directed forward, thus a very small part is protected by the shell; numerous gills arranged in rows around the nucleus, tail ends in a pigmented, star-shaped, expansion; minute shell with lateral expansions around the aperture.

Cardiopoda richardi Vayssière, 1904

Eight gills placed at the entrance to the pallial cavity; fin with obvious muscle bands, tail long and filamentous ending in a point; very pigmented expanse under the tail; retina of eye directed upwards (as in *Oxygyrus*).

PTEROTRACHEIDAE

Pterotrachea coronata Forskål, 1775

Body transparent and very elongate, colourless (12–100 mm); dark brown, slender nucleus, 4–5 times longer than wide, positioned at the back of the animal, which ends in a short slender tail; proboscis elongate; cylindrical eyes, the length of their axis is much greater than the width of the basal retina, denticulations under the eyes in older individuals.

Pterotrachea hippocampus Philippi, 1836

Nucleus thick, about half as wide as long; eyes triangular with the base of the retinal part widened; epidermis with scattered red dots in living specimens.

Pterotrachea scutata Gegenbaur, 1855a

Nucleus thick, a hyaline and gelatinous disc is present that covers the anterior part of the animal; eyes cylindrical in form but their bases are a little larger than those of *P. coronata*.

Pterotrachea minuta Bonnevie, 1920

Species small (2·5 cm); nucleus elongate, 3 times as long as wide; eyes wide at the base but the axial length is greater than that of *P. hippocampus*.

* Add, *Carinaria japonica* Okutani, 1955: body 62 mm in length; cuticle smooth with gelatinous tubercules; viscera triangular in outline; eye with broadly based, triangular retinal part: shell moderately high, carina wide.

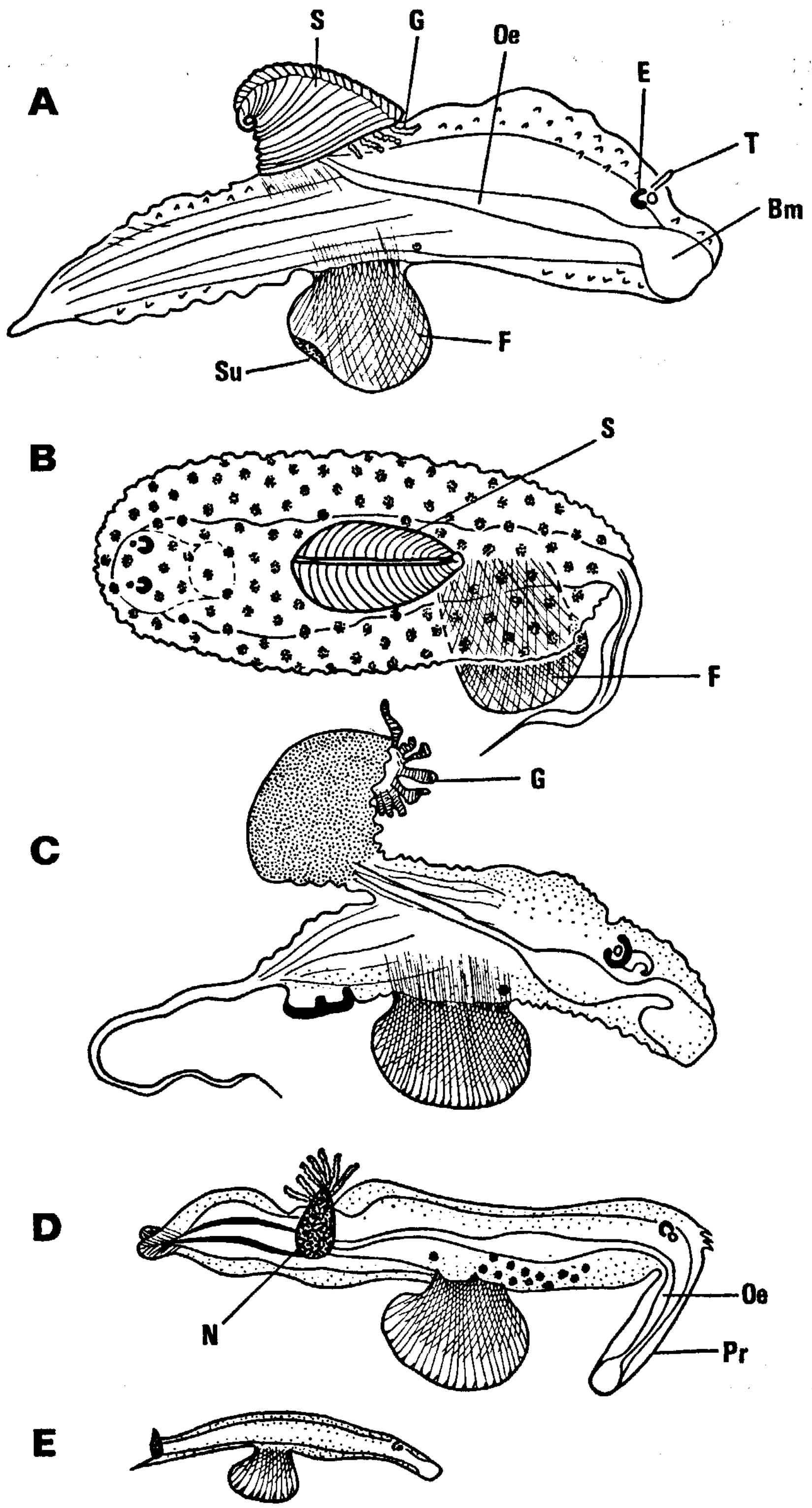


Fig. 4.—Adults of various female heteropods (redrawn after Tesch, 1949): A, *Carinaria lamarcki;* B, *Pterosoma planum* (from above); C, *Cardiopoda richardi;* D, *Pterotrachea hippocampus;* E, *Firoloida desmaresti:* Bm, buccal mass; E, eye; F, fin; G, gills; N, nucleus; Oe, oesophagus; Pr, proboscis; S, shell; Su, sucker; T, tentacle.

Firoloida desmaresti Lesueur, 1817b

Body colourless and transparent, small species (about 1·5 cm), nucleus situated in a terminal position; without tail, caudal filament and ovigerous cordon present in the female; elongate proboscis with short tentacles only in the male.

Little work has been done on the systematics of the families Carinariidae and Pterotracheidae since 1949; however, Richter (1968) from consideration of shell and radula characters has traced an evolutionary sequence for some recent species: *Atlanta fusca, A. inflata, Oxygyrus keraudreni, Atlanta peroni, Carinaria lamarcki, Cardiopoda placenta, Firoloida desmaresti,* and *Pterotrachea hippocampus.*

The position of *Oxygyrus* and *Firoloida* within the limits of the evolutionary sequence marks a new point of view which is in contrast to the older view that *Oxygyrus* was at the beginning and *Firoloida* at the end of a sequence of evolutionary events.

SEASONAL AND GEOGRAPHIC DISTRIBUTION

Following Tesch (1949), the geographical distribution of the heteropods is given in the Table I. The majority of the species are cosmopolitan and, above all, tropical and subtropical. Five species are peculiar to the Indo-Pacific region. Information recorded subsequent of Tesch (1949) has been reassembled in Table II.

TABLE I

The geographical distribution of the Heteropoda: +, present; –, absent.

Species	Atlantic	Mediterranean	Indo-Pacific
Oxygyrus keraudreni	+	+	+
Proatlanta souleyeti	+	+	+
Atlanta peroni	+	+	+
A. gaudichaudi	+	–	+
A. inclinata	+	–	+
A. lesueuri	+	+	+
A. helicinoides	+	–	+
A. inflata	+	–	+
A. fusca	+	+	+
A. turriculata	–	–	+
Carinaria lamarcki	+	+	+
C. galea	–	–	+
C. cithara	–	–	+
C. cristata	–	–	+
Cardiopoda placenta	+	–	+
C. richardi	+	–	+
Pterosoma planum	–	–	+
Pterotrachea coronata	+	+	+
P. hippocampus	+	+	+
P. scutata	+	+	+
P. minuta	+	+	+
Firoloida desmaresti	+	+	+

TABLE II

Geographical distribution of the Heteropoda: subsequent to Tesch (1949).

Geographical location	Sampling method and principal results	Species recorded	References
MEDITERRANEAN			
Malta	4 samples/year	*A. fusca*, *A. peroni*, *F. desmaresti*	Evans, 1968
Malta	Sampled Dec.–Jan.	*Atlanta* (not determined) *F. desmaresti*	Seguin, 1968
Algiers Banyuls-sur-Mer	Sampled Dec.–June, July	Larvae and adults: *Atlanta* spp., *O. keraudreni*, *C. lamarcki*, *Pterotrachea* spp., *F. desmaresti*	Franc, 1948, 1949a
Villefranche sur-Mer	Mar., Feb.		
Gulf of Naples	Annual seasonal cycle 1st max.: Feb.–Mar. 2nd max.: Oct.–Nov.	Larvae and adults: *A. inflata*, *A. lesueuri*, *A. peroni*, *A. fusca*, *A. megalope*, *P. souleyeti*, *O. keraudreni*, *C. lamarcki*, *P. hippocampus*, *P. coronata*, *P. minuta*, *F. desmaresti*	Richter, 1968
N. Med. west.	Seasonal 'Isaacs Kidd' samples; present in winter and spring	*C. lamarcki*, *P. coronata* and *P. hippocampus*	Franqueville, 1971
Southern zone: Golfe du Lion, Banyuls-sur-Mer	Annual cycle max.: summer and autumn	Larvae and adults: *A. lesueuri*, *A. inflata*, *A. peresi*, *F. desmaresti*. Larvae: *O. keraudreni*, *C. lamarcki*, *Pterotrachea* spp.	Thiriot-Quiévreux, 1967, 1968, 1970
Barcelona	Annual cruise	*A. peroni*, *A. helicinoides*	Vives, 1966
Tyrhennian Sea	Annual cruise	*A. peroni*, *A. helicinoides*, *O. keraudreni*, *F. desmaresti*	Vicente and Ehrhardt, 1964
ATLANTIC			
Brazil	Seasonal cruises	*A. peroni*, *C. lamarcki*, *Pterotrachea* spp.	Barth, 1968a,b
Gulf of Guinea	Seasonal cruises	*O. keraudreni*, *P. souleyeti*, *A. gaudichaudi*, *A. lesueuri*, *A. helicinoides*, *A. fusca*, *A. turriculata*, *C. lamarcki*, *C. placenta*, *P. coronata*, *P. scutata*, *F. desmaresti*	Frontier, 1968
Abidjan	Annual cycle, moderately frequent	*Atlanta* (not determined)	Seguin, 1970
Morocco	Seasonal cruises; taken in all seasons, although fewer present in autumn and winter	*O. keraudreni*, *P. souleyeti*, *A. fusca*, *A. inclinata*, *C. lamarcki*, *P. minuta*, *F. desmaresti*	Furnestin, 1961

TABLE II—*continued*

Geographical location	Sampling method and principal results	Species recorded	References
E. Atlantic	Atlantic cruises and *Galathea* Expedition	*O. keraudreni, A. peroni, A. gaudichaudi, A. lesueuri, A. inclinata, A. helicinoides, A. fusca, C. placenta, P. minuta, F. desmaresti*	Van der Spoel, 1970
N.E. Atlantic and North Sea	Plankton recorder (1948–1959)	*Atlanta* spp. (*peroni*), *F. desmaresti*	Vane, 1961
	Plankton recorder (1948–59), present in 8 of 12 years, most frequent in Aug., Sept., and Oct.	*A. peroni*	Vane and Colebrook, 1962
OTHERS			
Australia	D.S.L. (10–20 m)	*F. desmaresti*	Blackburn, 1956
New Zealand	Samples	Pterotracheidae, *Atlanta* sp.	Ralph, 1957 Pilkington, 1970
Chile	Cruises	*P. coronata, F. desmaresti*	Fagetti, 1958; Fagetti and Fischer, 1964
Japan	Cruises	*A. lesueuri, A. peroni, A. gaudichaudi, A. inclinata, A. inflata, A. fusca, A. turriculata, A. pacifica, O. keraudreni*	Tokioka, 1955 Taki and Okutani, 1962
Madagascar, Nosy-Bé	Samples	*O. keraudreni, P. souleyeti, A. peroni, A. gaudichaudi, A. inclinata, A. lesueuri, A. helicinoides, A. inflata, A. fusca, A. turriculata, C. placenta, F. desmaresti*	Frontier, 1963
Madagascar, Nosy-Bé	Annual seasonal cycle minimum: May, July (austral autumn) maximum: Sept.–Oct. (end of winter and beginning of austral spring)	idem. + *P. hippocampus*	Frontier, 1966b
Pacific coast of N. America	Various cruises	*C. lamarcki, P. scutata, P. minuta, P. coronata, P. hippocampus*	Dales, 1952

In the majority of published investigations, it must be noted that the heteropods are rarely studied for themselves, usually being cited in general zooplanktonic studies, or being included as 'pelagic molluscs' together with the pteropods. The quantitative variations have also been little studied, for numerically the heteropods are not a large component of the plankton: thus, Furnestin (1961) collected 300 specimens off Morocco in the course of seasonal sampling over a period of three years, with the maximum numbers in a single haul of 16 for *Oxygyrus*, 13 for *Atlanta fusca* and 18 for *A. inflata*. Frontier (1966b) obtained the greatest number so far reported in the region of Nosy-Bé, Madagascar. Three species were abundant, *A. helicinoides* (average of 43 per collection), *A. gaudichaudi* (27) and *A. lesueuri* (21). In 24 samples (horizontal tows in the course of one year) at an offshore station; the maximum number of individuals collected was in the case of *A. helicinoides* (1029), in comparison with 71,000 *Creseis acicula* taken at the same station. Richter (1968) in the course of three years in the Gulf of Naples collected 2,300 individuals in surface plankton tows, the most abundant species being *Atlanta inflata* (1478). The number of larvae is always markedly greater than that of the adults although it should be noted that differentiation between the larval and adult stages is rarely given. The numbers collected in the region of Banyuls (Thiriot-Quiévreux, 1968) in vertical tows (50–0 m) is very low and exceptionally 26 to 29 specimens of the larvae of *Atlanta* are taken in a tow. All these results indicate that in terms of quantitative importance the heteropod contribution is negligible in terms of the total biomass of the zooplankton.

The vertical distribution of the group is, for the same reason, practically unknown. A study of horizontal tows taken at four different depths in the neritic zone with a closing net (Thiriot-Quiévreux, 1968) shows a preferential distribution between the surface and 20 m for the larvae of *Atlanta* (at periods of abundance); the numbers are too low to be precise for the vertical distribution of the individual species. In general, heteropods are collected from surface waters (Tesch, 1949); but Lo Bianco (1909) recorded *Carinaria lamarcki* at depths of 30 m to 500 m and Hardy (1956) found one individual at 1000 m off the Hebrides. Dales (1952) remarked on the accumulation of carinarids in regions of upwelling.

With regard to the seasonal distribution of the Heteropoda, at least in the Mediterranean, there is a summer-autumn maximum (Vives, 1966; Richter, 1968, and Thiriot-Quiévreux, 1968) and in the North Atlantic (Vane and Colebrook, 1962). In the Australian region, the maximum is at the end of winter and the beginning of spring (Frontier, 1966b). The later work of Tesch (1949) contributed data on the geographical distribution of several species of the Atlantidae; thus *Atlanta gaudichaudi, A. helicinoides* and *A. inflata* are recorded from the Mediterranean. Unfortunately little work has been done in the Indo-Pacific region, and in particular our knowledge of the Carinariidae has not increased much in the last twenty years (except for Okutani, 1961).

MORPHOLOGY

Work on the anatomy of heteropods up to 1924 was reviewed by Tesch (1949); see for general anatomy and histology, Delle Chiaje (1843), Rang (1827, 1829, 1832), Leuckart (1854), Leydig (1851), Gegenbaur (1855a,b), Paneth (1885), MacDonald (1871), Rattray (1871), Kalschmidt (1912) and Reupsch (1912); for musculature, Warlomont (1886), Kalide (1888) and Wackwitz (1892); for the morphology of the foot, Huxley (1853), Fewkes (1883), Grobben (1888), Kalide (1888) and Tesch (1906); for the pharynx and radula, Buchmann (1824) and Rössler (1886); for kidney, heart, and circulatory system, Huxley (1850), Joliet (1883), Fahringer (1903) and Gerwerzhagen (1914); for statocyst, Ranke (1875), Claus (1876), Ilyin (1900), Retzius (1902) and Tschachotin (1908); for eyes, Schultze (1869), Grenacher (1892), Hesse (1900) and Hess and Gerwerzhagen (1914); for osphradium, Warlomont (1886); and for nervous system, Edinger (1877), Pelseneer (1892a,b) and Brüel (1915, 1921, 1924). Amongst these older works, the morphological descriptions of Leuckart (1854) and Gegenbaur (1855a,b) remain the basis for general zoological texts while Krasucki (1911) and Reupsch (1912) made important microscope observations on the genus *Pterotrachea.* Moreover, in general it is this latter genus that has been most studied. Among the work done since that of Tesch (1949), there are several papers on studies of a single species. Vannucci (1951) described the external morphology of *Firoloida desmaresti,* from an examination of animals mounted in glycerine. Furnestin (1961) made some histological observations of *Atlanta,* Fretter and Graham (1962) gave details of the morphology of *Carinaria lamarcki,* and Gabe (1966) made the first complete histological monograph on *Firoloida desmaresti.* The ciliary currents within the mantle cavity of species of the family Atlantidae were observed by Yonge (1941) who confirmed the tactile function of the osphradium, while Heymans (1969) states precisely the chemical nature (neutral and acid mucopolysaccharides with small amounts of proteins) of the connective tissue of the Pterotracheidae (*Pterotrachea* and *Firoloida*).

Gabe and Prenant (1950), working on *Pterotrachea,* described the histological characters of the radula sheath which they found to be analogous to those of *Firoloida desmaresti* (Gabe, 1966). The phylogenetic and ontogenetic significance of the radula of the Atlantidae is analyzed by Richter (1961). The alimentary canal of the Pterotracheidae is well known due to work of Gabe (1952, 1966). It comprises the buccal bulb with the radula and radula cartilages, two pairs of symmetrical salivary glands, the oesophagus, crop, stomach, intestine (divided into 3 regions) and the digestive gland. Composed of the same parts as those of *Pterotrachea,* the alimentary canal of *Firoloida* differs in that the proximal part of the intestine is simpler and there is less diversification of cell categories in the digestive gland.

The alimentary canal of the Atlantidae (Martoja and Thiriot-Quiévreux, 1972a,b) is very short and devoid of mucous glands. Single-celled glands are scattered in the buccal wall and the anterior portion of the oesophagus. In the crop, apocrine secretion takes place. The glandular activity is low in the stomach and lacking in the intestine. Every salivary gland consists of a terminal pouch, a glandular tube with three types of secretory cells, and a long collecting duct. The digestive gland comprises three cell-lines, the third one being specifically distributed.

The nervous system of the Heteropoda has been particularly well studied, and a synthesis of past work has been given by Bullock and Horridge (1965) in their general account of the nervous system of invertebrates. Gabe (1966) makes some supplementary observations on the histology of the ganglia of *Firoloida.* The strength of the evidence for neurosecretory phenomena in relation to the development of the reproductive organs is particularly strong in the heteropods (Gabe, 1951b, 1953, 1965a,b, 1966). The neurosecretory cells are located in the median-dorsal section of the cerebral ganglia; the mating and egg laying periods correspond to the impoverishment of acidophilic substances in the neurosecretory cells, while latent reproductive periods correlate with cells charged with acidophilic inclusions. Thiriot-Quiévreux (1971a) noted the presence of glucidic compounds in the cellular layer between the neurones and the neurilemma of the visceral ganglion of species of Atlantidae; the development of this layer coincides with the genital maturation in the female.

The eye of heteropods signify a remarkable development within the prosobranch Gastropoda. They are composed of three parts, an anterior segment containing a voluminous crystalline sphere, a middle truncated segment rich in black pigment and a posterior retinal segment dorsoventrally flattened, from which emerge the optic nerve fibres (Hesse, 1900; Bullock and Horridge, 1965; Gabe, 1966). The ultrastructure of the photoreceptor cells of the eye of *Pterotrachea* has been given in detail by Dilly (1969); these cells are organized in 5 parallel rows each separated from the other by clear supporting cells.

Barber and Dilly (1969) studied the fine structure of the statocyst of *Pterotrachea;* the ciliated cells ('hair cells') of this species are grouped in a macula and bear 'kinocilia' and 'microvilli'.

The morphological and histological characters of the male genital system are described by Gabe (1965c) for five genera of the Heteropoda. The structure of the testis is analogous to that of gonochoric prosobranchs, with atypical spermatogenesis in all the species studied (atypical spermatogenesis had previously been observed by Tuzet, 1936, in *Carinaria lamarcki* and by Rudi, 1952, in *Pterotrachea mutica*)*. The vas deferens, of which the epithelial cells of the distal part are rich in melanin, can be regarded as a rapid transport pathway to the seminal vesicle. The reservoir for spermatozoa is in the form of a tube wound on top of the vas deferens and also lined with a melanin-rich epithelium. The prostate portion varies in length according to the species and is extended by a ciliated groove which is analogous to that of other prosobranchs. The copulatory complex comprises a basal sac with a glandular outgrowth, the penis, and a second gland (which is equivalent to the flagellum of Leuckart, 1853) the cells of which resemble the glandular outgrowth. Gabe (1965c) suggested that there was a hormone conditioning by the testis of the form of the male tract, which is remarkable for its morphological uniformity in the five species studied.

The female reproductive system of *P. mutica* and *Firoloida desmaresti* (Gabe, 1951a, 1966) have been studied and show important differences between the two species. The structure of the ovary and the oviduct are relatively similar in the two species, oogenesis taking place in much the same way as in other Prosobranchia: however, the receptaculum seminalis of *Pterotrachea* contains spermatozoa whatever the stage of the ovarian cycle, whereas in *Firoloida* spermatozoa are present only in gravid females. As for the uterus, in *Pterotrachea* the accessory glands are large and voluminous comprising three types of glandular ducts, while in *Firoloida* there are no individual accessory glands but the epithelium of the uterus is secretory. An exocrine gland (or lateral gland) has been described in the female of *Firoloida*, the function of which appears to be correlated with the state of the reproductive system. An anomaly of the gonad was observed by Franc and Gabe (1951) in one *Pterotrachea coronata* which had normal male external characters

* *Pterotrachea mutico* (= *hippocampus*).

but with aberrant testicular tissue and a ciliated groove normal in form but with few mucous cells.

The Heteropoda illustrate a particularly important example of evolution within the single superfamily. The family Atlantidae is phylogenetically considered to be closest to the mesogastropodan gastropods, while the Pterotracheidae show the most extreme adaptation to pelagic life. The Carinariidae are intermediate between these two families. Nevertheless, Gabe (1966) showed the uniformity of morphological and histological characters of some organs in contrast to the extreme diversity of form. A study of the comparative morphology of the different organs of all the heteropod genera would contribute important evolutionary data, for there are no histological studies on the family Carinariidae, and their are significant gaps in the information on the family Atlantidae.

FOOD AND DIGESTION

The Heteropoda are carnivorous animals. The Carinariidae and Pterotracheidae swallow their prey whole—hyperids, salps, *Sagitta* (Tesch, 1949). Dales (1952) noted that *Carinaria* was present in plankton rich in salps, coelenterates and chaetognaths. No author, to my knowledge, has observed ingestion of Crustacea. The heteropods are very selective in their choice of prey and as a consequence are of great importance in the food pyramid. Hirsch (1915) describes the ingestion of prey by *Pterotrachea*. The prey is very quickly passed from the pharynx to the crop and so called 'digestion proper' occurs within a period of 4–20 h after the meal. Hirsch (1915) reported digestion as being intracellular, the process taking place inside absorbant cells of the digestive gland. In contrast Gabe (1952, 1966), believes that it is the intestine that plays the essential rôle in the absorption of food materials, digestion being extracellular and that the digestive gland is concerned with the elaboration of digestive enzymes. Richter (1968) describes the ingestion of a specimen of *Hyalocylix* or a *Styliola* (Pteropoda) within *Atlanta peroni*. This author distinguished two types of carnivores within the Heteropoda, the 'swallowers' ("Schilinger") comprising the Carinariidae and Pterotracheidae, and the 'scrapers' or 'tearers' ("Kratzer oder besser Reisser"), the Atlantidae.

Thiriot-Quiévreux (1969b) observed the capture by *Atlanta* of prey such as *Creseis*, gastropod veligers, or other *Atlanta* (larvae and adults). The prey is brought to the mouth by the movement of the foot, the *Atlanta* holds the shell of the captive animal with the sucker while the *Atlanta* inserts its buccal mass in the aperture of the shell. Due to the movement of the protracted radula, the body of the prey is torn and ingested. Its passage down the oesophagus is rapid, but the prey is kept some time in the crop before it is passed back into the stomach by means of muscular contractions. The movements of the food between stomach and digestive gland can be observed directly, particularly in *A. lesueuri* because it is so transparent, and digestion is completed in about 24 h after the start of this phase. In general, an *Atlanta* ingests but one prey at a time, the torn pieces filling the crop; however if the prey is very small (a veliger for example) I have observed the immediate capture of a second, but this never occurs during the course of digestion of previously captured prey. In the case of one individual, I was able to note the capture of a prey species, its digestion and, three days after, the capture of a second prey species.

DEVELOPMENT

Fol (1876) reported that *Atlanta peroni* and *Oxygyrus* produce isolated eggs while in *Carinaria* and *Pterotrachea*, the eggs are joined together as a tubular string which breaks up into variable lengths. Thiriot-Quiévreux (1969b) observed the eggs of two species of *Atlanta*, namely *A. quoyana* (*A. inflata*), in which the egg string is 1–10 mm in length and *A. lesueuri*, which lays isolated spindle shaped eggs about 300 μm in length. Lo Bianco (1888, 1889, 1909) noted the time of egg production for *Firoloida* (all year, but particularly in winter) *Pterotrachea coronata* (January to April), *Carinaria lamarcki* (March to June), *Atlanta peroni* (June to March at the surface, October to March in deep water) and *Oxygyrus keraudreni* (October to April). Dales (1952) first recorded the eggs of *Carinaria lamarcki* chiefly in April and in May, then in September, but eventually throughout the year.

Segmentation is total and spiral. Fol (1876) observed in detail the development of the embryo until hatching, when the larva is liberated and becomes planktonic. Thiriot-Quiévreux (1969b) studied the development of the planktonic larvae of *A. lesueuri* and defined three larval stages based on developmental criteria of the eye, foot and shell (see Fig. 5).

Several authors have described the external morphology of the veligers of different species of the Heteropoda (Krohn, 1860; Simroth, 1907; Franc, 1948, 1949a; Owre, 1964; Thiriot-Quiévreux, 1967, 1969a; Richter, 1968; Pilkington, 1970).

The larvae are characterized from the morphology and colour of the shell and velum.

DESCRIPTION OF THE KNOWN LARVAE OF THE HETEROPODA

This is given at a stage immediately prior to metamorphosis, from published reports and my own observations.

Atlantidae

All the Atlantidae larvae show a slit in the middle of the shell aperture, which is characteristic of this family.

Oxygyrus keraudreni

This has a clear, brown, globular shell, ornamented with flexuous ribs, and with a long notch visible at the external edge of the aperture, the velum is six-lobed the extremities being a vivid pink colour.

Proatlanta souleyeti

The veliger has a colourless shell which is slightly convex, with 3–3½ turns to the spire. The shell has a fine punctate ornamentation; the velum is six-lobed and colourless; one can distinguish the dark brown pigmented gut and the light brown digestive gland through the transparent shell.

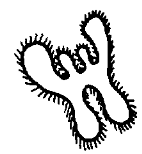
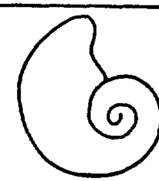
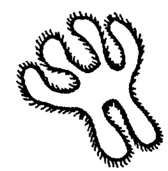
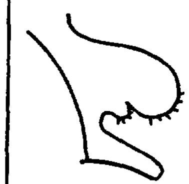
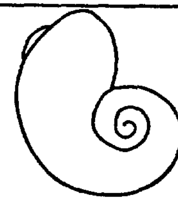
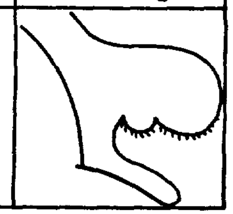
Atlanta lesueuri	Size	Shell	Velum	Eye (lens and pigmentary layer)	Foot
Stage I	300-400 µm				
Stage II	400-500 µm				
Stage III	500-600 µm				
Metamorphosis	About 600 µm		Idem		

Fig. 5.—Characteristics of larval stages of *Atlanta lesueuri* (after Thiriot-Quiévreux, 1969b)

Atlanta peroni

The shell of this veliger has 3½-4 turns to the spire, which are outlined in reddish violet; the velum is six-lobed with the lobes particularly long and bordered with a piping of reddish violet.

Atlanta peresi

The appearance of this species seems to be similar to that of *A. peroni*, but differs in having less a number of turns to the spire and in the presence of a small cusp on the second lateral tooth of the radula. A detailed examination of the veliger of *A. peroni* has still to be made.

Atlanta lesueuri

Immediately before metamorphosis, the veliger is approximately 500 μm in diameter with the shell having 3 turns to the spire; the turns are smooth, colourless and transparent; the velum is six-lobed, the lobes being unequal, with the lateral lobes very small and, whilst swimming, being held parallel to the anterior lobes; on some individuals, a brown piping edges the entire velum; the head, the opercular lobe, and the anterior part of the foot are completely coloured a pinkish brown; the digestive area at the centre of the spire is a clear yellow.

Atlanta fusca

A shell 500 μm in diameter has 3½ turns to the spire which, for the most part, is red-brown and yellow-brown in front; the shell aperture is oval with a deep groove; on the last turn of the spire, that part to the left of the groove is ornamented in relief with five, wavy longitudinal striae contained between two very marked rectilinear sides, the outer part exhibiting only longitudinal striae; the second and third turns are grooved with a fine longitudinal stria while the apex of the shell is punctate, transversely and between the striae; the whole shell is traced with very fine, tiny waves; the velum is six-lobed and colourless except at the tip of each lobe where there are spots of deep brown pigment; the lobes are flexible, the median lobe being held forward when swimming.

Atlanta quoyana (= *A. inflata*)

The shell, with 4½ turns to the spire, measures approximately 550 μm in diameter; the second, and the beginning of the third turn are ornamented with two longitudinal striae; the spires have a dark contour suture; the six-lobed velum is colourless with the lobes equal in size, but being more ridged than the preceding species; when swimming, the median lobes are orientated perpendicular to the anterior lobes; it is possible to see dark pigment on the head, the opercular lobe, and the anterior part of the foot; the digestive gland forms a characteristic violet brown mass at the centre of the spire.

Atlanta sp.

This veliger has a yellow-brown shell about 450 μm in diameter and 4½ turns to the spire; the second and third turns are ornamented with several longi-

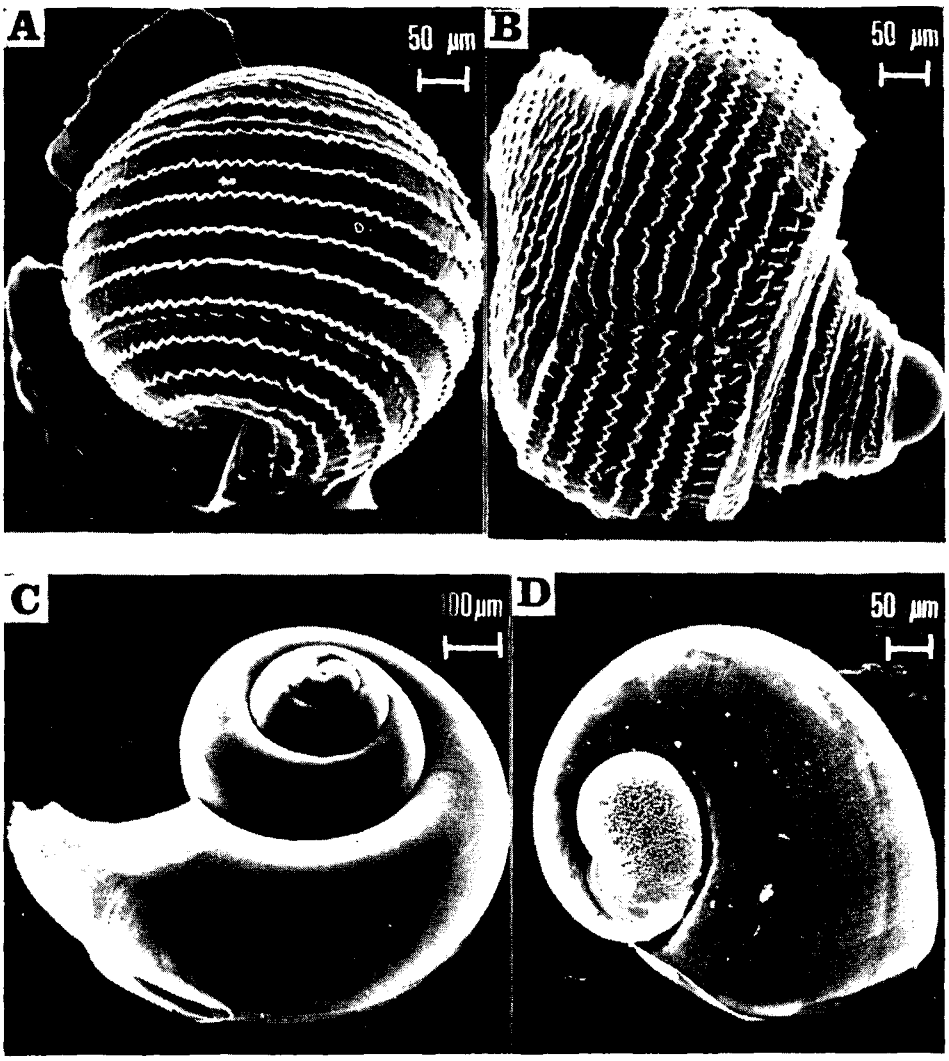


Fig. 6.—Scanning electron micrographs of various larval shells of heteropods: A, *Oxygyrus keraudreni;* B, *Atlanta fusca;* C, *A. peroni;* D, *Firoloida desmaresti.*

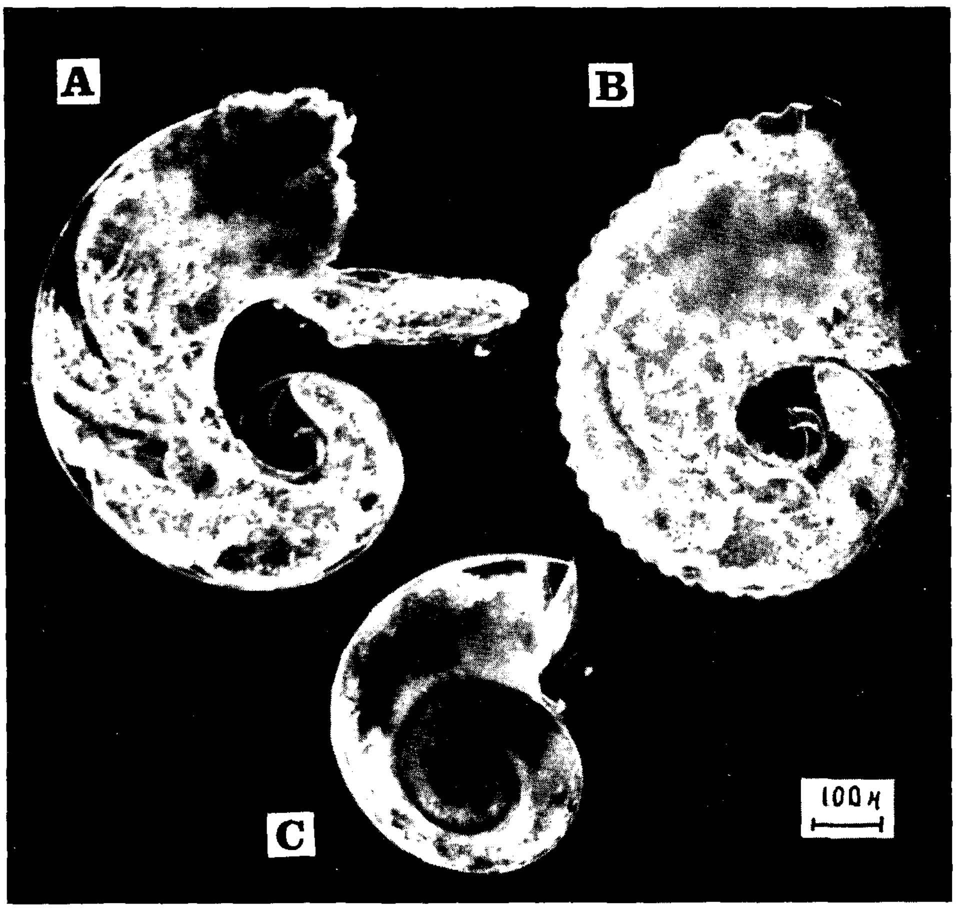


Fig. 7.—Larval shells of heteropods: A, *Pterotrachea* sp. 2 (opercular lobe opening); B, *Pterotrachea* sp. 1; C, *Carinaria lamarcki* (early stage); (after Thiriot-Quiévreux, 1969a).

tudinal striae; the velum is very similar to the preceding species; the head, foot and opercular lobe are a light brown colour, the mantle edge is brown, and the digestive gland is yellow.

Atlanta helicinoides

The shell can reach about 600 μm in diameter with 4½ turns to the spire; the second, third and beginning of the fourth have longitudinal striae; the centre of the shell is yellow and the contour suture of the spire a very constant yellow; the velum is essentially the same as the preceding species; the head and foot are faintly brownish, only the digestive part is dark yellow.

The last three species are difficult to distinguish. The velums are identical and only the ornamentation and the shell colour can be used for identification.

Carinariidae

Carinaria lamarcki (= *C. mediterranea*)

The shell of the veliger has a form similar to that of the Naticidae. It reaches more than 1 mm in diameter at metamorphosis with 4½ turns to the spire; the first turns are ornamented with fine longitudinal striate which are sometimes difficult to see; the velum is six-lobed, bordered with a fine brown piping, and with brown spots at the extremity of each long and flexuous lobe; the cylindrical appendix looks like a very mobile trunk; the tentacles are peculiarly developed, the right being longer than the left; the animal is a yellow-brown colour.

Pterotracheidae

Pterotrachea sp. 1 (= *P. minuta* of Richter, 1968, = *P. coronata* of Franc, 1948; Thiriot-Quiévreux, 1969a).

This is characterized by a thin shell, which is very transparent and traversed by about thirty transverse grooves; the veliger has a four-lobed velum, bordered by a brown piping and with a span of about 4 mm when the lobes are extended. This is the most frequently encountered species.

Pterotrachea sp. 2. (= *P. hippocampus* of Richter, 1968)

The veliger of this species is very close to the preceding species, but, the shell is entirely smooth and the point of the spire is more defined.

Pterotrachea sp. 3

The shell is smooth with 2 turns to the spire; the velum is four-lobed and bordered with a fine brown piping; the anterior right lobe is much enlarged in comparison with the other lobes, and the entire surface is pigmented brown as are the tips of the tentacles. This species had been described by Richter (1968), and has been seen in the region of Banyuls-sur-Mer and around Malta (Thiriot-Quiévreux, pers. obs.). It is almost impossible to distinguish with certainty the larvae of the three species of *Pterotrachea* and it is necessary to let them metamorphose. (In the case of one individual, Richter (1968) was able to observe the metamorphosis of *Pterotrachea* sp. 1.)

Firoloida desmaresti

The veliger has a pink-brown, globular shell, with 2 turns to the spire which measures 400 μm in diameter at metamorphosis; the shell is similar in form to veligers of the Naticidae; the velum is four-lobed and colourless except for the tips of the lobes which usually have brown spots.

ORGANOGENESIS OF THE LARVA

Franc (1949b) described the principal histological changes that take place at the time of metamorphosis of *Firoloida desmaresti*, and Thiriot-Quiévreux (1969b, 1971b) has observed the larval organization of many heteropod species. The following account follows the histogenesis of three larval stages and the metamorphosis of *Atlanta lesueuri.*

At Stage 1, the veliger has a shell secreted by the mantle edge, a velum, the foot in the form of a simple tongue, the gut showing advanced torsion and consisting of oesophagus, stomach, intestine and digestive gland. The radula is beginning to form and the first germ cells are apparent. The ganglia are present, in an ocular capsule which has the form of a small sphere enclosing a tiny lens and a spot of pigment. There is no larval nephridium but a definitive kidney is present; in contrast, there are larval and definitive hearts. It is only at Stage 2 that the primordia of the salivary glands and radula cartilage appear. The different cell types as seen in the adult digestive gland are formed. The posterior capsule lengthens and is slightly flattened. At the end of this stage future neurosecretory cells are differentiated. At Stage 3 the larval organization of the veliger is highly evolved and the development of the velum anticipates a long planktonic life. The foot differentiates, acquiring adult characters (sucker and swimming form). The form of the occular capsule is also analogous to the adult condition, the retinal cells of the posterior section having a well developed pigmentation. The first indication of the copulatory apparatus in males may be seen and takes the form of two small adjacent buds, which are the rudiments of the penis and flagellum. Metamorphosis involves important morphological changes, namely, the loss of the velum, the formation of the buccal extension, the elongation of the foot. The pigmentation of the intermediate segment of the occular capsule is particularly important in the control of the normal development of metamorphosis. The larval heart disappears. It is within the alimentary system that the principle histological changes occur—particularly with regard to the radula, the salivary glands, and the transformation of the posterior oesophageal region into the crop.

Except for some differences in histological detail in *A. quoyana* and *A. peresi*, the scheme of larval organization is identical throughout the genus *Atlanta*.

The general organization of the veliger of *Oxygyrus keraudreni* is very similar to that of *Atlanta*. The alimentary system and the nervous system have the same anatomy, the only distinguishing features being the development of the salivary glands, the radula and radula cartilage. The appearance of gill rudiments within the pallial cavity, the morphology of the opercular lobe and the position of the genital rudiment characterize this species.

The veliger of *Carinaria lamarcki* differs from the above species (*Oxygyrus keraudreni* and *Atlanta lesueuri*) in the morphology of its foot, the presence

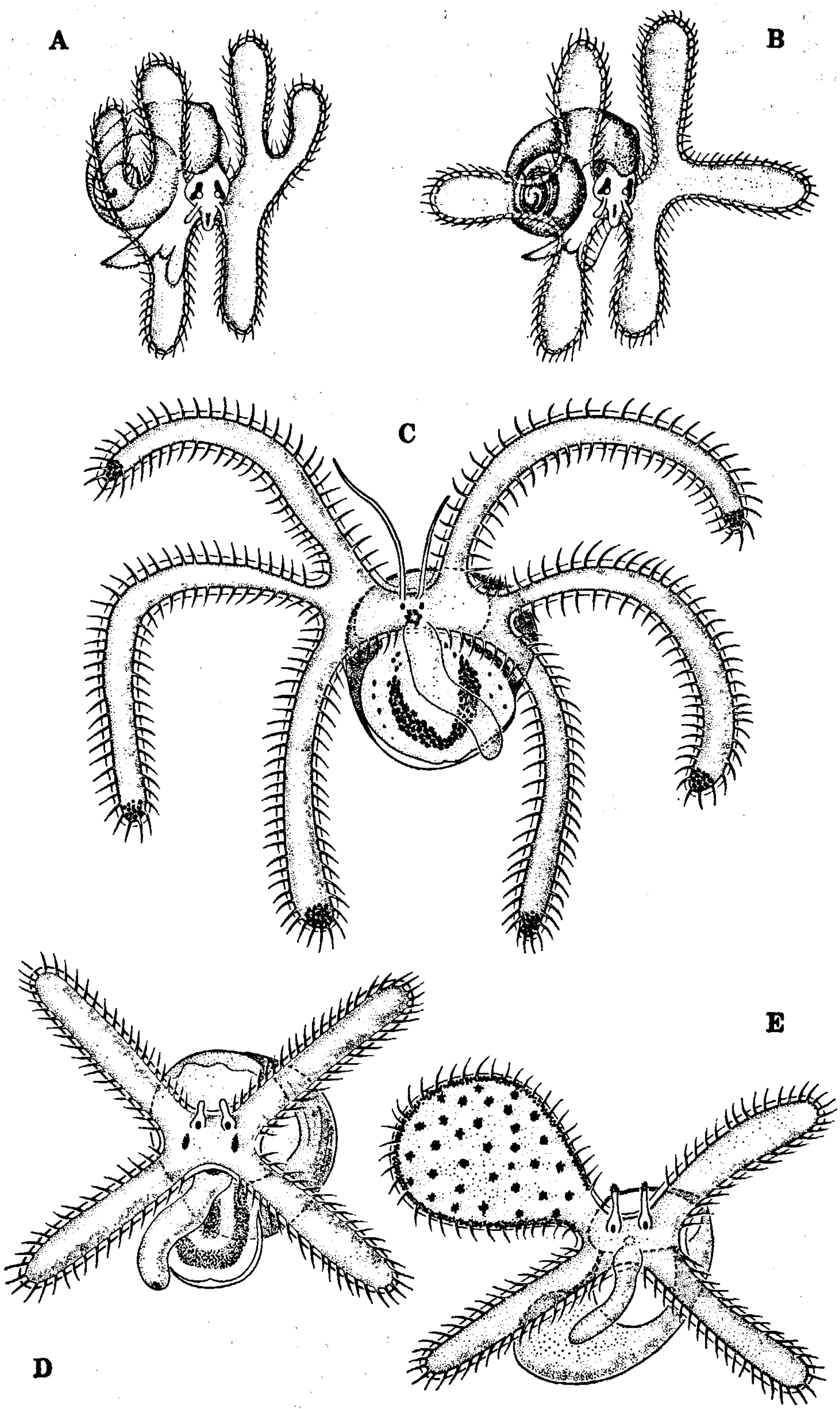


Fig. 8.—Swimming larvae of heteropods: A, *Atlanta lesueuri* (after Thiriot-Quiévreux, 1969b); B, *A. inflata* (after Thiriot-Quiévreux, 1969b); C, *Carinaria lamarcki;* D, *Firoloida desmaresti* (redrawn, after Franc, 1948); E, *Pterotrachea* sp. 3.

of mucous cells in the posterior part of the oesophagus and intestine, and by the arrangement of the digestive gland into two clearly unequal and opposite lobes. In contrast the morphology of the pallial cavity, the nervous system, and the formation of the buccal extension, are analogous to the preceding species, except that the salivary glands and the pigment bed of the eye are feebly developed, while the germinal rudiment is hardly to be seen.

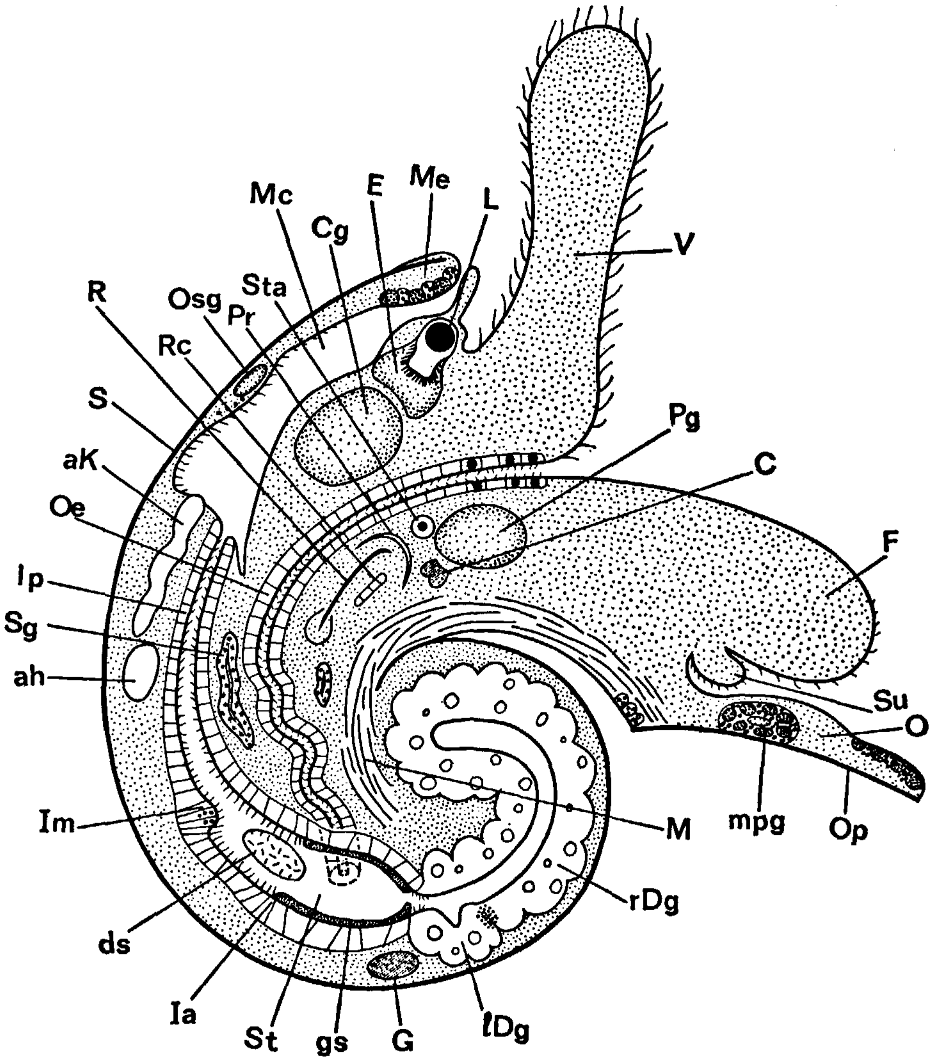


Fig. 9.—Internal anatomy of the larva of *Atlanta lesueuri* (stage III). after Thiriot-Quiévreux, 1971b: ah, adult heart; aK, adult kidney; C, rudiment of the copulatory apparatus; Cg, cerebral ganglion; ds, dental sheet; E, eye; F, fin; G, gonad; gs, gastric shield; Ia, anterior part of the intestine; Im, middle part of the intestine; Ip, posterior part of the intestine; L, lens; lDg, left digestive gland; M, muscle; Mc, mantle cavity; Me, mantle edge; mpg, pedal gland; O, opercular lobe; Oe, oesophagus; Op, operculum; Osg, osphradial ganglion; Pg, pedal ganglion; Pr, beginning of the proboscis; R, radula; Rc, radular cartilage; rDg, right digestive gland; S, shell; Sg, salivary gland; St, stomach; Sta, statocyst; Su, sucker; V, velar lobe.

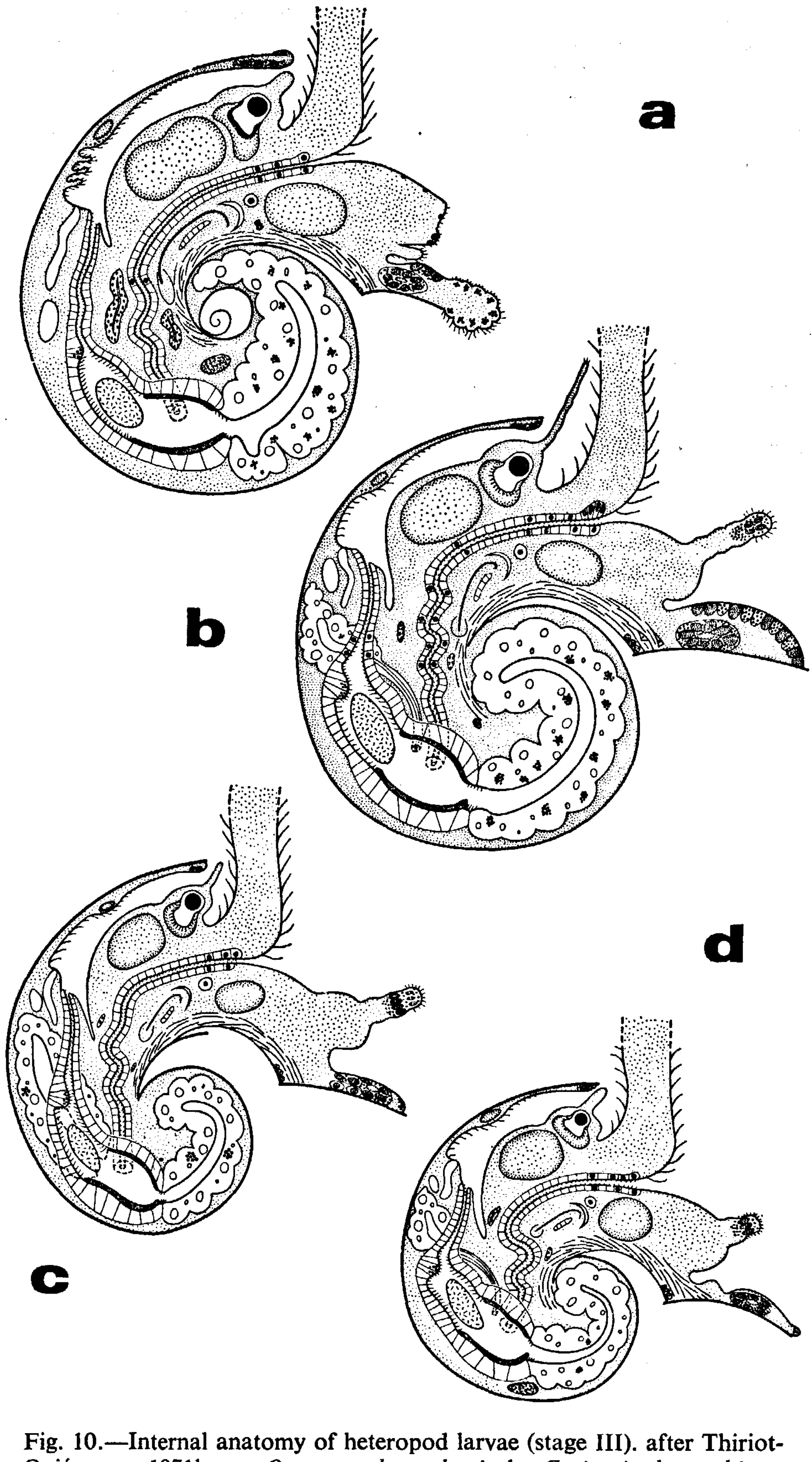


Fig. 10.—Internal anatomy of heteropod larvae (stage III). after Thiriot-Quiévreux, 1971b: a, *Oxygyrus keraudreni;* b, *Carinaria lamarcki;* c, *Pterotrachea coronata;* d, *Firoloida desmaresti.*

I

In comparison with *Carinaria* the veliger of *Pterotrachea* is little developed and there is no hypobranchial gland. The gut is analogous to that of *Atlanta*, except that the two opposing lobes of the digestive gland are subequal and the salivary glands are poorly developed. The pedal trunk has the same form as that of *Carinaria*, as does the nervous system. In contrast, the opercular lobe is peculiar to this species. The germinal rudiment is probably present but is very little developed.

The veliger of *Firoloida desmaresti* shows characters intermediate to those of *Carinaria* and *Pterotrachea*. The pallial cavity, the nervous system, and the anatomy of the gut are analogous to those of *Pterotrachea*, except that the digestive gland has the same form as that of *Carinaria*. The slight development of the salivary glands and the form of the buccal extension resemble both *Carinaria* and *Pterotrachea*. The opercular lobe is characteristic of this species. The germinal rudiment is well developed, and situated as in *Atlanta*. The appearance of cyanophilic granules in tegumentary cells is characteristic of approaching metamorphosis.

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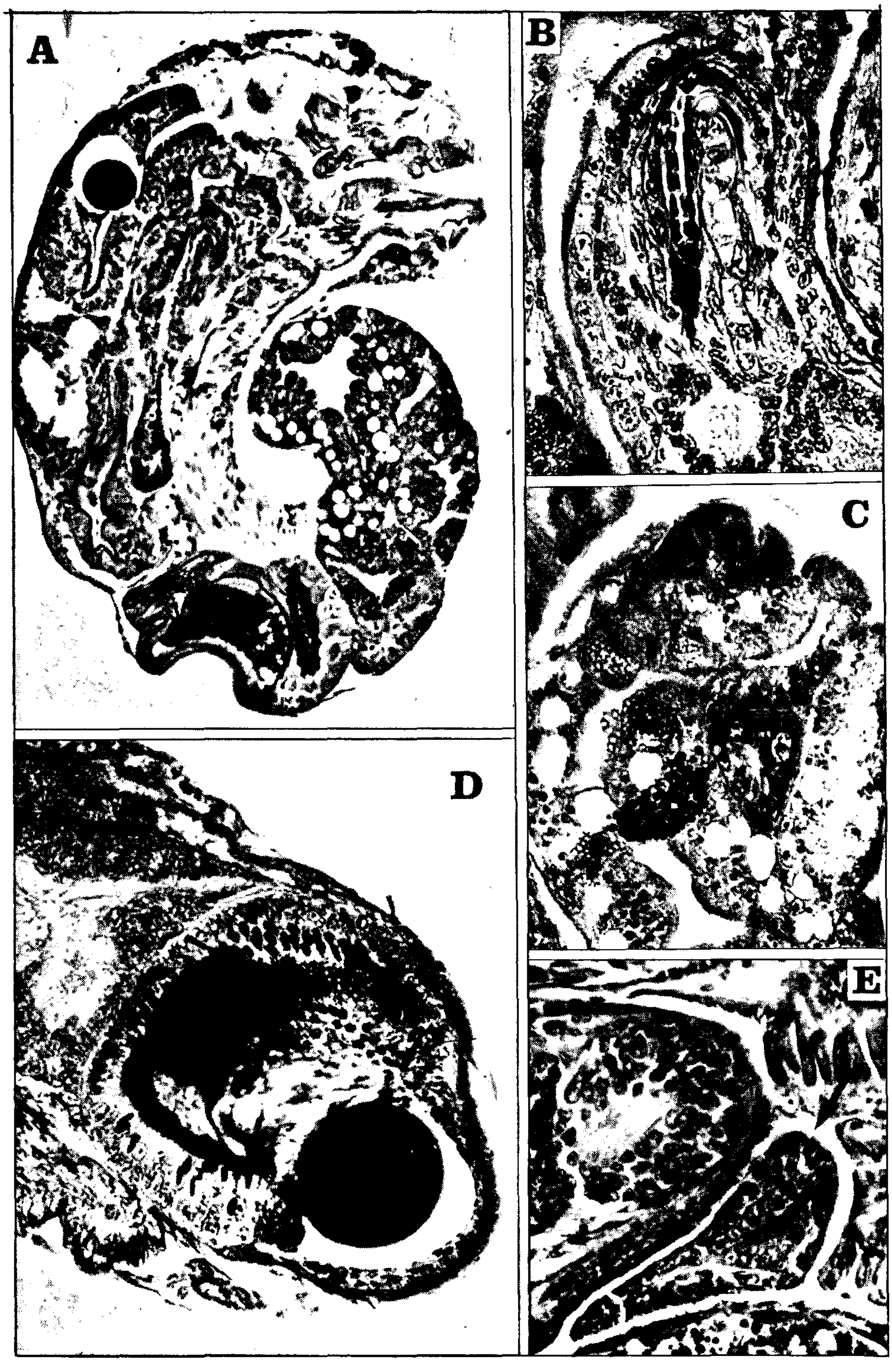

Fig. 11.—Histological sections of *Atlanta* larvae (after Thiriot-Quiévreux, 1969b). A, longitudinal section of *Atlanta lesueuri* (stage III) ×175; B, section through the buccal mass of *A. lesueuri* (stage III) ×440, note the radula and the radular cartilage; C, section through the digestive gland of *A. inflata* (stage III) ×440; D, section through the eye of *A. lesueuri* (metamorphosis) ×440; E, section through the rudiment of the copulatory apparatus (see the arrow) of *A. inflata* (metamorphosis) ×440.

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