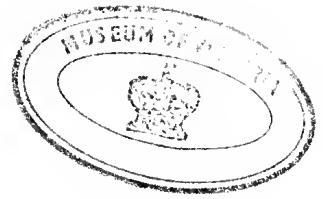






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A Revision of the Recent  
Xenophoridae of the World  
and of the Australian Fossil Species  
(Mollusca: Gastropoda)

by W.F. Ponder  
with appendix by W.F. Ponder and J. Cooper

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# A REVISION OF THE RECENT XENOPHORIDAE OF THE WORLD AND OF THE AUSTRALIAN FOSSIL SPECIES (MOLLUSCA, GASTROPODA)

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## SUMMARY

The 25 Recent species and subspecies of the Xenophoridae are reviewed. Three subgenera are recognized within the only genus, *Xenophora*: *Stellaria* (with 5 species and 1 subspecies), *Onustus* (with 4 species), and *Xenophora* s.s. (with 13 species and 2 subspecies). A brief outline of the fossil history of the group and a general account of the anatomy and habits are given. A new species (*X. granulosa* sp. nov.) from the central Indo-Pacific and three new subspecies are described, one from the Hawaiian Islands (*X. peroniana kondoi* subsp. nov.), one from the Gulf of Aden (*X. testigera profunda* subsp. nov.), and one from the Kermadec Islands (*X. neozelanica kermadecensis* subsp. nov.). The fossil *Xenophora* known from Australia are reviewed and a new Upper Pliocene — Lower Pleistocene subspecies (*X. flindersi ludbrookae* subsp. nov.) and an unnamed Upper Cretaceous species are described.

The shell, and where known the radula, operculum and anatomy, are described for each species. The distribution and synonymy of each species is also given in detail. All of the species-group names of fossil *Xenophora* are listed (Appendix, with J. Cooper).

Fossil species occurring outside Australia are not revised with the exception of a few which have relevance to the taxonomy of Recent species.

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## INTRODUCTION

The Xenophoridae is a small family of mesogastropods found on the continental shelves and slopes of most tropical and temperate regions of the world. They are especially notable for their peculiar habit of fixing foreign objects (shells, pebbles, etc.) to the dorsal surface of their shells, and thus they have earned the popular name of "Carrier Shells".

Morton (1958) has dealt with the habits and relationships of the Xenophoridae at some length and, more recently, Linsley and Yochelson (1973) discussed the habits of the family and compared it with the Middle and Late Devonian species of *Straparollus* (Euomphalidae) which also attached foreign objects to their shells.

The few taxonomic reviews of the Recent species on a world-wide basis have been confined to the last century (Reeve, 1842, 1843a, 1843b, 1845; Philippi, 1855; Fischer, 1879a; Tryon, 1886), more recent revisions being limited geographically (Clench and Aguayo, 1943 (Western Atlantic); Habe, 1953a (Japan); Adam & Knudsen, 1955 (West Africa), Beu, 1977 (New Zealand)). Mallory (1977a, b, 1978) has commenced a semi-popular monographic treatment of the family with excellent colour figures.

Mallory has also privately produced 7 numbers of "The *Xenophora* Newsletter" (Jan. 1976 – Dec. 1976), which was circulated to contacts of Mr Mallory known to be interested in the family.

This paper attempts to revise the taxonomy and distribution of the Xenophoridae. Unfortunately, the number of preserved animals available was very small and consequently most species and subspecies are defined on shell characters alone. The few specimens which have been available for anatomical examination appear to exhibit a general anatomical similarity between species although most of the material was in a poor state of preservation. Radular mounts have been made of a few specimens of several species but these too exhibit a close similarity. There are a number of fossil species described from the Tertiary rocks of the world and some species of *Xenophora* are also known from the Cretaceous. With the exception of the Australian forms, fossil species are not dealt with in detail in this revision because of the difficulty of obtaining adequate material for study. Fossil specimens of *Xenophora* have, however, been examined in several European Museums and in the NMV, AMS, USNM and BMNH and from this material, together with literature records, an attempt has been made to trace the evolution of the group in general terms (see 'Fossil History' below). Fossil records of Recent species are given in greater detail and a few fossil species are discussed where this is relevant to the taxonomy of a particular Recent species. A list of all named fossil species is given in the Appendix.

The family appears to be remarkably uniform in habits and shell form, all species probably being deposit feeders with a very uniform anatomy, radula and body form. The long ctenidial filaments of *Xenophora* are used for respiration and cleansing, not filter feeding (Morton, 1958) but the family is probably an offshoot from the stock that gave rise to the filter feeding Calyptraeidae, and is not as closely related to the deposit feeding Strombidae as previously thought (Morton, 1958).

## MATERIALS AND METHODS

Specimens have been borrowed from, or examined in, many of the world's major museums. Usually lists were compiled of locality data in each institution after identification of material. A small amount of preserved material was acquired for anatomical investigation but on the whole this has proved to be unsatisfactory for detailed work. Radulae were mounted in polyvinyl lactophenol and stained with picric acid. All dissections were done with a Wild M5 or M7 microscope with a drawing apparatus. A small amount of material was sectioned for histological examination. Some radulae were examined with a Scanning Electron Microscope after coating with gold.

Locality data have been compiled largely according to the "Times Atlas of the World" (1974 Edition).

A discussion on the taxonomic characters utilized in revising this group is given below.

#### ABBREVIATIONS

AMNH	American Museum of Natural History, New York.
AMS	The Australian Museum, Sydney.
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia.
BMNH	British Museum (Natural History), London.
BPBM	Bernice P. Bishop Museum, Honolulu.
DMNH	Delaware Museum of Natural History, Greenville, Delaware.
EBM	Zoological Museum, Humbolt University, East Berlin.
FMC	Field Museum, Chicago.
IRNSB	Royal Institute of Natural Sciences of Belgium, Brussels.
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts.
NHMG	Natural History Museum, Geneva.
NHMP	National Museum of Natural History, Paris.
NMNZ	National Museum, Wellington.
NMV	National Museum of Victoria, Melbourne.
NMW	National Museum of Wales, Cardiff.
NSMT	National Science Museum, Tokyo.
RGM	Royal Geological Museum, Leiden.
RNHL	Royal Natural History Museum, Leiden.
SAM	South Australian Museum, Adelaide.
USGS	United States Geological Survey, Washington D.C.
USNM	National Museum of Natural History, Washington D.C.
WAM	Western Australian Museum, Perth.
ZMA	Zoological Museum, Amsterdam.
ZMC	Zoological Museum, Copenhagen.

#### TAXONOMIC CHARACTERS USED

**The shell:** The main characters of the shell which are of value in separating species are as follows: (1) the amount and relative size of the foreign material attached to the surface, (2) the width of the peripheral flange, (3) the spire angle, (4) the dorsal sculpture and shape of the whorls, (5) the sculpture and shape of the base, (6) the umbilical characters, (7) the shape of the basal lip of the aperture, and (8) the colour, particularly of the base. The protoconch is rather uniform and is not described except where it differs from the usual type. Dimensions given are the maximum diameter of the shell (including peripheral shell structures) and the height and do not include any attached objects.

The species of *Xenophora* can be split into several morphological groups on shell characters, although these are not necessarily phylogenetic groupings.

- (a) Typical species of medium size showing heavy to moderate attachment of foreign objects, a narrow peripheral flange and a very narrow to closed umbilicus — e.g. *conchyliophora* (Born), *cerea* (Reeve), *corrugata* (Reeve), *pallidula* (Reeve), *japonica* Kuroda & Habe, *neozelanica* Suter, etc. (subgenus *Xenophora*).
- (b) Small to medium-sized species showing moderate to heavy attachment of foreign bodies, a narrow peripheral flange and a moderate umbilicus — e.g. *crispa* (König), *solaroides* (Reeve) (subgenus *Xenophora*).
- (c) Species of medium to large size, with medium to tall spires, straight whorl outline, rather narrow peripheral flange with only small objects attached, non-umbilicate — e.g. *infundibulum* (Brocchi), *flemingi* Beu (both fossil species) (subgenus *Xenophora*).
- (d) Species of medium size, with very little foreign material attached, digitate peripheral flange, and a very narrow umbilicus — e.g. *testigera* (Bronn) (subgenus *Stellaria*).
- (e) Large species with little foreign material attached, a moderate to wide umbilicus, a smooth to strongly sculptured base and a wide, simple peripheral flange — e.g. *chinensis* (Philippi), *gigantea* Schepman (subgenus *Stellaria*).
- (f) Large species with little foreign material attached, a wide umbilicus, strong radial sculpture on the base and a wide peripheral flange divided into tubular spines — e.g. *solaris* (Linné) (subgenus *Stellaria*).
- (g) Large species with very little foreign material attached, a wide umbilicus and a wide peripheral flange which is porcellanous ventrally — e.g. *indica* (Gmelin), *exuta* (Reeve), *caribaea* (Petit de la Saussaye) (subgenus *Onustus*).
- (h) Small species with wide umbilicus, little (or no?) foreign material attached, a narrow peripheral flange which is not porcellanous ventrally and simple, almost orthocline, axial riblets or growth lines dorsally — e.g. *patellata* (Deshayes), *bouryi* Cossmann, *rhytida* Cossmann (all Eocene, Paris Basin) (subgenus ?).

To separate all these groups as genera or subgenera would be unjustified but, clearly, some subdivision is necessary. The species *solaris* (group f) has very distinctive tubular peripheral spines but there is little else to justify its separation. The wide, simple, peripheral flange of group (e) differs from that of group (g) in being composed of a double shell layer and thus does not have its porcellanous layer exposed. These groups (e), (g) along with groups (c), (d), (f) and (h) have very little foreign material attached to their shells. Group (a) stands apart in containing the majority of species and presumably represents the basic or "typical" form of the family.

Several Cretaceous species such as *X. leprosa* (Morton) as redescribed and figured by Sohl (1960) are generally very similar to modern species of *Xenophora* in group (a), such as *X. conchyliophora*. Presumably the other "atypical" modern forms were derived from such an ancestral form by reduction of the size and number of objects cemented to the dorsal surface, the widening of the umbilicus and by an increase in the width of the peripheral flange. These developmental trends appear to have progressed along several lines (e.g. the forms attributed to "*Trochotugurium*" (group (e)) and to "*Onustus/Tugurium*" (group (g)) by various authors) and they are not necessarily correlated with one another. For example an increase in the width of the umbilicus is not necessarily correlated with any reduction of the size and number of objects fixed to the shell (as seen in the species in group (b)), and the reduction of the amount of attached material is not necessarily correlated with the formation of an umbilicus (e.g. group (c)).

Representatives of other groups (b), (c), (d), (g) and possibly (e), as well as group (a), have been in existence from the Paleogene but group (f) has no fossil record before the Pliocene. Cossmann (1915) recognized two Eocene species of the subgenus *Haliphoebus* (= *Stellaria*) in the European Eocene but these two species are probably not related to *Xenophora* (*Stellaria*) *solaris*. They lack hollow peripheral spines and are here included in group (h) along with a third Eocene species. A more detailed account of the fossil history of *Xenophora* is given below:

**The operculum:** The operculum shows some differences which are regarded as fairly important at the species level. To prevent confusion over the identification of opercular structures an explanatory diagram (Fig. 1) is provided.

This structure shows a fairly consistent pattern but there are variations on the basic type. To avoid needless repetition only the differences are given in the species descriptions. In general *Xenophora* opercula are roughly oval in most species with the outer edge (opposite the growing edge) usually worn away and rather ragged. The nucleus (the oldest or first-formed part of the operculum) is on the outer edge and is usually missing. It is characteristically displaced to the left but in some larger species and/or adults this displacement is not obvious and it appears to be mid-lateral. The outer surface is typically rather smooth, with concentric growth lines and often microscopic radial scratches. The inner surface is occupied by an attachment scar (that area of the operculum attached to the opercular lobe) and a non-attached area (free surface). The attachment scar occupies about half the inner surface and is usually kidney-shaped. A tongue of material (the central area) is deposited on top of the rest of the material of which the attachment scar is composed and projects into the attachment scar from its outer edge. The central area is continuous through the free surface but, because it is overlaid by concentric lamellate layers which follow the inner edge of the attachment scar, it is usually not obvious. The central area is laid down as a layer of radial units on top of the attachment scar which gives it a radially striate appearance. This radial layer extends to the right and left of the attachment scar, although not right to the edges of the operculum, and the outer concentric layer of the free surface is deposited on it. In a few species (e.g. *X. solaris*) the radial layer on the right side of the central area extends on to the attachment scar and becomes a narrow extension of the central area.

**The radula:** The radula shows surprisingly little differentiation between species. Figures of the radula of many of the species are given (Figs 7-12) but, in most cases, only one specimen was available for examination and only minor differences were exhibited between most species.

Each radular row consists of a rather large, usually squarish central tooth with a large median cusp and a few lateral cusps. The base of the tooth is usually simple. The pair of lateral teeth are more-or-less subtriangular to rectangular, rather short, their upper and lower sides nearly parallel. Each has a cutting edge which is usually simple, sometimes with a few weak denticles or small cusps and with a sharp, sometimes large cusp at its inner end. The two pairs of

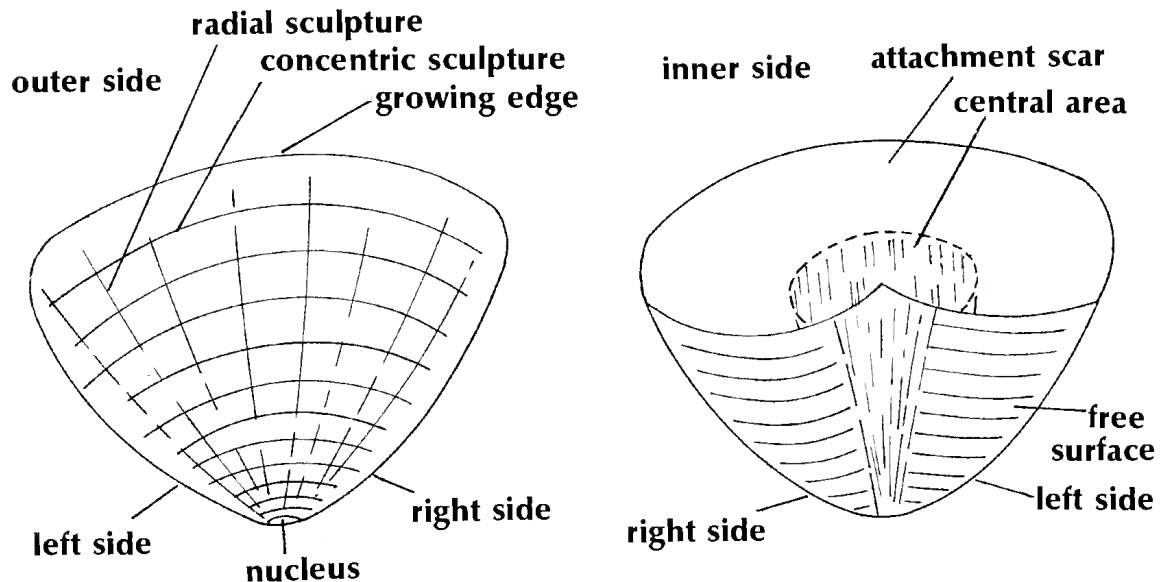


Fig. 1. Inner and outer side of generalized *Xenophora* operculum.



marginal teeth are long, curved, sometimes with weak denticles or smooth. Each inner marginal tooth bears a short thin wing-like plate which emerges from the outer base and runs up the tooth for a short distance. This structure has not been previously described in *Xenophora* and appears to be present in most of the species examined.

Because of the close similarity of the radulae of different species the descriptions given in the text outline only the distinctive features of each species.

**Anatomy:** The relative size of the ctenidium and the salivary glands and the shape and structure of the penis and female genital ducts appear to be of importance and these differences are noted in the anatomical account where known. More specific reference is avoided because of the small amount of material available to determine intraspecific variation. In general the anatomy of the family appears to be fairly uniform. An account of the anatomy of *Xenophora* follows.

## GENERAL ANATOMICAL ACCOUNT

Adams and Reeve (1850) were the first to describe the external appearance and locomotion of the living animal of *Xenophora* species. Mörch (1857) provided a description and figures of the animal of *Xenophora conchyliophora*, Bergh (1896) described the general anatomy, and Bouvier (1887) and Amaudrut (1898) have provided accounts of the nervous system and anterior alimentary canal respectively. Bergh (1904) figured some details of the anatomy of an Indo-Pacific *Xenophora* species (probably *X. cerea* (Reeve)). Morton (1958) described the external features of the living animal, the mantle cavity and the alimentary canal in some detail and outlined some features of the reproductive system in *X. neozelanica*.

The following brief account also concerns the anatomy of *X. neozelanica* based partly on Morton's account and the dissection of 4 Bouins-fixed specimens, 3 males and 1 female. Comparative notes are provided from observations on several other species. The material, in the majority of cases, was rather poorly preserved and, in all cases, examination of a particular species could only be based on 1 or a few specimens because of the lack of preserved material available for study. Details concerning the material used in this account are given under the heading "Anatomy" under each species in the taxonomic section.

**External features** (Figs 2, 4): The head, which is brightly pigmented in some species, bears a pair of long, cylindrical tentacles (tn) with eyes in short, bulb-like swellings near their outer bases. The long, muscular, extensile snout (sn) is bilobed distally and lies above the broad propodium (pr). This has a rounded anterior edge along which opens the anterior pedal mucous gland. The remainder of the foot is short. In *Xenophora neozelanica* and allied species the opercular lobe (opl) is relatively small and the operculum (op) is strong and thick, large in relation to the foot and extends beyond it posteriorly. The sole is broad in front and narrows along the metapodium. The narrow portion, according to Morton (1958), becomes keel-like during locomotion and does not function as a creeping sole. Linsley (*in litt.*), however, notes that the foot of *X. neozelanica* is hour-glass shaped and has a flattened sole over its total length which is capable of functioning as a creeping sole during righting behaviour and shell implantation. *Xenophora indica* (Fig. 4a, b), *X. chinensis* and allied species have only a slight suggestion of a sole on the metapodium and the opercular lobe is long and narrow, bearing a thin, flexible operculum. Behind the head lies the very muscular body column.

**Internal anatomy** (Figs 2, 3): A large ctenidium (ct) on the left and a massive rectum (r) mid-dorsally are the two most conspicuous features of the spacious mantle cavity. Alongside the deep embayment formed by the left side of the mantle edge runs the long, thread-like osphradium (os). The ctenidium is composed of long, narrow filaments which, although they have well developed rejection tracts, are not utilized in filter feeding (Morton, 1958). The anterior section of the ctenidium of several species is more conspicuously curved to the right than in *X. neozelanica*, so that it runs almost parallel with the anterior mantle edge to the rectum. A strip of hypobranchial gland (hg) lies between the ctenidium and the rectum. Just inside the muscular edge of the mantle there is a row of very short tentacles (t) and, on the right, a glandular swelling (g) lies inside the mantle edge, the secretions from which are presumably



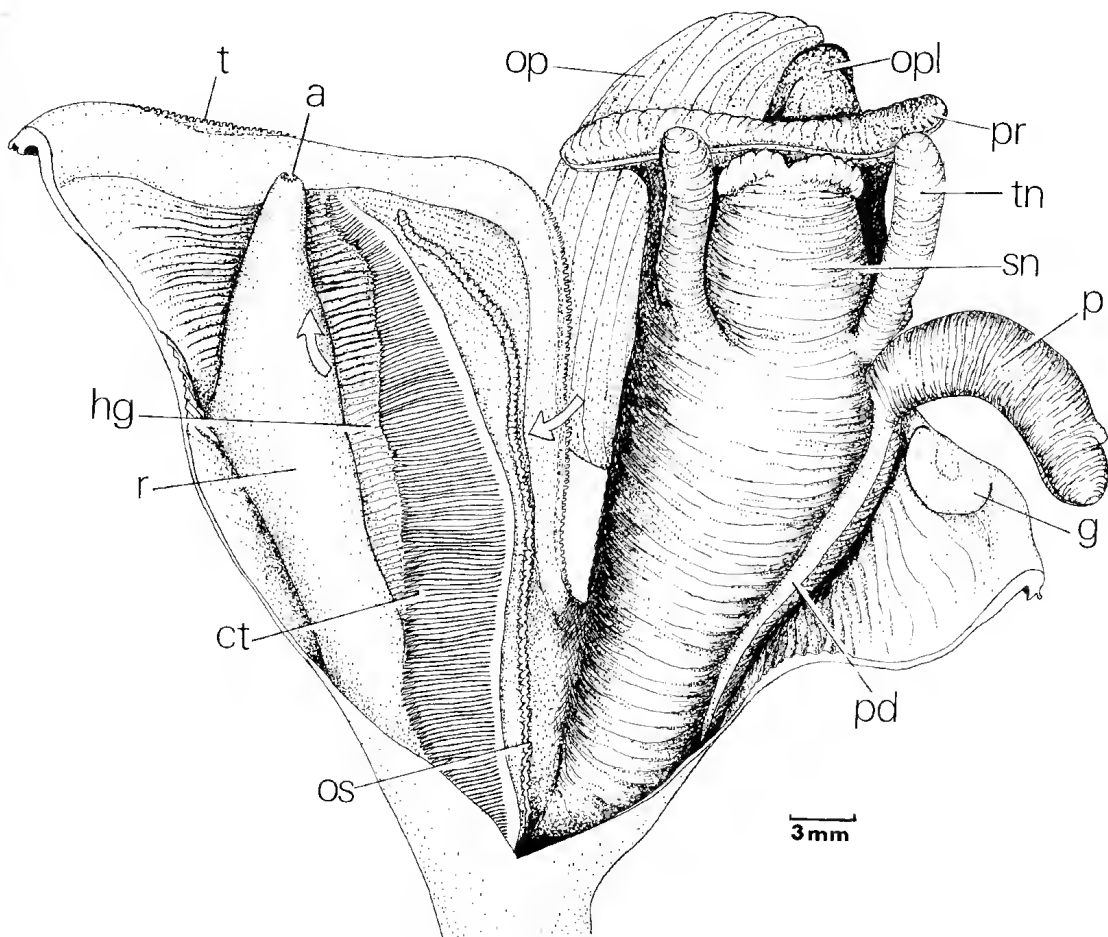


Fig. 2. *Xenophora (Xenophora) neozelanica neozelanica* Suter. Dorsal view of anterior end of animal, the mantle cavity opened mid-dorsally. The arrows show the probable direction of water flow through the mantle cavity. **a** — anus, **ct** — ctenidium, **g** — glandular pad, **hg** — hypobranchial gland, **op** — operculum, **opl** — opercular lobe, **os** — osphradium, **p** — penis, **pd** — vas deferens, **pr** — propodium, **r** — rectum, **sn** — snout, **t** — tentacles on mantle edge, **tn** — cephalic tentacle.

utilized in the disposal of the faeces. Species allied to *X. indica*, *X. chinensis* and *X. digitata* appear to lack the tentacular mantle edge, and the glandular pad, which is present in all species of *Xenophora* examined, appears to be smaller in some species than in *X. neozelanica*. In *X. solarioides* the glandular area is an elongate strip along the right side of the mantle edge.

The mouth opens between a pair of fleshy lobes (lips) at the end of the snout. A pair of small jaws (j) lie in the buccal cavity surrounded by the powerful buccal mass (bm) which contains the short, broad taenioglossan radula. The wide, thin-walled salivary ducts (sd) open into the buccal cavity after passing through the circum-oesophageal nerve ring which lies immediately behind the buccal mass. Two large, white, compact, externally smooth salivary glands (rsg, lsg) lie in the cephalic cavity alongside the mid-oesophagus. A very short anterior oesophagus (ao) passes through the nerve ring and contains prominent glandular dorsal folds. These structures become very inconspicuous in the mid-oesophagus (o) which is expanded into a thin-walled, crop-like structure. The narrow posterior oesophagus opens into the large stomach which consists of a very long style sac and a wide lumen containing a gastric shield (Morton, 1958 gives a detailed description of the stomach of *X. neozelanica*). The intestine runs anteriorly then loops posteriorly before it opens into the wide rectum which stores masses of small faecal pellets. Anteriorly the rectum is extended as a free papilla to the mantle edge.

The male (Figs 2, 14) has a very highly convoluted seminal vesicle which opens into a narrow pallial groove (pd). This runs along the right side of the trunk to the penis behind the right tentacle. The pallial groove appears to be thickened and glandular over the anterior half in one specimen of *X. neozelanica* possibly forming a region where prostatic secretion takes place,

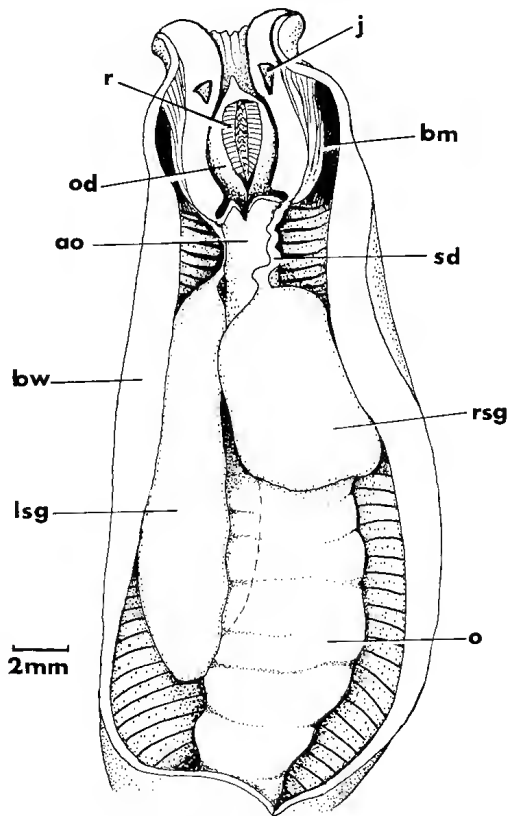


Fig. 3. *Xenophora (Xenophora) neozelanica neozelanica* Suter. Dorsal view of head and anterior body cavity opened mid-dorsally. The circum-oesophageal nerve ring has been removed. **ao** — anterior oesophagus, **bm** — buccal mass, **bw** — body wall, **j** — jaw, **lsg** — left salivary gland, **o** — mid-oesophagus, **od** — odontophore, **r** — radula, **rsg** — right salivary gland, **sd** — salivary gland duct.

but such thickening could not be seen in the other 2 specimens. The pallial groove is covered by a narrow flap of tissue along its whole length in *X. neozelanica* but in *X. digitata* most of the pallial groove within the mantle cavity is thickened and forms a narrow, closed prostate. In *X. neozelanica* the seminal groove continues along the posterior edge of the penis (p) to its tip which is not produced as a papilla. The penes of some species have accessory glandular or non-glandular structures and the seminal groove often terminates on a papilla. In *X. digitata* the seminal groove on the penis is closed over all but the distal portion and, in several other species, the groove is partially closed, although the extent of fusion was not readily discernible. The shape of the penis is variable within the group but appears to be fairly consistent within each species and is therefore used as a diagnostic structure (Fig. 14).

The structure of the female reproductive system, examined in *X. neozelanica* and *X. peroniana* (Figs 15, 16), is unusual amongst mesogastropods in having the very short pallial oviduct gland restricted to the posterior-most part of the mantle cavity. Ventral to the oviduct gland (capsule gland and albumen gland (ag)) lies a broad, muscular tube, the vagina (v), which opens to the posterior end of the mantle cavity a little behind the anterior end of the capsule gland. There it opens to become a simple groove covered by a narrow, thin flap of tissue, which runs along the right side of the neck to the right dorsal side of the propodium where it terminates just in front of the anterior edge of the foot in a small, shallow pocket. The short pallial section of the oviduct gland is continuous posteriorly with a section which protrudes into the visceral

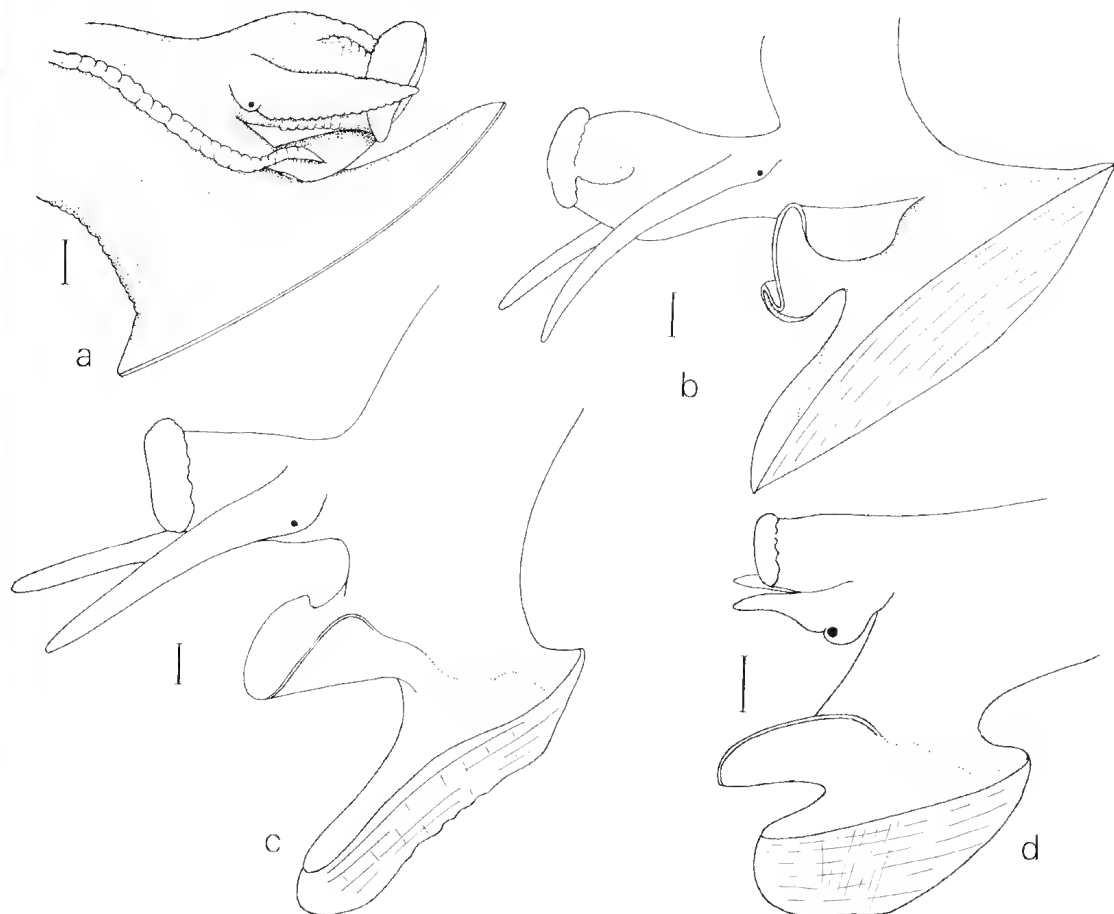


Fig. 4. Scale lines = 2 mm. *Xenophora (Onustus) indica* (Gmelin): (a) Right side of head and foot of female. (b) Left side of head and foot. *Xenophora (Stellaria) solaris* (Linné): (c) Left side of head and foot. *Xenophora (Xenophora) conchyliophora* (Born): (d) Left side of head and foot.

mass lying adjacent to the renal organ and the pericardium. The posterior end of the oviduct gland (rgo) doubles back on itself to lie against its inner face. This recurved part of the oviduct gland opens to the posterior part of the "vaginal tube" and its lumen is continuous with that of the rest of the oviduct gland which does not have any other opening. An anterior sperm sac (as), possibly homologous with the seminal receptacle of other mesogastropods, lies beneath the pallial oviduct gland and above the vaginal tube and contains a mass of sperm which appears to consist of both typical and atypical forms. Its narrow thin-walled (*X. peroniana*) or muscular (*X. neozelanica*) duct (das) enters the proximal part of the vaginal tube. The vaginal tube bifurcates posteriorly into a pair of narrow muscular tubes (bpvt) which emerge as long papillae (p) inside two large, rather thin-walled, posterior sperm sacs (ps). These spacious sacs are possibly homologous with the bursa copulatrix of other mesogastropods. They lie mostly behind the visceral oviduct gland and contain a dense mass of rather uniform, finely granular, poorly-staining material in which are embedded cyst-like objects (c) in the single specimen sectioned of each species. The identity of these cyst-like objects has not been established and the function of these sacs is obscure. The posterior-most sac is the larger and both have strongly plicated walls in *X. neozelanica* but the plications are weaker and fewer in *X. peroniana*. These walls are lined with a columnar epithelium and the cells, which are about 0.056 mm long, appear to be actively secretory. The modified renal oviduct (ro) is a muscular tube which is expanded distally, narrow and convoluted proximally and contains sperm. It opens into the ciliated muscular ventral lumen (vl) of the recurved part of the glandular oviduct, which also opens into the vaginal tube. This modified sperm-storing, renal oviduct is located in the posterior part of the bulge formed by the recurved oviduct gland.

The female genital tracts of the several other species observed appear to be generally similar to that of *X. neozelanica* and *X. peroniana* although differences were observed that may eventually prove to be very useful in the classification of the group. Unfortunately, the material available was not adequate to make detailed comparisons.

Copulation presumably takes place by the penis being inserted into the small, muscular vaginal opening. The position of this opening in the posterior part of the mantle cavity may account for the large size of the penis in *Xenophora* species. Fertilization probably occurs within the posterior part of the vaginal tube.

The eggs are small, up to 0.18 mm in the sectioned material of *X. neozelanica*, but nothing is known of their development or of the nature of the spawn in any species of *Xenophora*.

A small, heavily-plicate, renal organ lies in the posterior wall of the mantle cavity and it opens into the posterior end of the cavity.

The nervous system of *X. conchyliophora* is described in detail by Bouvier (1887). The circum-oesophageal ganglia are not particularly concentrated, the cerebral and pleural ganglia are in contact, the pedal ganglia are separated by rather long commissures and the buccal, visceral and both oesophageal ganglia are widely separated from the circum-oesophageal ring.

#### FOSSIL HISTORY

The earliest species of *Xenophora*\* are found in the Cretaceous and by the late Cretaceous the group was widespread. Most Cretaceous "species" are known from only one or a few poorly preserved specimens, but they are generally small and rather similar in form to *X. conchyliophora* (Born) in usually having a spire of medium height, a simple base and a closed or narrowly open umbilicus.

The genus diversified during the Paleogene when it probably gave rise to most of the forms existing today. It is difficult to assess the evolution of the group in detail, as many fossil species are very rare and have not been available for study. There are, however, some apparent lineages which assist in interpreting the present distribution and relationships of some of the Recent species. These are discussed below and summarized in Figure 5.

\*The species referred to in this discussion are listed in the Appendix where their full bibliographic details are given.

Cox (in Morton, 1958) was doubtful about the affinities of the two Jurassic genera *Jurassiphorus* and *Lamelliphorus*, named by Cossmann (1915) and placed by him in the Xenophoridae. No firm evidence is known to the writer which would, however, exclude these genera from the Xenophoridae except the lack of implantation of objects on the surface of their shells. A few genera in the Pseudophoridae, a supposed archaeogastropod group of uncertain affinities (Knight et al., 1960), show a close, although possibly superficial, resemblance to the Xenophoridae and one genus (*Protocalyptraea* Clarke, 1894) resembles the calyptraeids. Another species, *Sallya striata* Yochelson, 1956, from the Permian of North America, closely resembles *Jurassiphorus*, perhaps indicating a close relationship. If *Sallya* and *Jurassiphorus* were related this would extend the pseudophorids to the Jurassic. The pseudophorids (as recognized by Knight et al., 1960) are found in Silurian to Permian rocks and, because the Mesogastropoda are recognized as being in existence as early as the Ordovician (Knight et al., 1960), the possibility of some Pseudophoridae being mesogastropods and ancestral to the Xenophoridae-Calyptraeidae is not a remote one. Further evidence, such as shell structure studies is, however, required to substantiate this hypothesis. Examination of *Jurassiphorus caillaudianus* (d'Orbigny) and *Lamelliphorus* spp. in the IRNSB and the BMNH did not reveal any evidence of agglutination except that these species had rather irregular edges to their peripheral ornament suggesting the possibility of weak agglutination on the extreme edge of the periphery. No intact protoconchs were present in any of the specimens examined.

*Xenophora grasi* Matheron et al. from the Turonian of France is a peculiar, broadly umbilicate, low-spined species with strong dorsal and ventral spiral sculpture and a delicate peripheral flange. This species had acquired the habit of agglutinating objects but is otherwise (superficially?) similar to the Jurassic species *Jurassiphorus caillaudianus*. *Onustus tortilis* Peron from the Neocomian (Lower Cretaceous) of Yonne, France, appears to be similar to, and probably congeneric with, the Jurassic *Lamelliphorus* group. This in turn may have given rise to *X. plicata* (Zekeli) which bears similar strong, radial ribs. Thus, although the fossil record does not give any clear indication as to the origin of the group, it seems probable that it was derived from an ancestor of the *Lamelliphorus-Jurassiphorus* group some time in the Lower Cretaceous.

The earliest record of typical *Xenophora* is in the lowermost Upper Cretaceous (Cenomanian) of Texas (Stephenson, 1953: 152). The group does not become widespread until later in the Upper Cretaceous when xenophorids are recorded from North and South America, Egypt, Europe, Malagasy Republic and India. A species also occurs in north Western Australia, as recorded herein. These records are mostly based on poorly preserved individuals but they are in the main more-or-less typical *Xenophora* — that is, with a moderate to tall spire, with objects agglutinated on all whorls, with a narrow peripheral flange and usually with a small to absent umbilicus (the “*conchyliophora* group” for the purposes of this discussion). *X. onusta* (Nilsson) is widely recorded from the Senonian (Santonian to Campanian) of Europe although the variety of shell form in the figures available suggests that more than one species may be represented under this name. Very similar *Xenophora* in the Maastrichtian of North America are usually referred to as *X. leprosa* Morton and in Brazil *X. vasconcellosi* Oliveira has been described. These “species” undoubtedly gave rise to modern *Xenophora* and they are closely related to slightly older species in Europe (*X. plicata* (Zekeli) and *X. canaliculata* (d'Orbigny)) and North America (*X. umbilicata* (Tuomey)).

Two Indian Ocean species, *X. carnatica* Stoliczka, from the Campanian of southern India and *X. trangahinsis* Basse from the Maastrichtian of Malagasy Republic, are small, high-spined species that do not appear to have any close relationships with Tertiary species. Another species (*X. madagascariensis* Collignon) from the Maastrichtian of Malagasy Republic is low-spined and rather broadly umbilicate and may have relationships with Tertiary species such as *X. schroeteri* (Gmelin) (= *T. agglutinans* Lamarck).

*Xenophora* is not well represented in the Paleocene, being known from only two species from the Upper Paleocene of California (*X. simiensis* Nelson and *X. zitteli* Weaver).

By the Eocene the Xenophoridae was well established in the Tethyan area (i.e. Atlantic and Mediterranean), there being about 12 species from the Tethys Sea of Europe and North Africa and 3 from eastern North America. Records of unnamed species are known from the Eocene of



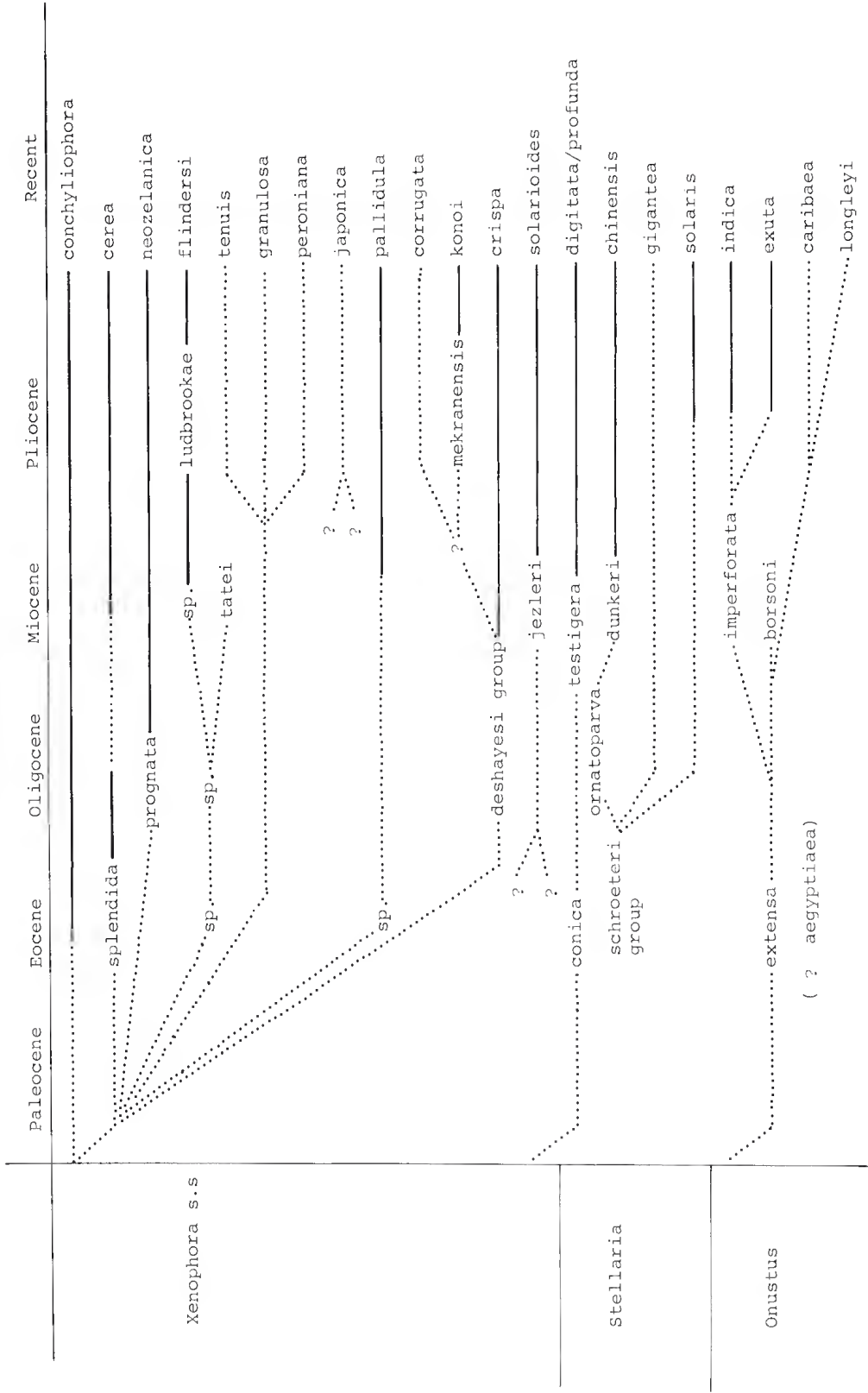


Fig. 5. Schematic table showing the possible relationships of the Recent species of *Xenophora*. Only a few key fossil species are indicated (for further explanation see text).



Jamaica (Trechmann, 1923), California (Vokes, 1939), Australia (herein) and Tonga (Ladd, 1970). Named Eocene *Xenophora* occur on the west coast of North America (California), Nigeria and New Zealand.

The Paris Basin Eocene species *X. patellata* Deshayes together with the much smaller *X. bouryi* Cossmann and *X. rhytida* Cossmann are a peculiar group of low-spired, widely umbilicate species exhibiting distinct orthocone axial sculpture, and little or no attachment of objects. They may be derived from the Cretaceous *X. grasi* but otherwise they do not appear to have any relatives.

The *conchyliophora* group is well represented in the Neogene of northern Europe and North America and may have reached the Indo-Pacific via the Tethys Sea. It is also possible that a westward or an eastwards (or both) migration occurred reaching at least to Tonga (Ladd, 1970), New Zealand (Beu, 1977), and Australia (herein) during the Upper Eocene. It is also possible that some of the modern Indo-Pacific species are derived from *Xenophora* resident in the Indo-Pacific during the Upper Cretaceous. The fossil record is generally poor in the Oligocene but *Xenophora* was established in southern Australia (herein) as well as in New Zealand (Beu, 1977). Some Miocene records of *Xenophora* from Indonesia belong to the *conchyliophora* group and appear to be very similar to, and probably conspecific with, *X. cerea* (Reeve). This species is, in turn, similar to *X. splendida* (Regny) from the Eocene — lower Oligocene of Italy, *X. cumulans* (Brongniart) from the Eocene of the Paris Basin and the *conchyliophora* group in the Paleogene of North America. Oceanic currents postulated for the Paleogene (Frakes & Kemp, 1972) show a generally westwards movement which would tend to support the eastern Pacific origin of animals with planktonic larvae.

The Paleogene members of the *conchyliophora* group seem to have given rise to several species groups, the most important in European Tertiary rocks being the species related to *X. deshayesi* (Michelotti). These appear to include *X. wemmelensis* Glibert (Eocene), *X. petrophora* Koenen (Upper Eocene-Oligocene), *X. deshayesi* (Oligocene-Miocene), *X. grateloupi* (d'Orbigny) (Miocene), *X. burdigalensis* (Grateloup) (Miocene), *X. infundibulum* (Brocchi) (Miocene-Pliocene) and *X. phoitalicum* (Sacco) (Pliocene). This group is characterized by rather large, evenly conical shells, with narrow, simple peripheral flanges and, in most but not all species, reduced areas of agglutination.

After the drying and subsequent flooding of the Mediterranean at the end of the Miocene (Hsii, 1972) an invasion occurred of a small *Xenophora*, *X. crispa* (König), which appears to have evolved from *X. burdigalensis*, a species very similar to *X. deshayesi*. It lives in the Mediterranean and eastern Atlantic today. *X. nigriensis* (Newton) from the Eocene of Nigeria is a small species very similar to *X. crispa* but, whereas it probably forms part of the same species complex, it is unlikely that it is directly ancestral, as the earlier forms of *X. crispa* are rather large and sometimes rather difficult to distinguish from *X. burdigalensis*.

Three Recent Indo-Pacific species with uncertain origins are *X. pallidula* (Reeve), *X. japonica* Kuroda & Habe and *X. gigantea* Schepman. The first two species are superficially similar and have been confused until recently. *X. pallidula* has an extensive Indian Ocean and central Indo-Pacific distribution and has a Miocene record in Indonesia and possibly India and Sri Lanka (recorded as *subextensum*, *agglutinans* and *cumulans* respectively). *X. japonica* has no known fossil history. It is now confined to the central Indo-Pacific from Japan to the Philippines, where it is sympatric with *X. pallidula*, and is also known from the Kermadec Islands north of New Zealand. Little can be said about its origin except that it is morphologically somewhat similar to *X. tatei* Harris from the Miocene of Victoria, Australia, and the two species may have shared a common ancestor in the *conchyliophora* group. It is likely, however, that these similarities are more superficial than real. *X. pallidula* can easily be derived from a *deshayesi*-like form but there is no evidence that it has any real relationships with the *deshayesi* group. This supposition is supported by a mould from the Middle Eocene of "British Somaliland" (= Somali Republic) in the BMNH (G. 78985) which is similar to *X. pallidula* in shape and size. If the species represented by this specimen is indeed ancestral to *X. pallidula* then an origin separate from the European *deshayesi* group would be likely. An Oligocene derivative of the *conchyliophora* group in Victoria, Australia, is morphologically very similar to *X. pallidula* and may be related.

*Xenophora gigantea* may have been derived from a *deshayesi*-like form but there is no fossil evidence to support this supposition. It is more probable that *X. gigantea* shared a common ancestry with *X. chinensis* in the early Tertiary.

*Xenophora digitata* Martens is clearly conspecific with *X. testigera* (Bronn) known from the Oligocene to the Pliocene of Europe and a new Indian Ocean subspecies described herein is interpreted as a remnant of a late Paleogene Tethyan distribution. *X. testigera* may have originated from the western Atlantic where it appears to be represented by a similar species, *X. conica* Dall, in the Eocene of Mississippi. The European material shows a tendency for this species to become relatively larger and broader with time.

During the early Miocene in the Americas forms evolved from the *conchyliophora* group which had strong spiral cords on their bases. This character is seen in 3 closely related Miocene species from Brazil (*X. braziliensis* White), Central America (*X. delecta* Guppy), and Florida (*X. textilina* Dall (Lower Miocene) and *X. delecta floridana* Mansfield (Upper Miocene)). A parallel form in Europe is seen in some Miocene specimens of *X. burdigalensis* a species similar to and presumably derived from *X. deshayesi*. A species of *Xenophora* was recorded and figured by Sacco (1896) from Italy as *X. deshayesi* which he later (1904) called *X. cf. cumulans* (Brongniart). This form ranges from the Oligocene to the Pliocene and sometimes also exhibits relatively strong basal spirals. It could be argued that the Mediterranean form migrated through the remnants of the Tethys Sea (Persian Gulf) which may have been open until the early Miocene (Gass, 1973), to give rise to the Recent *X. corrugata* (Reeve) which is restricted to the western Indian Ocean and which exhibits strong basal spirals and is generally similar to the *deshayesi* group. The Recent *X. konoi* Habe may have had an eastern Pacific origin during the Miocene from *X. delecta-textilina*. The westwards direction of oceanic currents in the Pacific would provide the dispersal mechanism for the larvae and this would be in keeping with Ladd's (1960) suggestion that many Indo-Pacific species may have an eastern Pacific origin. This hypothesis however, is not supported by the only known Tertiary record of a presumed ancestral form of *X. konoi*, the almost identical *X. mekranensis* (Newton) from the Pliocene of the Mekran coast of the Gulf of Oman.

An important group of European species which flourished in the Paleogene included *X. schroeteri* (= *agglutinans*) (Eocene), *X. subagglutinans* Glibert (Eocene), *X. subextensa* (d'Orbigny) (? Oligocene), and *X. solida* Koenen (Oligocene). This group is characterized by small, rather depressed shells, wide umbilicus and moderate agglutination. *X. ornatoparva* (Sacco), from the Oligocene of Italy, seems to have evolved from this group. This species in turn is similar to the Recent *X. chinensis* Philippi (= *P. calculiferus* Reeve), except that the base is not so strongly sculptured, and Sacco's suggestion that it is related to *X. calculifera* (i.e. *chinensis*) seems a reasonable one. The Pliocene *X. plioitalica* is probably not derived from *X. ornatoparva* as suggested by Sacco, because of the total extinctions that appear to have occurred in the Mediterranean in the late Miocene (Hsui, 1972). Instead *X. plioitalica* was probably derived from the *deshayesi* group of species, perhaps from a form close to *X. grateloupi* (d'Orbigny), this view being confirmed by an examination of Sacco's type specimen. The ancestral species to *X. chinensis* probably migrated through the Persian Gulf in the Oligocene, reaching Indonesia (as *X. dunkeri* Martin) and Japan (as *X. makiyamai* (Itoigawa & Nishikawa) ? = *Tugurium matsui* Ogasawara).

An unnamed fossil species was figured by Cossmann (1910: 52, pl. 3, figs 12-15) as *X. calculifera* from the Pliocene of Karikal, India. I have seen similar specimens from the Oligocene of Nari Beds, India, the Miocene and Pliocene of Sarawak and the Pliocene (?) of Java. The dorsal surface is similar to *X. chinensis*, but the base has relatively much stronger radial ribbing, and the peripheral flange is relatively narrow and simple as in typical *Xenophora*.

The origin of the common Indo-Pacific species *X. solariooides* (Reeve) is uncertain but it is unlikely that it shares a common ancestry with the superficially similar *X. crispa*. It is represented in the Miocene of India (*X. terpstrai* Dey), Java (herein) and Borneo (*X. jezleri* Cox).

*Xenophora solaris* (Linné), the type species of the subgenus *Stellaria*, has no known fossil history before the Pliocene, although it is probably derived from a *X. chinensis*-like ancestor in which the peripheral flange became digitate.

An Eocene species from Britain, *X. extensa* (Sowerby), is peculiar in having a thin, almost smooth shell showing only minute traces of attachment scars on the early whorls. It closely resembles Recent species placed herein in the subgenus *Onustus*. As in those species the wide peripheral flange is porcellanous beneath, but adult, and possibly even juvenile *X. extensa*, are imperforate, the umbilicus being plugged by a thickened callus. Two other Eocene species, *X. aegyptica* Oppenheim from Egypt and an unnamed form (known from a few moulds in the BMNH) from the Eocene-Oligocene (?) of Jamaica are taller spired but otherwise appear to be similar to *X. extensa* and species of the subgenus *Onustus* in general. A similar species, but one which possesses a narrow umbilicus, occurs in the Miocene of Italy (*X. depressa* Pantanelli, ? = *postextensa* (Sacco)) and *X. plioextensa* (Sacco) in the Italian Pliocene is probably also part of the same lineage. Another Miocene species, *X. borsoni* (Sismonda), the type of *Trochotugurium* Sacco, has a narrow (?), thin and fragile flange which, as in the type species of *Onustus*, *X. indica*, is porcellanous ventrally. Like *X. extensa* the umbilicus has a thick, porcellanous plug which is particularly conspicuous in broken shells (complete specimens have a narrow umbilical depression with a reflexed columellar callus). This species is rather similar in most features to the Recent *X. longleyi* (Bartsch) from the Caribbean. Typical *Onustus* is also represented by another Miocene species, *X. imperforata* (Gabb) from Central America which appears to be closest to *X. indica* and may not be ancestral to either of the Recent Caribbean species placed in *Onustus*. The origins of *X. indica* and *X. exuta* (Reeve) are uncertain, the only fossils being known from the Pliocene. They are possibly derived from a form similar to *X. extensa* which may have migrated into the Indo-Pacific via the Tethys Sea in the Eocene. *Xenophora oligostriata* (Sacco) in the Oligocene of Italy probably represents the earliest Tethyan *Onustus*\*. On the other hand a lineage leading from *X. extensa* through *X. imperforata* involving an eastern Pacific origin for one or both of the Indo-Pacific *Onustus* species is a more acceptable conclusion on the available evidence.

## BIOLOGY

**Locomotion:** The habits of *Xenophora conchyliophora* and *X. neozelanica* have been reviewed and discussed in some detail by Linsley and Yochelson (1973). During locomotion the "plantar surface" of the stromboid foot is "placed against the substrate, and the shell is lifted by extension of the muscular column. Next the shell is thrust forward for about half of its diameter, and it then falls forward. When the foot is being lowered to the substrate from its retracted position, the operculum is pointed straight down as though it would dig into the substrate. However, in observing the movement of *X. neozelanica* against a wide variety of substrates, the operculum was always found to be flat against the substrate, in the same plane as the plantar surface of the foot". Crozier (1919) describes the movement of *Xenophora (conchyliophora?)* involving an attachment of the anterior margin of the foot to the substrate "continuing with a smoothly flowing motion until the whole foot is in contact. The central portion of the foot is then pulled sharply away from the substratum, forming a very efficient sucker, since the anterior and posterior ends and the lateral margins remain firmly attached". The shell is then pulled forward. *X. flindersi* (Cotton & Godfrey) has an elongate, serrated operculum similar to that seen in the Strombidae and this may be used as a lever during locomotion in a similar way to that observed in the strombs.

*Xenophora* locomotion has been referred to as a "leaping motion" (Morton, 1958) a "one-legged stomp" (Linsley and Yochelson, 1973) and a "looping" or "gallop" (Crozier, 1919). No escape reactions were observed in *X. conchyliophora* with *Fasciolaria* (Berg, 1975), nor in *X. neozelanica* (Linsley and Yochelson, 1973) which were tested against starfish and "oyster drills". Berg (1975) records the rate of locomotion in *X. conchyliophora* as 233.5 cm/day.

The muscular column (trunk) is capable of extending to a height equal to that of the shell and lifting 2 or 3 times the weight of the shell and animal (Linsley and Yochelson, 1973). Righting the shell is achieved by the extension of the foot and column with the propodium digging into the substratum. A contraction of the column slowly pulls the shell over (Morton, 1958, Shank, 1969, Linsley & Yochelson, 1973, Berg, 1975).

\*The available material of this species is very poor so that its relationships cannot be accurately judged.

**Attachment of foreign objects:** The method of shell implantation is described in detail by Shank (1969) for *X. conchyliophora*, his description being quoted in full by Linsley and Yochelson (1973) who also described the process in *X. neozelanica*.

An object such as a dead shell is chosen and manoeuvred into position by the "proboscis" (= snout) or foot, being held between the snout and tentacle bases (in *X. conchyliophora*) or by the propodium of the foot (in *X. neozelanica*). The shell is raised and lowered by the powerful "trunk" and the foot (*X. conchyliophora*) or by the snout (*X. neozelanica*). In *X. conchyliophora* the object and shell are positioned, the shell surface cleaned and the object cemented, filling in gaps with sand or tiny pieces of debris to ensure a firm bond (this part of the process was not observed in *X. neozelanica*).

General discussion on the attachment of foreign objects by *Xenophora* and other molluscs is given by Vignon (1923) and Linsley and Yochelson (1973). In general bivalve shells are usually arranged with the inner side of the valve facing outwards and gastropods usually have their aperture uppermost and their vertical axes radially orientated.

Objects are generally attached to the edge of the periphery or the peripheral flange. As the shell grows the objects originally on the periphery lie across the shoulder of the succeeding whorl, to which they are also cemented. I have not seen any evidence to suggest that any species habitually implants the major foreign bodies initially on the shoulder although one fossil species (*X. lapiferens* Whitfield) has been cited as having attached objects on the middle of each whorl (Palmer, 1937). The specimens on which this species is based are very poor and it is probable that the peripheral attachment scars have been worn away. Linsley and Yochelson (1973) state that *X. lamberti* Sowerbie implants material at the suture, not at the periphery. This mistaken impression is due to the periphery of the type specimen being broken away beyond the line of implantation. Some species implant, usually to a limited extent, minute shell fragments, sand grains, etc., over the dorsal surface generally. Each species tends to select objects within a size-range characteristic of that species. The objects are usually dead mollusc shells but can also be pebbles, fragments of coral, brachiopod shells and any other small, solid objects. The selection of objects is presumably determined to at least some extent by the relative abundance of particular objects in the substrate that fall within the required size class.

**Feeding:** Shank (1969) observed that during feeding the proboscis of *X. conchyliophora* was extended and food ("microscopic algae") collected from the substrate beneath the shell. These observations have been confirmed by Berg (1975). Shank also observed that the animal buried its faeces in a hole in the substrate made by the snout which was then used to close the hole. This habit probably accounts for the large accumulation of faecal material stored in the rectum in all species examined suggesting that they are discharged only infrequently. Linsley (in Linsley and Yochelson 1973: 4) did not observe *X. neozelanica* burying its faeces but does not discount the possibility and noted that this species feeds beyond the margin of the shell as well as beneath it.

The gut contents of several species of *Xenophora* revealed miscellaneous detritus and a high silt content. *X. (Onustus) exuta* from near Yule Island, Gulf of Papua, however, had the stomach filled almost exclusively with Foraminifera (Miliolidae and Rotaliidae) and presumably feeds selectively. The faecal material consisted of small, greyish pellets composed mainly of the broken down forams. Berg (1975) noted that *X. conchyliophora* feeds selectively on fine, filamentous algae.

**Habits — a summary:** St. Jean (1977) has pointed out that "everything they (Xenophoridae) do seems to suggest means of eluding detection". She includes the feeding posture (foot lifted above the substrate), the method of locomotion (animal covered by the shell and no continuous trail), the habit of burying the faeces and the attachment of foreign material to the shell to provide excellent camouflage. The implanted material overhangs the periphery and provides a skirt or frill (in some species this is replaced by a wide peripheral flange) which raises the base and aperture above the substrate so that the animal can "safely graze and also facilitates its method of locomotion". There is little doubt that St. Jean's conclusions are essentially correct and they have been largely substantiated by Berg's (1975) work on *X. conchyliophora*. The species with little attached material generally live on soft, rather uniform bottoms, usually in relatively



deep water, so that implantation of objects on their surface would probably make them more conspicuous and therefore more susceptible to predation. Below the limits of light penetration visual predation ceases to be relevant so that deep-water species would have no advantage in being camouflaged.

**Reproduction:** There are no records known to the writer of the spawn or the larvae of any species of *Xenophora*. The protoconch of most species is small and multispiral (Fischer, 1873) and the apertural edge is bisinuate (Figs 12d, 13a, b, e, f) and thus a planktonic larval life is almost certain. A rather long planktonic larval life would help to account for the wide geographic ranges occupied by some species. A southern Australian species of *Xenophora* (*X. flindersi*) has a paucispiral protoconch (Fig 13c, d) and it is likely that this species, like many other gastropods in the same faunal area, undergoes direct development in contrast to the situation seen in close allies from most other areas (other striking examples of this phenomenon are found in the Conidae and Cypraeidae).

### TAXONOMY

**Introduction:** Reeve reviewed the Recent species of *Xenophora* in 3 works which all appeared at about the same time (1842, 1843a, 1843b). In the first, the *System of Conchology* (1842), the illustrations are the same as some of those published a few months later on plates 1 and 2 in the *Conchologia Iconica* and include 5 new names. The descriptions for these 5 new species were published in February, 1843 (not 1841 and 1842 as cited in the *System*, fide Duncan, 1937) and these predate the *Conchologia Iconica* figures and descriptions published in March, 1843. The third plate in the *Conchologia Iconica* was not published until March, 1845 and introduces 2 new species. Reeve cites *Proc. zool. Soc.*, 1845 as a reference for these names but they were not published in that journal.

Superfamily **Xenophoracea** (Pczelintzev & Korobkov, 1960)

Family **Xenophoridae** Philippi, 1853

(placed on official list of family names ICZN Opin. 715)

Synonyms: Onustidae H. & A. Adams, 1854.

Phoridae Gray, 1840 (*non* Curtis, 1833).

**Diagnosis:** Shell rather large, depressed-conical, with narrow to wide, simple to spinose peripheral flange sharply separating spire from base. Periostracum very thin or wanting. Aperture large, base broad, rather flattened, often umbilicate. Teleoconch usually with foreign objects attached in spiral series to peripheral flange and, sometimes, remainder of dorsum, at least on early whorls. Protoconch depressed-conical, multispiral, or, in one species, paucispiral; growth-lines and a single spiral cord usually the only sculpture. Operculum horny, nucleus lateral, with simple growth lamellae, sometimes with conspicuous radial striae or hollow radial ribs. Radula short, small, taenioglossan. Central teeth large, with few cusps, median cusp large. Lateral teeth short, with 1 prominent cusp and a long, often simple cutting edge. Marginal teeth curved, usually weakly dentate. Animal with elongate, narrow foot capable of stromboid motion. Head with long snout, cephalic tentacles with eyes at their outer bases. Ctenidium large, with long filaments. Stomach large, with crystalline style. No oesophageal glands; mid-oesophagus expanded to form a "crop". Salivary glands usually large. Male pallial genital tract usually an open groove, penis large. Oviduct gland short, posteriorly placed, with closed, blind pallial section continuous with a visceral (posterior) section. Vagina opens at posterior end of mantle cavity. Sperm sacs large, usually 1 anterior and 1 to several posterior. A narrow groove running from vaginal opening to antero-dorsal margin of foot. Nervous system with ganglia not concentrated. Eggs and larvae unknown but probably with free-swimming veliger stage in most species.

Genus **Xenophora** Fischer von Waldheim, 1807: 213

Type species: (S. D. Harris, 1897) *Xenophora laevigata* Fischer von Waldheim, 1807 (ICZN Opin. 715 (1964)) (= *Trochus conchyliophorus* Born, 1780: 333).

**Diagnosis:** As for family.

**Remarks:** Three subgenera are recognized.

KEY TO SUBGENERA OF *XENOPHORA* BASED ON SHELL CHARACTERS

1. Shell with ventral side of peripheral flange non-porcellanous .....2  
    Shell with ventral side of peripheral flange porcellanous ..... *Onustus*
2. Shell with wide peripheral flange, digitations or tubular spines around periphery,  
    foreign objects covering less than  $\frac{1}{4}$  of dorsal surface in adult ..... *Stellaria*  
    Shell with narrow, simple peripheral flange, foreign objects usually covering  
    more than  $\frac{1}{3}$  of the dorsal surface in adult ..... *Xenophora* s.s.

Subgenus *Xenophora* s.s.

Synonyms: *Phorus* Montfort, 1810: 159. Type species: *Phorus agglutinans* Montfort, 1810: 159.  
*Xenophorus* Philippi, 1849: 100 (*err. pro Xenophora*).  
*Endoptygma* Gabb, 1877: 302. Type species: *Phorus umbilicatum* Tuomey, 1854:  
 169.

**Diagnosis:** Shell with peripheral flange narrow, simple, non-porcellanous ventrally. Umbilicus moderate to closed. Foreign objects attached to all whorls and usually occupying more than  $\frac{1}{3}$  of the dorsal surface. Mantle edge tentaculate, foot typically with remnant of sole on metapodium, ctenidial filaments of moderate length. Operculum smooth externally, subtriangular to suboval, rarely stromboid.

**Remarks:** The type species designation and validity of the name *Xenophora* have been fully discussed by Palmer (1962). The inclusion of *Endoptygma* in the synonymy of *Xenophora* follows Sohl (1960: 96).

KEY TO RECENT SPECIES AND SUBSPECIES OF SUBGENUS *XENOPHORA* BASED ON SHELL CHARACTERS

1. Base with conspicuous spiral sculpture .....2  
    Base with weak spiral sculpture or spiral sculpture lacking .....5
2. Shell imperforate when mature .....3  
    Shell with moderate umbilicus when mature .....4
3. Shell with large foreign bodies attached dorsally and obscuring most of dorsal  
    surface; dorsal sculpture rugose; Indo-Pacific ..... *mekranensis konoï*  
    Shell with small foreign bodies attached dorsally, most of dorsal surface visible;  
    dorsal sculpture weak; Indian Ocean ..... *corrugata*
4. Shell, small, light, with subangle bordering umbilicus; Indo-Pacific .... *solaroides solaroides*  
    Shell of small to medium size, border of umbilicus not subangled; eastern  
    Atlantic-Mediterranean ..... *crispa*
5. Dorsal surface with strong, rounded, opisthocline ridges (often very irregular) .....6  
    Dorsal surface without strong opisthocline ridges .....14
6. Base with no umbilical depression in adult .....7  
    Base usually with an umbilical depression in adult .....11
7. Diameter usually more than 60 mm; New Zealand ..... *neozelanica neozelanica*  
    Diameter usually less than 55 mm; not New Zealand .....8



8. Basal lip of aperture with a low internal swelling; shell solid, with attached material over most of dorsal surface, Indo-Pacific-Australasia ..... 9  
 Basal lip of aperture without a low swelling internally; shell of light build, with attached material restricted to upper half of whorls, Indo-Pacific ..... *tenuis*
9. Base with strong radial lamellae; Kermadec Islands ..... *neozelanica kermadecensis*  
 Base with rather weak radial lamellae; not Kermadec Islands ..... 10
10. Base slightly to moderately concave, usually with brown radial markings; eastern Australia ..... *peroniana peroniana*  
 Base strongly concave, usually uniformly yellowish-white; Hawaiian Islands ..... *peroniana kondoi*
11. Protoconch multispiral; shell usually larger than 30 mm in diameter; not southern Australia ..... 12  
 Protoconch paucispiral; shell smaller than 50 mm in diameter; southern Australia ..... *flindersi flindersi*
12. Base with strong radial lamellae, without small brown blotches; Indo-Pacific ..... *cerea*  
 Base with weak to moderate radial growth lines, usually with small brown blotches ..... 13
13. Dorsal surface mostly covered; western Atlantic-Caribbean, eastern Pacific ..... *conchyliophora*  
 Dorsal surface with up to two-thirds uncovered; Indo-Pacific ..... *granulosa*
14. Shell of small to moderate size (up to 50 mm in diameter) with densely covered dorsal surface; base with very weak to weak spiral striae, often yellowish; western Pacific ..... *japonica*  
 Shell rather large (adults usually greater than 55 mm), with up to 1/3 of dorsal surface uncovered; base with moderate to weak spiral striae, usually white; Indo-Pacific ..... *pallidula*

**Xenophora (Xenophora) conchyliophora** (Born, 1780).

Figs 4d, 6c, 7a, 14l, 17a-h, 32.

*Trochus conchyliophorus* Born, 1780: 333, pl. 12, figs 21, 22. (No. 2045, Official List of Specific Names in Zoology, ICZN Opin. 715); Gmelin, 1791: 3584, Philippi, 1846: 52, pl. 2, figs 6-8.

*Astraea conchyliophora*. — Röding, 1798: 80.

*Astraea lapidifera* Röding, 1798: 80 (based on Chemnitz, 1781: pl. 172, figs 1688, 1789 (err. = 1689)).

*Astraea corallophora* Röding, 1798: 80 (*nomen nudum*).

*Trochus lithophorus* Blumenback, 1803: 64 (based on Chemnitz, 1781, pl. 172, figs 1688, 1689).

*Xenophora laevigata* Fischer von Waldheim, 1807: 213.

*Xenophora tricostata* Fischer von Waldheim, 1807: 213.

*Xenophora vulcanica* Fischer von Waldheim, 1807: 213.

*Xenophora mecandrina* Fischer von Waldheim, 1807: 214.

*Phorus agglutinans* Montfort, 1810: 159 (in part).

*Trochus agglutinans*. — Lamarck, 1822: 14 (*non* Lamarck, 1804).

*Phorus onustus* Reeve, 1842: 160, pl. 214, fig. 3, pl. 215, fig. 8; Reeve, 1843a: 161; Reeve, 1843b: pl. 1, figs 3a, b; Reeve, 1845, pl. 3, figs 3c, d (*non Trochus onustus* Nilsson, 1827, also a *Xenophora*).

*Xenophora trochiformis*. — H. & A. Adams, 1854: 363, pl. 40, fig. 2c; Fischer, 1879a: 448, pl. 6; Thiele, 1929: 250; Clench and Aguayo, 1943: 2, pl. 1, figs 1, 2; Palmer, 1963b: 10 (as *Trochus*), pl. 2, figs 1-3 (invalid designation of neotype); Rios, 1970: 57 (*non* Born, 1778).

*Xenophora conchyliophora*. — Philippi, 1855: 350, pl. 49, fig. 3; Tryon, 1886: 161, pl. 46, fig. 89; Dall, 1889: 290; Abbott, 1974: 143, pl. 4, fig. 1572; Rios, 1975: 65, pl. 18, fig. 265.

*Phorus conchyliophorus*. — Chenu, 1859: 323, figs 3216, 3217.

*Xenophora robusta* Verrill, 1870: 226; Strong, Hanna and Hertlein, 1933: 124, pl. 5, figs 8, 9 (holotype), pl. 6, figs 5, 6; Bourgeois, 1943: 37, pl. 7, figs 5, 6; Keen, 1958: 318, fig. 256; Keen, 1971: 463, fig 837; Abbott, 1974: 143.

*Xenophora corrugata*. — Watson, 1886: 463 (*non* Reeve, 1842).

*Xenophora conchyliophora robusta*. — Woodring, 1957: 78.

**Shell:** Of medium size, with a moderate spire ( $62^\circ - 93^\circ$ ), a narrow peripheral flange forming an irregular, cord-like flange around edge of base. Umbilicus narrow in juveniles, closed in mature specimens. Whorls convex, sculptured dorsally with fine, wavy, opisthocline riblets and very irregular folds, as well as prosocline axial growth rugae and low folds. Dorsal surface mostly obscured by attached foreign bodies (usually large). Base slightly convex to slightly concave, sculptured with fine, granulose, spiral and subspiral threads which cross weak, curved, collabral growth rugae. Colour yellowish-white with orange-brown, brown or purplish-brown radial streaks and/or blotches on base. Apertural callus and umbilical area brown, outer lip white (Fig. 17a-h).

#### Dimensions:

	height	diameter
Holotype of <i>tricostata</i>	53.75 mm	53.5 mm
Paratype of <i>mecandrina</i>	30.0	41.7
Holotype of <i>robusta</i> (from original description)	45.0	56.0
Figured specimens		
Large specimen of " <i>robusta</i> " (Punta Arena, BMNH)	52.0	60.0
Boynnton, Florida (AMS)	37.2	51.1

**Operculum:** Broadly oval, pale brown, rather thin, sub-opaque, smooth externally except for faint radial lines and growth striae. Growing edge strongly convex, sides weakly convex, nucleus slightly to the left of centre. Central area broad, with unusually conspicuous radial striate structure easily visible through rather thin free surface (Fig. 6c). Excellent figures provided by Bergh (1896, pl. 3, figs 22, 23). Most examples observed show little wear and consequently have a longer free surface (and therefore are broadly oval) than most species of *Xenophora* s.s.

**Radula:** Central teeth with narrow base, broad, rather short median cusp and 2 small lateral cusps. Lateral teeth subtriangular, with large, broad cusps. Marginal teeth smooth (Fig. 7a). See also Troschel, 1861: 190, pl. 16, figs 7, 7a, and Bergh, 1896, pl. 3, fig. 24. Bergh's illustration indicates a series of small plates on the outer side of the marginal teeth. These have not been observed in the material to hand, nor in any other species. The overall size of the radula of this species is relatively less than that of most other species of the genus.

**Anatomy:** Similar to that of *X. neozelanica*. Salivary glands large, left displaced posteriorly. Penis not observed but Mörch (1857) and Bergh (1896) give figures which show it to be long, with a flattened, expanded distal portion which bears a prominent, blunt papilla (copy of Bergh's figure, Fig. 14l). Head-foot shown in Fig. 4d. Material examined: off Martinique, Windward Ids, 47 m (AMS) (3 subadult females, sexually immature).

**Location of types and type localities:** *T. conchyliophorus*: Lost (fide F. Bachmayer in letter, Palmer, 1963b: 10). Clench & Aguayo (1943: 2) designated the type locality for *X. trochiformis* (Born) as Nassau, New Providence, Bahama Islands. As it was clearly their intention to give the type locality for the species now under consideration this locality is here designated the type locality of *T. conchyliophorus* Born.

- A. lapidifera* and *T. lithophorus* (based on same figures in Chemnitz): No specimens agreeing with these figures could be located in ZMC by the writer; "American Seas".
- X. laevigata*: Lost? It is possible that this is just a replacement name for *T. conchyliophorus*; "American Seas".
- X. tricostata*: Holotype, Zoological Museum, Moscow University (L. 77); "American Seas" (Fig. 17d, e).
- X. vulcanica*: Lost (fide V.N. Goryachev *in lit.*), "American Seas".
- X. mecandrina*: Holotype (?) and paratype, Zoological Museum, Moscow University (paratype L. 78) (Fig. 17f-h); "American Seas".
- T. agglutinans* Lamarck, 1822: NHMG, 3 specimens (1095/66, 67, 68); Antilles.
- P. onustus* Reeve: Lost? (not found in BMNH); West Indies.
- X. robusta*: Peabody Museum, Yale University (8882); La Paz, Lower California.

**Fossil records:** There are many records attributed to this species in the literature ranging from Eocene to Recent. The writer has not examined the relevant material so is unable to make his own assessment of the probable time range of *X. conchyliophora*.

**Other material examined:** *Georgia*: Off Brunswick (31°04'N, 79°42'W), 366 m (USNM).

*South Carolina*: 76 km E.S.E. of Charleston, 40 m (USNM). *North Carolina*: 40-43 km off Cape Fear, 26 m, 33 m (USNM). 63 km W.S.W. of Cape Hatteras, 635 m (USNM). N.E. of Cape Lookout, 64 m (USNM). *Gulf of Mexico*: 48 m (USNM); 18-24 m (AMS). Between Mississippi delta and Cedar Keys, 46-203 m (several lots) (USNM). *Florida*: Off Pensacola (ANSP). Off Apalachicola, 46 m (USNM). 24-56 km off Fort Walton, 24-35 m (MCZ). Off Destin, 18 m, 26 m (ANSP, USNM). Off Cape San Blas, 47 m, 55 m (USNM). Little Gasparilla Is. (ANSP). Tarpon Springs (USNM). Sanibel Is. (ANSP), 11 m (MCZ). Off Naples (ANSP). S.S.W. of John's Pass, 58 m (ANSP). Little Duck Key, Lower Florida Keys (ANSP). Bonefish Key, Florida Keys (ANSP). Washerwoman's Patch, off Marathon, Florida Keys (ANSP). 1.6 km E.S.E. of Marker 33 near Garden Cove, Key Largo (ANSP). Grassy Key (ANSP). Sugarloaf Key, 4 m (MCZ). 5 km off Molasses Reef East, Key Largo, 60-91 m (MCZ). W. of Everglades township, 55 m (AMNH), 36 m (FMC). S.W. of Egmont Key, 46 m (AMNH), 36 m (FMC). 29 km E. of Delray Beach, 503-549 m (USNM). Fort Dallas, Miami (MCZ). Biscayne Channel, Miami (ANSP, MCZ). Off Palm Beach, 73 m (ANSP), 55-91 m (MCZ). S.E. Alligator Reef Lighthouse (USNM). S.E. Keys (USNM). Off Fowey Light, 46-183 m (several lots) (USNM). Lake Worth (ANSP), 73 m (ANSP, FMC, MCZ, NMV, AMS). Daytona Beach (MCZ). Off Bear Cut, Miami, 33-36 m (USNM). Off Ragged Key (USNM), 137 m (USNM). Off Dry Tortugas, 33-36 m (USNM). S. of Dry Tortugas, 73 m (USNM). S.W. of America Shoals, Florida Keys, 146-183 m (USNM). Ajax Reef, 146-183 m (USNM). Sands Key, 128-165 m, 113 m (USNM). Off Cape Florida, 353 m (USNM). Off Key West, 11 m, 91 m, 165 m (USNM). *Mexico*: (*East Coast*): Cape Catoche, Yucatan, 46 m, 48 m (USNM). *British Honduras*: N.W. of Tom Owens Cay (16°15'N, 88°17'W), 51 m (ANSP). Twelve Feet Bank (17°19'N, 88°07'W), 12 m (ANSP). *Honduras*: Roatán Is. (USNM). *Panama* (*East Coast*): N.W. end of Gayard Is. (USNM). E. Colon (USNM). Taboguilla Is., 9 m (ZMC). *Bahamas*: Beach W. of Alice Town, North Bimini Is. (ANSP). Alice Town Flats, N. Bimini Is. (ANSP, MCZ). Tokas Cay, Bimini Ids (ANSP). S.W. of Elbow Cay, Great Abaco Is., 1-2 m (ANSP). Dundas Town, N.E. Coast, Great Abaco Is. (ANSP). 28 km W. off Hoffman Cay, Berry Ids (ANSP). Governors Harbour, Eleuthera Is. (ANSP, MCZ). Leafy Cay Beach, 1.6 km N.W. of Governors Harbour (MCZ). Nassau, New Providence Is. (USNM, MCZ). Simms, Long Is. (MCZ). Mathew Town, Great Inagua Is. (MCZ). Arthur's Town, Cat Is. (MCZ). Bennetts Harbour, Cat Is. (MCZ). *Cuba*: Golfo de

Batabano, 21°57'N, 82°32'W (USNM). Cayo Maja Figuro, S.W. of Santa Maria, off Punta Alegre (MCZ). Cayo Guajaba, Camaguey Province (MCZ). Cayo Hutia Reef (USNM). Cayo Levisa, 4-6 m (USNM). Varadero Beach (AMS). Guantánamo Bay, Oriente Province, outer beaches (ANSP). Cuzco Beach (MCZ). *Grand Cayman*: (ANSP). *Jamaica*: Montego Bay (USNM). W. of Mary Is., Port Antonio (AMNH). Portland (USNM). *Hispaniola*: Haiti (USNM). Dominican Republic (MCZ). Santo Domingo (ANSP). *Puerto Rico*: S.W. of Santa Isabel (USNM). Bahia de Anasco (MCZ). Point Guanajibo (ANSP). Bahia Bramadero (MCZ, USNM). *Virgin Islands*: St. Thomas Is. (ANSP, MCZ, USNM, ZMC). Beef Is., Sir Francis Drake Channel, 22-26 m (ANSP). N. of Towing Pt., Great Camanoe Is., 27 m (ANSP). Water Is. (USNM). Tortola Is. (USNM). St. John Is., 27 m (ZMC). *Leeward Islands*: Off English Harbour, Antigua Is., 904 m (USNM). *Windward Islands*: Off Martinique, 14°54'N, 61°04'W, 47 m (AMS). St. Anne's Bay, Martinique (AMNH). Grenadine Is. (AMNH). W. of Grenada Is., 11-15 m (ANSP). Off Lazaretto, Barbados Is., 137-146 m (USNM). Off Paynes Bay Church, Barbados Is., 91 m (USNM). Off Needhams Point, Barbados Is., 119-128 m (USNM). *Tobago*: 3 km S. of Fort George, Scarborough, 66 m (MCZ). *Aruba Island*: (ANSP, USNM). *Bermuda*: (ANSP). Off Somerset (ANSP). Off Spanish Point (ANSP). *Mexico (West Coast)*: Puerto Peñasco, Golfo de California (AMNH, FMC). Guaymas, Golfo de California (ANSP, AMNH, RNHL), 36-55 m (USNM, ANSP, FMC). S. end of San Marcos Is., Baja California (AMNH). Santa Ines area, 27°N, 112°W (AMNH). La Paz, Baja California (AMNH). Punta Arena area, Baja California (BMNH), 64 m, 82 m (AMNH). Cabo San Lucas, Baja California, 57 m (USNM). Los Frailes, Baja California (AMS). Punta Gorda, Baja California, 82 m, 146-164 m (AMNH). Mazatlán (ANSP). Maria Madre Is., Las Tres Marias (AMNH). *Panama (West Coast)*: Archipelago de las Perlas (USNM). San José Is. (USNM). S. end of E. beach, Playa Grande (USNM). E. side of Taboga Is., 12 m (ANSP).

**Other records:** *Brazil*: Off Amapá, 88 m. Off Maranhão. Off Ceará. Off Piauí. Off Rio Grande do Norte, 53-80 m. Off Recife, Pernambuco, 18 m. Off Alagoas, 31 m. Off Bahia, 58 m (All Rios, 1970). Off Fernando-Noronha Is., 13-46 m (Watson, 1886).

**General:** "West Indies generally, and northward to the vicinity of Cape Hatteras, where it is found in 30-40 fathoms (55-73 m)". Also in the southern Gulf of Mexico in 36-229 fathoms (66-419 m); the Gulf of Mexico and the Antilles, and along the Carolina Coast, in 14-111 fathoms (26-204 m) (Dall, 1889). West Mexican coast from Guaymas and La Paz in the Gulf of California to the Gulf of Tehuantepec, mostly off shore in depths of 45-50 fathoms (82-91 m) (Keen, 1971).

**Distribution:** Cape Hatteras, E. North America to Bahia, Brazil and on the west coast from Puerto Peñasco in the Gulf of California to the Gulf of Panama; mostly shallow water but a few records on the continental slope (down to 635 m) (Fig. 32).

**Remarks:** A detailed account of the complicated nomenclatural history of this species name is given in the proposals and comments in the *Bull. zool. Nomencl.* (Palmer, 1963a, 1963b; Robertson, 1963; Moore, 1963; Abbott, 1963 and Opinion 715, 1964).

Comparison of the shells of east and west coast specimens does not reveal any significant differences. This is not particularly surprising as both populations were probably continuous as recently as late Pliocene because of the sea connection that existed up to that time (Woodring, 1966). Insufficient time has elapsed to enable morphological differentiation to occur, as *X. conchyliophora*, like most species of *Xenophora*, is apparently very conservative. Woodring (1957) reduced *X. robusta* to subspecific status.

*Xenophora conchyliophora* has been recorded as a fossil from several localities in the central American region and in the south-eastern United States, perhaps dating back as far as the Eocene (Palmer, 1937, Woodring, 1957). *Xenophora zitteli* Weaver from the Martinez Group, California (Upper Paleocene) is poorly described and figured but appears to have a general similarity with *X. conchyliophora* as has *X. stocki* Dickerson from Rose Canyon, California (Upper Eocene) and *X. hawleyi* Loel and Corey from the Vaqueros Formation, California (Lower Miocene).

**Xenophora (Xenophora) cerea** (Reeve, 1845).

Figs 7c, 14j, k, 18d-f, 20f, g, 23a-i, 33.

*Phorus cereus* Reeve, 1845: pl.3, fig. 9.*Trochus agglutinans*. — Cuvier, 1849: 112, pl.41, figs 3, 3a (*non* Lamarck, 1804).*Xenophora cerea*. — H. & A. Adams, 1854: 363; Fischer, 1879a: 440, pl.44, fig. 2.*Xenophora corrugata*. — Philippi, 1855: 346, pl.48, fig. 1; Tryon, 1886: 159, pl.45, figs 81, 82; Uchiyama, 1902: 2, pl.22, figs 2, 3; Schepman, 1909: 203; Habe, 1953a: 176, text fig. 6; Habe, 1964: 57, pl.16, fig. 6; Okutani, 1972: 83, fig. 20; Ladd, 1977: 16, pl.21, figs 10-12 (*non* Reeve, 1842).*?Onustus trochiformis*. — Bergh, 1904: pl.8, figs 1-4.*Xenophora torrida* Kuroda and Ito, 1961: 257, pl.16, fig. 11.*Xenophora turrida* (sic!). — Kira, 1962: 33, pl.15, fig. 7.

**Shell:** Depressed to moderately elevated (spire angle 70°-100°), with narrow peripheral flange, convex whorls, and umbilicus closed in mature specimens, narrowly open in juveniles. Foreign objects often large and cover much of dorsal surface. Dorsal sculpture of fine, wavy, opisthocline riblets, growth lines, and rounded, prominent, very irregular rugae, both opisthocline and prosocline, giving surface a somewhat warty appearance. Base slightly concave to slightly convex, usually with umbilical depression; sculptured with heavy, irregular radial (collabral) lamellae crossed by subspiral striae which sometimes thicken into weak spiral cords, especially over inner half of base. Spiral sculpture rendered gemmate at points of intersection with radials and is conspicuous to almost absent. Colour white or yellowish-white to dark chocolate brown (Figs 18d-f, 20f, g, 23a-i).

**Dimensions:**

	height	diameter
Holotype	16.2 mm	24.0 mm
Figured paratype	13.8	20.0
Paratype	12.2	16.7
Average specimen (Swain Reefs, AMS)	42.1	46.5
Small (mature) specimen (New Britain, AMS)	24.2	31.0
Holotype of <i>X. torrida</i> (from original description)	34	38
? Paratype of <i>X. torrida</i> (ANSP)	29.6	36.8
Figured specimens		
Eniwetok, Marshall Ids (USNM)	23	27.35
Near Michaelmas Cay, Queensland (AMS)	42	54
Off Tosa, Japan (USNM)	38.1	51.35

**Operculum:** Subtriangular, rather thin yellowish-brown, opaque, with closely-spaced concentric lamellae externally. Nucleus displaced to left, sometimes markedly; central area broad.

**Radula:** Central teeth subtriangular, with broad triangular median cusp and two pairs of short lateral cusps. Lateral teeth subrectangular, with simple, straight cutting edge with very indistinct irregularities. Marginal teeth curved, rather narrow, with minute denticles on cutting edges (Fig. 7c).

**Anatomy:** Similar to that of *X. neozelanica*. Penis long and narrow, simple, with a papilla-like termination (Fig. 14j). Material examined: Kukum, E. of Honiara, Guadalcanal, British Solomon Ids, 2-9 m (AMS) (1 small adult male); 3.2 km off Baie Ternay, W. coast of Mahé, Seychelles, 49 m (BMNH) (1 male); off Cape Cleveland, Queensland, 29 m (WAM) (1 male).



**Location of types and type localities:** *P. cereus*. Holotype and 2 paratypes, BMNH (197784); Isle of Luzon, Philippines, H. Cuming Coll. (a third paratype is *X. solaroides* (Reeve)) (Fig. 23a-f).

*X. torrida*. Holotype in Kaisei Hospital, Ohama, Nishinomiya City, Japan, in Kuroda Coll. Paratype (?), ANSP (244689); Tatsugahama, Kii, Japan (Figs 23g, h) (this specimen marked paratype *ex* Ito but there is no mention of it in the original description). Southwestern coast of Kii Peninsula, collected with lobster fishing nets.

**Fossil material examined:** Miocene: "Locality O", Tjilang, Java (2 fragmentary specimens, RGM, 11141). Kembang Sokkoh, near Jogjakarta, Java (1 fragment of base, RGM 11143). Goenoeng Spolong, near Jogjakarta, Java (3 immature, RGM, 47213 (Fig. 18d-f), RGM, 11139). All the Miocene specimens appear to agree closely with Recent specimens of *X. cerea* but because of their poor condition are referred rather tentatively to this species. Pliocene: Thuvu Group, Viti Levu, Fiji (USNM, 175049) (recorded as *X. corrugata* by Ladd (1977)).

**Other material examined:** Zanzibar: 0.4 km W. of Chumbe Is., S.W. Zanzibar, E. Africa, 22-26 m (ANSP). Indian Ocean: Mauritius (AMS). N.W. Bay, Mahé, Seychelles, (BMNH). 3.2 km off Baie Ternay, W. coast Mahé, Seychelles, 49 m (BMNH). Cargados, 55 m (BMNH). Red Sea: Elat, Gulf of Aqaba (ZMC). Off Elat, 40-49 m, 62-80 m (Tel Aviv Univ.). Japan: 73 m (AMS). Izu-Shichito Ids, S.E. of Izu Peninsula, 160-218 m (Tokai Fish. Res. Lab.) Kii Suido Wakayama, 55 m (AMS), 73 m (ANSP) (*torrida* var). Tosa (AMS), (ANSP) (*torrida* var). Tatsugahama, Kii (ANSP). Tsuken Reef, Okinawa Is. (ANSP). Off Itoman, Okinawa Is., 73-91 m (BPBM). Off Kiyau, Okinawa Is., 73-91 m (BPBM). China Sea: Macclesfield Bank, 59 m (BMNH). Philippines: Legazpi, S. Luzon, 271 m (AMS). N.E. Burias Is., 36 m (USNM) (*torrida* var). Lady Is., Bohol Strait, off Bohol Is., 199-234 m (WAM). S.E. of Balabac Is., Sulu Sea, 55 m (WAM). Indonesia: Off Piru Bay, Seram (Ceram), Moluccas, 26-47 m (WAM). Kai Ketjil (Noehoerowa), 5°32'S, 132°41'E. Moluccas, 27-37 m (WAM). Off Kepulauan Kai, Moluccas, 5°38'S, 132°55'E, 90 m (ZMC). Off Banda Elat, W. coast of Kai Besar, Kepulauan Kai, Moluccas, 49-64 m (WAM). E. side of Mitduan Reef, W. coast of Kai Besar, 46 m, 36-55 m (WAM). Auri Kepulauan, Teluk Irian (Geelvink Bay), 33-36 m, Irian Barat (ANSP) (*torrida* var), 36-46 m (ANSP). 1.6 km E. Dauuio Is., Padeaido Kepulauan, 1°15'S., 136°30'E (ANSP). North Western Australia: 11 km N. of Long Is., Off Onslow, 51 m (WAM). Between Malus and Gidley Ids, Dampier Arch., 18-26 m (WAM). Between Gidley and Rosemary Ids, Dampier Arch., 24-33 m (WAM). 11-13 km N. of Delambre Is., Dampier Arch., 40 m (WAM). Delambre Is., Dampier Arch. (WAM). Northern Australia: 241 km N.W. of Darwin (ANSP). Arafura Sea, near Darwin (ANSP). Queensland: Cairns Reef, 0-9 m (DMNH). Michaelmas Cay, 84 m (AMS). Bramble Reef (AMS, DMNH). 8 km E.N.E. of Brook Light, Brook Is., 4.5 m (DMNH). Palm Is. (DMNH). Off Cape Cleveland, 29 m (WAM). Black Is., Langford Reef, 33 m (AMS). Off Mackay, 55 m (AMS). Gillett Cay, Swain Reefs, 64-73 m (AMS). Between High Peak and Swain Reefs, 82 m (AMS). South Keppel Is., 27-36 m (AMS). North West Isle, Capricorn Group (AMS). Wide Bay, 64 m (AMS). ? Moreton Bay, 13 m (AMS) (1 juvenile). Admiralty Islands: 40-155 m (BMNH). New Britain: Rabaul (AMS) (some *torrida* var). Rabaul Harbour (ANSP), 37 m (ANSP) (both *torrida* var). Solomon Islands: Kukum, 1.5 km E. of Honiara, 2-9 m (AMS). Marshall Islands: W. of Jieroru Is., Eniwetok (USNM). New Caledonia: (AMS). Fiji: Nandi Bay, Viti Levu, 9-35 m (AMS). Pitcairn Island: 55-82 m, 119-128 m (USNM).

**Distribution:** Tropical Indo-Pacific including Red Sea, Tropical E. Africa, the islands of the western Indian Ocean, tropical Australia, Western Pacific as far north as southern Japan and east to Fiji, the Marshall Ids and Pitcairn Is; shallow sublittoral to 270 m but mostly between 30-80 m (Fig. 33).

**Remarks:** This wide-ranging, very variable species (compare Figs 20f, g, 23a-i) has long been known as *X. corrugata* (Reeve) but that species, as shown herein, is restricted to the Indian Ocean.

A chocolate-brown variety has been named *X. torrida* and this is not uncommon in New Britain and New Caledonia where it grades into the typical colour form of *X. cerea* from which it cannot be otherwise distinguished.



*Xenophora cerea* is similar in shell characters to *X. conchyliophora*, being most readily separated by the stronger basal radial sculpture of *X. cerea*, its often less-pronounced brown colouration of the apertural glaze, and the lack of the brown blotches on the base which are so characteristic of *X. conchyliophora*. The American species tends to agglutinate more small shell fragments and sand grains to the dorsal surface of the shell than *X. cerea* and, partly because of this, its dorsal surface is generally more completely covered. The differences given above, however, are of a minor nature and the two species could even be interpreted as being only subspecifically distinct if it were not for the considerable differences observed in the opercular, radular, and penial characters. Another similar species, *X. mekranensis konoï* Habe, differs in having a relatively higher spire, more strongly convex whorls and usually a strongly spirally-ribbed base. A form with an unusually weakly-sculptured base is shown in Figure 16e for comparison with *X. cerea*.

The names *X. subconica* Boettger, 1883 and *X. birmanica* Noetling, 1901 are based on internal moulds from the Miocene of Sumatra and Burma respectively. Both species names are clearly based on members of the *conchyliophora* group which resemble *X. cerea* in size, shape and agglutination pattern. They may represent either an ancestral form of *X. cerea* (to which the Indonesian Miocene records listed above would probably also belong) or, more likely, should be regarded as the same species as *X. cerea*. The available material does not, however, enable a positive judgement to be made.

Reeve's type specimens of *X. cerea* are juveniles and this fact has been largely responsible for the confusion in subsequent identification. Comparison of Reeve's material with juvenile specimens of the species here regarded as *X. cerea* has shown them to be conspecific.

One specimen from off Cape Cleveland, Queensland has a peculiar plate-like flange on the penis unlike that seen in the other 2 males examined (Fig. 14k). Specimens have been examined from the Seychelles and Honiara, Solomon Ids and all of these differ from the Cape Cleveland specimen in having a simple, long, tapering penis. The operculum in the Cape Cleveland specimen and in a similar specimen from off South Keppel Island (AMS, C86710), have closely-spaced, raised, concentric lamellae on the outer surface. This closely resembles the sculpture on the operculum of specimens of *X. cerea* and *X. mekranensis konoï*, although it is somewhat finer and the nucleus is more displaced to the left than in other available material of *X. cerea*. Possibly these two Queensland specimens represent an unnamed species or subspecies with closely similar shell features to *X. cerea* but on the available material they cannot be satisfactorily distinguished. Clearly a much larger amount of preserved material is required to establish whether or not more than one species is encompassed by the present interpretation of *Xenophora cerea*.

Bergh (1904; pl.8, figs 1-4) figured the penis, the mantle edge, and the otocyst of "*Onustus trochiformis*" from the Philippines. The illustration of the penis resembles that of the typical form of *X. cerea* and consequently Bergh's diagrams are referred to this species.

The known distribution of this species (Fig. 33) is separated into Western Indian Ocean — Red Sea and central Indo-west Pacific blocks. Material available from both areas cannot be distinguished consistently and it is assumed that this apparent break in distribution is probably due to a collecting artifact.

### ***Xenophora flindersi* (Cotton and Godfrey, 1938).**

Two subspecies of *X. flindersi* are recognised, the shells of both being distinguished from other species by their rather flat, imperforate bases which are almost devoid of spiral sculpture, and their paucispiral protoconchs (Fig. 13c, d). The fossil subspecies (*ludbrookae* nov.) has numerous sand grains embedded in the exposed parts of the dorsal surface, a habit retained to a much lesser extent in the smaller Recent subspecies.

**Xenophora (Xenophora) flindersi flindersi** (Cotton & Godfrey, 1938).

Figs 6d, e, 7b, 13c, 14a, 17k-m, 22g, h, 34.

*Xenophora tatei*. — Verco, 1909: 270 (non Harris, 1897).

*Onustus peronianus*. — Cotton & Godfrey, 1932: 38, pl.1, fig. 4; Cotton (in Verco), 1935: pl.14, fig. 6 (non Iredale, 1929).

*Onustus flindersi* Cotton & Godfrey, 1938: 205.

*Xenophora flindersi*. — Cotton, 1957: 123.

**Shell:** Depressed to moderate spire (spire angle  $80^{\circ}$ - $103^{\circ}$ ), peripheral flange very narrow, barely distinguishable from rest of base. Protoconch large, paucispiral (Fig. 13c). Umbilicus closed in adult, narrowly open in juveniles. Attached foreign objects obscure most of dorsal surface, a few scattered sand grains and shell fragments attached in areas not covered by large objects. Whorls convex, sculptured dorsally with fine opisthocline riblets and predominantly prosocline irregular rugae. Base almost flat to very lightly concave, sculptured with rather fine and regular growth lines and very inconspicuous, close, subspiral to oblique striae at right angles to growth lines. Colour white dorsally, base yellowish-white to white with very indistinct pale brown spots scattered behind basal part of outer lip; aperture white (Figs 17 k-m, 22g, h).

**Dimensions:**

	height	diameter
Holotype (from original description)	9 mm	18 mm
Largest specimen seen (figured), St. Francis Is., South Australia (AMS)	41.3	49.5
Coffin Bay, South Australia (NMV)	19.5	29.4

**Operculum:** Stromboid, elongated, nucleus mid-lateral but because of growth pattern appears terminal. Edges almost parallel, each with about 5 sharp serrations; growing edge strongly convex. External surface smooth except for weak growth lines, inner surface with central area transformed into a heavy, narrow rib extending from outer edge to just over half way through attachment scar towards inner edge. Colour light horny brown. The serrated portion (about half the length of the operculum) freely projects beyond the opercular lobe (Fig. 6d, e).

**Radula:** Central teeth subcircular, with moderate median cusp and two short lateral cusps. Lateral teeth triangular, with large, triangular cusp near inner edge and very indistinct serrations along remainder of cutting edge in a few teeth. Inner marginal teeth very finely serrate, existence of wing-like plate not fully confirmed. Outer marginal teeth smooth (Fig. 7b).

**Anatomy:** Similar to that of *X. neozelanica*. Mantle-edge tentacles short and blunt and appear to be restricted to the left side. Salivary glands very small, the right the larger. Penis of moderate length, approximately parallel-sided except for the distal portion being slightly expanded; with a short, blunt, subterminal papilla (Fig. 14a). Material examined: Petrel Bay, St. Francis Is., South Australia, 20-30 m (AMS) (1 male, 1 female).

**Location of type and type locality:** Holotype, SAM (D. 13615); 27-37 m, Petrel Bay, St. Francis Is., South Australia (3 other specimens in SAM from this locality) (Fig. 17k, l).

**Fossil records:** None known.

**Other material examined:** *South Western Australia:* 1 km S.E. of Mistaken Is., King George Sound, 27 m (WAM). *South Australia:* Petrel Bay, St. Francis Is., 20-30 m (AMS). Dredged between St. Francis and Smooth Ids, 20-30 m (AMS). Coffin Bay, 37 m (NMV). "Cape Don" (? Cape Donington, Port Lincoln), 13 m (NMV).

**Distribution:** King George Sound, south Western Australia to Port Lincoln, western South Australia; in 20-40 m (Fig. 34).

**Remarks:** The shell of this species is most similar in general appearance to that of *X. japonica* Kuroda & Habe but differs in having a more finely and regularly sculptured base, a lower spire and a narrower umbilicus. *X. peroniana* Iredale is apparently not sympatric with this

species, is larger and the shell has a more irregularly and strongly sculptured base, which is usually coloured with axial streaks of red-brown and is more concave than that of *X. flindersi flindersi*.

The protoconch of *X. flindersi* is paucispiral (Fig. 13c) and in this respect differs from all of the other Recent and fossil species of *Xenophora* that the writer has examined. The Upper Pliocene-Pleistocene ancestor of *X. flindersi flindersi*, *X. flindersi ludbrookae* nov., has a similar protoconch but has a much larger shell. The unusual stromboid operculum of *X. flindersi flindersi* also distinguishes it from any other living *Xenophora*.

***Xenophora (Xenophora) flindersi ludbrookae* n. subsp.**

Figs 13d, 17i, j.

*Xenophora neozelanica*. — Ludbrook, 1978: 126, pl.13, figs 7-11 (non Suter, 1908).

**Shell:** Rather large, heavy, with moderate to depressed spire (spire angle  $85^{\circ}$ - $100^{\circ}$ ), peripheral flange narrow, slightly set off from rest of base. Umbilicus closed in adults and subadults, narrowly open in juveniles. Protoconch large, of about  $1\frac{1}{2}$  whorls (Fig. 13d). Attached foreign objects obscure most of dorsal surface; numerous sand grains attached (or the scars they leave) over most of remainder of dorsal surface. Whorls convex, sculpture very irregular, mostly obscured by attached objects (small and large), surface very rough but no strong folds appear to be present. Base weakly convex, a weak depression in umbilical area, sculptured with regular, distinct growth rugae and traces of exceedingly fine spiral striae. Basal lip of aperture slightly and evenly thickened when mature, edge regularly concave (Fig. 17i, j).

**Dimensions:**

	height	diameter
Holotype	46.9 mm	58 mm
Largest paratype (WAM 70.15)	42.3	63.0

**Location of type and type locality:** Holotype, WAM (76.2473); Roe Plain, Eucla Basin, Western Australia at Hampton Microwave Repeater Tower, in spoil from foundation holes, coll. E. & N. Zeffert, Jan. 1976 (Fig. 17i, j). Paratype, WAM (70.15); same locality, coll. M. Archer & B. Muir, 3 Dec. 1969 (1 adult). Paratype WAM (69.490); same locality, coll. T. A. Darragh, M. Archer and G. W. Kendrick, 5 March 1969 (1 subadult) 5 paratypes NMV P28431a, b, P28428-30, same data as last. 2 paratypes, AMS (C.90093); same locality, coll. W. F. & J. M. Ponder, 7 Feb. 1972 (1 adult, 1 subadult). 5 paratypes, WAM (77.589); Roe Plain, pit 1.5 km N. of Hampton Microwave Repeater Tower, basal 0.4 m of carbonate sand, coll. V. A. Ryland, G. W. & W. E. Kendrick, Sept. 1976 (5 juveniles including specimens with intact protoconchs). All lowest Pleistocene or Upper Pliocene.

**Other fossil material examined:** *Lower Pleistocene: Western Australia:* Jandakot, Perth Basin, "Frank Paulik's Bore", lot 6, W. side Semple Road, coll. J. G. Hastings, 7 June 1967 (WAM, 70.1161). *Lowest Pleistocene or Upper Pliocene: Western Australia:* Roe Plain, 76 km W. from Eucla Motel along Eyre Highway, coll. H. P. Salter, 21 Sept. 1970 (WAM, 70.817) (1 small specimen).

**Distribution:** Roe Plain and Perth, south Western Australia, Lower Pleistocene and possible Upper Pliocene.

**Remarks:** The new subspecies differs from *X. flindersi flindersi* in its larger, heavier shell and in the much greater density of sand grains agglutinated to the exposed parts of the dorsal surface. The new subspecies was identified as *X. neozelanica* by Ludbrook (1978) from which it can be distinguished by its smaller size, flatter base, much weaker basal sculpture, the habit of agglutinating sand grains over the exposed dorsal parts of the shell, and the protoconch characters, *X. neozelanica* having a typical multispiral protoconch.

The shell from Jandakot is tentatively assigned to this subspecies. It is in good condition dorsally but the base is represented by only a few fragments. It has all of the essential features of the subspecies but is smaller (29.2 mm diameter, 26.4 mm height) and has a taller spire (spire angle  $73^{\circ}$ ).

This subspecies is named for Dr N. H. Ludbrook of South Australia as a small tribute to her fine work on the Tertiary and Quaternary molluscs of southern Australia.

***Xenophora (Xenophora) tatei* Harris, 1897.**

Figs 13b, 19a-e.

*Xenophora (Tugurium) tatei* Harris, 1897: 254, pl.7, figs 7a, b; Chapman, 1922: 11.

**Shell:** Spire depressed (spire angle 95°-104°); peripheral flange narrow, set off at distinct angle from rest of base. Umbilicus almost completely closed by inner lip callus, but umbilical depression remains distinct. Attached objects obscure much of dorsal surface (60-80%), a few scattered sand grains attached to free surface. Whorls convex, tending to be angled in middle, sculptured with opisthocline fine, wavy riblets and heavy undulating cords crossed by rather weak, irregular growth lines. Base slightly convex, with weak, curved, radial growth lines and very fine subspiral striae (Fig. 19a-e).

**Dimensions:**

	height	diameter
Holotype	27.9 mm	44.3 mm
Figured specimen (Topotype, AMS)	24.3	37.0

**Location of type and type locality:** BMNH (G5538); Muddy Creek, Victoria (Balcombian, Miocene) (= Lower Beds) (Fig. 19a-c).

**Other fossil material examined:** *Miocene (Balcombian):* Victoria "Lower beds" (Muddy Creek Marl), Clifton Bank, Muddy Creek, near Hamilton (NMV, AMS). Balcombe Clay, Fossil Beach, Balcombe Bay, Mornington (NMV, AMS). Fyansford Formation, Red Hill, Shelford (FL\* 69) (NMV). *Miocene (Bairnsdalian):* Victoria: Section 4A, Parish of Murgheboluc, near junction of Bruces Creek and Barwon River (FL 100) (NMV).

**Other records:** *Miocene (Balcombian):* Victoria: Grices Creek (Chapman, 1922); Newport and Altona (Dennant & Kitson, 1903).

**Distribution:** Balcombian to Bairnsdalian (Middle Miocene) of Victoria, Australia.

**Remarks:** The shell of this extinct species differs from other similar species by its finely sculptured, somewhat convex base and marked umbilical depression. The form of the base is somewhat like that of *X. conchyliophora* but it differs in having weaker sculpture, and it is also similar to that of subadult *X. peroniana peroniana*.

Dennant & Kitson (1903: 113) record *X. tatei* from Camperdown and Lower Moorabool (Victoria) and Chapman (1922: 11) records it from Bird Rock Cliffs, Torquay, Victoria. All of these localities are Janjukian in age (Upper Oligocene) and only the specimen from Bird Rock Cliffs can be located (T. A. Darragh, *in litt.*). This specimen differs in detail from *X. tatei* and probably represents an unnamed forerunner of that species (see below).

It is probable that *X. tatei* evolved from the Oligocene type represented by the Bird Rock Cliffs specimen and similarly *X. peroniana peroniana* may have had a common ancestry with *X. tatei*. There is, however, little evidence available to support this view, other than their general morphological similarity and geographical proximity. In fact, the youngest specimens of *X. tatei* are thin-shelled and widely umbilicate and consequently quite dissimilar to *X. peroniana*. This umbilicate form is represented by a few fragmentary examples (from Murgheboluc) but appears to be very similar to *X. tatei* in other features. The umbilicus in the specimens occupies approximately ¼ of the total diameter of the base.

The shell of *X. tatei* is most like that of *X. japonica* Kuroda & Habe and it is possible that these two species had a common ancestry, although this similarity is, again, possibly superficial and the case is not strengthened by the prominent umbilicus seen in the Murgheboluc specimens.

\*FL = National Museum of Victoria fossil locality number



The protoconch of *X. tatei* is multispiral (Fig. 13b) and typical of the majority of other species in the genus but differs considerably from the other southern Australian species *X. flindersi*.

### Discussion on Additional Records of Australian Tertiary *Xenophora*

A specimen from the Miocene of South Australia (Morgan Limestone, River Murray cliffs, 0.4 km above Morgan (lowest bed); NMV, P13162) is much larger than *X. flindersi ludbrookae* (101 mm maximum diameter of mould). This specimen probably represents the forerunner of *X. flindersi* and, because of its size and the extreme coarseness of the agglutination scars (Fig. 19 i-k) is probably not closely related to *X. tatei*, the common Miocene species of Victoria. Another specimen (Fig. 19 f-h) presumed to be conspecific with the Morgan Limestone specimen, is a juvenile from Cadell Marl, River Murray cliff, 6.4 km below Morgan (Miocene, Balcombian) (NMV, P48589). This shell has a multispiral protoconch but lacks the conspicuous radial striae on the dorsal surface characteristic of *X. tatei* and has numerous small sand grains agglutinated on its surface between the larger scars. A single featureless mould (74.5 mm maximum diameter) and a fragmentary mould are known from the Nullarbor Limestone (Miocene) (WAM, 69.1521 and W.A. Geol. Surv. F6751).

A single well-preserved shell from the Upper Oligocene of the Jan Juc Formation, Bird Rock Cliffs, Torquay, Victoria (NMV, P13178) is similar to *X. flindersi ludbrookae* in size (67.2 mm maximum diameter, 45 mm in height) but has coarser radial lamellae on the base and a more conspicuous umbilical depression (Fig. 18 a-c). There is no trace of any spiral or subspiral sculpture on the base and the dorsal surface is similar, being more heavily agglutinated than in *X. tatei*, but lacks conspicuous arenaceous agglutination, although traces of this seem to be present. The conspicuous radial striae on the dorsum seen in *X. tatei* are relatively well developed. It is suggested above that this specimen has some similarity with *X. pallidula*.

The oldest known Tertiary *Xenophora* from Australia is a single broken specimen from the Upper Eocene (27 km from Walpole, along Thomson road, S.W. Australia, WAM. 67.180). It is a typical member of the *conchyliophora* group, being strongly agglutinated, but the surface features are worn and the base is broken away. The umbilicus is narrow but no other details can be discerned.

In an attempt to interpret the rather meagre data available it appears that a *Xenophora* of the *conchyliophora* group reached south west Australia (and New Zealand) in the mid to late Eocene. By the late Oligocene the genus had spread to the Otway Basin of Victoria (there is no record of *Xenophora* in the relatively rich Upper Eocene faunas of Victoria and South Australia) and by the Miocene occurred in the Eucla, Murray and Otway Basins. At least two species existed in the Miocene, a large (unnamed) species in the Murray Basin (possibly conspecific with the Eucla Basin species) and a smaller species in the Otway Basin (*X. tatei*). By the Pliocene *X. tatei* appears to have become extinct but *Xenophora* persisted in the Eucla Basin to give rise to *X. flindersi ludbrookae* and eventually, *X. flindersi flindersi*.

None of the other Australian fossil *Xenophora* are named herein because the available material is considered to be inadequate for proper description and interpretation.

### *Xenophora* sp.

Fig. 18 g-i.

**Shell:** Of moderate size, with medium spire (spire angle  $74^{\circ}$ – $91^{\circ}$ ), base concave, whorls strongly convex. Peripheral flange with about 10 agglutination scars on body whorl in largest specimen. Shoulder of last two whorls with only small, weak scars. All material internal moulds (Fig. 18 g-i).

#### Dimensions:

	height	diameter
Figured specimen	36.5 mm	49.5 mm
Largest specimen	50 (estimated)	57.8



**Material examined:** Maastrichtian (Upper Cretaceous): Miria Marl, N.W. Carnarvon Basin, Western Australia (4 specimens, all Bureau of Mineral Resources, Canberra, stations SK5 22 (2 specimens), B7c (1 specimen (figured)), B30s (1 specimen)).

**Remarks:** These specimens are the first of the genus known from the Cretaceous of Australasia. Unfortunately they are moulds, although the size and shape and the pattern of the agglutination scars indicate that this species was probably a member of the *conchyliophora* group. It closely resembles illustrations of *X. onusta* (Nilsson) which has been recorded from the Cretaceous (Upper Senonian and Maastrichtian) of E. Madagascar (Malagasy Republic) (Cottreau, 1922; Basse, 1931). Similar specimens have been recorded from the Upper Cretaceous of Europe (the type locality of *X. onusta* is Germany), Egypt, Brazil and the U.S.A. (the latter as *X. leprosa* (Morton) and *umbilicata* (Tuomey)).

***Xenophora (Xenophora) peroniana peroniana*** (Iredale, 1929).

Figs 8c, 14i, 16, 20d, 21d-l, 34.

*Xenophora tatei*. — Hedley, 1903: 357 (*non* Harris, 1897).

*Xenophora* sp. Allan, 1927: 57, text fig.

*Onustus peronianus* Iredale, 1929: 172.

*Xenophora corrugata*. — Ripplingale & McMichael, 1961: 51, pl. 4, fig. 21; Cernohorsky, 1972: 89 (in part), pl. 23, fig. 2 (*non* Reeve, 1842).

*Xenophora peroniana*. — Macpherson & Gabriel, 1962: 133, fig. 157.

**Shell:** Moderately elevated (spire angle  $70^{\circ}$ – $94^{\circ}$ ), peripheral flange narrow, about 12-13% of total width of base, usually set off at an angle to rest of base. Umbilicus closed in adults, narrowly open in juveniles. Row of foreign objects very prominent, obscuring more than 50% of dorsal surface. Whorls convex, sculptured dorsally with fine opisthocline riblets and very irregular rugae, the most prominent opisthocline and others prosocline (following the fine growth lines), resulting in an irregularly "warty" surface. Base slightly concave to almost flat, sculptured with fine, irregular, subspiral (oblique) striae which run at right angles to strongly curved, fairly distinct to weakly lamellate growth lines. Lower lip of aperture somewhat thickened in mature specimens, often with a distinct internal thickening in middle of lip and usually with a weakly sinuate edge. Colour yellowish-white dorsally, base yellowish-white with collabral lines of chocolate brown. Callus white, columella white, but with a brown blotch around umbilical region in many specimens (Figs 20d, 21d-l).

**Dimensions:**

	height	diameter
Lectotype	30.5 mm	46.6 mm
Figured specimens		
Off Moreton Bay, S. Queensland (AMS)	33.12	46.7
Off Fraser Is., S. Queensland (AMS)	29.05	40
	24	31.56
Large specimen. Off Bateman's Bay, New South Wales (AMS)	41.1	54.1

**Operculum:** Suboval to subrectangular, nucleus displaced to about left  $\frac{1}{3}$  although often appears to be midlateral if worn. Growing edge strongly convex, sides convex to angular. External surface smooth except for weak concentric growth lines; central area broad, slightly thickened, traceable through free surface as a broad, slightly thickened zone. Free area with conspicuous, closely spaced, concentric lamellae.

**Radula:** Central teeth with rather narrow base, median cusp large, triangular, with 3 small lateral cusps on each side. Lateral teeth rectangular, with small, sharp cusp. Marginal and lateral teeth sometimes with very slightly dentate cutting edges (Fig. 8c).

**Anatomy:** Similar to *X. neozelanica*; penis long and slender, similar to that of *X. cerea* (Fig. 14i). Salivary glands large, subequal. Material examined: S.E. of Broken Bay, New South Wales, 139-146 m (AMS) (2 males, 2 females); N.E. of Woolgoolga, N.S.W., 165 m (2 males, 3 females).

**Location of type and type locality:** Lectotype (here chosen), AMS (C. 104143) and 4 paralectotypes (C. 74844); trawled off Botany Bay, New South Wales, Australia, 91-128 m (Fig. 21d-f), 2 paralectotypes, off Port Kembla, 115-132 m (AMS, C. 16319).

**Fossil records:** None known.

**Other material examined:** *Australia: Victoria:* Off Lakes Entrance (SAM, NMV), 110 m (NMV). N. of Deal Island, Bass Strait, 91 m (NMV). *New South Wales:* Off Eden, Twofold Bay, 73-183 m (AMS). Off Tathra, Bega, 146 m (AMS). N.E. of Montague Is., 110-128 m, 164 m (AMS). Off Burrewarra Point, Bateman's Bay, 91 m (AMS). Off Burrill Lake, Ulladulla (AMS). Off Jervis Bay, 64-73 m (AMS). Off Shoalhaven, Nowra, 73-110 m (AMS). Off Wollongong-Port Kembla, 115-137 m, 183 m (AMS). Off Stanwell Park, 91 m (AMS). Off Wattamolla, Royal National Park, 64-73 m, 110 m (AMS). Off Sydney area, 60-457 m (several lots) (AMS). E. of Tuggerah, 164-183 m (AMS). Off Port Stephens (AMS), 55 m (ANSP). Off Cape Hawke, 82 m (AMS). 24 km S. E. of Forster, 100 m (AMS). 6 km off Tuncurry, 36 m (AMS). Off Manning River, 82-91 m (AMS). N.E. of Woolgoolga, 165 m (AMS). *Queensland:* E. of Moreton Bay, 75-80 m, 115-175 m (AMS). N. E. of Cape Moreton, Moreton Is., 115-137 m, 183 m (AMS). Off Caloundra, 73 m, 128 m, 183 m (AMS). E. S. E. of Noosa Heads, 37 m, 128 m (AMS). Wide Bay (AMS). Off S. end of Fraser Is., 201-219 m (AMS). Off Bundaberg (AMS). Off North Reef, in Capricorn Channel, 134 m (AMS). *W. Tasman Sea:* Taupo Gyot, E. of Newcastle, 154-164 m (AMS).

**Distribution:** Bass Strait, Victoria, to Capricorn Channel southern Queensland, eastern Australia, on the continental shelf and upper continental slope and on Taupo Gyot, W. Tasman Sea (37-457 m) (Fig. 34).

**Remarks:** Iredale (1929) introduced this name without designating a type, or giving a description or dimensions. He did, however, differentiate his species from *X. neozelanica* stating that "The Australian shells do not reach the size of the examples from New Zealand and are comparatively broader and less elate" and thus the name is here considered to be validly introduced. He mentions 3 lots of material, all of which could be considered syntypes; viz:— (1) specimens recorded as *X. tatei* by Hedley from off Port Kembla, (2) a "large series collected by Howell" and (3) specimens figured by Allan (1927). He relates that Howell's specimens have "shown that though the Recent shell is certainly separable from the fossil it is scarcely distinguishable from the Neozelanic species". As Howell's material was probably the main series Iredale had in hand when differentiating the new taxon, and because the whereabouts of Allan's figured material is not known, Howell's specimens are taken to be the series which Iredale based his description on. The label of the one large lot collected by Howell is in Iredale's hand but the name *X. peroniana* does not appear on it, nor is there any other indication that it is type material. This state of affairs is not, however, uncommon with the types on which Iredale based his names. A specimen from the Howell series has been designated as a lectotype above (Fig. 21d-f).

The shell of this species differs from that of other Recent *Xenophora* in its medium size, the thickening in the middle of the lower apertural lip (more strongly developed in the new subspecies described below) and by the rather flat, rather weakly sculptured base lacking any umbilical depression in adults. The shells of *X. cerea* and *X. conchyliophora* are similar in size and dorsal features to *X. peroniana*, but differ in basal characters. *Xenophora cerea* differs from *X. peroniana* in having a more convex base with a weak to moderate umbilical depression and all specimens have strong radial lamellae with weaker, rather flat (but distinct) spiral lirae, which are often broken up to give the outer part of the base a pustulose appearance. *Xenophora conchyliophora* has a similarly shaped base to that of *X. cerea*, but also differs from *X. peroniana* in the much weaker sculpture which consists of weak to moderate threads or growth lines, the weak spiral threads usually very irregular.

Another similar species is *X. tenuis* Fulton but that species has a thinner shell, strongly stepped whorls, and a very finely sculptured base which lacks any radial coloration. The base of *X. tenuis* is flatter than in *X. peroniana*, the edge of the lower lip is evenly concave and there is no internal thickening.

A few specimens of *X. peroniana peroniana* from southern Queensland resemble *X. cerea* in having a heavily sculptured base, the radial lamellae being sharp and dark brown (Fig. 20d). It is possible that a zone of interbreeding between *X. cerea* and *X. peroniana* exists but it is more probable that the similarity is coincidental. Similar specimens of *X. cerea* occur in southern Japan at the northern limit of its range (Fig. 20g). There is some evidence to suggest that, where the ranges of *X. cerea* and *X. peroniana peroniana* overlap in southern Queensland, *X. cerea* is found in shallower water on the continental shelf than *X. peroniana peroniana* which is typically found on the outer edge of the continental shelf and the upper continental slope.

*Xenophora peroniana* was referred to *X. tatei* by Hedley (1903) but the Recent species differs in its more flattened and more coarsely sculptured base, the thickened lower (basal) lip, and the lack of an umbilical depression in adults.

This species and the following, *X. neozelanica*, are apparently very closely related and probably shared a common origin. They are contrasted under *X. neozelanica*.

***Xenophora (Xenophora) peroniana kondoi* n. subsp.**

Figs 8d, 21m-o, 34.

*Xenophora peroniana*. — Quirk & Wolfe, 1974: 8; Kay, 1979: 183, fig. 63 k-m (*non* Iredale, 1929).

**Shell:** Similar to *X. peroniana peroniana* but with a more strongly concave base which bears crisper sculpture. Dorsal surface as in *X. peroniana peroniana*. Base merges with peripheral flange which is not set off at an angle as in *X. peroniana peroniana* because of its greater concavity. Basal sculpture of distinct collabral growth lines, distinctly lamellate near centre, crossed by spiral striae (becoming subspiral near periphery), rendered gemmate at points of intersection; relatively stronger in juvenile specimens than in juveniles of *X. peroniana peroniana*. Inner lip somewhat thickened internally in basal portion in adults, with a prominent low swelling within even subadult specimens; edge sinuate. Colour yellowish-white, apertural callus white. A few specimens have lower lip edged with brown and base with diffuse brown collabral streaks (Fig. 21m-o).

**Dimensions:**

	height	diameter
Holotype	30.5 mm	42.2 mm
Paratype	30.6	43.1

**Operculum:** Identical to that of *X. peroniana peroniana*.

**Radula:** Similar to that of *X. peroniana peroniana* but the central teeth have a slightly wider base and the lateral teeth are more triangular in shape (Fig. 8d).

**Anatomy:** Not known.

**Location of type and type locality:** Holotype, USNM (335064); U.S. Fisheries Commission Station 3810, 97-386 m, S. coast of Oahu Island, in fine coral sand, with 12 paratypes (Fig. 21m-o).

**Fossil records:** None known.

**Other material examined:** *Hawaiian Islands: Laysan Island:* 238-271 m (USNM). *Oahu:* 329-411 m (DMNH). Off Waikiki Beach, Honolulu (BPBM). Off Sand Island, Honolulu (BPBM). Keehi Lagoon, Honolulu (BPBM). Off Fort Kamehameha, Honolulu (BPBM). Off Ewa Beach, Mamala Bay (BPBM), 256 m (DMNH). S. coast Oahu, 334-483 m (USNM).

*Molokai*: Molokai Channel, 213 m (G. Mallory coll.). S. coast, 128-181 m, 233-238 m, 168-388 m (USNM). *Maui*: N. coast Maui, 174-288 m, 278-279 m (USNM). N. E. coast Maui, 181-193 m (USNM).

**Distribution:** Hawaiian Islands; 120-450 m (Fig. 34).

**Remarks:** This subspecies appears to be restricted to the Hawaiian Islands. Although widely geographically separated from *X. peroniana peroniana*, the differences in the two forms are slight and are considered to be of subspecific value only. This is especially the case when specimens from the northern end of the range of *X. peroniana peroniana* are contrasted with *X. peroniana kondoi*. Specimens from the Capricorn Channel, Queensland are almost indistinguishable from Hawaiian shells, the similarity being enhanced by their yellowish-white bases and white apertural margins. The same remarks apply for the separation of the new subspecies from allied species as for the typical subspecies.

The lack of additional records of *X. peroniana* from areas between eastern Australia and Hawaii may be a collecting artifact but other examples of disjunct distribution between these two areas are known (e.g. *Bursa latitudo latitudo* Garrard, 1961 and *B. latitudo wolfei* Beu, 1980).

The new subspecies is named for Dr. Y. Kondo, recently retired from the Bernice P. Bishop Museum, Honolulu, as a small tribute to his many contributions to malacology.

***Xenophora (Xenophora) neozelanica neozelanica* Suter, 1908.**

Figs 2, 3, 8a, 13a, 15, 20h, 34.

*Xenophora neozelanica* Suter, 1908: 346, text fig. (radula), pl. 26, figs 1, 2; Finlay, 1927: 391; Beu, 1977: 230, figs 1, 3, 4, 6, 9-12.

*Xenophora corrugata*. — Suter, 1913: 278, pl. 15, fig. 13; Morton, 1958: 89 (*non* Reeve, 1842). (See Beu, 1977 for detailed synonymy).

**Shell:** Very similar to *X. peroniana* in most features but with relatively coarser basal sculpture and reaching a much larger adult size (up to about 1½ times maximum adult size of *X. peroniana*). Spire angle 62°–84°; umbilicus closed in adults and subadults, narrowly open in juveniles; much of dorsal surface (40-70%) obscured by attached foreign bodies; a few sand grains and small objects attached to free surface. Apertural glaze brown to colourless; base with conspicuous brown collabral markings (Fig. 20h).

**Dimensions:**

	height	diameter
Holotype (from original description)	35 mm	68 mm
Beu (1977: 231) gives the range as:		
low spired specimen	45.3	83.6
normal specimen	41.0	70.0
normal specimen	40.8	59.3
tallest specimen seen	50.7	61.2

**Operculum:** Subrectangular, brown, with coarse to weak concentric growth lines on outer surface; growing edge moderately convex; nucleus appears to be mid-lateral. Central area broad, weakly discernible through free surface as a broad, slightly thickened zone. Free surface thickened, with conspicuous concentric lamellae.

**Radula:** Central teeth with about 4 small cusps on either side of median cusp; lateral teeth triangular, cusp small; marginal teeth smooth (Fig. 8a). Also figured by Suter (1908: 346, figure in text).

**Animal:** "Exposed parts are cream white in colour, tinted or delicately lined with orange or reddish brown" (Morton, 1958).

**Anatomy:** Penis rather short, broad with a short projection near distal end on opposite side to sperm groove (Fig. 2). See general anatomical account for other details (Figs 2, 15). Material



examined: Trawled, Colville Channel, Hauraki Gulf, New Zealand (AMS) (3 males and 1 female).

**Location of type and type locality:** Holotype (TM 857) and paratype (TM 858), New Zealand Geological Survey, Lower Hutt; 16 km W. of Cuvier Island, 59 m.

**Fossil records:** Opoitian (early-mid Pliocene) to Waipipian (late Pliocene) of Hawkes Bay, North Island (Beu, 1977).

**Material examined:** Many specimens in NMNZ and AMS.

**Distribution:** Northern North Island, New Zealand, as far south as eastern Bay of Plenty on the east coast and Kapiti Island on the west coast (Beu, 1977); on the continental shelf (Fig. 34).

**Remarks:** Beu (1977) has discussed the fossil history of *Xenophora* in New Zealand. One species (*X. prognata* Finlay, 1926) ranges from the Upper Eocene to the Lower Miocene (and possibly to the Middle Miocene) and was probably ancestral to *X. flemingi* Beu, 1977 which ranges from the Lower Miocene to the Middle Miocene and apparently lived in deeper water. An unusual feature of *X. flemingi* is the very narrow zone of agglutination, most of the dorsal surface being naked. The three New Zealand species are non-umbilicate when adult or subadult, with moderate to weak basal sculpture and with a narrow peripheral flange. In the writer's opinion *X. prognata* would be more usefully regarded as chrono-subspecies of *neozelanica* as the two forms are clearly very similar morphologically and probably form a continuous lineage.

Although the shell of *X. neozelanica* closely resembles that of *X. cerea* and *X. peroniana* they are here regarded as separate species on the basis of the long, and presumably separate lineage of the New Zealand form. There are also some apparent, although minor, anatomical differences (particularly in the shape of the penis) between the three species. The completely closed umbilicus and lack of an umbilical depression in the shells of the three New Zealand taxa are also features which distinguish them from *X. cerea* and *X. tatei*. Some shells of *X. neozelanica* have 2 spiral rows of small, rather indistinct brown blotches on the base, as seen in some specimens of *X. conchyliophora*, but not observed in most other species. This colour pattern, together with the frequently dark brown coloration of the basal callus and a general similarity in other shell features shared by both species, suggests that *X. neozelanica* and *X. conchyliophora* are possibly closely related and, as suggested above, may have had a common ancestry in the Eocene. There is little doubt that the closest living relative to *X. neozelanica* is *X. peroniana*, both species sharing a similar shell, operculum and radula and being generally anatomically very similar.

***Xenophora (Xenophora) neozelanica kermadecensis* n. subsp.**

Figs 8b, 14b, 24a-f, 34.

*Xenophora corrugata*. — Oliver, 1915: 524 (*non* Reeve, 1842).

*Xenophora neozelanica*. — Powell, 1958: 81 (*non* Suter, 1908).

*Xenophora cerea*. — Beu, 1977: 230 (*non* Reeve, 1845).

**Shell:** Moderately elevated (spire angle 80°–95°). Peripheral flange narrow, distinctly down-turned from base. Foreign objects large, obscuring nearly all of dorsal surface (more than 70%), a few scattered sand grains and other minute objects attached to exposed surface. Umbilicus closed; no umbilical depression in adult. Whorls moderately to strongly convex, subangled in centre of each whorl; dorsal sculpture of close, fine opisthocline riblets and heavy, very irregular folds crossed by weaker, very irregular prosocline folds and growth rugae, the result giving the free surface a "warty" appearance. Base (excluding peripheral flange) very lightly convex (almost flat), with strong, curved, raised growth lamellae which cross moderately strong, close spiral cords. Lower apertural lip thickened within when fully mature, sometimes forming a weak internal bulge in its middle section; columella thick and heavy. Colour white dorsally, columella white, basal callus colourless, or with orange-brown radial streaks, columella and lower apertural lip edged with brown; base yellowish-white, strongest axial lamellae dark reddish-brown (Fig. 24a-f).



**Dimensions:**

	height	diameter
Holotype	41 mm	58.1 mm
Figured paratype	42.8	54.2
Large specimen (Fig. 24e)	38	55

**Operculum:** Like that of *X. neozelanica neozelanica*.

**Radula:** Central teeth similar in shape to those of *X. neozelanica neozelanica* but with 3 lateral cusps and a relatively longer central cusp. Lateral teeth subrectangular, cusp moderate, sharp. Inner marginal teeth sometimes very finely serrate, outer marginal teeth smooth (Fig. 8b).

**Anatomy:** Like that of *X. neozelanica neozelanica*. Penis relatively longer and narrower than *X. neozelanica neozelanica*, with a small, very short projection a short distance behind distal end (Fig. 14b). Material examined: Paratypes (2 males).

**Location of type and type localities:** NMNZ, holotype (M.F. 30899), 46 paratypes (M.F. 22014), 2 paratypes AMS (C. 110194); off Hutchinson Bluff, Raoul Is., Kermadec Ids, 84-113 m, 24 August 1972, R.V. "Acheron" on rubble bottom (Fig. 24a-d).

**Fossil records:** None known.

**Other material examined:** *Kermadec Ids: Raoul Is:* (AMS). 274-219 m (NMNZ). Between Bells Flat and Hutchinson Bluff, 110-121 m; 110-165 m (NMNZ). Off Bells Flat, 219-165 m (NMNZ). Off N.W. end, 146-219 m (NMNZ). Off Fleetwood Bluff, 135 m (NMNZ). Off Smith Bluff, 69 m (NMNZ). *Nugent Is.:* 165-146 m (NMNZ). *Dayrell Is.:* 247-267 m (NMNZ).

**Distribution:** Kermadec Islands, north of New Zealand; 84-274 m.

**Remarks:** The Kermadec Islands *Xenophora* shares the shell characters of three closely related species, *X. peroniana*, *X. cerea*, and *X. neozelanica*. The shells of these three species differ only in minor respects but there are also a few significant differences in the operculum, radula and penis. The closest species morphologically and geographically is *X. neozelanica* and the Kermadec Islands population is here considered to be only subspecifically distinct from that species. The large amount of material available of the new subspecies is surprisingly consistent in shell characters.

The shell of this subspecies is closest to *X. cerea* in its basal sculpture but differs in having a less obvious umbilical depression and the spiral sculpture is not so noticeably pustulose. The lower apertural lip and columella are thicker than in *X. cerea* and the external opercular sculpture is simple, not lamellate. The shell of *X. peroniana peroniana* is similar in size, shape and colour to *X. neozelanica kermadecensis* but is of lighter build, has weaker basal sculpture (both radial and spiral elements being relatively finer) and has a thinner columella. There is also somewhat more of the dorsal surface exposed in *X. peroniana peroniana* and the primary dorsal sculpture is weaker. The shell of *X. neozelanica neozelanica* is larger, with relatively weaker basal sculpture; the radial rugae on the base being less obviously lamellate and the spiral sculpture finer and weaker. There is also relatively more of the dorsal surface exposed in most specimens of *X. neozelanica neozelanica* and the base is usually slightly concave whereas it is nearly flat in *X. neozelanica kermadecensis*. The penis of *X. neozelanica kermadecensis* differs from that of the typical subspecies in being longer and narrower, with a smaller subterminal accessory bulge. Both *X. cerea* and *X. peroniana peroniana* appear to lack this accessory structure.

There are a large number of endemic species of molluscs at the Kermadec Islands (Oliver, 1915) so that the differentiation of the local shallow water *Xenophora* is not particularly surprising.

**Xenophora (Xenophora) tenuis** Fulton, 1938.

Figs 21a-c, 34.

*Xenophora tenuis* Hirase, 1934: 57, pl.89, fig. 3 (*nom. nud.*); Fulton, 1938: 56, pl.3, fig. 5; Fulton, 1939: 236; Habe, 1953a: 177, figs 9, 10; Kira, 1962: 32, pl.15, fig. 6.

**Shell:** Moderately elevated (spire angle 92°). Peripheral flange narrow, down-turned from base. Foreign objects of medium size, about half of dorsal surface usually exposed (the lower half of each whorl). Umbilicus closed, no umbilical depression. Whorls strongly convex, subangled in centre of each whorl; dorsal sculpture of close, fine opisthocline riblets and heavy, irregular folds crossed at right angles by rather weak growth lines and a few prominent ridges. Base almost flat to lightly concave, with very weak collabral growth lines crossed by close, very fine, subspiral striae rendered minutely granular at points of intersection. Lower apertural lip simple, thin, regularly concave. Colour yellowish-white to white; paratype with two rows of small, very pale, yellowish-brown spots on base (Figs 21a-c).

**Dimensions:**

	height	diameter
Holotype	32 mm	43.5 mm
Tosa Bay (NSMT)	24.8	37.3

Operculum, radula and anatomy unknown.

**Location of type and type locality:** BMNH (1937.7.13.7-8) holotype and one paratype; Kii, Japan (Figs 21a-c).

**Fossil records:** None known.

**Other material examined:** *Japan* (USNM). Shiono-misaki (Kii), Wakayama Province, 146 m (MCZ, AMS, NMV). Tosa Bay Shikoku (USNM, NSMT), 137 m, 183 m (ANSP). Satsuma, Kyushu, 31-36 m (AMNH). *China Sea:* Okinawa, Ryukyu Islands (ANSP). "East China Sea" (NSMT). *Indian Ocean:* Salha de Malha Bank, Mauritius—Seychelles Ridge, 60-70 m (AMS).

**Distribution:** Southern Japan and probably the China Sea; one specimen from western Indian Ocean; 30-185 m (Fig. 34).

**Remarks:** The shell of this species is similar to those of both *X. peroniana* and *X. conchyliophora*, but is lighter in build. The main distinguishing features are the white, somewhat flattened to slightly concave, imperforate base with its very fine sculpture, and the distinctly stepped whorls with their lower half more-or-less free of attached foreign objects. *X. tenuis* does not appear to have any fossil record but may possibly share a common ancestry with *X. peroniana* which is the most similar species in shell features.

The Indian Ocean record is based on a unique specimen and, although the data associated with it is almost certainly reliable, additional records from the Indian Ocean should be obtained before its presence there can be fully confirmed. The specimen agrees in nearly every respect with Japanese material except that the base is a little more strongly concave and there is a weak thickening of the basal lip.

**Xenophora (Xenophora) granulosa** n. sp.

Figs 12c, 14h, 22a-f, 34.

**Shell:** Moderately elevated (spire angle 75°-90°), with narrow peripheral flange, rather solid, with convex whorls, umbilicus narrowly open in mature specimens. Foreign objects usually small, at least lower half of whorls usually exposed, and often up to about ¾ of dorsal surface exposed. Dorsal sculpture of coarse, wavy opisthocline rugae over which run fine, slightly more strongly opisthocline riblets. Base flat to slightly concave in median region, markedly depressed in umbilical region, with narrow umbilicus almost hidden by reflected inner lip in adult. Peripheral flange forms a narrow, wavy, down-turned rim at outer edge of base. Base sculptured with regular, rather fine collabral ribs crossed by subspiral striae, which are rendered

weakly gemmate at points of intersection with collabral sculpture. Aperture simple, basal lip very strongly concave, weakly and uniformly thickened in mature specimens. Colour yellowish-white to pale yellow brown dorsally, base white, sometimes with a zone of pale brownish-yellow spots just inside peripheral flange and around umbilical region. Holotype with uniformly white base (Fig. 22 a-f).

**Dimensions:**

	height	diameter
Holotype	32 mm	50 mm
Large paratype (from 290-310 m)	36.0	54.7
Largest specimen seen. Balicasag Is., Bohol, Philippines (G. Mallory Colln).	40	63

**Operculum:** Oval, thin, translucent, yellowish-brown to pale yellow, smooth externally except for weak radial growth lines and faint radial striae. Nucleus displaced to left of centre. Central area broad, with weak radial striae, visible through free surface.

**Radula:** Central teeth with 1-3 small cusps on each side of a triangular, sharp median cusp. Lateral teeth with a single broad cusp on inner side, rest of cutting edge simple. Marginal teeth with broad, hooked distal ends lacking cusps or denticles. Inner marginal teeth with basal plate-like projection (Fig. 12c).

**Anatomy:** Similar to that of *X. neozelanica* but with smaller, subequal salivary glands, the right placed more anteriorly, about half way along the left. Penis very long, slender, simple, with an open penial groove along its ventral side. Material examined: Holotype (male). 22°17'S, 167°13'E (1 male) (Fig. 14h).

**Location of type and type locality:** Holotype (NHMP) and 3 paratypes (1 damaged) (NHMP); 1 paratype (AMS, C. 116768) 22°17'S, 167°12'E, New Caledonia, 390 m, P. Bouchet, O.R.S.T.O.M. (Fig. 22 d-f).

**Localities of additional paratypes:** *New Caledonia:* 5 paratypes (NHMP) 22°19'N, 167°11'E, 290-310 m; 5 paratypes (NHMP) 22°17'S, 167°13'E, 400 m; 1 paratype same data as last (AMS, C. 116768).

**Fossil records:** None known.

**Other material examined:** *South China Sea.* 366 m (G. Mallory Colln) (1 specimen). *Philippines.* 14°N, 120°17.5'E, Mindoro Strait, 194-195 m (NHMP); Balicasag Is., Bohol, Philippines, 183 m (G. Mallory Colln) (1 specimen). *New Britain.* Talili Bay, Rabaul, 55-73 m (AMS) (1 subadult and 2 juvenile specimens). *Mauritius.* Off Port Louis, 245 m (ZMC).

**Distribution:** Mauritius, Indian Ocean, South China Sea to New Britain and New Caledonia in 55 to 400 m (Fig. 34).

**Remarks:** This species resembles *X. tenuis* in most features including the basal coloration and dorsal features. The base, however, is more strongly sculptured in the new species and has a distinct umbilicus in mature material. It is possible that *X. tenuis* and *X. granulosa* should be regarded as subspecies but until the animal of *X. tenuis* is known, close relationship cannot be firmly established.

There is a general similarity with *X. pallidula* but that species is easily distinguished by its usually weaker basal sculpture, much weaker dorsal sculpture and penial characters. The small amount of attached foreign material dorsally and the lack of radial colour markings on the base distinguishes *X. granulosa* from *X. peroniana* and *X. neozelanica*. Although there is a general similarity in penial characters between *X. peroniana peroniana*, *X. neozelanica* and *X. granulosa* the operculum of *X. granulosa* is thinner and more transparent than in the other two species.

**Xenophora (Xenophora) corrugata** (Reeve, 1842).

Figs 9d, 25a-c, 28f-h, 35.

*Phorus corrugatus* Reeve, 1842: 160, pl.214, fig. 5; Reeve, 1843a: 163; Reeve, 1843b: pl.3, fig. 6.*Xenophorus caperatus* Philippi, 1849: 100.*Xenophora corrugata*. — H. & A. Adams, 1854: 363; Philippi, 1855: 346, pl.48, fig. 1; Fischer, 1879a: 441, pl.8 (2 figures); Tryon, 1886: 159, pl.45, Figs 81, 82, Barnard, 1963: 68; Biggs, 1973: 363.*Xenophora caperata*. — Philippi, 1855: 349, pl.49, fig. 2; Biggs & Grantier, 1960: 388; Biggs, 1973: 363.? *Xenophora philippinarum*. — Paetel, 1887: 501 (*nomen nudum*).

**Shell:** Moderately elevated (spire angle 80°-94°), umbilicus closed in adult, open in immature specimens. Whorls convex, often subangled in middle of shoulder, concave at narrow peripheral flange. Foreign objects generally rather small leaving the centre part of the whorls more-or-less uncovered. Dorsal sculpture of fairly coarse, opisthocline, wavy riblets and prosocline broad axial folds and indistinct growth lines. Base slightly convex to very slightly concave. Strong spiral ribs (5-7) on inner half of base, subspiral lirae on outer half. Narrow, close collabral growth lamellae cross spiral sculpture, points of intersection nodulose. Colour pale yellowish-brown to yellowish-white, sometimes with a few pale brown spots or collabral streaks on base (Figs 25a-c, 28f-h).

**Dimensions:**

	height	diameter
Holotype of <i>P. corrugatus</i>	40.5 mm	62.0 mm
Large specimen (Zanzibar, BMNH)	50.0	81.5
Average specimen (Bahrain, Persian Gulf, ZMC) (figured)	30.7	45.0

**Operculum:** Suboval, with all sides convex, rather thin, pale brown; nucleus displaced slightly to left; smooth externally except for weak concentric growth lines. Central area broad, sometimes yellowish.

**Radula:** Central teeth subtriangular, median cusp broad, triangular, with 3 small cusps on either side. Lateral teeth rather small, with simple cutting edge and a prominent basal projection. Marginal teeth long, smooth, inner marginal teeth with small accessory plate (Fig. 9d).

**Anatomy:** Not known.

**Location of types and type localities:** *P. corrugatus*. BMNH, holotype (1950.8.28.18); described from unknown locality, H. Cuming Colln. Type locality here designated as Zanzibar, East Africa (Fig. 25a-c). *X. caperatus*. Location of type unknown; described from unknown locality.

**Fossil records:** None known. All records of fossil *X. corrugata* appear to be based on misidentifications.

**Other material examined:** *South Africa:* "Morewood Cove", 49 m (IRNSB). N.E. of Durban, 38 m, 124-128 m (USNM). Natal (DMNH). Tongaat, Natal Province (DMNH). Umhlanga Rocks, N. coast of Natal (AMS). *Mozambique:* 129 km S.S.W. of Ponta da Barra Falsa (USNM). Mocambique City (ANSP). *Zanzibar Island:* (AMS, BMNH). 2 km W.N.W. of Zanzibar, 11-15 m (ANSP). *Somali Republic:* 14km N. of Mogadiscio (ANSP). *Gulf of Oman:* 40 km E. of Daba, 79 m (MCZ). 25°54'N, 56°46'E, 95 m (RNHL). *Persian Gulf:* 56 km E.N.E. of Al Fujayrah, 205 m (MCZ). *Trucial Coast:* 11-27 m (several lots) (RNHL). E. of Qatar, 22 m, 26 m, 31 m (RNHL). Bahrain, 15-29 m (several lots) (RNHL), 23 m, 33 m (ZMC). Ras Tannurah, Bahrain (ANSP, FMC, DMNH). Tarut Bay, Arabia (ANSP, DMNH, AMS). 116 km E.N.E. of Bahrain Lightship, 23 m (AMS). 27°48'N, 50°12'E, 53 m (RNHL). 27°29'N, 49°36'E, 17 m (RNHL). 27°58'N, 49°41'E, 20 m, 23 m (RNHL). 28°20'N, 48°56'E, 20 m

(RNHL). 28°32'N, 49°20'E, 35 m (RNHL). West of Khark Is., 13 m, 29 m (ZMC). Kuwait (USNM). Khor-al-Basam, near Abu Dhabi, Trucial States (BMNH) (recorded by Biggs, 1973). Eastern Khor, Trucial States (BMNH) (recorded by Biggs, 1973 as *X. caperata*). *Pakistan*: Karachi (USNM). *Sri Lanka*: (AMS, BMNH). Gulf of Mannar, 9 m (DMNH). 19 km N. of Trincomalee (FMC). Off S. coast, 62 m (BMNH). *India*: Madras (BMNH). Tuticornin, Madras, dredged (BMNH). Tranquebar, Madras (ZMC).

**Other records:** *South Africa*: From off Umtwalumi (south of Durban) to Umuoti (north of Durban) and off Amatikulu River, Zululand, 22-46 fathoms (40-84 m). 29°58'S, 31°02'E, 49 m (all from Barnard, 1963). *Gulf of Oman*: Kuh-i-Mubarak (Biggs & Grantier, 1960).

**Distribution:** S.E. India and Sri Lanka, Pakistan, Persian Gulf and tropical east Africa, 0-200 m, mostly in rather shallow water (Fig. 35).

**Remarks:** The shell of this species differs from those of *X. cerea*, *X. conchyliophora*, *X. neozelanica*, *X. flindersi*, *X. granulosa*, *X. tenuis* and *X. peroniana* in having weaker axial folds on the dorsum which are prosocline, not opisthocline in orientation, and in having a more regular arrangement of generally smaller attached objects, revealing more of the surface of the shell. The flat base is also distinctive with its strong spiral ornament and closed umbilicus (when mature). The shell of *X. mekranensis konoii* is similar in basal sculpture but differs markedly in dorsal sculpture and in being umbilicate to sub-umbilicate when mature. The operculum of *X. corrugata* is similar to those of *X. peroniana* and *X. neozelanica*, those species differing in their lack of any distinct external opercular sculpture from the opercula of *X. mekranensis konoii* and *X. cerea*, both the latter being sculptured with distinct, concentric lamellae.

This species name has been wrongly applied to the Indo-Pacific species *X. cerea* by most authors. Examination of Reeve's type material has shown that the name *X. corrugata* must be used for the Indian Ocean species previously known as *X. caperata* Philippi. Two large specimens from Zanzibar in the Cuming collection (BMNH) closely resemble the type of *X. corrugata* and possibly the holotype came from this locality, which is here designated as the type locality of the species.

*Xenophora caperata* was originally described from unknown locality but Philippi (1855) redescribed and figured (for the first time) his species and noted that it was found on the east coast of Africa. It is conspecific with Reeve's *corrugata* as far as can be judged from Philippi's excellent figures.

The fossil record of *X. corrugata* of Nuttall & Sealy (1961) is based on a specimen which appears to be *X. chinensis*.

*Xenophora philippinarum* "A. Adams, Philippi" was introduced by Paetel (1887) in a list of the specimens in his collection. This name does not appear to have been published elsewhere and must be regarded as a *nomen nudum*. A single specimen labelled *Xenophora (Phorus) philippinarum* Adams from "the Philippines" was located in the EBM (probably ex Paetel) and this appears to be a juvenile specimen of *X. corrugata*.

A name sometimes encountered on specimens and in the literature (St. Jean, 1972: 42; Travis, 1974: 143; Mallory, 1977: 3) is *X. spirata*. This name appears never to have been properly introduced and must be regarded as a *nomen nudum*. Mrs St. Jean (*in litt.*, 1978) has provided the writer with a photograph of "*spirata*" which proves to be *X. corrugata*.

### ***Xenophora (Xenophora) mekranensis konoii* Habe, 1953.**

Figs 7d, 20e, 25d-i, 35.

*Xenophora caperata*. — Schepman, 1909: 203 (*non* Philippi, 1851).

*Xenophora konoii* Habe, 1953a: 176, text figs 3-5; Habe, 1964: 57, pl.16, fig. 5.

*Xenophora konai* (sic!). — Ladd, 1977, pl.22, figs 1-3.

**Shell:** With rather tall to moderate spire (spire angle 62°-80°), of light build, with narrow peripheral flange set off at distinct angle from rest of base. Umbilicus narrow, almost closed by narrowly reflected columellar callus in mature specimens, open in sub-adults and juveniles.



Attached objects tend to be well spaced but large (often rather long), usually about 50% of dorsal surface visible between objects. Whorls strongly convex, sculptured with close, rather sharp, fine opisthocline riblets and heavy opisthocline folds crossed at right angles by very fine, regular growth lines which render the opisthocline riblets finely scabrose. Base slightly convex, with about 4, usually strong, spiral cords on inner half of base, innermost bordering umbilicus. Outer half of base with irregular, subspiral sculpture broken into close, disjointed pustules by fine, radial growth lamellae. Umbilicus with a few weak spiral cords and prominent radial lamellae. Colour white dorsally, creamy white to white ventrally (Figs 20e, 25d-i).

#### Dimensions:

	height	diameter
Holotype	52.7 mm	54.8 mm
Figured specimens		
W. of Gantheaume Bay, Western Australia (WAM)	31.7	37.8
Off Sorsogon, Luzon Is., Philippine Ids (AMS)	37.5	47.2

**Operculum:** Suboval, yellowish-brown, rather thin, with closely set lamellae on outer surface; nucleus markedly displaced to left (left  $\frac{1}{4}$ ), growing edge convex, sides nearly straight. Concentric lamellae of outer surface conspicuously visible through attachment scar; central area displaced to left half of attachment scar, very slightly thickened. Free surface with weak, very closely spaced lamellae.

**Radula:** Central teeth with 3 short cusps on either side of median cusp. Lateral teeth with a blunt cusp, inner ventral edge projects beyond cusp; marginal teeth smooth (Fig. 7d).

**Anatomy:** Similar to *X. neozelanica*; salivary glands large, subequal in size. Material examined: W. of Gantheaume Bay, Western Australia, 27°35'S, 115°14'E, 146 m (WAM) (1 immature male; penis represented by a very small papilla).

**Location of type and type locality:** NSMT, holotype, 45262; Bungo Channel, between Kyushu and Shikoku (Fig. 25d-f).

**Fossil material examined:** Pleistocene: Santo, New Hebrides (USGS) (recorded by Ladd, 1977).

**Other material examined:** *Indian Ocean:* Mauritius, 245 m (ZMC). Off S. coast, Sri Lanka, 62 m (BMNH). 19 km N.W. of Port Blair, S. Andaman Is., 90 m (ANSP). *Thailand:* 9°10'N, 98°06'E, 30 m (ZMC). 8°46'N, 97°46'E (USNM). *China Sea:* (BMNH); Hong Kong (BMNH). *Philippines:* Off Sorsogon, S. Luzon (AMS). Bohol Strait, 95 m, 110 m (WAM). Jolo Is., Sulu Archipelago, 38 m (ZMC). Sirun Is., Sulu Archipelago, 38 m (USNM). *Indonesia:* Ternate, Halmahera, 31-42 m (WAM). Butung Strait, Sulawesi (Celebes), 68 m (USNM). Kai Ketjil, Kepulauan Kai, 27-36 m (WAM). Banda Elat, W. coast Kai Besar, Kepulauan Kai, 49-55 m (WAM). W. of Babi Is., Wokam, Kepulauan Aru, 110-238 m (WAM). Maikoor, Kepulauan Aru, 110-113 m (WAM). Between Wowoni and Buton Ids 75-94 m (ZMA). 9°00.3'S, 126°24.5'E, Timor Sea, 112 m (ZMA). *Australia: Western Australia:* W. of Shoal Point, 292 m (WAM). W. of Gantheaume Bay, 146 m (WAM). N.W. of Carnarvon, 138 m (WAM). W. of Point Cloates, 133 m (WAM). Between Shark Bay and Onslow (WAM). N.W. of Anchor Is., off Onslow, 119 m (WAM). *Queensland:* Off Cape Cleveland, Townsville, 29 m (WAM).

**Distribution:** Indian Ocean (Mauritius, Sri Lanka, Andaman Ids), central Indo-Pacific, north-west Australia and possibly Queensland; 27-292 m (Fig. 35). The single record from Queensland needs to be confirmed.

**Remarks:** The Pliocene species *X. mekranensis* (Newton, 1905) from the Mekran Coast is very similar to *X. konoii* and is almost certainly conspecific judging from the original material in the BMNH. Unfortunately, the specimens are mostly in poor condition, all being extracted from nodules, so that minor differences between the two forms are difficult to establish with certainty.

Consequently the name based on the Recent form is here tentatively retained and given subspecific status.

This species is sympatric with *X. cerea* (Reeve) although the two species do not appear to be collected together often. Their shells are readily distinguished by the taller spire, the more convex whorls and the stronger basal spirals of *X. mekranensis konoii*. The shell of *X. corrugata* (Reeve) has a similar base to that of *X. mekranensis konoii* but can be distinguished by its shorter spire and its more closely arranged and generally smaller agglutinated objects. The lower half of its whorls are usually free but in *X. mekranensis konoii* it is the spaces between the objects that reveal the majority of the dorsal surface. *Xenophora corrugata* also has much weaker dorsal sculpture and a completely closed umbilicus in the adult. *Xenophora mekranensis konoii* and *X. cerea* are, however, similar in opercular and radular characters and appear to be more closely related to one another than to *X. peroniana*, *X. corrugata* or *X. neozelanica*.

***Xenophora (Xenophora) pallidula* (Reeve, 1842).**

Figs 6f, g, 9a, b, 12d, 14f, g, 20a-c, 28i-k, 36.

*Phorus pallidulus* Reeve, 1842: 160, pl. 214, fig. 4; Reeve, 1843a: 162; Reeve, 1843b: pl. 1, fig. 4.

*Xenophora pallidula*. — H. & A. Adams, 1854: 363; Philippi, 1855: 347, pl. 48, fig. 2; Lischke, 1874: 56, pl. 3, figs 1-3; Fischer, 1879a: 444, pl. 54; Tryon, 1886: 160, pl. 44, fig. 79; Studer, 1889: 266; Sowerby, 1894: 38; Uchiyama, 1902: 2, pl. 22, figs 4-6; Schepman, 1909: 203; Thiele, 1925: 106, pl. 46, fig. 21; Habe, 1953a: 173, figs 12, 13; Kira, 1962: 32, pl. 15, fig. 5b,c; Barnard, 1963: 69; Kuroda, Habe and Oyama, 1971: 139, 91, pl. 21, fig. 1.

**Shell:** Large, of rather light build, with moderate to high spire (spire angle  $65^{\circ}$ - $92^{\circ}$ ), with lightly to moderately convex whorls. Protoconch of about  $4\frac{1}{2}$  whorls, dark brown, with axial ribs and weak spiral striae (Fig. 12d). Umbilicus small, sometimes closed in adult but usually only partially covered by inner lip. Attachment of large foreign objects obscures much of shell surface although usually about  $\frac{1}{3}$  or more of dorsal surface unaffected. Dorsal sculpture of distinct, close, wavy, opisthocline riblets which cross irregular prosocline folds and growth lines. Base nearly flat to slightly concave, weakly convex in most juveniles; peripheral flange narrow, produced downwards from rest of base. Base sculptured with fine to moderate subspiral, usually wavy, striae which cross rather distinct, curved collabral growth lines. Colour white to pale yellowish-white (Figs 20a-c).

**Dimensions:**

	height	diameter
Holotype	51.0 mm.	71.7 mm.
Large specimen, Batangas Bay Philippines (AMS)	51.0	87.7
New South Wales (AMS)	45.0	71.0
Tall-spired specimen (Andaman Islands, AMS)	58.7	69.4

**Operculum:** Suboval, brown, somewhat thickened, opaque, with rugose to inconspicuous growth lamellae or striae on outer surface. Nucleus mid-lateral, all edges convex. Central area conspicuous, median, broad and yellowish in colour; free surface with dense concentric lamellae (Fig. 6f, g).

**Radula:** Central teeth subrectangular, with triangular median cusp of moderate size and about 4 small cusps on either side. Lateral teeth rather small, subrectangular, with simple cutting edge. Marginal teeth smooth, with small accessory plate on inner marginal teeth (Figs 9a, b). Figured previously by Thiele (1925: pl. 46, fig. 21).

**Anatomy:** Similar to *X. neozelanica*; salivary glands of moderate size, subequal; mantle edge with very small tentacles; sole of foot moderately well-developed, eyes small. Penis observed in mature and immature state: long, slightly tapering, with terminal papilla at distal end (Fig. 14f).

Immature specimen with short, broad proximal portion and narrow distal portion (Fig. 14g). Material examined: trawled off New South Wales, between Port Stephens and Hawkesbury River, 366-411 m (AMS) (1 submature male); S.E. of Crowdy Head, New South Wales, 402-548 m (AMS) (1 immature male); same locality, 366 m (AMS) (1 mature male); S. of Sugar Loaf Point, New South Wales, 457 m (AMS) (1 female); S.E. of Clarence River, New South Wales, 405 m (AMS) (1 female); Sagami Bay, Japan, 150-226 m (ZMC) (1 male).

**Locality of type and type locality:** BMNH, holotype (1950.8.28.17); coast of Japan, H. Cuming Colln. (Fig. 20a-c).

**Fossil material examined:** Several lots (in RGM) identified as *X. pallidula* (by Martin, 1905) from Java are small or broken specimens and their positive identification is impossible. One lot is *X. solarioides jezleri*, several are *X. cf. cerea* (see above) and only one specimen can be identified with reasonable certainty as *X. pallidula* (Figs 28i-k) and is from "Locality R", Tjkarang, Java (Miocene), RGM 11136, together with an unidentifiable fragment.

**Other fossil records:** Summarized by Wissema (1947) but all need to be confirmed.

**Other material examined:** *South and East Africa:* Capetown (MCZ). Durban, Natal, 329 m (BMNH), 54 m (AMNH). Zululand coast, Natal Province (ZMC), 183 m (USNM), 16-32 km E., 292-329 m (USNM, BMNH, RNHL, DMNH). Off Pemba Is., Tanzania, 329 m (BMNH). *Mauritius:* (BMNH). *Oman:* Off Oman, 21°50'N, 59°52'E, 1046 m (BMNH). *India:* Nagappattinam, S.E. India, 137-146 m (BMNH, DMNH). Travancore Coast, S.E. India, 658 m (BMNH). *Andaman Sea:* W. coral bank, W. coast Andaman Ids, 55-64 m (BMNH). Andaman Ids, (BMNH, AMS). 48 km W. of Twin Ids, 10°39'N, 97°06'E, 274-292 m (ANSP). 120 km E.S.E. of Phuket Is., W. Thailand, 503-512 m (ANSP). 7°40'N, 97°08'E (ANSP). *Japan:* (AMS, USNM). Kuma Makagai, 732 m (BMNH). Misaki, Kanagawa ken, 35°30'N, 140°30'E (ANSP). Irozaki, 115-128 m (USNM). Tokyo Bay (MCZ). Chiba, Tokyo Bay, 183 m (ANSP). Sagami Bay (USNM), 146 m (DMNH), 150-226 m (ZMC). Suruga Bay, 227 m (USNM). Mikawa, Sea of Japan, 91 m (FMC). Wakayama area, S. Honshu (ANSP). Kii (Shiono-misaki), Wakayama (ANSP, AMS), 183 m (DMNH). Tanabe, Wakayama (ANSP, USNM). Minabe, Wakayama, 55 m (ANSP). Kyoto Province, Honshu, 73 m (USNM). Awaji Is., Seto Naikai (ANSP). Tosa Bay, Shikoku, 110 m (ANSP, MCZ, AMNH, DMNH), 55-183 m (FMC). Kagoshima Gulf, Kyushu, 155 m (USNM). Nagasaki, Kyushu (ZMC). S.W. of Kyushu, 32°17'N, 128°11'E, 208 m (ZMC). *Philippines:* Batangas Bay, Luzon (USNM, DMNH), 238-362 m (5 lots) (USNM), 391 m (USNM), 250 m (AMS). N. of Ambil Is., Lubang Ids, Luzon, 187 m (USNM). Calapan, Mindoro, 198 m (USNM). Off Tablas Is., 183-210 m (BMNH). Tagapula Is., E. of Masbate Is., 197 m (USNM). Sibugay Is., E. of Masbate Is., 197 m (USNM). N.E. of Point Domorong, Masbate Is., 249 m, 280 m (USNM). W. of Borocay Is., N. Panay, 571 m (USNM). N. end Palawan Passage (USNM). W. of Destacado Is., Samar Sea, 146 m (USNM). Pacijan Is., Camotes Ids, 290m, 345m (USNM). Bohol (AMNH). Talisay, Cebu, Bohol Strait, 161 m, 296 m, 265 m (USNM). S.W. of Mactan, Bohol Strait, 302 m (USNM). Off Zamboanga, Mindanao (AMNH). N.W. Jolo, Sulu Archipelago, 340 m (USNM). *Indonesia:* S. of Padang, Sumatra, 470 m, 614 m (EBM). 8°29'S, 114°40'E, Selat Bali, 200 m (ZMC). Sebuku (=Sibuko?) Bay, East Kalimantan, Borneo, 558 m (USNM). Cape Lassa, Sulawesi (Celebes), 5°36'S, 120°28'E, (USNM). *Australia: Queensland:* N.E. Raine Is., c.1000 m (AMS). *New South Wales:* S.E. of Clarence River, 405 m (AMS). S.E. of Crowdy Head, 366, 402-548 m (AMS). N.E. of Port Stephens, 384 m (AMS). Between Hawkesbury River and Port Stephens, 366-411 m (AMS).

**Other records:** West coast, Malagasy Republic, 12°42.4'S, 48°14.3'E, to 18°54'S, 43°55'E, in 245-810 m (*vide* R. Kilburn *in litt.*; A. Crosnier Colln, O.R.S.T.O.M.).

**Distribution:** Indian Ocean from South Africa to Oman and India, central Indo-Pacific, southern Japan south to eastern Australia; 50-1050 m, mostly on the continental slope (Fig. 36).

**Remarks:** This widely ranging species shows some variation in size, in the height of the spire and in the strength of the basal sculpture. The shell cannot readily be confused with that of any other Recent species except young shells with *X. japonica* (see under *X. japonica* for comparative remarks) and with *X. granulosa* which differs in its much stronger dorsal sculpture.

This species habitually attaches large, often elongate shells in a radial fashion, so that they presumably function in the same way as the digitations on some other species. The points of attachment of the objects are often extended somewhat beyond the edge of the free periphery giving the periphery a subdigitate appearance.

The records from New South Wales extend the range of this species into temperate Australia for the first time. Martens (in Studer, 1889) has recorded *X. pallidula* from E. of Noosa Heads (southern Queensland) in 1408 m but the writer has not seen the material on which this record is based.

***Xenophora (Xenophora) japonica* Kuroda and Habe, 1971.**

Figs 9c, 14c-d, 23j-m, 36.

*Xenophora japonica* Kuroda & Habe, 1971 (in Kuroda, Habe & Oyama, 1971): 138, 91; pl.21, figs 2-4; Okutani, 1972: 83, fig. 19.

**Shell:** Small, with depressed to moderate spire (spire angle 81°-102°) rather solid, with narrow peripheral flange. Very similar to *X. pallidula* in most respects except the base, which, in adults, tends to be more flattened and has weaker or obsolete spiral sculpture. In addition foreign objects are more closely spaced and relatively larger, resulting in a smaller percentage of uncovered dorsal surface than in *X. pallidula*. The base is uniform yellowish-white to orange-brown and the apertural callus and the dorsal surface are white (Fig. 23j-m).

**Dimensions:**

	height	diameter
Holotype	24 mm	43 mm
Paratypes	26	54
	23.5	48.3
(all above from original description)		
Figured paratypes	25.7	35.0
	24.4	35.5
Off Adyagan Island, Philippines (USNM)	26.5	40.5
Kermadec Ids (NMNZ)	27.6	33.9

**Operculum:** Oval, with all edges convex, brown, rather thin, subopaque. Outer surface with weak concentric striae only. Central area relatively narrow, slightly thickened, partly obscured over free surface by lamellate growth lines.

**Radula:** Central teeth with very large median cusp and 3 lateral cusps on each side. Lateral teeth with rather large cusp; marginal teeth smooth (Fig. 9c).

**Anatomy:** Similar to *X. neozelanica* and *X. pallidula* but with the rectum placed further back in the mantle cavity. The large, asymmetrical salivary glands are like those of *X. neozelanica* and different from the smaller, symmetrical glands of *X. pallidula*. Penis long, slender, with a rather long subterminal papilla (Fig. 14c-d). Material examined: Sagami Bay, Japan (ZMC) (1 male).

**Location of type and type locality:** Biological Laboratory, Imperial Household, Tokyo, holotype and 2 paratypes; 3 paratypes NSMT, 43506 (Fig. 23j-m); Sagami Bay, Joga-Shima, WNW 5 km, in 200-300 m.

**Other material examined:** *China Sea:* Tung Sha Tao (Pratas Is.), 183 m, 256 m, 420 m (USNM). "Trawled off Taiwan" (AMS). *Japan:* (BMNH). Joga-shima, Sagami Bay (MCZ). Sagami Bay (ANSP). Misaki (BMNH), 91-110 m (BPBM), 150-225 m, 376 m (ZMC), Suruga Bay, 104 m (USNM). Kii (Shiono-misaki) (NMV, AMS), 110 m (USNM). Tanabe (USNM, ANSP), 64 m (USNM). Seto Naikai (Inland Sea) (BPBM). Awaji Is., Seto Naikai (ANSP). Tosa Bay, Shikoku (ANSP). Kagoshima Gulf, Kyushu (USNM), 128 m, 106 m (USNM). Hondo, 32°30'N, 130°20'E, 106 m (USNM). *Philippines:* N. of Burias Is., S. Luzon, 192 m (USNM). Off Adyagan Is., E. Masbate (USNM). S.W. of Destacado Is., E. Masbate, Samar Sea, 216 m,



247 m (USNM). *Kermadec Islands*: 6 km N.N.E. of Herald Is., Raoul Is., 1188-1225 m (NMNZ).

**Distribution:** Southern Japan to the Philippines; one specimen recorded from the Kermadec Ids; 60-1225 m but mostly on the continental shelf (Fig. 36).

**Remarks:** Although similar to one another, *X. pallidula* and *X. japonica* do not often occur living together and, when they do, one species is usually predominant. They have a fairly extensive common geographical range but *X. pallidula* is much more widespread. The differences in the size and basal features noted above, and the denser clothing of the dorsal surface of *X. japonica* with foreign objects than seen in most specimens of *X. pallidula*, are the main shell characters distinguishing the two species. Many juveniles, however, are difficult to distinguish. The radular and opercular characters are similar but the central teeth of the radula have a longer median cusp in *X. japonica*. The penial features of the two species appear to be similar judging from the available material (cf. Fig. 14c-f).

Okutani (1972: 83) has indicated that *X. japonica* is a "hard bottom" dweller associated with *Cryptopecten vesiculosus* (Dunker) and that *X. pallidula* is a sandy or muddy bottom dweller frequently associated with *Glycymeris rotunda* (Dunker).

A single specimen from deep water off the Kermadec Islands, N.E. of New Zealand, is indistinguishable from Japanese shells and suggests the possibility that this species may be more widely distributed on the continental slopes of the south western Pacific than the available material indicates.

### ***Xenophora (Xenophora) crispa* (König, 1825).**

Figs 26a-g, 38.

*Trochus crispus* König, 1825: pl.5, fig. 58.

*Xenophora caperata*. — Petit de la Saussaye, 1857: 249, pl.10, figs 3-5; Nordsieck, 1968: 96, pl.15, fig. 56: 31 (*non* Philippi, 1849).

*Xenophora mediterranea* Tiberi, 1863: 157, pl.6, fig. 1; Locard, 1897: 486; Adam & Knudsen, 1955: 2, pl.1, figs 1-5, text fig. 1A (radula); Le Loeuff *et al.*, 1971: 501.

*Xenophora senegalensis* Fischer, 1873: 123 (new name for *X. caperata* Petit de la Saussaye, 1857: 249, *non* Philippi, 1849); Locard, 1897: 488, pl.22, figs 18, 19; Nordsieck, 1968: 96, pl.15, figs 56: 30; Le Loeuff *et al.*, 1971: 501, fig. 3 (radula).

*Xenophora commutata* Fischer, 1879b: 211.

*Xenophora trinacria* Fischer, 1879b: 211 (based on Philippi, 1836, pl.10, fig. 26); Franchis, 1894: 184, pl.3, figs 4a-b, 5.

*Xenophora cavellieri* Rochebrune, 1883: 178 (syntype figured by Adam & Knudsen, 1955: 6, pl.1, fig. 4).

*Xenophora crispa* var. *elatior* Sacco, 1896: 22, pl.2, fig. 23.

*Xenophora crispa* var. *depressior* Sacco, 1896: 22, pl.2, fig. 25.

*Xenophora crispa*. — Cerulli-Irelli, 1914: 386, pl.50, figs 28-35; Nordsieck, 1968: 96, pl.15, figs 56: 30. (See Franchis (1894), Sacco (1896), Cerulli-Irelli (1914) and Caprotti (1967) for more detailed synonymy).

**Shell:** Of rather small size, solid, with moderate to low spire (spire angle 60°-94°). Umbilicus rather wide, deep, partly covered by inner lip. Foreign objects obscure much of dorsal surface and are frequently large. Whorls flat to moderately convex, sculptured with opisthocline to spiral wavy riblets which cross irregular, weak growth folds and lines. Base rather flat, peripheral extension set off at an angle to it, sculptured with prominent spiral threads and collabral growth lines, points of intersection more-or-less beaded. Spiral sculpture does not enter umbilicus. Colour yellowish-white to yellowish-brown (Fig. 26a-g).



**Dimensions:**

	height	diameter
Syntypes of <i>X. mediterranea</i>	19.35 mm	28.7 mm
	23.6	30.7
Holotype of <i>X. senegalensis</i>	10.9	16.7
Recent, Oran, Algeria, Mediterranean (large specimen, Dautzenberg Colln, IRNSB)	33.4	42.0
Recent, Melilla, Spanish Morocco, Mediterranean (AMS)	26.0	36.5
Recent, West Africa (specimen figured by Adam & Knudsen, 1955), one of the largest seen from this area	19.3	26.9

(See Le Loeuff *et al.* (1971) for biometric analysis of west African populations).

**Operculum:** Oval, rather thin, yellowish-brown, transparent, all sides convex, smooth externally except for very weak concentric striae. Nucleus displaced slightly to left. Central area narrow, darker brown than rest of operculum, thickened, somewhat obscured over free surface by weak lamellae. Figured and described by Petit de la Saussaye (1857: 250, pl.10, fig. 5).

**Radula:** See Adam and Knudsen (1955: 3, fig. 1) and Le Loeuff *et al.* (1971: fig. 3).

**Anatomy:** Penis strongly bent back, contracted and transversely rippled with the exception of the distal extremity, flattened in the form of a sickle, with the point enlarged and terminating in two small, rounded lobes (free translation from Adam & Knudsen, 1955: 3). Remainder of anatomy not known.

**Location of types and type localities:** *T. crispera*. Not known; type locality here designated Asti, Italy (Astian, Upper Pliocene).

*X. mediterranea*. NHMP, 2 syntypes; Algeria (Fig. 26d-f).

*X. senegalensis*. NHMP, holotype; West Africa, between Senegal and the Gabon River (Fig. 26g).

*X. commutata*. NHMP (?); Altavilla, Sicily ("Astesian" =? Astian, Upper Pliocene).

*X. trinacria*. Not known. Based on Philippi (1836: 183, pl.10, fig. 26); Panormus, near Palermo, Sicily (Upper Pliocene).

*X. cavelleri*. NHMP, 2 syntypes; mouth of the Casamence River, Senegal, W. Africa, in 150 m (Fig. 26a-c).

*X. crispera* var. *elator*. Museo geol. Torino; Bordighera, Italy, Pliocene (here designated; locality of Sacco's figured specimen).

*X. crispera* var. *depressior*. Museo geol. Torino; Ceriale, Italy, Pliocene (here designated; locality of Sacco's figured specimen).

**Fossil records:** There are extensive records of this species from the Pliocene and Pleistocene of Italy (see Sacco, 1896, Cerulli-Irelli, 1914 and Caprotti, 1964). A large number of fossil specimens held in several museums (notably the Turin Geological Museum and the BMNH) have been examined.

**Other material examined:** *France:* Cap Breton (USNM). *Spain:* Off Valencia (ZMC). La Azohia (Mazarrón) (AMS). *Sardinia:* (USNM, RNHL, BMNH). *Sicily:* 36°43'N, 13°36'W, (USNM). Sicily Channel, 180-240 m (AMS). *Tunisia:* Cap Serrat, 170 m (BMNH). *Algeria:* Golfo di Bone, Annaba (USNM). Algiers (BNMH). Cherchell (ANSP, IRNSB). Beni-Saf (IRNSB). Oran (RNHL, IRNSB). *Morocco:* 1072 m, 1335 m (USNM). Melilla (ANSP, MCZ, DMNH, AMNH, EBM, AMS, RNHL). 35°26'N, 04°15'W, 212 m (USNM). *Senegal:* 183 m (AMNH). 19 km off Cape Blanc, 70 m (AMS). 16°N (EBM) Dakar (BMNH) 13°43'N, 17°23'W (ZMC). *Portuguese Guinea:* Off Cape Roxo, 120 m (BMNH). *Guinea:* 10°22'N,

16°22'W, 41-55 m (ZMC). 9°24'N, 14°48'W, 50-51 m (ZMC). 9°20'N, 14°15'W, 32 m (ZMC). *Sierra Leone*: 7°29'N, 13°38'W, 74-78 m (ZMC). *Liberia*: 6°03'N, 10°25'W, 44 m (ZMC). 5°59'N, 10°27'W, 62 m (ZMC). 5°06'N, 9°34'W, 78 m (ZMC). *Gulf of Guinea*: 4°50'N, 2°49'W, 60-65 m (ZMC). 4°17'N, 7°11'W, 135 m (ZMC). 4°N, 9°E (EBM). 3°55'N, 6°08'E, 53 m (ZMC). *Gabon*: 2°03'S, 9°05'E, 50 m (ZMC). 2°09'S, 9°27'E, 260-650 m (ZMC). *Angola*: 7°19'S, 12°40'E, 47 m (ZMC). Mocamedes (AMNH). *Atlantic Ocean*: 16°17'N, 22°51'W (EBM). 16°50'N, 25°04'W, 41-50 m (ZMC).

**Other records:** *Atlantic Ocean*: Azores, 1440 m (Locard, 1897). Cape Verde Ids, Saint Vicente Is., 75 m, 90 m, 105 m (Locard, 1897). Between 3°05'S and 16°36'S, West Africa, 74-225 m (Adam & Knudsen, 1955).

**Distribution:** Western half of the Mediterranean Sea, Azores and West Africa (Senegal to Angola); 30-1440 m (Fig. 38).

**Remarks:** Several authors including Sacco (1896) have regarded *X. crispa* and *X. mediterranea* as a single species (although Sacco recognized several varieties). Careful comparison of Pliocene and Recent shells has failed to reveal any significant differences which would serve to separate them as species or subspecies, except that some of the fossil shells are somewhat larger (up to about 55 mm in diameter) and in some the columella tends to cover the umbilicus. Smaller (subadult) fossil shells and many of the adult specimens are identical to Recent shells.

Nordsieck (1968) recognized three species, *X. crispa* (Mediterranean), *X. caperata* (Atlantic), and *X. senegalensis* (Cape Verde Ids and the Azores), presumably not aware that Fischer (1873) proposed the name *senegalensis* to replace *caperata* Petit de la Saussaye, non Philippi. The usage of the name *X. caperata* for West African specimens of *X. crispa* is discussed at length by Adam & Knudsen (1955).

The names *X. trinacria* and *X. commutata* are both based on fossil forms and were intended as replacement names for *X. crispa* (König) which Fischer (1879b) regarded as being unidentifiable. Subsequent authors have mostly regarded the fossil and Recent forms as being unidentifiable although varieties or subspecies are often recognized. Examination of Pliocene, Pleistocene and Recent material has indicated a close similarity, suggesting that only one taxon need be recognized. This conclusion was also reached, in large part, by Adam & Knudsen (1955) who also synonymized *X. senegalensis* and *X. cavelleri* with *X. mediterranea*, which they regard as probably the same species as *X. crispa*, although they did not formally place the two names in synonymy. Le Loeuff *et al.* (1971) have advanced statistical and ecological data as a means of separating *X. mediterranea* and *X. senegalensis*. They argue that the shell of *X. mediterranea* is nearly twice the size of that of *X. senegalensis*, exhibits weaker basal sculpture, and has a proportionately slightly higher spire. *X. mediterranea* lives on the continental slope and is therefore in colder water than *X. senegalensis* which lives on the continental shelf between 35 and 50 m. As the observed differences could equally well be interpreted as ecological variation exhibited within a single species, the more conservative approach is adopted here.

The shell of *X. crispa* is similar to that of *X. solaroides* (Reeve) but is larger and heavier, has stronger basal sculpture, and the umbilicus is not bordered by a distinct angulation. These two species appear to have arisen quite independently as discussed above (see under "Fossil History"). *X. crispa* probably evolved from *X. burdigalensis* Grateloup, a Miocene species. A few Miocene records have been attributed to *X. crispa* but all of those examined by the writer are based on misidentifications or specimens with dubious locality data.

**Xenophora (Xenophora) solarioides solarioides** (Reeve, 1845).

Figs 10a, 12b, 14e, 27a-j, 37.

*Phorus solarioides* Reeve, 1845: pl.3, fig. 8, A. Adams & Reeve, 1850: 50, pl.17, fig. 6.*Xenophora solarioides*. — H. & A. Adams, 1854: 363, pl.40, figs 2a, b; Philippi, 1855: 346, pl.46, fig. 6; Brazier, 1877: 3; Fischer, 1879a: 447, pl.44, fig. 3; Watson, 1886: 464; Tryon, 1886: 159, pl.44, fig. 77; Melvill & Sykes, 1899: 227; Uchiyama, 1902: 12, pl.22, fig. 1; Hedley, 1907: 482; Schepman, 1909: 202; Yen, 1942: 209; Wissema, 1947: 85, pl.4, figs 98-100; Habe, 1953a: 173, text fig. 11; Habe, 1964: 57, pl.16, fig. 3.*Onustus javanicus* Gray, 1857: 131 (based on figure of *Phorus* sp., Gray, 1850: 26, pl.122a, fig. 1, and Adams and Reeve, 1850:50, pl. 17, fig. 6).*Xenophora (Phorus) australis* Souverbie & Montrouzier, 1870: 423, pl.14, fig. 4.*Xenophora australis*. — Fischer, 1879a: 436, pl.66, fig. 2; Wissema, 1947: 86, pl.4, figs 101-103; Rippingale & McMichael, 1961: 51, pl.4, fig. 22; Cernohorsky, 1972: 89, pl.23, fig. 1.*Xenophora cerea*. — Fischer, 1879a: 440, pl.44, fig. 2 (*non* Reeve, 1845).**Shell:** Small, of rather light build, spire usually rather depressed (spire angle 85°-111°), widely umbilicate, dorsal surface largely obscured by relatively large foreign objects. Umbilicus deep, rather wide, partly covered by inner lip, bordered by a subangulation. Whorls convex, sculptured with fine, close, opisthocline, wavy striae crossed by irregular growth lines. Base flat to lightly convex, narrow peripheral extension set off at angle. Basal sculpture of 3-6 spiral cords over inner half and usually several weak spiral threads within umbilicus. Collabral growth striae rather fine to moderate, usually rendering spiral cords gemmate. Outer half of base with weak, gemmate spiral to subspiral threads or axial growth threads only. Colour yellowish-white, aperture white (Fig. 27a-j).**Dimensions:**

	height	diameter
Holotype of <i>P. solarioides</i>	10.6 mm	19.1 mm
Syntype of <i>X. australis</i> (from original description)	15	27
Small mature specimen (Bowen, Queensland, AMS)	13.5	19.0
Large specimen (Nouméa, New Caledonia, AMS)	20.1	31.6

**Operculum:** Oval, thin, yellow, transparent, with outer surface smooth except for very weak concentric and radial striae; all sides convex. Nucleus displaced slightly to left. Central area whitish, opaque, rather narrow, slightly thickened, easily visible through free surface.**Radula:** Central teeth subcircular, with 2 small, sharp cusps on either side of median cusp. Lateral teeth with moderate sized, rather blunt cusps. Marginal teeth weakly serrate in some specimens. Accessory wing-like structure not observed on inner marginal teeth (Figs 10a, 12b).**Animal:** Proboscis "yellow at the tip and on the under surface, but pink between the tentacles, which are straight, rigid, and opaque dead-white; the eyes are black and conspicuous" (Adams & Reeve, 1850).**Anatomy:** Similar to *X. neozelanica* except that the metapodium lacks any clear indication of a sole and the gill filaments are relatively longer. The mantle edge is smooth on the right side and has short, blunt tentacles on the left side. The penis is rather long and slender, the distal portion only slightly swollen and appears to be glandular. A deep cleft continuous with the penial groove runs through the distal portion to the extremity of the penis (Fig. 14e). There is no papilla. Material examined: trawled in the vicinity of the Keppel Ids, Keppel Bay, Queensland, Australia, 10-50 m (AMS) (2 males, 3 females).

**Location of types and type localities:** *P. solariooides*: BMNH, holotype (1953.4.7.47); Island of St. Nicolas and Cebu, Philippines, in sandy mud in 11 m (Fig. 27f-g).

*X. australis*: NHMP (4 syntypes); Nouméa Bay, New Caledonia (Fig. 27a-e).

*O. javanicus*: Not known; Java.

**Fossil material examined:** Pliocene: Cape Possession, Papua, Papua New Guinea, 1 specimen (Bureau of Mineral Resources, Canberra, F. 7184). South Flank of Petak anticline near Toeri, west of Tjepoe, middle Rembang, eastern Java, from blue clays above foraminiferal marl, 1 specimen (Natural History Museum, Basel, H16970).

**Other fossil records:** Pliocene: Atjeh, Sumatra (Wissemma, 1947). Plio-Pleistocene: Locality 102, Nias, Malay Archipelago (Wissemma, 1947).

**Other material examined:** *Red Sea*: Off Nuweiba el Tarabin, 132-146 m, Gulf of Aqaba (Tel Aviv Univ.). Off Abu Samra, Gulf of Aqaba, 46-132 m (Tel Aviv Univ.). Elat, Gulf of Aqaba (ZMC). Off Elat, 38-91 m (Tel Aviv Univ.). Off Gesirath Farun, Gulf of Aqaba, 64-73 m (Tel Aviv Univ.). *Zanzibar*: 2 km N.W. of Ras Nungwi, 15 m (ANSP). *Malagasy Republic*: 96 km N.E. of Cape St. André (USNM). Off Nossi Bé, 31 m, 36 m (ANSP). *Amirante Islands*: 51 m (BMNH). *Seychelles*: 57 m, 71 m (BMNH). N.W. Bay, Mahé (BMNH). Anse Etoile, Mahé (BMNH). *Sri Lanka*: Mannar (BMNH). *India*: Off Mangalore, Malabar Coast, 48-55 m (BMNH). S.E. of Vishakhapatnam, N.E. India, 58 m, 79 m (ANSP). *Andaman Islands*: (DMNH, BMNH). N.W. of Port Blair, South Andaman Is., 49 m, 90 m (ANSP). *Burma*: 24 km S. of Sittwe (Akyab), N. Burma, 30 m (ANSP). *Thailand*: (ZMC). 105 km N.N.W. of Phuket Is., Andaman Sea, 58 m (ANSP). 8°21'N, 98°14'E, 15 m (ZMC). *Vietnam*: Nha Trang, 10-15 m (ZMC). *Philippines*: 1.6 km E. San Nicolas Shoals Light, Manila Bay, Luzon, 18 m (ANSP). Bataan, Manila Bay, Luzon, 15 m (DMNH). Corregidor Is., Manila Bay, Luzon, 20 m, 10-18 m (DMNH), 10-18 m (ANSP). Tabaco, S. Luzon (ANSP). "Gigante Ids", Visayan Sea, 47 m (USNM). Visayan Sea, 11°37'N, 123°31'E, 33 m (BMNH). Cebu, Bohol Strait (USNM). Bohol Strait, 110-128 m (WAM). Laoy Is., off Bohol Is., 110 m (WAM). 14 km W. of Cape Melville, Balabac Is., Palawan, 36-49 m (WAM). Off Malanipa, Basilan Strait, 18-36 m (BMNH). Sulu Archipelago (WAM). Tataan Ids, Sulu Archipelago, 33 m (USNM). 5°36'S, 132°55'E, 35 m (ZMC). *Malaysia*: 16-25 km from Balambangan Is., Sabah, 29 m (WAM). *Indonesia*: Straits of Malacca (EBM). E. coast of Sumatra (EBM). Bangka Strait (EBM). Off Belitung, 3°30'S, 107°30'E (EBM). Java Sea (EBM). Sunda Strait (USNM, EBM), 16 m, 25 m, 45 m (ZMC). N. of Jakarta, 22 m, 25 m (ZMC). Selat Bali, 70-150 m (ZMC). Makasar, S. Sulawesi (Celebes), 25 m, 35 m (ZMC). Ambon (Amboina), Moluccas, 13-19 m (ZMC), 110-115 m, 144-157 m (WAM). Tjirebon, Djawa (Java) (RNHL). Semarang, Djawa (Java) (EBM). Dangar Besar, 8°26'S, 117°40'E, (RNHL). 8 km N. of Selaru, Kepulauan Tanimbar, 51-58 m (WAM). 9 km W. of Selaru, Kepulauan Tanimbar, 46-64 m (WAM). Auri Ids, Teluk Irian (Geelvink Bay), Irian Barat, 36-46 m (ANSP). N.E. of Roemwakon Is., Aoeri Ids, 37-46 m (ANSP). Japen Is., Teluk Irian, 18-29 m (ANSP). N.W. of Walir Is., Kepulauan Kai, Moluccas, 79-86 m (WAM). Kai Besar, Kepulauan Kai, 33-37 m (WAM). *Papua New Guinea*: Yule Is., Papua, 22-33 m (AMS). W. end Manuabada (Local) Is., Port Moresby, Papua, 18-22 m (AMS). Marua Is., Collingwood Bay, Papua (AMS). N. coast, New Guinea (AMS). New Ireland (BMNH). *Australia*: *Western Australia*: 160 km N. of Carnarvon (WAM). 11-16 km N. of Long Is., Onslow, 51 m, 76 m, 95 m (WAM). N.W. of Anchor Is., Onslow, 84 m (WAM). N. of Delambre Is., Dampier Archipelago, 40-42 m (WAM). 22 km W. of Eaglehawk Is., Dampier Archipelago, 26 m (WAM). 60 km W. of Cape Jaubert, 40 m (WAM). W. of Cape Bossut (WAM). 16-32 km W. of Lagrange Bay, 22-46 m (WAM). 58 km S.W. of Adele Is., Buccaneer Archipelago (WAM). Troughton Is., Bonaparte Archipelago, 91 m (WAM). N.W. Holothuria Banks, 69 m (BMNH). Off Cassini Is., 60 m (BMNH). *Northern Australia*: Clarence Strait, N.W. of Charles Point, Darwin, 33 m (WAM). S. of Bathurst Is., 51 m (WAM). 161 km N. of Croker Is., 124 m (WAM). 68 km N.E. of Croker Is., 62 m (AMS). Gulf of Carpentaria (ANSP). *Queensland*: Sweers Is., Gulf of Carpentaria, 28 m (AMS). Mapoon, Cape York, 18 m (AMS). Arafura Sea, 10°39'S, 140°29'E, 49 m (AMS). Darnley Is., Torres Strait (WAM). Cape York, 5-22 m (BMNH). Albany Passage, Torres Strait, 7-26 m (AMS). 8 km N. of Clack Reef, Flinders Group, Princess Charlotte Bay, 33 m (WAM, DMNH). Lizard Is. (BMNH). Hope Ids, Cooktown, 9-18 m (AMS). Cairns Reef,



Cooktown, 11-18 m (AMS). Low Isles (AMS); 6-11 m (AMS, WAM). Port Douglas (DMNH). Ellis Beach and Trinity Bay, Cairns (AMS). Dunk Is., Rockingham Bay (ANSP). 8 km E.N.E. of Brook Is., Lighthouse, Rockingham Bay, 4-5 m (DMNH). Bramble Reef, off Ingham (DMNH). Magnetic Is., Townsville (AMS). Cape Cleveland, Townsville, 29 m (WAM). Cape Bowling Green, S. of Townsville, 29 m (WAM). Bowen (AMS). Whitsunday Is. (AMS). Lindeman Is., Whitsunday Passage (AMS). Keppel Bay (WAM), 46 m, 137 m (AMS). N. Keppel Is., Keppel Bay, 7 m (AMS). Great Keppel Is., Keppel Bay, 13-14 m (AMS). North West Is., Capricorn Group (AMS). Port Curtis, Gladstone (AMS). Burnett Heads, Bundaberg, 55 m (AMS). Wide Bay, Fraser Is., 100 m (AMS). Off Caloundra (AMS). E. of Moreton Bay, 115-166 m (AMS). *New South Wales*: Off Yamba, 49 m (AMS). *New Caledonia*: (ANSP, USNM). 5 km N.E. of Dumbéa Passage, Nouméa, 15 m (ANSP). Baye Papaye, Nouméa (AMS). Nouméa, 6-22 m (ANSP), 1-3 m (AMS). *Fiji*: Moni Bay, W. Viti Levu, 18-24 m (ANSP, USNM).

**Distribution:** Tropical Indian Ocean, Red Sea, central Indo-Pacific and western Pacific including the Australian east coast as far south as northern New South Wales; mostly in shallow water; depth range 1-170 m (Fig. 37).

**Remarks:** This species differs from all other Recent species in its small shell which has a wide umbilicus bordered by a subangulation, a densely clothed dorsal surface and spirally sculptured base. It is similar, but not closely allied to, *X. crispa* as discussed under that species.

The syntypes of *X. australis* are larger specimens than the type of *solarioides* but the examination of a large series of shells has indicated that only a single species can be recognized. There is some variation in shell characters, particularly in size, and in the strength of the basal sculpture. Large specimens tend to lack, or have a weakly developed, umbilical subangulation.

The name *O. javanicus* appears to have been first introduced by Gray (1857) and is based on the drawing published by Adams & Reeve (1850) under the name *solarioides*, which it certainly appears to be.

The fossil forerunner of this species is *X. jezleri* Cox, 1948 (Fig. 27k-l) from Borneo and its synonym *X. terpstrai* Dey, 1961 from India. These, and Miocene specimens from Java and Okinawa, agree very closely with *X. solarioides* except that the umbilical area is separated from the base by a weaker subangulation and the basal sculpture is relatively coarser. These differences are minor and consequently *X. jezleri* (= *terpstrai* Dey) is here regarded as a chrono-subspecies of *X. solarioides* as already suggested by Nuttall (1965: 169).

The known records of *X. solarioides jezleri* are: Dent Peninsula, Sabah (= British North Borneo) (type locality of *X. jezleri*) Upper Miocene or Pliocene. Quilon, Kerala, India (type locality of *X. terpstrai*) (Miocene) (not examined). Yonabaru Clay, Shimijiri Group, Okinawa (as *Xenophora* sp. MacNeil, 1960: 48, pl.2, figs 8, 12) U.S. Geological Survey, USNM (Miocene) (examined). "Locality K", west part of district of Tjidamar, Buitenzorg, Java (recorded in part as *X. pallidula* by Martin (1905)) RGM (Miocene) (examined).

The subgeneric classification of this species is somewhat problematic as it has a less distinct metapodial sole than other species of *Xenophora* s.s., a character which allies it with the species in *Stellaria* and *Onustus*. The tentaculate left mantle margin, the narrow peripheral flange and the relatively densely clothed dorsal surface all suggest placement in *Xenophora* s.s. Perhaps *X. solarioides* is a survivor from the original stock from which *Onustus* and *Stellaria* sprang, a view possibly supported by the open umbilicus of the shell, a character which influenced Cossmann (1915) to place *X. solarioides* together with *X. calculifera* (= *chinensis* herein) in *Trochotugurium*. Other characters which seem to ally *X. solarioides* with *Stellaria/Onustus* more than with *Xenophora* s.s. are the simple, very thin operculum (although this is probably more a function of size, small specimens of most species having a thinner, less abraded operculum) and the apparently glandular, slightly swollen distal end of the penis. Unfortunately neither of the latter characters is restricted to any of the subgenera although they are more typical of the species in *Onustus* and *Stellaria* than those in *Xenophora* s.s. The only two characters shared by all the species in *Stellaria* are the wide peripheral flange of the shell and the restricted agglutination of objects on the dorsal surface. *Xenophora solarioides* lacks both of these shell characters and the peripheral flange also lacks a porcellanous ventral surface which excludes it from *Onustus* as defined herein. Consequently it seems best classified in *Xenophora* s.s.



Subgenus **Stellaria** (Schmidt MS) Möller, 1832: 130.  
(*non Stellaria* Nardo, 1834 or Bonaparte, 1838)

Type species: (monotypy) *Trochus solaris* "Lamarck" = Linné, 1764: 645.

Synonym: *Haliphoebus* Fischer (in Kiener), 1879a: 450.

Type species: (monotypy) *Trochus solaris* Linné, 1764.

**Diagnosis:** Shell large, widely umbilicate, with wide peripheral flange which is simple in some species or is digitate or divided into numerous long, hollow, narrow, parallel-sided spines. Attached foreign objects small, covering little of dorsal surface. Mantle edge mostly smooth. Ctenidial filaments very long; foot lacks metapodial sole. Operculum smooth externally; subtriangular to suboval.

**Remarks:** The species included in *Stellaria* share several characters that are not found in combination in *Xenophora* s.s. These include the expanded peripheral flange, the nearly smooth dorsal surface and a wide to moderate umbilicus. There are no tentacles on the mantle edge, the ctenidial filaments are relatively longer than in species of *Xenophora* s.s. and there is little or no trace of a metapodial sole. The long, hollow spines of *X. solaris* have been considered by other authors sufficient justification for the separation of that species in a monotypic subgenus of the genus. This single character is not, in the writer's view, sufficient reason for separating *X. solaris* from the other, apparently related, species here included in *Stellaria*.

The genus name *Stellaria* was overlooked until 1953 when Habe (on the advice of Dr H. Rehder) reintroduced the name (Habe, 1953b) to replace *Haliphoebus* over which it has priority.

#### KEY TO RECENT SPECIES OF THE SUBGENUS *STELLARIA* BASED ON SHELL CHARACTERS

1. Shell with long, tubular spines on periphery ..... *solaris*  
Shell with peripheral flange simple or digitate .....
2. Shell with peripheral rim strongly digitate ..... *testigera*  
Shell with peripheral rim simple .....
3. Shell with strong spiral and radial sculpture on base .....  
Shell with radial sculpture on base, spiral sculpture lacking ..... *gigantea*
4. Strong spiral sculpture over entire base..... *lamberti*  
Strong spiral sculpture over inner half of base only ..... *chinensis*

#### ***Xenophora (Stellaria) solaris*** (Linné, 1764).

Figs 4c, 6a, 10b, 13e, 29k-m, 39.

*Trochus solaris* Linné, 1764: 645 (refers to Buonanni, 1684: pl.366 and Rumphius, 1705: pl.20, fig. K); Linné, 1767: 1229; Gmelin, 1791: 3569; Lamarck, 1822: 10; Hanley, 1855: 319; Philippi, 1846: 51, pl.11, figs 2, 3; Dodge, 1958: 187.

*Astraea polaris* (? *err. pro solaris*) Röding, 1798: 79 (based on Chemnitz, 1781: pl.173, figs 1700, 1701).

*Phorus solaris*. — Reeve, 1842: 160, pl.214, figs 1, 2; Reeve, 1843a: 161; Reeve, 1843b: pl.2, figs 5a-b.

*Onustus solaris*. — H. & A. Adams, 1854: 362, pl. 40, fig. 1c.

*Xenophora solaris*. — Fischer, 1879a: 428, pl.3, fig. 1; Tryon, 1886: 162, pl.47, figs 92, 93; Braga, 1952: 89, pl.5, fig. 7.

*Xenophora (Onustus) solaris*. — Schepman, 1909: 205.

*Xenophora solariformis* Tesch, 1920: 73, pl.133, figs 214a-c.

*Haliphoebus solaris*. — Habe, 1953a: 178, fig. 14; Dodge, 1958: 189.

*Stellaria solaris*. — Habe, 1953b: 214; Dance, 1966: pl.16; Dance: 1967: 15.

*Stellaria solaris paucispinosa* Kosuge and Nomoto, 1972: 4, pl.1, figs 5, 6.

**Shell:** Depressed (spire angle  $92^{\circ}$ - $102^{\circ}$ ), with peripheral flange represented by 10-20 long, narrow, tubular, blunt spines. Inner peripheral flange a narrow, weakly scalloped ridge from which spines arise at right angles to periphery. Peripheral spines and ridge about 45% total diameter of base. Umbilicus deep, wide, all whorls visible within, partly covered by inner lip. Row of foreign objects usually restricted to about first  $2\frac{1}{2}$ -4 whorls, usually small, attached to spines. Whorls slightly convex, sculptured dorsally with fine, opisthocline, somewhat wavy ribs often rendered finely granular by very inconspicuous, close, prosocline growth striae. More prominent growth rugae form fairly regular axial undulations, which become very prominent ridges on last half of body whorl of large shells. Base convex, with strong, close collabral ribs (becoming lamellate within umbilicus) crossed by weak spiral striae forming granules at points of intersection. Colour uniformly pale yellowish-brown (Figs 29k-m).

#### Dimensions:

	height	diameter
Probable original of Chemnitz figures 1700-1.	39.0 mm	83.0 mm
Holotype of <i>S. solaris paucispinosa</i> (from original description)	56.3	93.0
Holotype of <i>X. solariformis</i> (from original description)	—	57.0
Large specimen (Saudi Arabia, AMS)	55.0	126.8
Figured specimen (Persian Gulf, BMNH)	37.7	68.8

**Operculum:** Thin, yellow, growing edge strongly convex, nucleus at about left  $\frac{1}{3}$ . Sides nearly straight. External surface smooth except for concentric growth lines and closely spaced radial striae. Central area broad, yellowish-white, opaque (remainder of operculum semi-transparent); a thin extension to right side of attachment scar. Central area conspicuous through free surface which has close, weak concentric lamellae (Fig. 6a).

**Radula:** Central teeth with 2 cusps on either side of the rather small median cusp. Lateral teeth sub-rectangular, with sharp cusps and very weakly serrate cutting edge. Marginal teeth finely serrate (Fig. 10b).

**Anatomy:** Similar to *X. neozelanica* except that the gill filaments are relatively longer, the mantle edge is smooth except for very short papillae on the left side, there is no distinct sole on the metapodium and the salivary glands are of medium size, the left being nearly twice the length of the right. Penis not known. Head-foot shown in Fig. 4c. Material examined:  $28^{\circ}58'N$ ,  $49^{\circ}34'30'E$ , Persian Gulf, 49 m (ZMC) (3 females).

**Location of types and type localities:** *T. solaris*: Dodge (1958) noted that this species is not represented in the Linnean collection but that Linné gave the specimen (possibly his only one) on which his first description (1764) was based to Queen Louisa Ulrica, and that shell is now in the University of Uppsala. This specimen is therefore, regarded as the holotype. The two figures cited by Linné (1764) therefore, have no type status. The locality given by Linné (1764) is Java.

*A. polaris*: Based on Chemnitz, 1781, pl.173, figs 1700, 1701. A specimen in the ZMC marked original of figs 1700-1701 is not in fact that specimen. However, another specimen in

that Museum does agree extremely well with figures 1700-1701 and is probably the figured specimen; Nicobar (Fig. 29k-l).

*X. solariformis*: Station XVIII, Noil Lioe, between Pene and Niki-Niki, Timor, Indonesia; Pliocene. Location of holotype not known.

*S. solaris paucispinosa*: Holotype, Coral Museum, Tatsukushi, Tosa-Shimizu City, Japan; paratypes California Academy of Sciences, San Francisco, BMNH, USNM; off Aden, Gulf of Aden, 85 m.

**Fossil record:** Pliocene: Timor (type locality of *X. solariformis*).

**Other material examined:** *Gulf of Aden:* (USNM). *Red Sea:* Off Mersat, Abu Samran, Gulf of Aqaba, 183-229 m (Tel Aviv Univ.). Eritrea coast, Ethiopia (AMNH). *Gulf of Oman:* Al Khaburah, Oman, 44-47 m (MCZ). Daba, Oman, 79 m (MCZ). 25°38'N, 56°26'E, 73 m (BMNH). 25°50'N, 57°07'E, 91-95 m (MCZ). Chah Bahar, Iran, 30 m (AMNH), 19 km S.W., 110-121 m (MCZ). 37 km W. of Ras Beris, E. of Chah Bahar, 110-123 m (MCZ). *Persian Gulf:* W. of Vadasht, Saudi Arabia, 26°46'N, 56°47'E, 46-48 m (MCZ). S.E. of Larak Ids, Strait of Hormuz, 64 m (ZMC). S.E. of Bandar e Lengeh, 26°05'N, 55°33'E, 77 m (RNHL). 26°55'N, 53°08'E, 65 m (ZMC). N.E. of Qatar, 50 m (RNHL). Rás-e Barkan, 29°07'N, 49°56'E, 41 m (ZMC). W. of Bushehr, 28°58'N, 49°34'E, 49 m, 32 m (ZMC). 85 km W.S.W. off Khark Is., 44 m (ZMC). Kuh-i-Manner, 82 m (BMNH). *Pakistan:* 19 km S. of Gwatar Bay, border of Pakistan and Iran, 109 m (MCZ). 21 km S. of Astola Is., 90-101 m (MCZ). 84 km S.S.E. of Ormara, 7 m (MCZ). W. of Ras Muari, 121-122 m, 93-100 m, 75 m (MCZ). 84 km S.W. of Karachi, 80-82 m (MCZ, USNM). 168 km S.W. of Karachi, 88-91 m (MCZ). 257 km S. of Karachi, 110 m (MCZ). S. of Korangi, Karachi, 18-20 m, 51-55 m (MCZ). Karachi (ANSP). *India:* Mandvi, Gulf of Kutch, Gujarat, 57 m (MCZ). 50 km S. of Dwarka, Gujarat, 50-52 m (MCZ), 139 km W., 108-114 m (MCZ). Off Mangrol, Gujarat, 101 km at 70-72 m, 31 km at 62-64 m (MCZ). 71 km S.S.W. of Veraval, Gujarat, 71-79 m (MCZ). 172 km W. Janjira, S. of Bombay, 95-100 m (MCZ). 64 km W. of Arrah, 17°54'N, 72°27'E, 46-55 m (MCZ). Goa, near Panjim, W. coast (USNM). Tranquebar, Coromandel coast, Bay of Bengal (ZMC). Madras, Coromandel coast, Bay of Bengal (ANSP, BMNH). 20°37'N, 87°33'E, Bay of Bengal, 68 m (ZMC). *Bangladesh:* 144 km S. of Chittagong, 22 m (ANSP). *Burma:* 27 km E.S.E. of Sittwe (Akyab), 55 m (ANSP). 56 km S.E. of the Irrawaddy Delta, 22 m (ANSP), 64 km S., 29 m (ANSP). Preparis North Channel, 53 m (ANSP). 91 km N.W. of Tavoy Is., 39 m (ANSP). *Andaman Islands:* Diligent Strait, South Andaman Is., 38 m (ANSP). Port Blair (BMNH), 18-22 km N.N.W. of Port Blair, South Andaman Is., 49 m, 90 m (ANSP). *Thailand:* 40 km N.N.W. of Phuket Is., 42 m (ANSP). Songkhla, Gulf of Siam, S. Thailand (MCZ). Phuket (BMNH). *Malaya:* Selangor (ZMC). *Singapore:* (USNM, ANSP, AMS, NMW, BMNH). *China Sea:* (USNM, AMS). South China Sea, 3°34.4'N, 110°13.0'E, 115 m (BMNH). 3°32.6'N, 110°12.7'E, 117-91 m (BMNH). *Philippines:* Lingayen Gulf, Luzon (DMNH). San Fernando Point, Lingayen Gulf, 82 m (USNM). Subic Bay, Bataan, Luzon, 60 m (USNM). Tayabas Bay, Manila, Luzon (AMS). Daram Is., Samar Sea, 48 m (USNM). Samar Sea, 64 m (USNM). Marinduque Is., 100 m (USNM). Masbate, Masbate Is. (DMNH). Malampaya Bay, N. Palawan, 55-91 m (DMNH). Malampaya Sound, N. Palawan, 26-46 m (USNM). Palawan (ANSP). Carigara Bay, Leyte Is. (DMNH), 27-36 m (FMC). *Indonesia:* Straits of Malacca (USNM). W. Coast of Borneo (WAM). Makassar Strait, 50 m (ZMC). Madura, Djawa (Java) (RNHL). Moluccas (USNM). Ambon (Amboina) (IRNSB). *Malaysia:* W. Bangney Channel, off Balambangan Is., Sabah (N. Borneo) (WAM). Marudu Bay, Sabah (N. Borneo) (DMNH), 22-36 m (ANSP, USNM).

**Other records:** *Mozambique:* Inhambane (Braga, 1952, fide Barnard, 1963).

**Distribution:** Northern Indian Ocean, Red Sea, Persian Gulf and central Indo-Pacific with only one record from mid-east Africa; on the continental shelf in 18-200 m (Fig. 39).

**Remarks:** Dodge (1958) discussed at length the history of this species and the figures on which Linné based his name.

The subspecies name *paucispinosa* Kosuge & Nomoto was introduced for specimens from the Gulf of Aden. These authors cited 3 minor sculptural differences, a greater number of whorls having objects attached to them and fewer spines as the reasons for distinguishing their subspecies. Although some other material seen from the Red Sea — Persian Gulf area agrees with Kosuge's material, other specimens from the same area agree well with typical *X. solaris* or are intermediate. On the available evidence the differences cited by Kosuge & Nomoto do not seem to indicate anything more than a local variation. A heavily agglutinated specimen from the Persian Gulf is figured (Fig. 29m).

A study of the figures and description of the holotype of *X. solariformis* Tesch from the Pliocene of Timor indicates that this specimen appears to fall within the range of variation of Recent specimens of *X. solaris*. The only distinguishing feature noted by Tesch is the granulation of the dorsal axial sculpture in the fossil form which he maintains is not present in Recent specimens. This is not the case, Recent specimens, particularly those in the eastern part of the range of the species, tend to develop granulose sculpture on the axials.

There does not appear to be any fossil record below the Pliocene and the relationships of this species to others in the genus are not obvious. The spinose development of the periphery is presumably an adaptation to raise the base from the substrate in the same way as the large attached objects or the wide peripheral flange do in some other species.

### ***Xenophora (Stellaria) testigera digitata* Martens, 1878.**

Figs 10d, 14m, 30a-c, 38.

*Xenophora digitata* Martens, 1878: 135; Adam & Knudsen, 1955: 7, pl. 1, figs 6-9, text fig. 1B; Le Loeuff *et al.*, 1971: 501.

**Shell:** Medium spire (spire angle 75°-86°), solid, with peripheral flange divided into 8-10 (usually 8) prominent, blunt digitations each bearing a foreign object distally. Umbilicus small, about ½ covered by inner lip. Whorls almost flat, sculptured with wavy spiral to sub-spiral lirae crossed by irregular growth lines. Base lightly convex, with distinct collabral growth lines which are lamellate within umbilicus, and with a trace of spiral ornament (Fig. 30a-c).

#### **Dimensions:**

	height	diameter
Holotype	38.2 mm.	56.3 mm.
Large specimen (S.W. Africa, Natal Museum)	65.0	80.7

**Operculum:** Oval, brown, all sides convex. Nucleus very slightly displaced to left. Exterior smooth except for concentric growth lines. Central area small, thickened, not easily distinguishable through free surface, which is sculptured with close concentric lamellae.

**Radula:** Central teeth with rather large, triangular median cusp with about 3 small, irregular denticles on either side. Lateral teeth subrectangular, with a short, broad cusp on inner edge of cutting edge; a small basal process sometimes present on inner basal edge. Marginal teeth smooth (Fig. 10d). Also figured and described by Adam & Knudsen, 1955: 9, fig. 1B.

**Anatomy:** Similar to that of *X. neozelanica* except that the very thick mantle edge lacks any tentacles, the foot has no sole and the salivary glands are subequal and of medium size. The eyes are very small. The penis is extremely large, flattened, with a simple flattened distal portion bearing, in 2 of the 4 specimens, an irregular glandular frill; sperm groove closed over along all but the distal section, terminating at distal end. A laterally subspinose ridge runs along the sperm duct in the median as well as, in some specimens, the proximal, sections of the penis (Fig. 14m). Material examined: N. of Port-Gentil, Gabon, West Africa (IRNSB) (4 males, 2 females).

**Location of type and type locality:** Holotype, EBM, 29316; "Gazelle" Stn, 10°6.9'N, 17°16'W, 274m, West Africa (Fig. 30a-c).

**Fossil records:** None known.



**Other material examined:** *Senegal*: 14°53'N, 17°32'W, 457m (FMC). Off Cape Verde, 457m (FMC). *Portuguese Guinea*: Bijagos Ids, Bissagos Bank, 266-350m (BMNH). *Gulf of Guinea*: 2°09'N, 9°27'E, 260-650m (ZMC, AMS). *Gabon*: 294m (USNM). N. of Port Gentil (IRNSB). *Congo*: Off Pointe Noire, 200m (ANSP), 295-305m (ANSP). *South-West Africa (Namibia)*: Approx. 240km N.N.W. of Walvis Bay, 329-366m (Natal Museum).

**Other records:** Cape Verde to Angola from 100m to 440m (Le Loeuff *et. al.*, 1971: 507). Between 10°05'N and 7°16'S, West Africa, in 230-440m (living material); empty shells between 0° and 10°39'S, 170-263m (Adam & Knudsen, 1955).

**Distribution:** Senegal to Namibia, West Africa; 100-650m (Fig. 38).

**Remarks:** The distribution and ecology of this species have been discussed recently by Le Loeuff *et. al.* (1971). It cannot be confused with any other Recent species but is clearly conspecific with the Tertiary species *X. testigera* (Bronn, 1832). The Recent and fossil forms are here regarded as chrono-subspecies. *X. testigera testigera* ranges from the Oligocene to the Pliocene of Europe (see Sacco, 1896: 24, pl. 10, figs 1, 2) and is very similar to *X. testigera digitata* and presumably ancestral to it. The shell of the fossil subspecies has stronger and more oblique (almost spiral) riblets dorsally and much stronger spiral sculpture on the base than that of the living subspecies. In addition the digitations in the fossil form are relatively shorter than in the Recent one. *X. conica* Dall, from the Eocene of Mississippi, also appears to be related to *X. testigera* but is smaller (diameter 18mm).

The subgeneric placement of this species is not completely satisfactory, although it agrees with *X. solaris* in having a relatively smooth shell, a smooth mantle edge, and in lacking a distinct metapodial sole. The penial characters are very different from any other species of *Xenophora*. Possibly *testigera* represents a separate, early off-shoot from the *Stellaria* group at a point when the ancestral *Stellaria* species were little differentiated from *Xenophora* s.s. The discordant shell features are the relatively narrow peripheral flange (except for the digitations) and the small umbilicus.

***Xenophora (Stellaria) testigera profunda* n. subsp.**

Figs 30d-f, 40.

**Shell:** Very similar to *X. testigera digitata* but differs in its lighter shell, finer dorsal sculpture which is opisthocline not subspiral, and more numerous digitations (10-13 on the body whorl compared with 8-10 in *X. testigera digitata*). Spire angle 76° (Fig. 30d-f).

**Dimensions:**

	height	diameter
Holotype	46.1 mm.	60.6 mm.
Paratype	50.5	63.2

Operculum, radula and anatomy unknown.

**Location of type and type locality:** Holotype BMNH (19787) and 8 paratypes, 1 adult, 3 subadults (fragmentary) and 3 juveniles (in poor condition), BMNH (19788); 1 paratype (adult) AMS (C.116767); 12°04'06"N, 50°38'36"E, off the coast of Somali Republic, N.E. Africa, 655-732m, 2 May 1934, John Murray Expedition, Station 176 (Fig. 30d-f).

**Locality of additional paratypes:** 13°14'24"N, 46°14'12"E to 13°13'24"N, 46°10'00"E, 457-549m, off Aden, Democratic Republic of Yemen, Gulf of Aden, John Murray Expedition, Station 35, 4 paratypes, BMNH (19789).

**Distribution:** Gulf of Aden and northernmost E. Africa, 450-730m (Fig. 40).

**Remarks:** Although known only from two samples (13 specimens), the new subspecies, being located in the Indian Ocean and the Gulf of Aden is very widely isolated from the Recent Atlantic subspecies. Presumably they either had a common ancestor in *X. testigera* which was present in the Mediterranean Sea during the early Miocene and late Oligocene and which could



have migrated into the then open Persian Gulf, or the Atlantic population of *X. testigera* may have migrated around South Africa during a rise in sea temperatures and then retreated northwards along both coasts of Africa. The absence of records from deep-water investigations along the eastern coast of South Africa suggests that a Mediterranean origin is the more likely one.

The new subspecies differs from *X. testigera testigera* and *X. testigera digitata* in its thinner shell, more numerous digitations and much weaker dorsal and basal sculpture.

***Xenophora (Stellaria) chinensis chinensis* (Philippi, 1841).**

Figs 10c, 14n, 29c-g, 40.

*Trochus chinensis* Philippi, 1841: 8 (not homonymous with *Trochus sinensis* Gmelin, 1791).

*Phorus calculiferus* Reeve, 1842: 161, pl. 215, fig. 7; Reeve, 1843a: 162; Reeve, 1843b: pl. 1, fig 1.

*Onustus calculiferus*. — H. & A. Adams, 1854: 362.

*Xenophora chinensis*. — Philippi, 1855: 348, pl. 49, fig. 1.

*Xenophora calculifera*. — Fischer, 1879a: 438, pl. 7, fig. 1; Tryon, 1886: 159, pl. 44, figs 75, 76; Altena, 1942: 40; Habe, 1953a: 177, text figs 16, 17; Habe, 1964: 57, pl. 16, fig. 4; Ladd, 1977: 16, pl. 22, figs 4-6.

*Xenophora (Tugurium) calculifera*. — Schepman, 1909: 205.

**Shell:** Depressed, about twice as wide as high (spire angle  $95^\circ$ ) with moderately wide, simple, peripheral flange (30-37% of total base diameter). Umbilicus broad, deep, all whorls visible within, partly covered by inner lip, partially filled by an overlapping series of very fragile periostracal leaves emerging from the crest of each collabral lamella and easily eroded away completely. Row of foreign objects usually narrow, the objects small, most of dorsal surface exposed. Whorls slightly convex, sculptured dorsally with fine but distinct, opisthocline, granular, close-set, somewhat irregular ridges crossed at right angles by undulating growth rugae. Base very lightly convex, with close, moderately strong spiral ridges crossed by radial (collabral) ridges, the points of intersection forming distinct beads; radials weakly lamellate within umbilicus. Colour pale yellowish-brown to yellowish-white, aperture largely white (Fig. 29c-g).

**Dimensions:**

	height	diameter
Large specimen (near Manila, Philippines, AMS)	45.0 mm	81.8 mm
Figured specimen (W. of Dirk Hartog Is., Western Australia, WAM)	46.0	68.9

**Operculum:** Almost identical to that of *X. solaris*.

**Radula:** Central teeth with 3 cusps on either side of the rather large, sharp median cusp. Lateral teeth rectangular, with small cusps; marginal teeth smooth (Fig. 10c).

**Anatomy:** Similar to that of *X. neozelanica* but the mantle edge is smooth except for a few short papillae on left side, the foot has no sole and the opercular lobe is relatively larger. The salivary glands are large, the left slightly larger; the gill filaments are very long; the eyes minute and the snout has a weak lateral ridge distally on each side. Penis in submature specimen rather short with a swollen, probably glandular, distal end deeply dissected longitudinally by the penial groove (Fig. 14n). Material examined: Off Cape Possession, near Yule Is., Gulf of Papua (AMS) (1 submature male, 1 immature male, 1 immature female).

**Location of types and type localities:** *T. chinensis*: Location not known; China. *P. calculiferus*: Not located in BMNH, assumed lost; locality unknown.

**Fossil material examined:** Pliocene: Son dé beds, Java (stn 11151) (3 specimens) (RGM) (Fig. 29f, g). Seria Formation, Sarawak, Borneo (BMNH, 170/6) (3 specimens). Kankasanturai, N. of Jaffna, Sri Lanka (BMNH, G. 51081-2) (2 specimens). Near Tanga, Tanganyika (= Tanzania) (this specimen was recorded by Nuttall & Sealy (1961) as *X. corrugata* but examination of the material suggests it is probably a specimen of *X. chinensis*). Pleistocene: Santo, New Hebrides (USNM) (recorded by Ladd, 1977).

**Other fossil records:** Upper Miocene: Rembang, Java (Pannekoek, 1936). Pliocene: Kendeng Beds, East Java (Altena, 1942).

**Other material examined:** *Red Sea:* (BMNH). *Persian Gulf:* 26°05'N, 55°33'E, 77m (RNHL). "Kuh-i-Mannaar" (BMNH). *Andaman Islands:* 19km N.W. of Point Blair, South Andaman Is., 90m (ANSP). *Burma:* 104km W. of Tavoy City, 62m (ANSP). 56km W. of Tavoy Is., 68m (ANSP). *Thailand:* 88km W. of Ranong, 73m (ANSP). *Singapore:* (USNM, AMS). "Tangong Katong" (NMW). *South China Sea:* 5°04'N, 110°45'E, 130m (BMNH). 3°34.4'N, 110°13'E, 115m (BMNH). *Hong Kong:* (EBM, USNM). Off Cape St. Mary (AMS). 22°25'N, 114°25'E, 20m (BMNH). *China:* (ANSP, FMC). Off Hainan Tao Is. (ANSP, BMNH). *China Sea:* (USNM, AMS). *Japan:* (USNM). *Philippines:* Linapacan Strait, 84m (USNM). Luzon (USNM). Batangas Bay, Batangas, Luzon, 4m (WAM). Tacbue Point, Leyte, 113m (USNM). Laoy Is., Bohol Strait (WAM). Makibojoc Bay, Bohol Is., 64-91m (WAM). South Panglao Is., off Bohol Is., 73-141m (WAM). *Indonesia:* Butung Strait, W. of Butung Is., Sulawesi (Celebes), 68m (USNM). N.W. of Tajandu, Palau Palau Is., Moluccas, 128m (WAM). W. Wasir Is., off Wokam Is., Kepulauan Aru, Moluccas, 22-45m, 57-73m (WAM). W. of Udjir Is., off Wokam Is., Kepulauan Aru, Moluccas, 91-95m (WAM). 12.4km S.W. of Maikoor Wokam Is., Kepulauan Aru, Moluccas, 58-77m (WAM). *Australia:* *Western Australia:* Dampier Archipelago (WAM). Between Shark Bay and Onslow (WAM). W. of North West Cape, 123-128m, 137m (WAM). 16km N. of Long Is., Onslow, 95m (WAM). W. of Dirk Hartog Is., 130m (WAM). W. of Shoal Point, 110m (WAM). *Papua:* Off Yule Is., 27m (AMS). 2km off Cape Possession, 22-33m (AMS).

**Other records:** *Japan:* Wakayama Pref., Honshu (Habe, 1953a). *Taiwan:* (Habe, 1953a).

**Distribution:** Red Sea, Persian Gulf, eastern Indian Ocean and central Indo-Pacific north to Japan and south to Papua; 4-140m (Fig. 40).

**Remarks:** The shell of this species is easily distinguished from all other Recent species, except *X. lamberti* Souverbie, by its wide umbilicus and (usually) heavily spirally ridged base. The shell of *X. dunkeri* Martin, 1879 (Fig. 29a, b) from the Miocene of Java has a slightly flatter base with a narrower peripheral flange and the basal sculpture is broken into squarish "granules", the spirals being relatively weaker than in the Recent *X. chinensis*. It is, however, identical to shells of *X. chinensis* in all other features and is here regarded as a chrono-subspecies.

The Japanese Miocene *Tugurium matsuo*i Ogasawara, 1976 and *T. makiyamai* Itoigawa & Nishikawa, 1976 are probably based on the same species and appear from the examination of topotypes and the original description and figures to be related to *X. chinensis*, not to *X. exuta* as their authors maintained.

This species is closest to *X. lamberti*, which differs in its more rapidly descending peripheral flange, the strong spirals on the base persisting to the inner edge of the peripheral flange, its more convex base and its narrower umbilicus.

Overlapping sheets of periostracum are seen in the umbilicus of the shell of most specimens of this species collected alive and not subjected to any form of cleaning. They are extremely fragile and are found in both sexes. Their function is unknown and similar structures have not been observed in any other species.\*

\*Since this paper went to press similar structures have been observed in a living specimen of *X. (S.) gigantea*.

**Xenophora (Stellaria) lamberti** Souverbie, 1871.

Figs 28a-e, 40.

*Xenophora lamberti*. Souverbie, 1871: 334; Souverbie, 1872: 54, pl. 1, fig. 5; Fischer, 1879a: 435, pl. 44, fig. 1.

*Tugurium lamberti*. — Mallory, 1977b: 8, fig. on p. 10.

**Shell:** Depressed (spire angle  $104-108^\circ$ ) with moderately wide peripheral flange. Umbilicus rather narrow, deep, covered by reflexed callus of inner lip in adult, open in juvenile. A row of rather small foreign objects on peripheral flange of all whorls of teleoconch, about half of dorsal surface of each whorl exposed. Whorls weakly convex, sculptured dorsally with close, fine but distinct opisthocline riblets crossed by fine prosocline growth lines. Base strongly convex, sharply separated from peripheral flange, sculptured with strong, collabral riblets crossed by close, narrow spiral cords in juvenile. Spiral sculpture increases in strength in adult and axial sculpture weakens. Colour white (Fig. 28a-e).

**Dimensions:**

	height	diameter
Holotype	26.6 mm	52.2 mm
Small specimen	15.4	32.6

Operculum, radula and anatomy unknown.

**Location of type and type locality:** Musée d'Histoire Naturelle, Bordeaux, France, holotype; Ile des Pins, New Caledonia (Fig. 28a, b).

**Fossil records:** Pleistocene: Quarry at Banat-Ouloup, Ouvéa Is., Loyalty Islands (Doiteau Colln, New Caledonia) (Fig. 28c-e).

**Distribution:** New Caledonia and Loyalty Islands (Fig. 40).

**Remarks:** This species is known only from the holotype and a small specimen collected in Pleistocene deposits in the Loyalty Islands. The holotype could be a fossil judging from the condition of the shell so that it is possible that this species is now extinct.

Mallory (1977b) places this species in "*Tugurium*" (= *Onustus* herein) but the ventral surface of the peripheral flange is covered with a smooth, non-porcellanous layer of shell, forming the typical double layered flange of *Stellaria*. The nearest relative of this species appears to be *X. (Stellaria) chinensis* with which it is contrasted above.

The impression that *X. lamberti* fixes material to the sutural area of the shell, not to the periphery (Linsley & Yochelson, 1973) is incorrect, the peripheral flange being partly broken away in the type specimen. The (secondary) sutural attachment of objects is that normally seen in most species of *Xenophora*. Those objects which are initially attached to the periphery of the juvenile or subadult and protrude beyond the shell margin will eventually lie on the upper part of the whorl immediately below, as the shell grows, and become cemented to it.

**Xenophora (Stellaria) gigantea** Schepman, 1909.

Figs 29h-j, 40.

*Xenophora gigantea* Schepman, 1909: 204, pl. 13, fig. 1.

*Trochotugurium giganteum*. — Habe, 1953a: 177, figs 1, 2.

*Tugurium (Trochotugurium) giganteum*. — Kilburn, 1973: 562, fig. 5 (radula).

**Shell:** Large, thin, with moderate spire (spire angle  $81-84^\circ$ ), with wide, simple peripheral flange (about 35% of total width of base). Umbilicus distinct, deep, all whorls visible within, partly covered by inner lip. Narrow row of foreign objects on all whorls, most of dorsal surface exposed. Whorls very slightly convex, sculptured dorsally with distinct opisthocline, rather wavy

riblets crossed by fine prosocline growth lines. Base convex, smooth except for weak growth lines, which become lamellate in umbilicus. Colour pale brown to yellowish-white (Fig. 29h-j).

#### Dimensions:

	height	diameter
Holotype (from original description)	60 mm	98 mm
Off Ponta Falsa, Mozambique (from Kilburn, 1973: 562)	63	111

**Operculum:** Rather thin, subopaque, brown, with distinct concentric growth lines externally. All sides convex; nucleus at approximately left  $\frac{1}{3}$ ; central area yellowish to brown, slightly thickened, broad, a very narrow extension to left side of attachment scar (less obvious than in *X. solaris*), partially obscured over free surface by concentric lamellae.

**Radula:** Kilburn, 1973: 563, fig. 5.

**Anatomy:** Not known.

**Location of type and type locality:** Holotype and paratype, ZMA, 2532; "Siboga" Stn. 38, 7°35.4'S, 117°28.6'E, Flores Sea, Indonesia, 521m, "in coral" (Fig. 29h-j).

**Fossil records:** None known.

**Other material examined:** *South Africa:* Durban, Natal, 274m (DMNH). *Mozambique:* Bazaruto Is., 600m (AMNH). *Chagos Archipelago:* 4°58'42"S, 73°16'24"E, 494m (BMNH). *Singapore:* 18m (USNM). *Taiwan:* (ANSP). *Japan:* (AMNH, AMS). Mikawa, 128m (USNM). Shiono-misaki (Kii) (FMC, AMS). Tosa Bay, Shikoku (ANSP), 311m (FMC), 274m (DMNH). *Philippines:* Tayabas Bay, W. of Batangas, Luzon (AMS). N.W. of Basilan Island, Sulu Archipelago, 64m (USNM). *Indonesia:* Kepulauan Kai, Moluccas, 345m (ZMC). *Western Australia:* 220 km NW of Port Hedland, 507m (AMS). *Eastern Australia:* E. of Tweed Heads, New South Wales, 28°01'-27°58'S, 154°00'E, 550m (AMS).

**Other records:** *Mozambique:* Off Ponta da Barra Falsa, 530m (Kilburn, 1973). *Malagasy Republic:* 23°36.0'S, 43°29.6'E, 600-610m, 22°21.6'S, 43°04.3'E, 450m, 12°26.2'S to 48°13.0'E, 2°53.3'S, 48°09.4'E, in 350-705m (several lots) (*vide* R. Kilburn *in litt.*; from A. Crosnier Colln., O.R.S.T.O.M.).

**Distribution:** South Africa (off Durban) to Mozambique, E. Africa, Chagos Archipelago, Indian Ocean, and the central Indo-Pacific (southern Japan to north-western Australia and northern New South Wales); 60-700m (one record at 18m needs to be confirmed) (Fig. 40).

**Remarks:** This species probably evolved from the same group as *X. chinensis*, perhaps migrating through the Tethys Sea during the late Eocene or Oligocene. Unfortunately, however, there is no known fossil record of this species.

Morphologically and in size the shell of *X. gigantea* is closest to *X. chinensis* but it can be readily distinguished by the lack of spiral sculpture on the base. The opercula of the two species also differ, that of *X. gigantea* being thicker and less oblique than that of *X. chinensis*.

Subgenus **Onustus** Swainson, 1840: 352.

Type species: (subsequent designation Gray, 1847: 158) *Onustus indicus* (Gmelin, 1791) = *Trochus indicus* Gmelin, 1791: 3575.

Synonyms: *Onustus* *err. auct.*

*Tugurium* P. Fischer (*in* Kiener) 1879: 450. Type species: (subsequent designation Cossmann, 1888: 192) *Xenophora indica* (Gmelin, 1791) = *Trochus indicus* Gmelin, 1791.

*Trochotugurium* Sacco, 1896: 27. Type species: (original designation) *Tugurium (Trochotugurium) borsoni* ("Bellardi") Sisonda, 1847:50.

**Diagnosis:** Shell thin, with wide peripheral flange simple or weakly digitate, porcellanous below. Umbilicus narrow to wide, sometimes plugged with callus. Foreign objects attached to



periphery on few to all whorls, small and inconspicuous, leaving most of shell surface exposed. Foot lacks sole on metapodium, mantle edge smooth, ctenidial filaments very long. Operculum radially ridged externally or almost smooth, bearing only very fine radial striae.

**Remarks:** Gray (1847: 158) included both *Trochus indicus* and *T. solaris* in the genus *Onustus* but in his introduction (p.129) he states that he lists "the first name given to the genus and the type on which it was founded, and then to accumulate the synonyma around the genus. Where a succeeding author has referred to a different species as the type of the genus, I have given the name in a new line, as at some future period that type may be proved really to belong to a different genus". It is therefore clear, that Gray intended *T. indicus* as the type species of *Onustus* as *T. solaris* was listed on a new line below *T. indicus*.

There have been differences of opinion as to whether *Onustus* represents a genus distinct from *Xenophora*. The porcellanous ventral surface of the peripheral flange seems sufficient justification for subgeneric separation, but because of the overall general similarity of all other characters, generic separation from *Xenophora* is not advocated here. The anatomical characters of *Onustus* and *Xenophora* s.s. differ slightly, *Onustus* species having longer ctenidial filaments than species of *Xenophora* s.s. and lacking a distinct metapodial sole. The opercular lobe is very long and the mantle edge smooth but in other features the anatomy resembles that of species of *Xenophora* s.s. The differentiating anatomical features of *Onustus* are also shared by most species of *Stellaria*, but they, like the species of *Xenophora* s.s., do not have the porcellanous layer exposed on the ventral side of the peripheral flange, because it is composed of two shell layers, not one as in *Onustus*.

When Sacco (1896) tentatively introduced *Trochotugurium* for the Italian fossil species *Tugurium* (i.e. *Onustus*) *borsoni* he stated that it was closely related to *Tugurium* but differed in having a taller spire and almost closed to closed umbilicus. This subgenus name has been used for *X. gigantea* Schepman (by Habe, 1953a) and *X. longleyi* (by Clench & Aguayo, 1943). Sacco (1896) mentioned the narrow, but fragile peripheral flange of *X. borsoni* of which only a trace has been preserved in a few specimens. Examination of some of his material in the Geological Museum, Turin, shows that one specimen still retains a fragment of the flange which is the same type as that seen in Recent *Onustus* species. The only observable difference between *Trochotugurium* and *Onustus* appears to be the narrow umbilicus of *X. borsoni*. This is not considered to be of sufficient importance to warrant subgeneric separation.

There are 4 Recent species of *Onustus*; 2 in the Indo-Pacific and 2 in the Western Atlantic. In both areas, each pair of species is sympatric and the two species of each pair more closely resemble one another than either of the other species.

#### KEY TO RECENT SPECIES OF THE SUBGENUS *ONUSTUS* BASED ON SHELL CHARACTERS

1. Peripheral flange (in adult) with small objects attached ..... 2
  - Peripheral flange (in adult) with no objects attached ..... 3
2. Base with spiral ridge near junction with peripheral flange ..... *caribaea*
  - Base evenly convex, radial lamellae at junction with peripheral flange ..... *longleyi*
3. Peripheral flange with scalloped edge ..... *exuta*
  - Peripheral flange with simple edge ..... *indica*

#### ***Xenophora* (*Onustus*) *indica*** (Gmelin, 1791).

Figs 4a-b, 6b, 11a, 12a, 14s, 31c-f, 41.

*Trochus indicus* Gmelin, 1791: 3575 (based on Chemnitz, 1781: pl.172, figs 1697,1698); Lamarck, 1822: 11.

*Phorus indicus*. — Reeve 1842: 161, pl.215, fig. 6; Reeve, 1843a: 161; Reeve, 1843b: pl.1, fig 2.

*Phorus exutus*. — Adams & Reeve, 1850: 50, pl.17, fig. 7 (*non* Reeve, 1842).



*Xenophorus helvaceus* Philippi, 1852: 44.

*Onustus exutus*. — H. & A. Adams, 1854: 362, pl.40, figs 1, 1a, 1b (*non* Reeve, 1842).

*Onustus indicus*. — H. & A. Adams, 1854: 362; Gray, 1857: 131 (cites Figures in Gray, 1850: pl.122a, figs 2a-g); Melvill & Sykes, 1899: 227; Habe, 1953a: 180, fig. 15.

*Xenophora helvacea*. — Philippi, 1855: 343, pl.47, fig. 1; Fischer, 1879a: 432, pl.53.

*Xenophora indica*. — Philippi, 1855: 344, pl.47, figs 4, 5; Fischer, 1879a: 433, pl.9, fig. 1.

*Xenophora wagneri* Philippi, 1855: 345; pl.47, figs 2, 3; (based on Schubert & Wagner, 1829: pl.229, figs 4062a, 4062b and Reeve, 1843b: pl.1, fig. 2).

*Xenophora (Tugurium) indica*. — Tryon, 1886: 161, pl.46, figs 92, 93.

*Xenophora (Tugurium) helvacea*. — Tryon, 1886: 162, pl.47, fig. 96.

**Shell:** Depressed (spire angle  $92^{\circ}$ - $100^{\circ}$ ), with rather wide, simple (but often ragged), thin peripheral flange (30-35% of total diameter of base). Umbilicus prominent, deep, all whorls visible within, partly covered by inner lip. Row of foreign objects restricted to first few whorls of teleoconch, the last 2-3 whorls completely free of attachments. Whorls slightly convex, peripheral flange concave dorsally. Dorsal surface sculptured with distinct, somewhat irregular, opisthocline, close-set riblets, these often broken up by distinct, irregular growth lines running at right angles to them. Base lightly convex to almost flat with a concave portion near outer edge bordered on its outside by a low fold bearing 0-4 weak, spiral ridges which are rendered weakly gemmate by distinct, rather regular, close-set collabral growth ridges which traverse the entire base, become subfoliate within umbilicus and terminate abruptly at junction with peripheral flange. Peripheral flange porcellanous below. Colour yellowish-white to pale orange-brown, base often white, sometimes with an orange-brown band at edge of base; surface shining (Fig. 31c-f).

#### Dimensions:

	height	diameter
Lectotype of <i>Trochus indicus</i> (lacks peripheral flange)	22.5 mm	44.7 mm
Lectotype of <i>X. wagneri</i>	38.3	68.1
Large specimen (Tin Can Bay, Queensland, AMS)	40.0	83.5

**Operculum:** Elongately oval, brown, rather thin; growing edge convex. Nucleus at about left  $\frac{1}{3}$ ; right end rather sharply pointed, sides nearly straight to slightly concave or convex. Sculptured with heavy, radial ridges on outer surface which are rendered minutely foliate by dense concentric lamellae. Central area slightly thickened, broad, yellowish, mostly obscured over free surface by concentric, close lamellae (Fig. 6b).

**Radula:** Central teeth with large, broad median cusp and 3 small lateral cusps on each side. Lateral teeth subrectangular, with small, sharp cusp at inner end, cutting edge with a few small, blunt cusps. Marginal teeth with sharp denticles (Figs 11a, 12a).

**Animal:** Adams & Reeve (1850) note (as *P. exutus*) that the tentacles are longer and the eyes smaller than in *P. solarioides* and the eyes are in only very slight swellings. Several sketches of the animal published by Gray (1850, pl.122a, figs 2a-g) are apparently based on living specimens. Head-foot shown in Fig. 4a, b.

**Anatomy:** Similar to *X. neozelanica* but with relatively longer ctenidial filaments, much smaller eyes, short lateral ridges on snout (Fig. 4a, b), a smooth mantle edge, no sole on the metapodium and relatively smaller salivary glands, those of *X. indica* being about  $\frac{1}{2}$  the size of those of *X. neozelanica*. Penis parallel-sided, rather short, heavy, with an expanded distal portion. There appears to be glandular tissue interspersed amongst the muscular tissue of the distal portion, especially in the vicinity of the penial groove which is deep and pronounced in this area (Fig. 14s). Material examined: Off North Keppel Is., Queensland, Australia, 51 m (AMS) (2

females, 1 mature and 1 semi-mature male); E. of Keppel Ids, Keppel Bay, Queensland, 46-49 m (AMS) (3 females).

**Location of types and type localities:** *T. indicus*. Based on Chemnitz, 1781, pl.172, figs 1697, 1698. The original specimen is in the ZMC, together with two other specimens (Fig. 31c, d). The figured specimen is here designated lectotype; India.

*X. helvaceus*: Location of type not known; China Seas?

*X. wagneri*: Based on Schubert & Wagner, 1829, pl.229, figs 4062a, b, and Reeve 1843b, pl.1, fig. 2. The original specimen of Schubert & Wagner's figure is in the ZMC (Fig. 31e-f) and is here designated lectotype; East Indian Seas.

**Fossil material examined:** Pliocene: Seria Formation, Sarawak, BMNH (LAP276/7) (1 juvenile specimen).

**Additional material examined:** *Zanzibar*: W. of Ukombi Is., 11-16 m (ANSP). W. of Chumbe Is., 22-26 m (ANSP). 3 km E. of Nyange Is., 18-40 m (ANSP). *Malagasy Republic*: S.W. of Nossi Bé, 37 m, 64 m (ANSP). 11 km S. of Nossi Bé, 16 m (MCZ). 29 km N.E. of Nossi Bé, 29 m (ANSP). *Seychelles*: W. coast of Mahé, 36 m (BMNH). *Maldivé Islands*: Miladunmadulu Atoll (ANSP). E. of Fadippolu Atoll, 4-64m (ANSP). Kendikolu Is., 42-46m (ANSP). *Sri Lanka*: Gulf of Mannar (ANSP). *India*: Cochin (BMNH). Madras (BMNH). *Burma*: 16km S. of Akyab, 30m (ANSP). *Thailand*: Phuket Is. (ANSP, ZMC). Songkhla, Gulf of Siam (ANSP). *Singapore*: (ANSP). "China": (ANSP). *Hong Kong*: (AMS, EBM, BMNH). *Philippines*: Corregidor Is., Manila Bay, Luzon, 11-20m (ANSP). *Indonesia*: Sunda Strait, 52m (ZMC). S. of Wowoni Is., Sulawesi, 75-94 m (ZMA). Between Wowoni and Buton Ids, 4°20'S, 122°58'E, 75-94m (ZMA). Piru Bay, Ceram, 49-64m (WAM). W. Borneo, 0°30'S, 107°5'E (EBM). Auri Ids, Teluk Irian (Geelvink Bay), 31-36m (ANSP). N.W. of Walir, Kepulauan Kai, 80-84m (WAM). Kai Ketjil, 36m (WAM). Elat Bay, Kepulauan Kai, 49-64m (WAM). Maikoor, Kepulauan Aru, 60-64m (WAM). Trangan, Kepulauan Aru, 38-51m (WAM). W. Wokam, Kepulauan Aru, 40-57m (WAM). Udjir Is., Kepulauan Aru, 69-75m (WAM). *Australia*: *Western Australia*: S.W. of Jurien Bay, 146m (WAM). W. of Shoal Point, 110m (WAM). N.W. of Bluff Point, 99m, 130m (WAM). W. of Shark Bay, 73m (WAM). N. of Dirk Hartog Is., 73m (WAM). N.W. of Carnarvon, 128-130m (WAM). 16km W. of Bernier Is., 73m (WAM). W. of North West Cape, 122-128m, 137m (WAM). 23km W. of Eaglehawk Is., Dampier Archipelago, 26m (WAM). 11-13km N. of Delambre Is., 40m (WAM). 64km W. of Cape Jaubert, 40m (WAM). 32km N. of Adele Is., Bonaparte Archipelago, 73m (WAM). N.W. Holothuria Banks (13°08'S, 126°04'E), 55m (BMNH). 208 and 240km E.N.E. of Troughton Is., 91m (WAM). *Northern Territory*: Off Anson Bay (AMS). Clarence Strait, N.W. of Charles Point, 27m, 33m (WAM). S. of Bathurst Is., 53-59m (WAM). Off Port Darwin (AMS). Tree Point, Darwin (AMS). *Queensland*: Off Mornington Is., Gulf of Carpentaria (AMS). W. of Cape York, 51m (BMNH). Off Townsville (AMS). Off Cape Manifold (AMS). Keppel Bay, 27 m, 46-49m, 51m (AMS). Off Wide Bay, 55 m, 97 m (AMS). 40km S.E. of Double Is. Pt., 60m (AMS). Off Tin Can Bay (AMS). Off Caloundra (AMS). Off Mooloolaba, 128m (AMS). Off Jumpin Pin, 27°44'S; 153°28'E, 46m (AMS). Off S. Stradbroke Is., 47-58m (AMS). Off Southport (AMS). *New South Wales*: Off Tweed Heads (AMS). Off Evans Head (AMS).

**Other records:** South eastern Malagasy Republic, 25°11.2'S, 47°14.7'E, 85-90m (*vide* R. Kilburn, *in litt.*, A. Crosnier Colln., O.R.S.T.O.M.).

**Distribution:** Tropical Indian Ocean (excluding Arabian Sea), central Indo-Pacific and western-most Pacific (Hong Kong to southern Indonesia), northern and tropical-subtropical eastern and western Australia; 4-150m (Fig. 41).

**Remarks:** The three species' names in the synonymy are all clearly based on the one species. The type of *T. indicus* is a small, very worn specimen with the peripheral flange ground down to the periphery (Fig. 31c, d). The type of *X. wagneri* (Fig. 31e, f) is a rather worn shell but the periphery has been only slightly ground away, and *X. helvacea* is based on a specimen in excellent condition with the slightly ragged edge of the periphery untouched.

This species has a wide range over the tropical Indo-west Pacific and is sympatric with *X. (Onustus) exuta* throughout much of the area it occupies except eastern Australia and the northern and western parts of the Indian Ocean where only *X. indica* occurs. The shells of the two species can be readily distinguished by the scalloped peripheral flange of *X. exuta*, that of *X. indica* being simple. The peculiar radial sculpture on the operculum of *X. indica* is unique.

The shell of *X. (O.) imperforata* (Gabb) from the Miocene of Santo Domingo appears to be very similar to that of *X. (O.) indica* except that the umbilical area is almost closed by the reflexed columella.

***Xenophora (Onustus) exuta* (Reeve, 1842).**

Figs 11b, 13f, 14q-r, 31i-k, 41.

*Phorus exutus* Reeve, 1842: 161, pl. 215, figs 9, 10; Reeve, 1843a: 162; Reeve, 1843b: pl. 2, fig 7.

*Onustus exutus*. — H. & A. Adams, 1854: 362; Brazier, 1877: 3; Habe, 1953a: 179, text figs 7, 8; Kira, 1962: 32, pl. 15, fig. 4.

*Xenophora exuta*. — H. & A. Adams, 1854: 362, pl. 40, figs 1a, b; Philippi, 1855: 348, pl. 48, fig. 4; Fischer, 1879a: 430, pl. 22, figs 1, 2; Tryon, 1886: 161, pl. 46, figs 90, 91; Uchiyama, 1902: 2, pl. 22, figs 7-9; Yokoyama, 1927: 176, pl. 47, fig. 10; Nomura, 1935: 198, pl. 10, figs 25a, b.

*Tugurium exutum*. — MacNeil, 1960: 47, pl. 12, fig. 10; Kuroda, Habe & Oyama, 1971: 139, 92, pl. 20, figs 1, 2.

**Shell:** Similar to *X. (O.) indica* in general features but with a strongly and evenly undulating edge to the peripheral flange (and therefore suture on spire whorls) and a sharp angulation separating base and umbilicus (only a weak subangulation in *X. (O.) indica*). Peripheral flange wider (up to 40% of total diameter of base) than in *X. (O.) indica*. Attachment of foreign material restricted to first 1-2 whorls of teleoconch and material attached is usually minute and frequently not retained. Colour uniformly pale yellowish-brown, surface shining (Fig. 31i-k).

**Dimensions:**

	height	diameter
Large specimen (China, BMNH)	40.0 mm	97.5 mm
Figured specimen (off False Entrance, Western Australia, WAM)	33.5	63.7

**Operculum:** Almost identical to that of *X. solaris*.

**Radula:** Central teeth with small median cusp and 3 rather large lateral cusps on each side. Lateral teeth subrectangular, a sharp cusp at inner end and weak denticles on cutting edge. Marginal teeth smooth (Fig. 11b).

**Anatomy:** Similar to that of *X. indica*. Penis long, slender, with rather small distal portion; penial groove terminates in small papilla. Glandular expansion of distal portion on opposite side of penis to penial groove (Fig. 14q, r). Material examined: Off Cape Possession, near Yule Is., Gulf of Papua (AMS) (1 male and 4 semi-mature females).

**Location of type and type locality:** Holotype could not be located in BMNH; locality not known in original description but given as China by Reeve (1843b).

**Fossil material examined:** Pliocene: Nakoshi sand, Okinawa (USGS) (recorded by MacNeil, 1960). Vanua Levu, Fiji (USNM) (recorded by Ladd, 1972).

**Additional fossil records:** Pliocene: Kanazawa, Honshu (Yokoyama, 1927) and Shikoku, Japan (Nomura, 1935), and Formosa (Nomura, 1935).

**Other material examined:** *China:* (ANSP, ZMC, USNM). Tung-sha Tao (Pratas Is.), 62-311m (several lots) (USNM). "China Seas" (NMV). *Hong Kong:* (NMV); 36m (ANSP,



BMNH); 18m (AMS). Lamma Channel (AMS). *Taiwan*: (NMV). Off Anping (ANSP). Tainan Beach (AMNH). *Japan*: Sagami Bay (ANSP). Tateyama (ANSP). Kii (Shiono-misaki) (USNM, ANSP, NMV, NMW). Awajishima Is. (USNM). Mikawa, 18-37m (AMNH). Tosa Bay, 36m (ANSP), 37m (MCZ). Nagasaki (ZMC). *Philippines*: Off San Fernando, N.W. Luzon, 340m (USNM). Batangas Bay, Luzon (USNM). W. Samar Is., 91m (USNM). Sindangan Bay, Mindanao (USNM). *Malaysia*: W. Banguay Channel, off Balambangan Is., Sabah (N. Borneo), 46m (WAM). Off Brunei, 4°44'N, 113°23'E (USNM). *Indonesia*: Waija, Ceram (ZMA). 10°12.2'S, 124°27.3'E, Timor Sea, 73m (ZMA). *Papua New Guinea*: 43km off Cape Possession, near Yule Is. (AMS). *Western Australia*: W.S.W. of False Entrance, 146m (WAM). N. of Long Is. off Onslow, 51m, 76m, 95m (WAM). N.W. of Anchor Is. off Onslow, 119m (WAM). 208km E.N.E. of Troughton Is., 91m (WAM). *Northern Australia*: Jones Shoal, Port Essington (Darwin Mus.). Melville Is., Northern Territory (AMS). Gulf of Carpentaria (ANSP).

**Distribution:** Central Indo-Pacific from southern Japan to southern Indonesia, tropical western Australia, northern Australia and Papua; 18-340m (Fig. 41).

**Remarks:** The similarity of *X. indica* and *X. exuta* is apparently somewhat superficial for not only are there important shell differences, as noted above, but there are also substantial differences in the opercular and penial characters. The specimen described by Adams & Reeve (1850) showing the external features of the animal and identified as *P. exutus* is *X. (O.) indica* as shown by the form of the shell and the radially sculptured operculum.

***Xenophora (Onustus) longleyi* Bartsch, 1931.**

Figs 11c, 14o, 31g, h, 42.

*Xenophora longleyi* Bartsch, 1931: 1, pl. 1.

*Tugurium (Trochotugurium) longleyi*. — Clench and Aguayo, 1943: 5, pl. 1, figs 5, 6.

*Tugurium longleyi*. — Abbott, 1974: 143, fig. 1575.

**SHELL:** With moderate spire (spire angle about 80°), with wide, simple peripheral flange (about 50% of total base width). Umbilicus distinct, deep, partly covered by inner lip. Row of foreign objects on all whorls, usually relatively small, most of dorsal surface exposed. Whorls slightly convex; peripheral flange distinctly concave dorsally, porcellanous beneath. Dorsal sculpture of opisthocline, rather wavy riblets crossed by fine prosocline growth lines. Base strongly convex, sculptured with strong collabral growth lines which become lamellae in a deep furrow at outer edge of base and terminate abruptly at inner edge of flange. Colour yellowish-white (Fig. 31g, h).

**Dimensions:**

	height	diameter
Holotype (from original description)	85 mm	144 mm

**Operculum:** Subtriangular, brown, growing edge moderately convex, nucleus at left  $\frac{1}{3}$ , sides very lightly convex, almost straight. Smooth externally with very weak concentric growth lines and radial striae. Central area rather narrow, very slightly thickened, yellowish-brown, slightly obscured over free surface by very weak growth lines.

**Radula:** Central teeth with constricted base, a short, broad median cusp and about 4-5 minute lateral cusps on each side. Lateral teeth very short, deep, cusp small, cutting edge smooth. Marginal teeth smooth (Fig. 11c).

**Anatomy:** Similar to *X. indica*, but snout lacks distal lateral ridges. Salivary glands very long and slender, subequal in size. Penis simple, slightly tapering, of moderate length, with a blunt terminal papilla (Fig. 14o). Material examined: Bonaire Trench, Venezuela, 11°25'N, 68°23'W, 496m (AMS) (1 submature and 1 immature male); S. of Guayama, Puerto Rico, 17°47'N, 66°04'W, 412-439m (USNM) (1 female).

**Location of type and type locality:** Holotype, USNM (382689) and paratype USNM; off and S. of Loggerhead Key, Dry Tortugas, Florida, 179-229m (Fig. 31g, h).

**Other material examined:** *North Carolina:* 120km S.E. of Cape Fear, 452m (USNM). *Atlantic Ocean:* Hudson Canyon, 39°30'N, 72°10'W, 91m (ANSP). *Gulf of Mexico:* Off Padre Is., Texas, 366-435m (MCZ). *Florida:* Off Pensacola (USNM). 225km S.W. of Egmont Key, 366m (AMNH). Dry Tortugas (ANSP, USNM), 360m, 402m (USNM, AMS), 32km S.E. of Tortugas, 214m (AMS). Off Key West (USNM, FMC, ANSP), 214m (AMNH, MCZ). 80km S. of Key West, Florida, 214m (BMNH). Straits of Florida (USNM), 214m (USNM). *Cuba:* Habana, 457-731m (MCZ). Matanzas, 686-704m. (MCZ). Bahia Cochinos, 329-347m (MCZ). Off Sagua La Grande, 521-548m (MCZ). Off Cayo Coco, 402m (ANSP, MCZ). *Puerto Rico:* N.W. of San Juan, 366-439m (USNM). S. of Guayana, 17°47'N, 66°04'W, 412-439 m (USNM). 18°18'N, 66°3'W, 366-439m (MCZ). *Virgin Islands:* N. of St. Thomas Is. (USNM, FMC). *Lesser Antilles:* St. Croix Is., 435m (MCZ). Frederiksted, St. Croix Is., 377-565m (ZMC). Off St. Kitts, 448m, 457m, 494m (MCZ). *Curacao:* (USNM). *Venezuela:* S. Bonaire Trench, 11°25'N, 68°23'W, 496m (AMS). *Brazil:* Off Recife, Pernambuco, 640m (ex *Challenger*) (BMNH).

**Distribution:** Gulf of Mexico, Caribbean Sea (Florida, Cuba, Puerto Rico, Virgin Ids and the Lesser Antilles, Venezuela) and Brazil; 210-about 695m (one record at 91m needs to be confirmed. The maximum depth given is an approximation because the greatest recorded depths are given as a range, the greatest being 457-731m and 686-704m, 695 representing the largest mean of these ranges.) (Fig. 42).

**Remarks:** This species is one of the largest in the family, having a very wide, ragged peripheral flange to which rather large objects are usually attached. The base differs from that of the other living members of the subgenus *Onustus* in being markedly convex and in having lamellate radial sculpture. These two characters alone serve to distinguish *X. (O.) longleyi* from *X. (O.) caribaea*, with which it is sympatric.

This species is not closely related to any living species (the most similar being *X. caribaea*), nor has it any obvious fossil ancestors. A somewhat similar species is *X. (O.) borsoni* from the Miocene of Italy, the shell of which differs in its smaller size, narrower, very fragile peripheral flange and narrow umbilicus which is plugged with callus.

***Xenophora (Onustus) caribaea* Petit de la Saussaye, 1857.**

Figs 11d, 14p, 31a, b, 42.

*Xenophora caribaea* Petit de la Saussaye, 1857: 248, pl. 10, figs 1, 2; Fischer, 1879a: 429, pl. 65, fig. 1; Watson, 1886: 462.

*Xenophora (Tugurium) caribaea*. — Tryon, 1886: 162, pl. 47, figs 97, 98; Dall, 1889: 291; Rios, 1975: 66, pl. 18, fig. 266.

*Tugurium (Tugurium) caribaeum*. — Clench & Aguayo, 1943: 3, pl. 1, figs 3, 4.

*Tugurium caribaeum* — Abbott, 1974: 143, fig. 1574.

**Shell:** Rather large, thin, with rather depressed spire (spire angle 85°-90°) and wide peripheral flange (about 44% of total diameter of base). Umbilicus deep, moderately wide. Whorls 8-8½, flat to lightly convex in upper half, concave in middle, peripheral flange flat dorsally. Foreign objects small, rather widely spaced, attached at regular intervals around edge of peripheral flange over all whorls of teleoconch. Dorsal sculpture of rather coarse, wavy, opisthocline riblets which cross curved prosocline growth rugae. Base strongly convex in middle portion, sloping evenly into umbilicus; outer portion of base a rounded ridge separated from inner base by a wide groove. Outer basal ridge with a few spiral riblets which cross weak collabral growth lines. Remainder of base with weak, but distinct, growth rugae and very faint spiral lirae which persist inside umbilicus. Basal margin of aperture strongly sinuous. Colour yellowish-white, aperture and peripheral flange white (Fig. 31a, b).

**Dimensions:**

	height	diameter
Syntypes (from original description)	35 mm	65 mm
	40	70



**Operculum:** Very similar to that of *X. longleyi* but free area more thickened by coarse concentric lamellae.

**Radula:** Similar to that of *X. (O.) longleyi* except that the lateral cusps on the central teeth are slightly larger and sharper and some lateral teeth have extremely weak denticles on the cutting edge (Fig. 11d).

**Animal:** Small relative to shell, whitish, tentacles long with large eyes; opercular lobe larger than foot (Dall, 1889).

**Anatomy:** Similar to *X. indica*, but snout without distal lateral ridges and salivary glands globular and of moderate size. Penis similar to that of *X. indica* except that the expanded distal portion has a prominent papilla emerging from a short, deep groove (Fig. 14p). Material examined: Off Guadeloupe, 16°26'N, 61°36'W, 274m (AMS) (1 male, 1 female).

Location of types and type locality: 2 syntypes, NHMP; Marie-Galante Island, Lesser Antilles, 37-132m (Fig. 31a, b).

**Other material examined:** *Gulf of Mexico:* 96km S.W. of Cape San Blas (MCZ). W. of Cape San Blas (AMS). E. Gulf of Mexico, 183-201m (ANSP). Off Mobile, Alabama (USNM). 29°17'N, 87°40'W, 338-366m (USNM). 29°30'N, 86°56'W, 347m (USNM). Between Mississippi Delta and Cedar Key, 203m, 161m (USNM). *Florida:* Egmont Key, 293m (AMNH). W. of Egmont Key, 366-427m (AMNH). Anna Marie Is., 166m (AMNH). 145km S.W. of Egmont Key, 183m (AMNH). 225km S.W. of Egmont Key, 366m (AMNH). Off Pensacola (USNM). Off St. George Is., 205m (USNM). Alligator Reef, Lower Florida Keys, 183m (ANSP). W. of Tampa, 18-36m (MCZ). Palm Beach, 137m (MCZ), 128m, 46m (FMC). Boynton Beach, 146m (FMC). Off Key West, 24°21'N, 82°42'W, 214m (USNM). Dry Tortugas (BMNH), 128m (USNM), 220m (FMC). *Mexico:* Yucatan, 154m, 174m (MCZ). *Bahamas:* Little Bahama Bank, 618m (USNM). 11km off Great Isaac, Bimini Ids, 283m (MCZ). *Cuba:* Off Rio Jarnco, Habana Province, 457m (MCZ). Matanzas, 320m, 366m, 521m (MCZ). Bahia de Cochinos, Santa Clara, 91-585m (several lots) (MCZ). Off Santa Clara Prov., 439m, 457m (MCZ). Off Caibarien, Santa Clara Prov., 439-467m (several lots) (MCZ). Sagua La Grande, Santa Clara, 485m (MCZ). N. Santa Clara Prov., 356-475m (several lots) (MCZ). Nicholas Channel off N. Cuba, 22°50'N, 79°27'W (USNM). Cayo Coco, Camagüey Prov., 329-411m (several lots) (MCZ). Punta Alegre, Camagüey Prov. (ANSP), 347-475m (several lots) (MCZ). Cayo Romano, Camagüey Prov., 329m, 448m, 466m (MCZ), 466m (FMC). Old Bahama Channel, 347-421m (MCZ). Cabo Cruz, 377m (MCZ). Off Sagua de Tanamo, Oriente Prov., 549m, 521m (MCZ). Santiago de Cuba, 527m (MCZ). *Jamaica:* Entrance to Port Royal, 183m (MCZ). *Puerto Rico:* Punta Figuero, 146-329m (USNM, AMS). *Virgin Ids:* N.W. Anegada Is. (USNM). S. Frederiksted, St. Croix Is., 329m (MCZ). Off St. Thomas, 435m (MCZ). *Lesser Antilles:* Saba Bank, off Saba Is., 274m (MCZ). 17°33'N, 63°35'W, 146-329m (AMNH). Montserrat, Leeward Ids, 219m (MCZ). S.E. of Antigua, 16°26'N, 61°36'W, 274m (AMS). Off Guadeloupe, 274m (AMS, MCZ), 320m (MCZ). Off Barbados, 134m, 256m (MCZ), 183m (USNM). *Curacao:* Off Recife, Pernambuco, 640m (BMNH).

**Additional records:** *Brazil:* Off Salvador, 55m (Rios, 1970). Off Concoicas, Bahia and Tramandai (Rios, 1975).

**Distribution:** North-eastern Gulf of Mexico, Caribbean Sea and Brazil; 55-640m (one record at 18-36m needs to be confirmed). Nearly all records are greater than 100m (Fig. 42).

**Remarks:** The shell of this species can be readily distinguished from *X. (O.) longleyi* by its smaller size and the less convex base which has a ridge around its outer edge just inside the peripheral flange. The base of *X. (O.) longleyi* is evenly convex. The penis of the two species also differs significantly (Fig. 14o, p).

*Xenophora (O.) caribaea* tends to occupy shallower water than *X. (O.) longleyi*, the average depth for the latter species being about 400-430m whereas that of *X. (O.) caribaea* is about 300-330m.

The Brazilian material on which the record of *X. caribaea* by Watson (1886) was based consists of *X. caribaea* and a specimen of *X. longleyi*.

## LIST OF RECOGNIZED RECENT TAXA IN THE FAMILY XENOPHORIDAE

This list is compiled in the order in which the species appear in the text.

Genus *Xenophora* Fischer von Waldheim, 1807.

Subgenus *Xenophora* s.s.

*conchyliophora* (Born, 1780). Western Atlantic and eastern Pacific.

*cerea* (Reeve, 1845). Indo-Pacific.

*flindersi flindersi* (Cotton & Godfrey, 1938). Southern Australia.

*peroniana peroniana* (Iredale, 1929). South-eastern Australia.

*peroniana kondoi* n. subsp. Hawaiian Islands.

*neozelanica neozelanica* Suter, 1908. North Island, New Zealand.

*neozelanica kermadecensis* n. subsp. Kermadec Islands.

*tenuis* Fulton, 1938. Southern Japan, China Sea and western Indian Ocean.

*granulosa* n. sp. South China Sea to New Caledonia and Mauritius.

*corrugata* (Reeve, 1842). North-western Indian Ocean.

*mekranensis konoii* Habe, 1953. Indian Ocean and central Indo-Pacific.

*pallidula* (Reeve, 1842). Indian Ocean, central Indo-Pacific, eastern Australia.

*japonica* Kuroda & Habe, 1971. Southern Japan to the Philippines;

Kermadec Islands.

*crispa* (König, 1825). Western Mediterranean Sea and West Africa.

*solarioides solarioides* (Reeve, 1845). Indo-Pacific.

Subgenus *Stellaria* Möller, 1832.

*solaris* (Linné, 1764). Indian Ocean and central Indo-Pacific.

*testigera digitata* Martens, 1878. West Africa.

*testigera profunda* n. subsp. Gulf of Aden and northernmost East Africa.

*chinensis chinensis* (Philippi, 1841). Indian Ocean and central Indo-Pacific.

*lamberti* Soubervie, 1871. New Caledonia (possibly extinct).

*gigantea* Schepman, 1909. Indian Ocean, and central Indo-Pacific and north-eastern Australia.

Subgenus *Onustus* Swainson, 1840.

*indica* (Gmelin, 1791). Indian Ocean, central Indo-Pacific and north-eastern Australia.

*exuta* (Reeve, 1842). Central Indo-Pacific, including tropical Western Australia.

*longleyi* Bartsch, 1931. Gulf of Mexico, Caribbean Sea and Brazil.

*caribaea* Petit de la Saussaye, 1857. North-eastern Gulf of Mexico, Caribbean Sea and Brazil.

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#### APPENDIX

#### A LIST OF THE TERTIARY AND CRETACEOUS SPECIES TAXA ASSIGNED TO THE XENOPHORIDAE

By W. F. Ponder and J. Cooper, British Museum (Natural History).

The following list includes as complete a compilation as we have been able to assemble of the fossil taxa assigned to the Xenophoridae. We have not included any species older than Cretaceous as none of these is probably xenophorid in the strict sense. The original reference and a broad locality and age are given for each species. In most cases no attempt is made to indicate relationships or synonymy although some discussion on many of the species is found in the main body of the text. In the right-hand column the original generic and subgeneric combination is followed by a tentative indication of genus and subgenus.

<i>aegyptica</i> Oppenheim, 1906: 258, pl. 21, fig. 10a, b. Egypt, Eocene.	<i>Xenophora</i> ( <i>Xenophora</i> ) <i>Xenophora</i> ( <i>Xenophora</i> )
<i>agglutinans</i> Lamarck, 1804: 51. Lamarck, 1806: pl. 15, fig. 8. France, Eocene. Syn. of <i>schroeteri</i> Gmelin.	<i>Trochus</i>
<i>annosus</i> Conrad, 1869: 42, pl. 1, fig. 4. An architectonicid ( <i>vide</i> Dall, 1892: 362).	<i>Onustus</i>
<i>aquensis</i> d'Orbigny ("1847") 1852: 41. Based on Grateloup, 1847-48: pl. 1, figs 3, 4 (as <i>Trochus conchyliophorus non</i> Born). France, Lower Miocene.	<i>Phorus</i>  <i>Xenophora</i> ( <i>Xenophora</i> )
<i>aringus</i> de Gregorio, 1885: 70. Italy, Pliocene.	<i>Xenophora</i> <i>Xenophora</i> ( <i>Xenophora</i> )
<i>bartonensis</i> (Edwards MS) Newton, 1891: 218. Barton, England, Upper Eocene. <i>Nomen nudum</i> . Syn. of <i>schroeteri</i> Gmelin.	<i>Xenophora</i>

- bellardi* Michelotti, 1840: 14.  
Italy, Pliocene?  
Syn. of *testigera* Bronn (*vide* Sacco, 1896: 24). *Trochus*
- benettiae* Sowerby, 1815: 224, pl. 98 (2 figures)  
Britain, Eocene.  
Syn. of *schroeteri* Gmelin. *Trochus*
- birmanica* Noetling, 1901: 280, pl. 18, figs 21, 21a.  
Burma, Miocene. *Xenophora*  
*Xenophora (Xenophora)*
- borsoni* (Bellardi MS) Sismonda, 1847: 50.  
Based on Michelotti, 1847: 175, pl. 7, fig. 1.  
Italy, Middle Miocene. *Phorus*  
*Xenophora (Onustus)*
- bouryi* Cossmann, 1888: 193, pl. 7, figs 36-38.  
France, Eocene. *Xenophora (Haliphoebus)*  
*Xenophora (subgenus?)*
- brasiliensis* White, 1887: 196, pl. 10, figs 13, 14.  
Maury, 1925: 79, fig. 13.  
Brazil, "Eocene" (= Lower Miocene). *Phorus*  
*Xenophora (Xenophora)*
- brongniarti* Bronn, 1831b: 569.  
Based on d'Eichwald, 1859: pl. 11, fig. 22a, b.  
Russia, Tertiary. *Trochus*  
*Xenophora (Xenophora)*
- burdigalensis* Grateloup, 1847: pl. 1 (caption),  
pl. 1, fig. 1 (as var. of *T. conchyliophorus*).  
France, Miocene. *Trochus*  
*Xenophora (Xenophora)*
- calculifera* Cossmann, 1910: 52, pl. 3, figs 12-15 (*non*  
Reeve).  
Karikal, S.E. India, Pliocene.  
See remarks on p. 14. *Xenophora (Tugurium)*  
*Xenophora (subgenus?)*
- canaliculatus* d'Orbigny, 1842: 180, pl. 176, figs 13, 14.  
France, Senonian (Upper Cretaceous) *Phorus*  
*Xenophora (Xenophora)*
- carnatica* Stoliczka, 1868: 247, pl. 19, fig. 24.  
South India, Upper Cretaceous. *Xenophora*  
*Xenophora (Xenophora)*
- cleopatras* Cuvillier, 1933: 35, pl. 6.  
Egypt, Eocene. *Xenophora*  
*Xenophora (Xenophora)*
- coelatus* Delpey, 1948: 22, pl. 5, fig. 1.  
Malagasy Republic, Upper Cretaceous. *Onustus*  
*Xenophora (Xenophora)*
- colligens* (Bonelli MS) Michelotti, 1840: 14.  
Italy, Miocene.  
Syn. of *testigera* Bronn (*vide* Sacco, 1896: 24). *Trochus*
- commutata* Fischer, 1879b: 211.  
Italy, Pliocene.  
Syn. of *crispa* König. *Xenophora*
- confusus* Deshayes, 1832: 243, pl. 31, figs 3, 4.  
France, Eocene. *Trochus*  
*Xenophora (Xenophora)*
- conica* Dall, 1892: 361.  
Mississippi, U.S.A., Eocene. *Xenophora (Tugurium)*  
*Xenophora (Stellaria)*
- crispus* König, 1825: pl. 5, fig. 58.  
Italy, Pliocene. *Trochus*  
*Xenophora (Xenophora)*



- cumulans* Brongniart, 1823: 57, pl. 4, fig. 1a-c.  
France, Eocene.
- delectus* Guppy, 1876: 529, pl. 28, fig. 10  
Maury, 1917: 134, pl. 23, figs 8, 9.  
Pilsbry, 1922: 385, pl. 32, figs 7, 8.  
Woodring, 1957: 77, pl. 22, figs 1, 2, 4.  
Dominican Republic, Miocene.
- depressa* Pantanelli, 1886: 125, pl. 5, figs 6, 7.  
Italy, Miocene.
- depressior* Sacco, 1896: 22, pl. 2, fig. 24.  
(as var. of *crispa*).  
Italy, Pliocene.  
Syn. of *crispa* König.
- deshayesi* Michelotti, 1847: 173.  
Italy and France, Miocene.
- discoideum* Sowerby, 1813: 36.  
Recorded as a *Xenophora* by Newton, 1891: 219.  
Barton, England, Upper Eocene.  
This species is probably an architectonicid.
- dunkeri* Martin, 1879: 71, pl. 12, fig. 7.  
Martin, 1905: 253, pl. 37, fig. 606.  
Java, Miocene.  
Subspecies of *chinensis* Gmelin herein.
- elatespirata* Sacco, 1896: 21, pl. 2, fig. 21 (as var. of  
*deshayesi*).  
Italy, Miocene.  
Syn. of *deshayesi* Michelotti.
- elator* Sacco, 1896: 22, pl. 2, fig. 23 (as var. of *crispa*).  
Italy, Pliocene.  
Syn. of *crispa* König.
- elatuscula* Sacco, 1896: 25, pl. 3, fig. 2 (as var. of *testigera*).  
Italy, Miocene-Pliocene  
Syn. of *testigera* Bronn.
- eocenica* Abbass, 1967: 48, pl. 6, figs 3-6.  
Egypt, Upper Eocene.
- expansior* Sacco, 1896: 24 (as var. of *infundibulum*).  
Italy, Pliocene.  
Syn. of *infundibulum* Brocchi.
- extensus* Sowerby, 1821: 140, pl. 278, figs 2, 3.  
England, Eocene.
- farinesi* de Serres, 1831: 75.  
Syn. of *infundibulum* Brocchi (*fide* Sacco,  
1896: 23).
- flemingi* Beu, 1977: 233, figs 2, 5, 7, 8, 10, 13-17.  
Southland, New Zealand, Lower Miocene.
- floridana* Mansfield, 1930: 121, pl. 18, figs 5, 6 (as  
subspecies of *delecta*).  
Florida, Miocene.
- Trochus*  
*Xenophora* (*Xenophora*)
- Phorus*
- Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Stellaria*)
- Xenophora*
- Phorus*  
*Xenophora* (*Xenophora*)
- Solarium*
- Xenophora*
- Xenophora* (*Stellaria*)
- Xenophora*
- Xenophora*
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora*
- Trochus*  
*Xenophora* (*Onustus*)
- Trochus*
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Xenophora*)

- gigas* auct. non Borson, 1821, = *borsoni*  
Sismonda, 1847.  
(*Trochus gigas* Borson, 1821 is a *Pleurotomaria*, fide Sacco, 1896: 27).
- gracilior* Sacco, 1896: 25, pl. 3, fig. 7 (as var. of *plioitalicum*).  
Italy, Pliocene.  
Syn. of *plioitalicum* Sacco. Tugurium
- grasi* (Matheron MS) Roman & Mazeran, 1920: 42, pl. 4, figs 28, 28a, pl. 5, fig. 15a-b.  
France, Turonian (Cretaceous). Xenophora  
Xenophora (subgenus?)
- gratteloupi* (sic) = *grateloupi* d'Orbigny, ("1847") 1852: 7.  
France, Miocene. Phorus  
Xenophora (Xenophora)
- gravesianus* d'Orbigny, ("1847") 1850: 312.  
France, Eocene. Phorus  
Xenophora (Xenophora)
- grayi* Palmer, 1953: 23, pl. 2, fig. 7.  
Florida, Eocene. Tugurium  
Xenophora (subgenus?)
- haliaensis* Daresté de la Chavanne, 1911: 270.  
Algeria, Tertiary. Xenophora (Tugurium)  
Xenophora (subgenus?)
- hawleyi* Loel & Corey, 1932: 269, pl. 63, fig. 12.  
California, U.S.A., Lower Miocene. Xenophora  
Xenophora (Xenophora)
- helvetica* (Mayer *nomen nudum*) Rutsch, 1929: 44.  
Mayer, 1872 (in Kaufmann): 504 (*nomen nudum*).  
Switzerland, Miocene. Xenophora  
Xenophora (Xenophora)
- This name is introduced in synonymy by Rutsch but is accompanied by a description and is thus a valid introduction of the name.
- humilis* Conrad, 1847: 285.  
Conrad, 1848: 116, pl. ii, fig. 46.  
Harris & Palmer, 1947: 259, pl. 30, fig. 2.  
Mississippi, U.S.A., Oligocene. Phorus  
Xenophora (Xenophora)
- imperforatus* Gabb, 1873: 241.  
Type figured by Pilsbry, 1922: 385, pl. 31, figs 3, 4.  
Dominican Republic, Miocene. Onustus  
Xenophora (Onustus)
- infundibulum* Brocchi, 1814: 352, pl. 5, fig. 17.  
Italy, Pliocene. Trochus  
Xenophora (Xenophora)
- insignis* Kner, 1850: 17, pl. 3, fig. 10.  
Lemberg, Maastrichtian (Upper Cretaceous). Phorus  
Xenophora (Xenophora)
- italica* Grateloup, 1847: pl. 1 (caption), pl. 1, fig. 2 (as var. of *T. conchyliophorus*).  
Italy, ?Miocene. Trochus  
Xenophora (Xenophora)
- jezleri* Cox, 1948: 20, pl. 1, fig. 11a-c.  
British N. Borneo, "Neogene" (= Upper Miocene or Pliocene).  
Subspecies of *solaroides* Reeve herein. Xenophora  
Xenophora (Xenophora)
- koeneniana* Sacco, 1896: 25 (as var. of *subextensum*).  
Based on Koenen, 1867: pl. 12, fig. 6.  
Germany, Oligocene. Tugurium  
Xenophora (?Xenophora)

- lapiferens* Whitfield, 1892: 227, pl. 34, figs 6-9.  
New Jersey, U.S.A., Eocene. *Xenophora*  
*Xenophora (Xenophora)*
- leprosa* Morton, 1834: 46, pl. 15, fig. 6.  
Sohl, 1960: 96, pl. 10, figs 19, 23-7.  
Alabama, U.S.A., Maastrichtian (Upper Cretaceous). *Trochus*  
*Xenophora (Xenophora)*
- ludbrookae* Ponder n. subsp.  
Subspecies of *flindersi* Cotton & Godfrey.  
South Australia, Upper Pliocene — Lower Pleistocene. *Xenophora (Xenophora)*  
*Xenophora (Xenophora)*
- lyellianus* Bosquet, in Lyell, 1852: 300, 315.  
Deshayes, 1864: 963; 1866, pl. 64, figs 25, 26.  
Belgium, Eocene. *Phorus*  
*Xenophora (Xenophora)*
- This name was introduced in a list but with a brief differentiating statement so we consider it to be valid. It is based on Nyst, 1843: 376, pl. 36, fig. 18a-c.
- madagascariensis* Collignon, 1951: 103,  
pl. 16, figs 6, 6b.  
Malagasy Republic, Maastrichtian (Upper Cretaceous). *Xenophora (Trochotugurium)*  
*Xenophora (Xenophora)*
- makiyamai* Itoigawa & Nishikawa, 1976: 147, pl. 35, figs 7,  
8.  
Bihoku Group, Japan, Miocene. *Tugurium*  
*Xenophora (?Stellaria)*
- matsuoii* Ogasawara, 1976: 61, pl. 13, figs 11, 12.  
Japan, Miocene *Tugurium*  
*Xenophora (?Stellaria)*
- mekranense* Newton, 1905: 301, pl. XVII, figs 8-10.  
Mekran Coast, Pliocene. *Tugurium*  
*Xenophora (Xenophora)*
- minutus* Zekeli, 1852: 61, pl. 11, fig. 4a-c.  
A juvenile of *Astrarium radiatum* Zekeli, *vide* Stoliczka,  
1865: 59. *Phorus*
- nigeriense* Newton, 1922: 51, pl. 4, figs 20, 21.  
Nigeria, Eocene. *Tugurium*  
*Xenophora (Xenophora)*
- nummulitifera* Deshayes, 1864: 965, pl. 64, figs 27-30.  
Paris Basin, France, Eocene. *Xenophora*  
*Xenophora (Xenophora)*
- oligostriatum* Sacco, 1896: 26, pl. 4, fig. 2.  
Italy, Lower Oligocene. *Tugurium*  
*Xenophora (?Onustus)*
- onustus* Nilsson, 1827: 12, pl. 3, fig. 4.  
Sweden, Maastrichtian (Upper Cretaceous). *Trochus*  
*Xenophora (Xenophora)*
- ornatoparva* Sacco, 1896: 25, pl. 3, figs 4, 5 (as var. of  
*subextensum*).  
Italy, Lower Oligocene. *Tugurium*  
*Xenophora (Stellaria)*
- pagodaeformis* Sacco, 1896: 28, pl. 4, fig. 5 (as var. of  
*borsoni*).  
Italy, Miocene. *Tugurium*
- Syn. of *borsoni* Sismonda (from examination of author's  
material).
- parisiensis* Grateloup, 1847: pl. 1 (caption), pl. 1, figs 3, 4  
(as var. of *T. conchyliophorus*).  
France, Eocene. *Trochus*  
Syn. of *schroeteri* Gmelin.

- patellatus* Deshayes, 1832: 240, pl. 31, figs 5-7.  
France, Eocene.
- petrophora* Koenen, 1892: 847, pl. 53, figs 3-5.  
Germany, Oligocene.
- plicatus* Zekeli, 1852: 62, pl. 11, fig. 5a, b.  
Austria, Upper Cretaceous.
- plicomphalus* Pusch, 1837: 110, pl. 10, fig. 7.  
Poland (= Ukrainian SSR), "Tertiärkalke".
- plioextensum* Sacco, 1896: 27, pl. 4, fig. 3.  
Italy, Pliocene.
- plioitalicum* Sacco, 1896: 25, pl. 3, fig. 6.  
Italy, Pliocene.
- postextensum* Sacco, 1896: 26, pl. 3, figs 8, 9, pl. 4, fig. 1.  
Italy, Miocene.  
Probably a synonym of *depressa* Pantanelli.
- prognatus* Finlay, 1926: 228, pl. 59, figs 15, 16 (fig. 16 is a specimen of *X. flemingi* (Beu, 1977: 232)).  
New Zealand, Oligocene.  
A subspecies of *neozelanica*.
- reclusa* Conrad, 1854: 289, pl. 17, fig. 6a, b.  
Conrad, 1855: 262.  
Harris & Palmer, 1947: 258, pl. 30, figs 15-18.  
Mississippi, U.S.A., Eocene.
- rhytida* Cossmann, 1900: 51 (357), pl. 26 (5), figs 22, 23.  
France, Eocene.
- rugata* Abbass, 1967: 49, pl. 6, figs 1, 2.  
Egypt, Upper Eocene.
- scaldensis* Glibert, 1958: 24, pl. 12, fig. 20a (as subspecies of *deshayesi*).  
Belgium, Pliocene.
- schröeteri* Gmelin, 1791: 3575.  
Based on Schröter, 1783, 1784: 716, pl. 7, figs 2, 3.  
France ("Courtagnon" (Schröter, 1783: 716), Paris Basin), Eocene.
- Schröter (1783: 716) refers to pl. 3, fig. 15 in error as stated in Vol. II (1784), pp. IV-V.
- scrutarius* Philippi, 1844: pl. 3, fig. 37.  
Germany, Oligocene.
- simiensis* Nelson, 1925: 422, pl. 55, figs 7a-c.  
California, "Eocene" (= Upper Paleocene).
- simpsoni* Stanton, 1893: 133, pl. 29, figs 4-6.  
Colorado, Turonian (Cretaceous).
- solariformis* Tesch, 1920: 73, pl. 133, fig. 214a-c.  
Timor, Pliocene.  
Syn. of *solaris* Linné.
- Trochus*  
*Xenophora* (subgenus?)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Phorus*  
*Xenophora* (*Xenophora*)
- Trochus* (*Phorus*)  
*Xenophora* (*Xenophora*)
- Tugurium*  
*Xenophora* (*Onustus*)
- Tugurium*  
*Xenophora* (*Xenophora*)
- Tugurium*
- Onustus*
- Xenophora* (*Xenophora*)
- Xenophora*
- Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (subgenus?)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Trochus*
- Xenophora* (?*Stellaria*)
- Trochus*  
*Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (subgenus?)
- Xenophora*



- solida* Koenen, 1867: 149, pl. 12, fig. 5a-c.  
Germany, Lower Oligocene.
- splendida* Vinassa de Regny, 1886: 251, pl. 17, figs 16a, b.  
Venetian Alps, Italy, Eocene.
- stocki* Dickerson, 1916: 502, pl. 37, fig. 4a, b.  
California, U.S.A., Upper Eocene.
- subagglutinans* Glibert, 1938: 56, pl. 2, fig. 2.  
Belgium, Eocene.
- subconchyliophorus* d'Orbigny, 1850: 414.  
Based on Deshayes, 1824: 242, pl. 31, figs 1, 2.  
France, Eocene.
- subconica* Boettger, 1883: 70, pl. 5, fig. 14a, b.  
Sumatra, Miocene.
- subextensus* d'Orbigny ("1848") 1852: 7.  
Based on *Trochus extensus* Nyst, 1843: 375, pl. 36, fig. 9a-c  
(non Sowerby, 1821).  
Belgium, Upper Middle Oligocene.
- suezi* Abbass, 1977: 127, pl. 5, fig. 6.  
Egypt, Miocene.
- tatei* Harris, 1897: 254, pl. 7, figs 7a, b.  
Victoria, Australia, Miocene.
- tauroturrita* Sacco, 1896: 25, pl. 3, fig. 3 (as var. of  
*testigera*).  
Italy, Miocene.  
Syn. of *testigera* Bronn.
- terpstrai* Dey, 1961: 58, pl. 5, figs 9, 10.  
India, Miocene.  
Syn. of *solarioides jezleri* Cox.
- testigerus* Bronn, 1831: 61.  
Sacco, 1896:24, pl. 3, fig. 1.  
Italy, Pliocene?  
Known from several European localities, Oligocene to  
Pliocene.
- testudinarium* Benoist, 1878: LXXXVIII.  
France, Miocene.  
*Nomen nudum*
- textilina* Dall, 1892: 361.  
Gardner, 1947: 561, pl. 62, figs 31, 32.  
Florida, Lower Miocene.
- tortilis* Peron, 1900: 140, pl. 3, figs 2, 2<sup>1</sup>, 2<sup>2</sup>.  
France, Neocomian (Lower Cretaceous).
- trangahinsis* Basse, 1931: 54, pl. 9, figs 17, 18.  
Malagasy Republic, Maastrichtian (Upper Cretaceous).
- transiens* Sacco, 1896: 23 (as var. of *crispa*).  
Based on Hörnes, 1856: pl. 44, fig. 13.  
Austria, Lower Miocene.
- Xenophora*  
*Xenophora* (?*Stellaria*)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora* (*Trochotugurium*)  
*Xenophora* (?*Stellaria*)
- Phorus*
- Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Phorus*
- Xenophora* (?*Stellaria*)
- Xenophora* (*Xenophora*)  
*Xenophora* (*Xenophora*)
- Xenophora*  
*Xenophora* (*Xenophora*)
- Xenophora*
- Xenophora*
- Phorus*  
*Xenophora* (*Stellaria*)
- Xenophora*
- Xenophora*
- Xenophora* (*Xenophora*)
- Onustus*  
*Xenophoridae*?
- Xenophorus*  
*Xenophora* (*Xenophora*)
- Xenophora*
- Xenophora* (*Xenophora*)

- trinacria* Fischer, 1879: 211. *Xenophora*  
Based on Philippi, 1836: 185, pl. 10, fig. 26.  
Sicily, Pleistocene.  
Syn. of *crispa* König.
- turicensis* (Mayer MS) [Mousson, J.R.A.?], 1862?: 34. *Xenophora*  
Mayer in Kaufmann, 1872: 504.  
Switzerland, Miocene.  
*Nomen nudum*.
- umbilicaris* Solander in Brander, 1766: 10,  
pl. 1, figs 4, 5. *Trochus*  
Preocc. by *Trochus umbilicaris* Linné, 1758.  
Syn. of *schroeteri* Gmelin
- umbilicatus* Tuomey, 1854: 169. *Phorus*  
Alabama, U.S.A., Senonian (Cretaceous).  
A probable synonym of *leprosa* Morton (*vide* Sohl, 1960:  
96).
- ustjurtensis* Alekseev, 1963: 56, pl. 12, figs 12-14. *Xenophora*  
Pre-Arals, Russia, Paleogene. *Xenophora* (subgenus?)
- vasconcellosi* Oliveira, 1957: 18, pl. 2 figs 4, 5. *Xenophora*  
Brazil, Maastrichtian (Upper Cretaceous). *Xenophora* (*Xenophora*)
- venatrix* (Edwards MS) Newton, 1891: 219. *Xenophora*  
England, Middle Eocene.
- Nomen nudum*.
- wemmelensis* Glibert, 1938: 55, pl. 2, fig. 1. *Xenophora* (*Xenophora*)  
Belgium, Eocene. *Xenophora* (*Xenophora*)
- zitteli* Weaver, 1905: 118, pl. 12, fig. 8. *Xenophora*  
California, U.S.A., Upper Paleocene. *Xenophora* (*Xenophora*)

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**Figs 6-42**

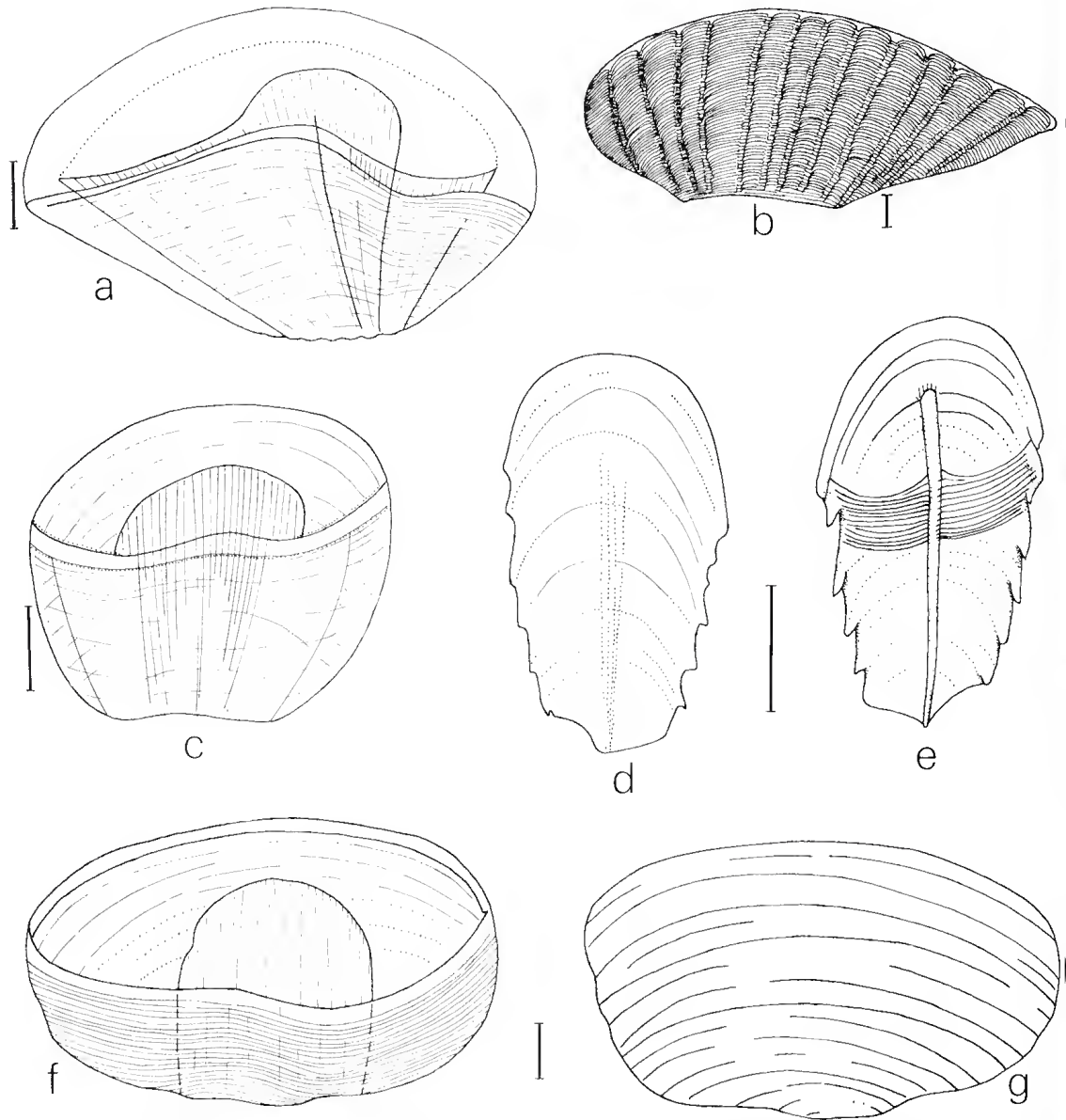


Fig. 6. Opercula of *Xenophora*: Scale lines = 2 mm. (a) Inner side of operculum of *Xenophora (Stellaria) solaris* (Linné). S.S.W. of Dwarka, India. (b) Outer side of operculum of *Xenophora (Onustus) indica* (Gmelin). Off Wide Bay, Queensland. (c) Inner side of operculum of *Xenophora (Xenophora) conchyliophora* (Born). Lake Worth, Florida. (d, e) Outer (d) and inner (e) sides of operculum of *Xenophora (Xenophora) flindersi flindersi* (Cotton & Godfrey). St. Francis<sup>s</sup> Island, South Australia. (f, g) Inner (f) and outer (g) sides of operculum of *Xenophora (Xenophora) pallidula* (Reeve). Between Port Stephens and Hawkesbury River, New South Wales, Australia.

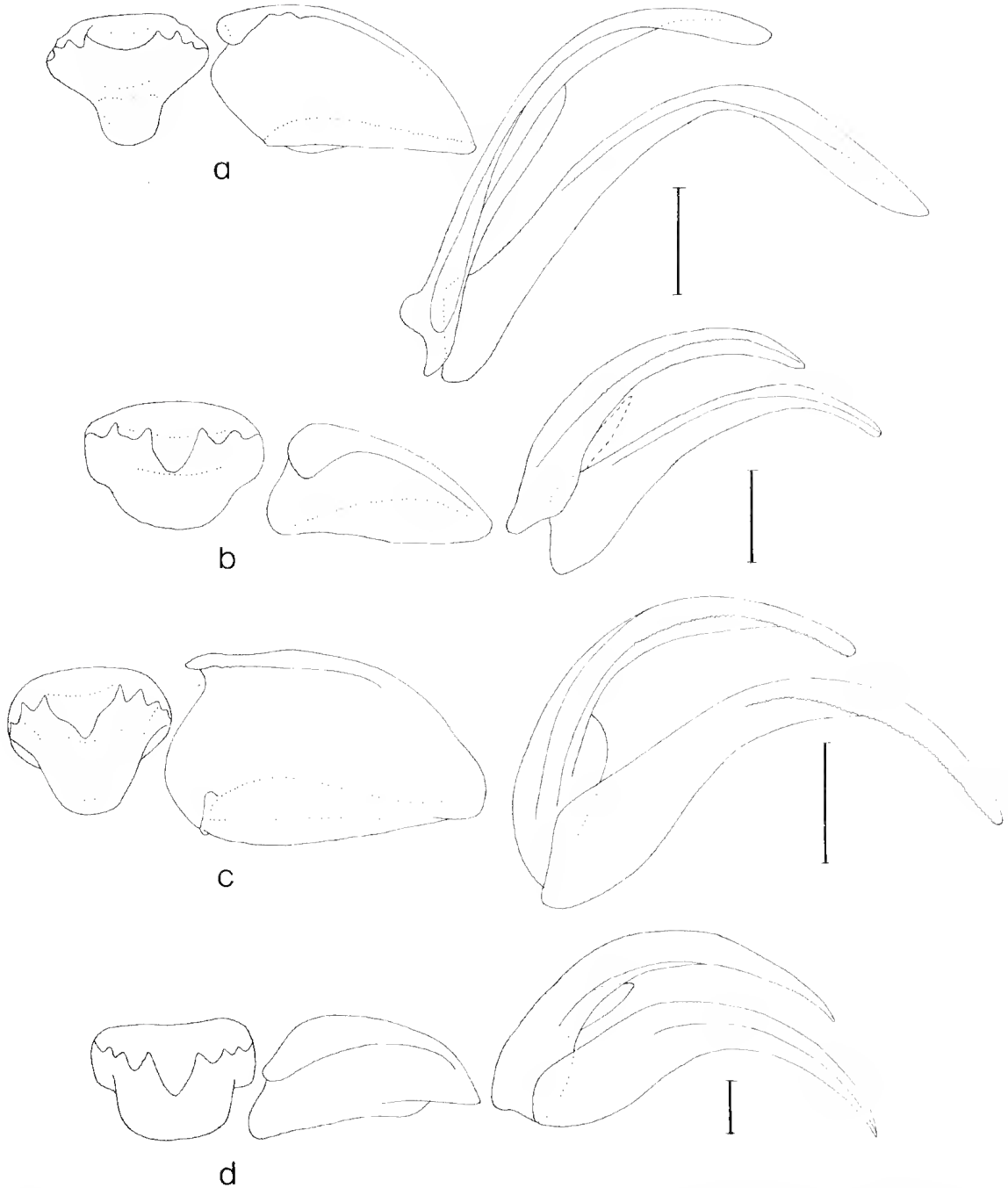


Fig. 7. Radulae of *Xenophora* (*Xenophora*) species: Scale = 0.1 mm. (a) *X. (X.) conchyliophora* (Born). Off Martinique. (b) *X. (X.) flindersi flindersi* (Cotton & Godfrey). Coffin Bay, South Australia. (c) *X. (X.) cerea* (Reeve). Mahé, Seychelles. (d) *X. (X.) mekranensis konoii* (Habe). W. of Gantheaume Bay, Western Australia.



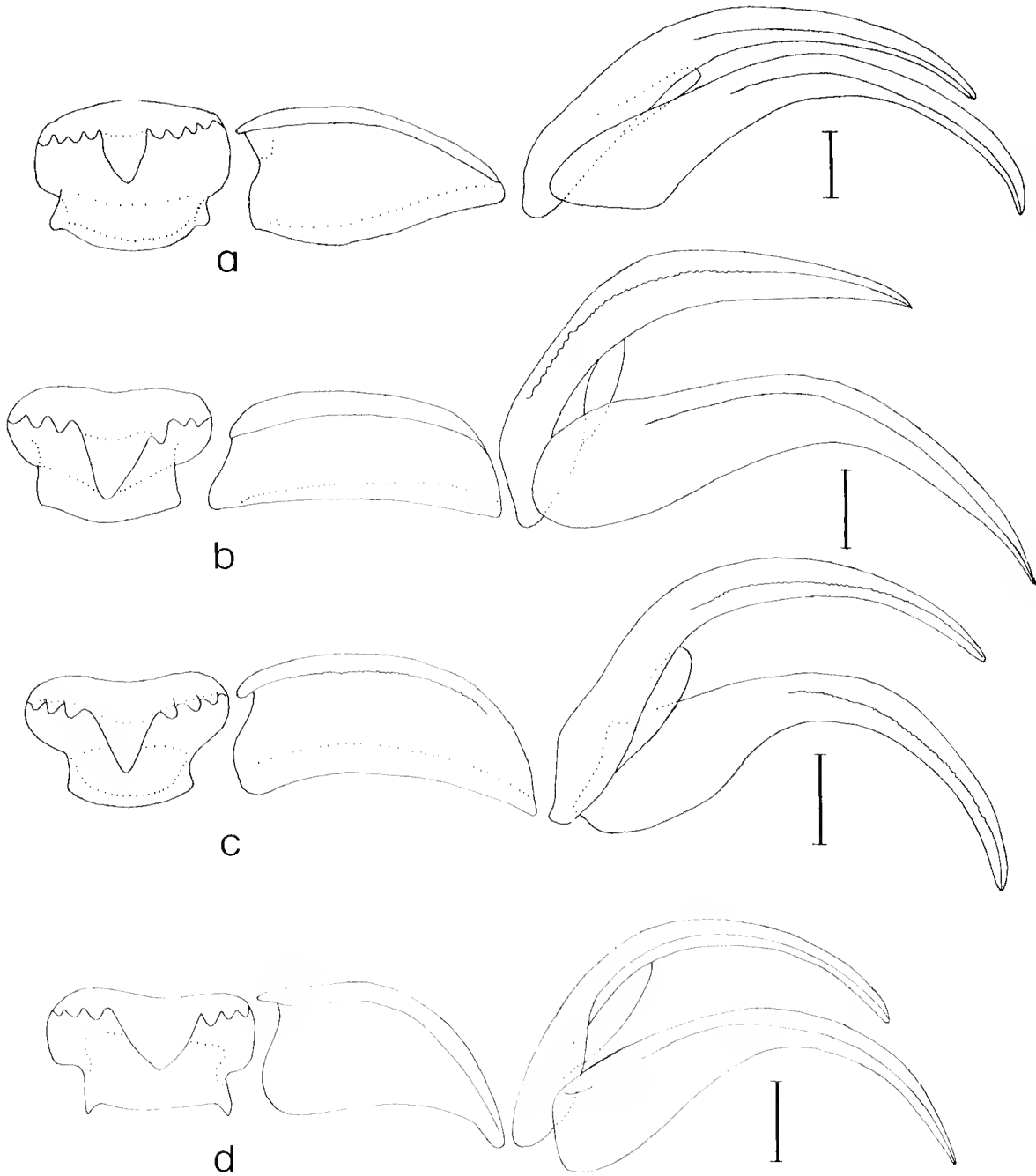


Fig. 8. Radulae of *Xenophora* (*Xenophora*) species: Scale = 0.1 mm. (a) *X. (X.) neozelanica neozelanica* Suter. Colville Channel, New Zealand. (b) *X. (X.) neozelanica kermadecensis* n. subsp. Paratype. (c) *X. (X.) peroniana peroniana* (Iredale). Off Broken Bay, New South Wales, Australia. (d) *X. (X.) peroniana kondoi* n. subsp. Off Maui Is., Hawaiian Islands.

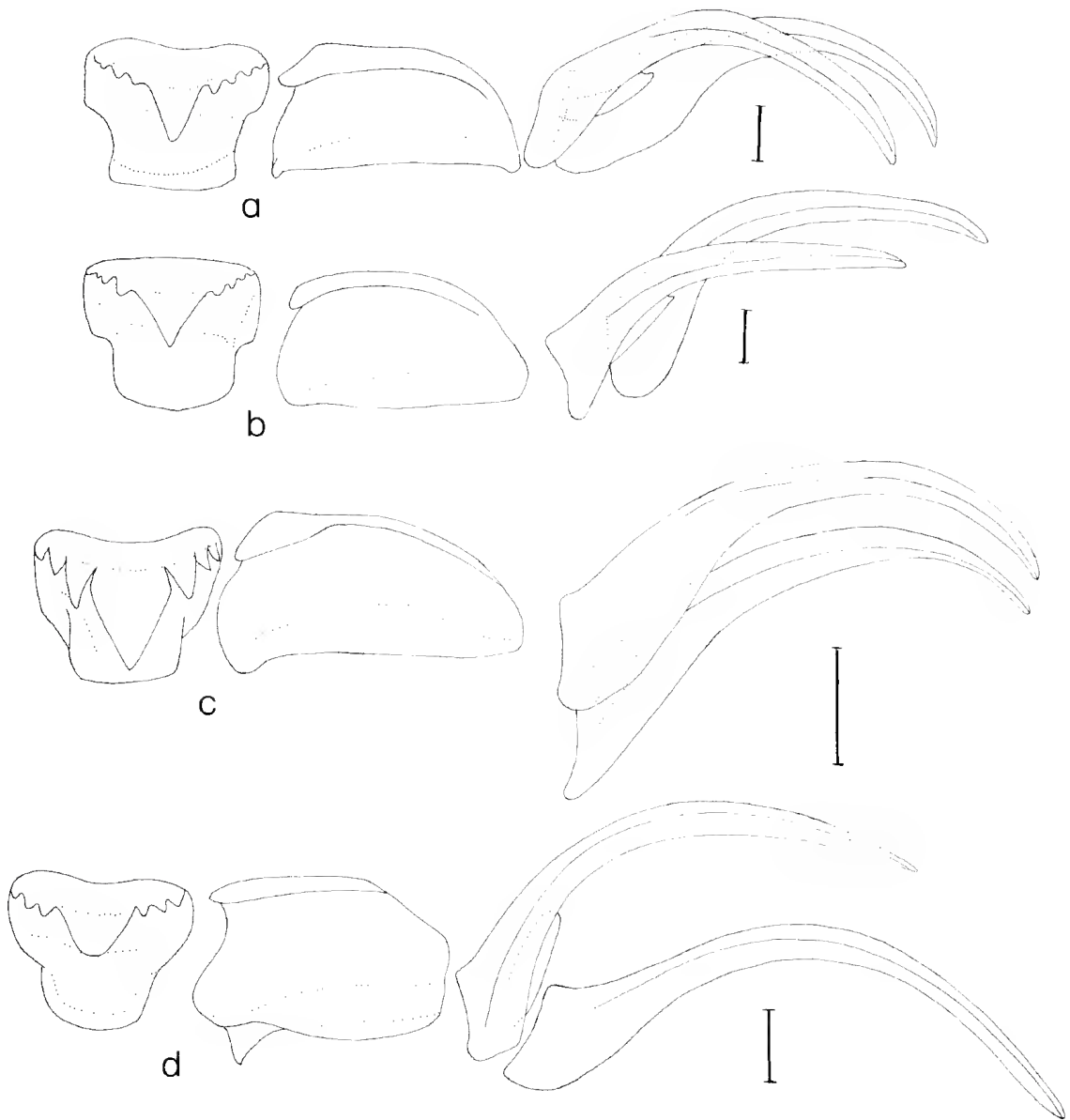


Fig. 9. Radulae of *Xenophora* (*Xenophora*) species: Scale = 0.1 mm. (a, b) *X. (X.) pallidula* (Reeve). (a) Sagami Bay, Japan, (b) Between Port Stephens and Broken Bay, New South Wales, Australia. (c) *X. (X.) japonica* Kuroda & Habe. Sagami Bay, Japan. (d) *X. (X.) corrugata* (Reeve). Bahrain, Persian Gulf.

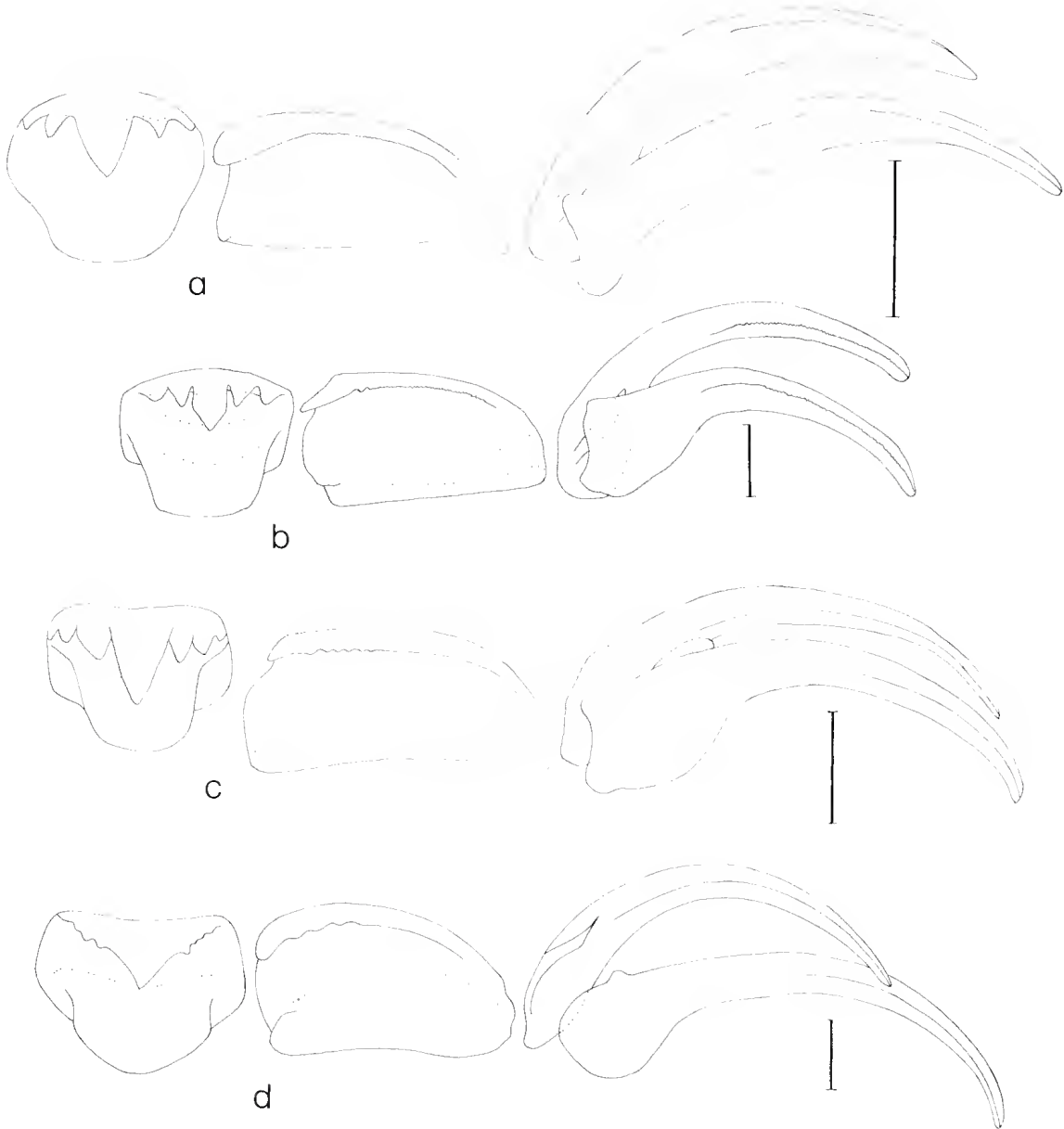


Fig. 10. Radulae of *Xenophora* (*Xenophora*) and *Xenophora* (*Stellaria*) species: Scale = 0.1 mm. (a) *X. (X.) solarioides solarioides* (Reeve). Off North Keppel Is., Queensland, Australia. (b) *X. (S.) solaris* (Linné). S.S.W. of Dwarka, India. (c) *X. (S.) chinensis chinensis* (Philippi). Cape Possession, Gulf of Papua, Papua New Guinea. (d) *X. (S.) testigera digitata* Martens. N. of Port Gentil, Gabon, West Africa.

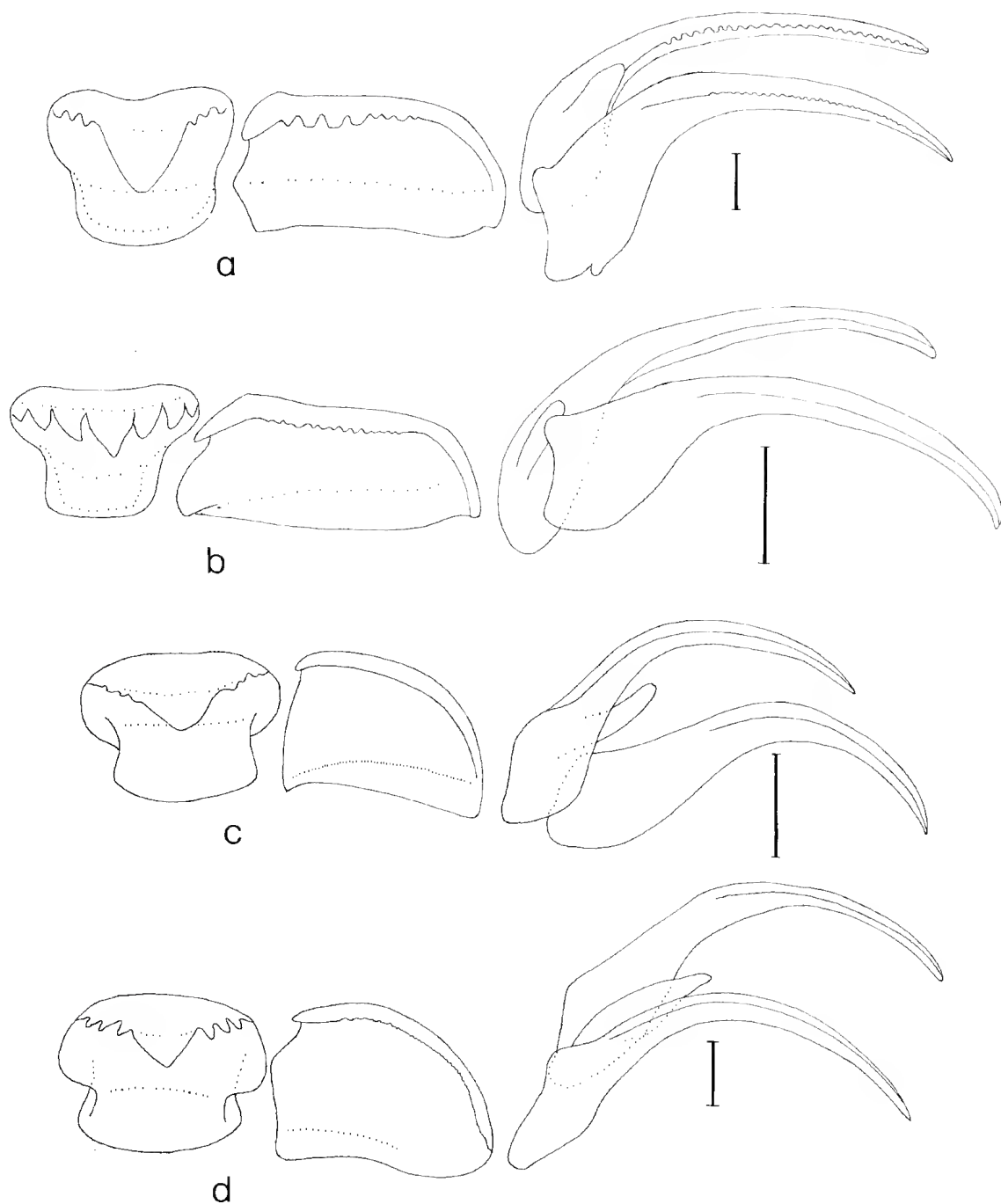


Fig. 11. Radulae of *Xenophora (Onustus)* species: Scale = 0.1 mm. (a) *X. (O.) indica* (Gmelin). Off North Keppel Is., Queensland, Australia. (b) *X. (O.) exuta* (Reeve). Off Cape Possession, Gulf of Papua, Papua New Guinea. (c) *X. (O.) longleyi* Bartsch. South of Guayama, Puerto Rico. (d) *X. (O.) caribaea* Petit de la Saussaye. Off Guadeloupe, Leeward Ids.

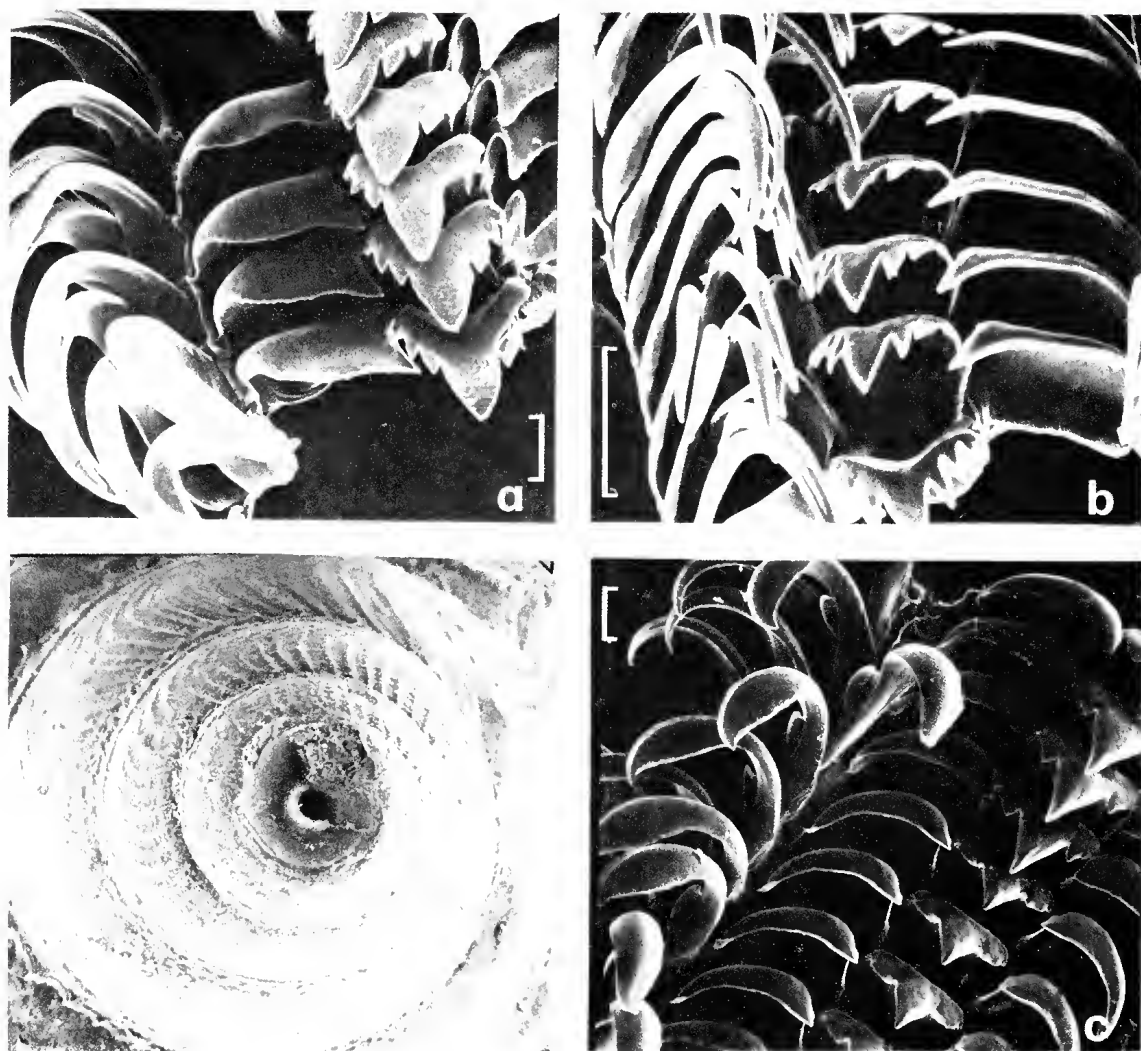
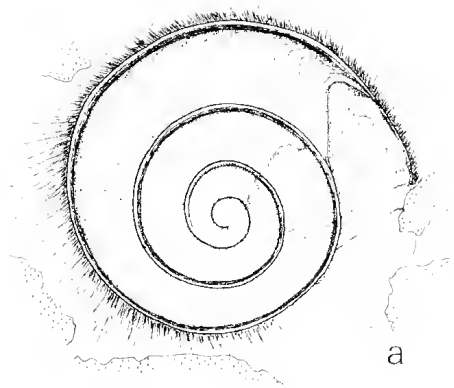


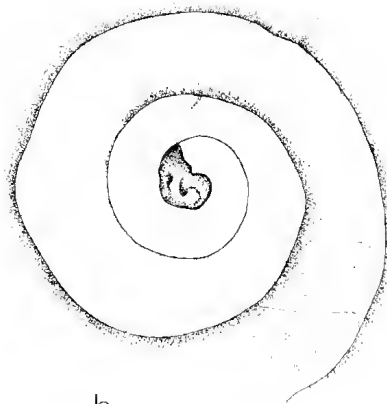
Fig. 12. (a-c) Radulae of *Xenophora* species: Scale = 0.1 mm. (a) *X. (O.) indica* (Gmelin). Off North Keppel Is., Queensland. (b) *X. (X.) solarioides* (Reeve). Baye Papaye, Nouméa, New Caledonia. (c) *X. (X.) granulosa* n. sp. Holotype. (d) Protoconch of *X. (X.) pallidula* (Reeve). Off Rainie Is., Queensland (AMS).

Fig. 13 (facing page). Protoconchs of *Xenophora* species: All to same scale. (a) *Xenophora (Xenophora) neozelanica neozelanica* Suter. Off Doubtless Bay, New Zealand (NMNZ, 25777). (b) *Xenophora (Xenophora) tatei* Harris. Miocene, Muddy Creek, Victoria, Australia (AMS, F1916). (c) *Xenophora (Xenophora) flindersi flindersi* (Cotton & Godfrey). Coffin Bay, South Australia (NMV). (d) *Xenophora (Xenophora) flindersi ludbrookae* n. subsp. Pliocene-Lower Pleistocene, Roe Plain, Western Australia (WAM 77.589). (e) *Xenophora (Stellaria) solaris* (Linné). S.S.W. of Dwarka, Gujarat, India, 79-88 m. (MCZ). (f) *Xenophora (Onustus) exuta* (Reeve). Off Yule Island, Papua New Guinea (AMS, C74807).

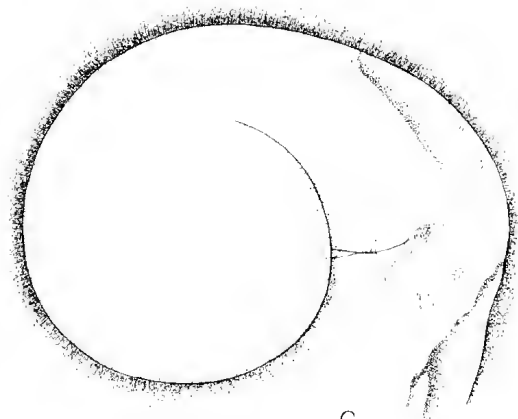




a



b

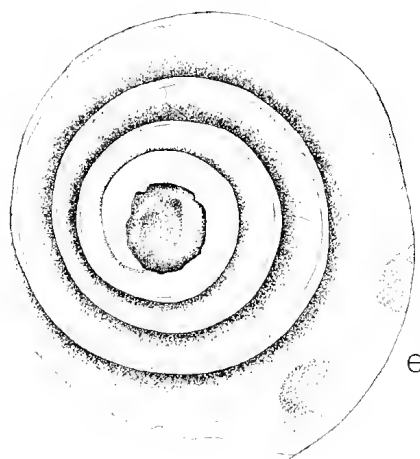


c

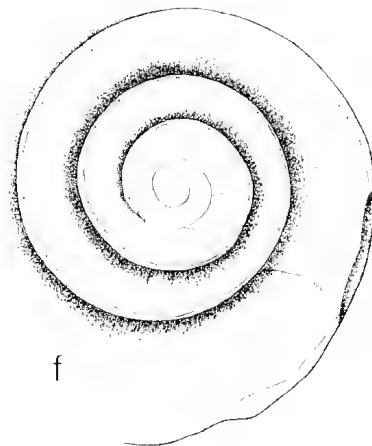


d

0.5 mm



e



f

Fig. 14 (facing page). Male genitalia of *Xenophora* species: (a) *Xenophora (Xenophora) flindersi flindersi* (Cotton & Godfrey). (b) *Xenophora (Xenophora) neozelanica kermadecensis* n. subsp. Paratype. (c, d) *Xenophora (Xenophora) japonica* Kuroda & Habe. (d) Enlargement of distal end of penis. (e) *Xenophora (Xenophora) solarioides solarioides* (Reeve). (f, g) *Xenophora (Xenophora) pallidula* (Reeve). (f) Mature. (g) Immature. (h) *Xenophora (Xenophora) granulosa* n. sp. (i) *Xenophora (Xenophora) peroniana peroniana* (Iredale). (j, k) *Xenophora (Xenophora) cerea* (Reeve). (j) Adult, Seychelles. (k) Immature, Queensland. (l) *Xenophora (Xenophora) conchyliophora* (Born). After Bergh (1896). (m) *Xenophora (Xenophora) testigera digitata* Martens. (n) *Xenophora (Stellaria) chinensis chinensis* (Philippi). (o) *Xenophora (Onustus) longleyi* Bartsch. (p) *Xenophora (Onustus) caribaea* Petit de la Saussaye. (q, r) *Xenophora (Onustus) exuta* (Reeve). (r) Enlargement of distal end of penis. (s) *Xenophora (Onustus) indica* (Gmelin).

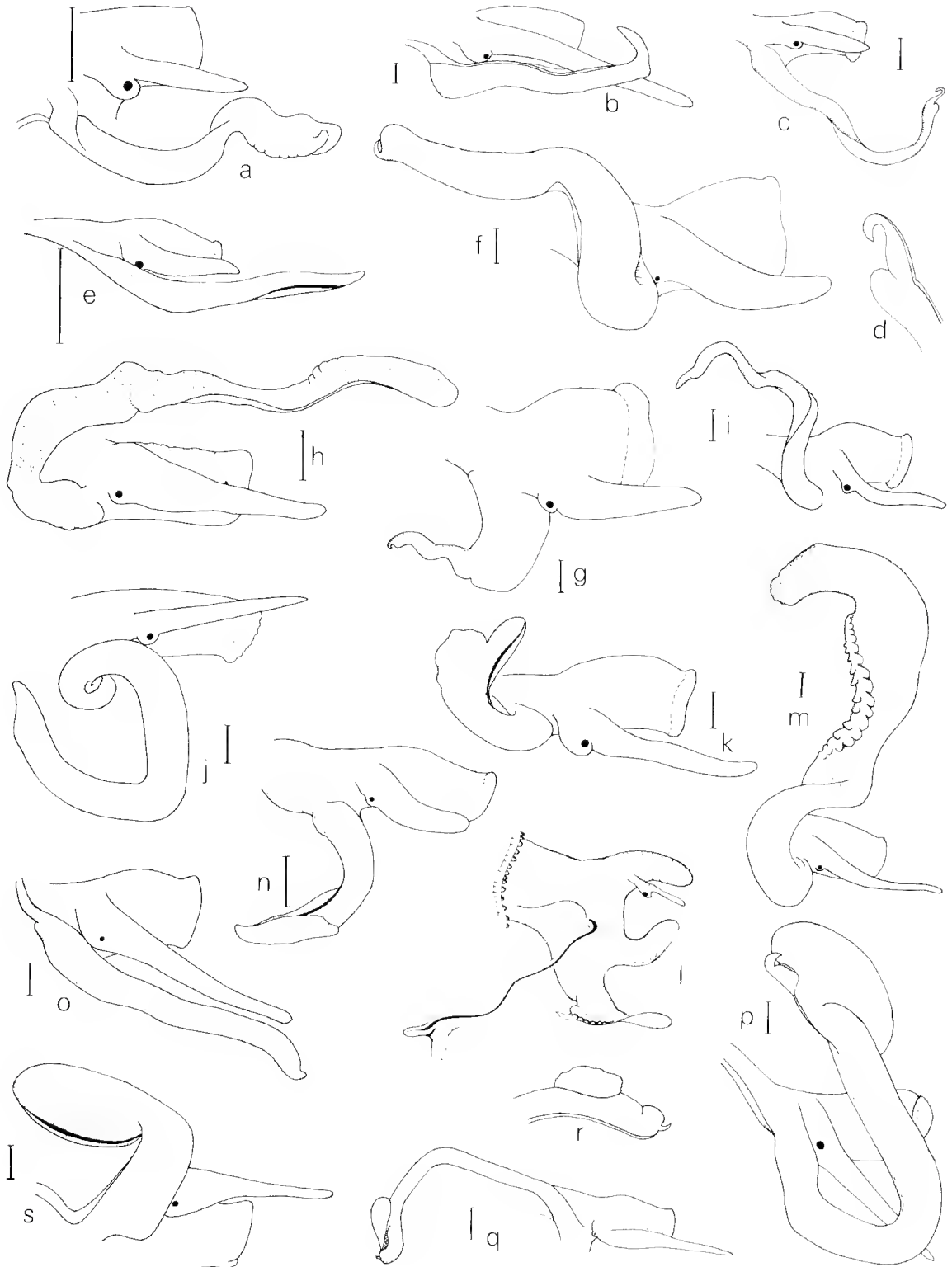
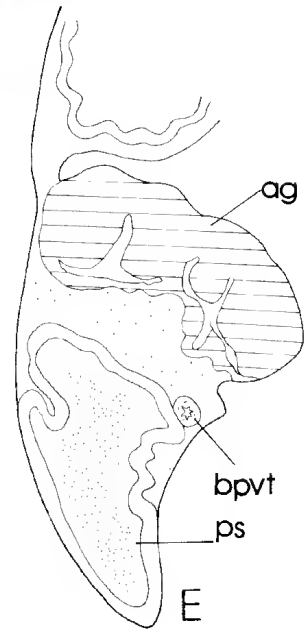
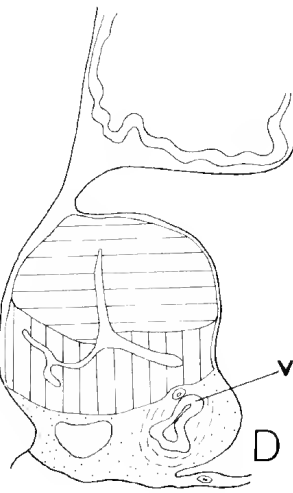
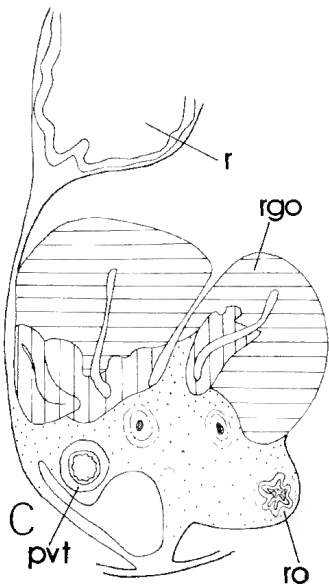
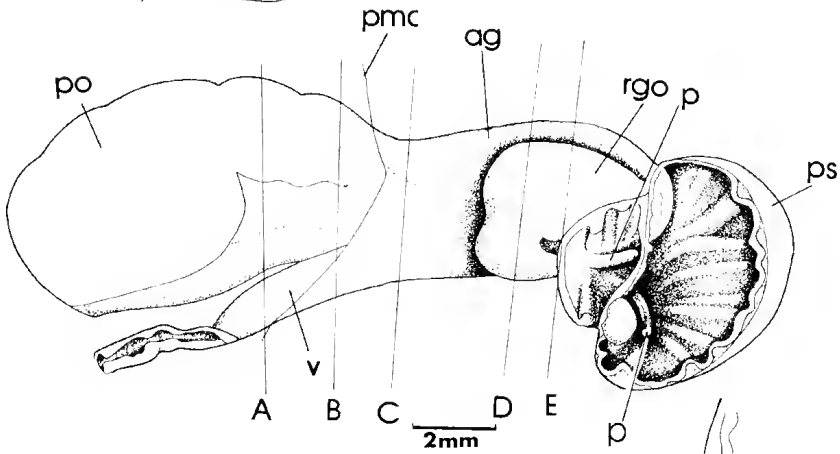
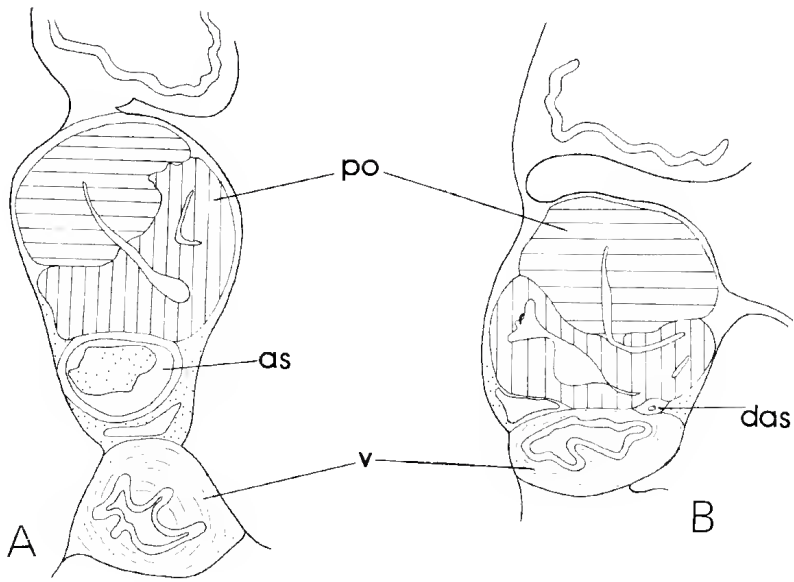


Fig. 15 (facing page). Female genitalia of *Xenophora (Xenophora) neozelanica neozelanica* Suter. A lateral view of the glandular part of the oviduct from the left side. The lines A-E represent the sections so numbered. ag — albumen gland, as — anterior sperm sac, bpvt — bifurcate posterior ventral tube, c — cyst-like structure, das — duct of anterior sperm sac, p — papilla, pmc — posterior limit of pallial cavity, po — pallial oviduct, ps — posterior sperm sac, pvt — posterior ventral tube, r — rectum, rgo — recurved part of glandular oviduct, ro — renal oviduct, v — vaginal tube, vl — ventral lumen.





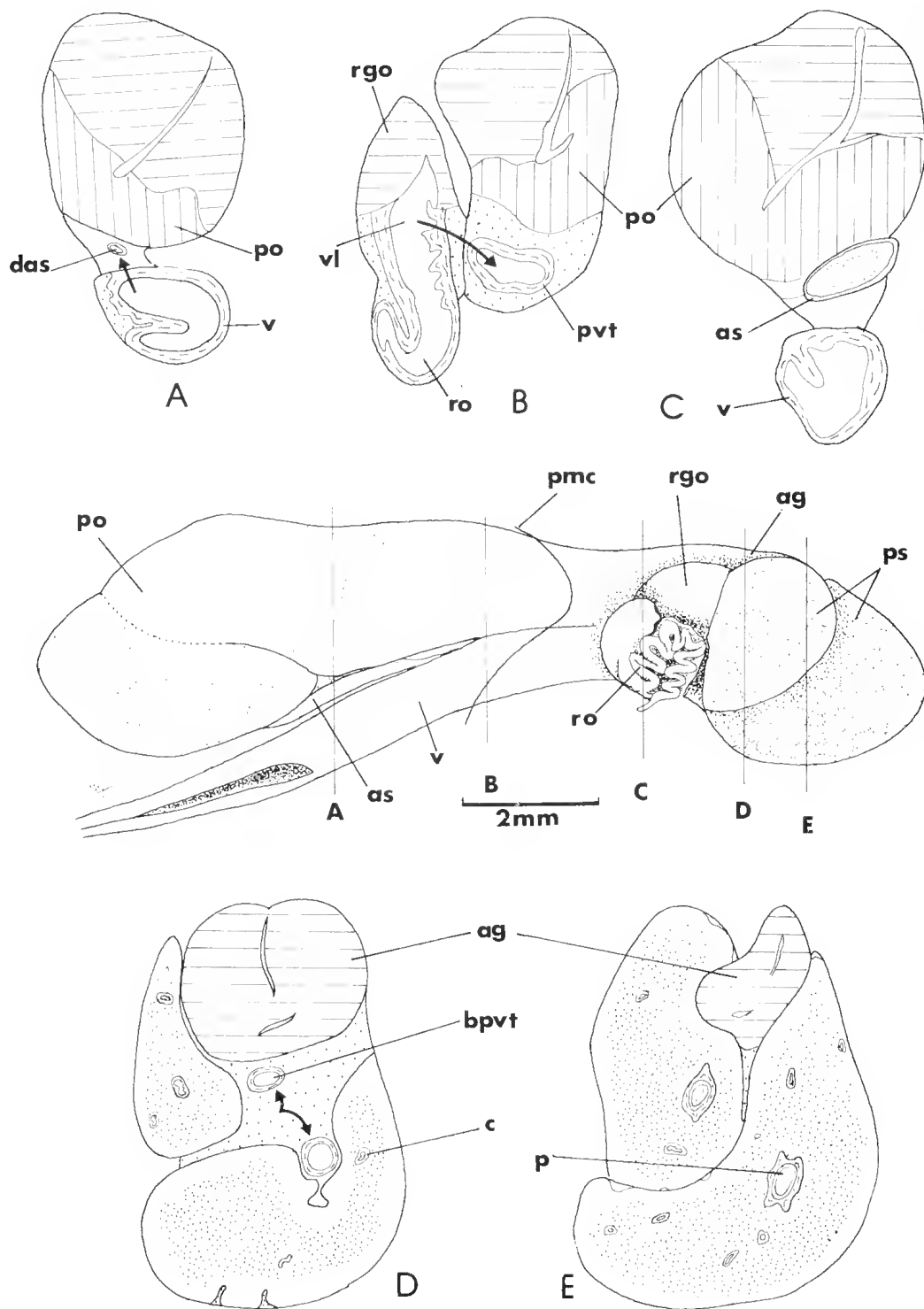


Fig. 16. Female genitalia of *Xenophora (Xenophora) peroniana peroniana* (Iredale). A lateral view of the glandular part of the oviduct from the left side. The lines A-E represent the sections so numbered. Key to letters used as abbreviations for the names of structures given in explanation of Fig. 15.

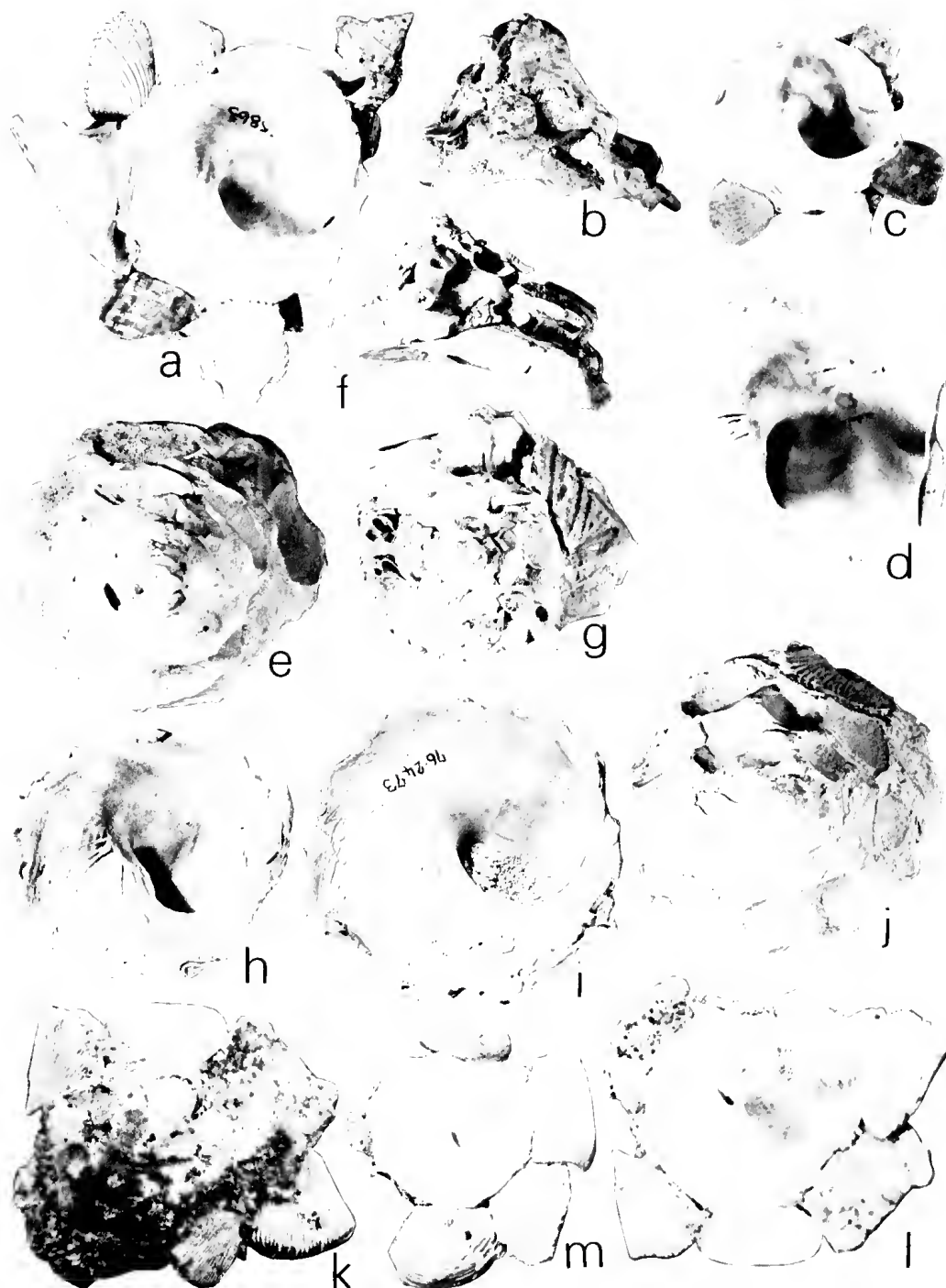


Fig. 17. *Xenophora* (*Xenophora*) *conchyliophora* (Born). (a) Boynton, Florida, U.S.A. (AMS, C.75863). Diam. 51.1 mm. (b, c) Punta Arena, Gulf of California (BMNH). Diam. 60 mm. (d, e) Holotype of *Xenophora tricostata* (Zoological Museum, Moscow University, L77). Diam. 53.5 mm. (f-h) Paratype of *Xenophora mecandrina* (Zoological Museum, Moscow University, L78). Diam. 41.7 mm. *Xenophora* (*Xenophora*) *flindersi ludbrookae* n. subsp.: (i, j) Holotype (WAM, 76.2473). Diam. 58 mm. *Xenophora* (*Xenophora*) *flindersi flindersi* (Cotton & Godfrey): (k, l) Holotype (SAM, D.13165). Diam. 18 mm. (m) Coffin Bay, South Australia, 37 m (NMV). Diam. 29.4 mm.

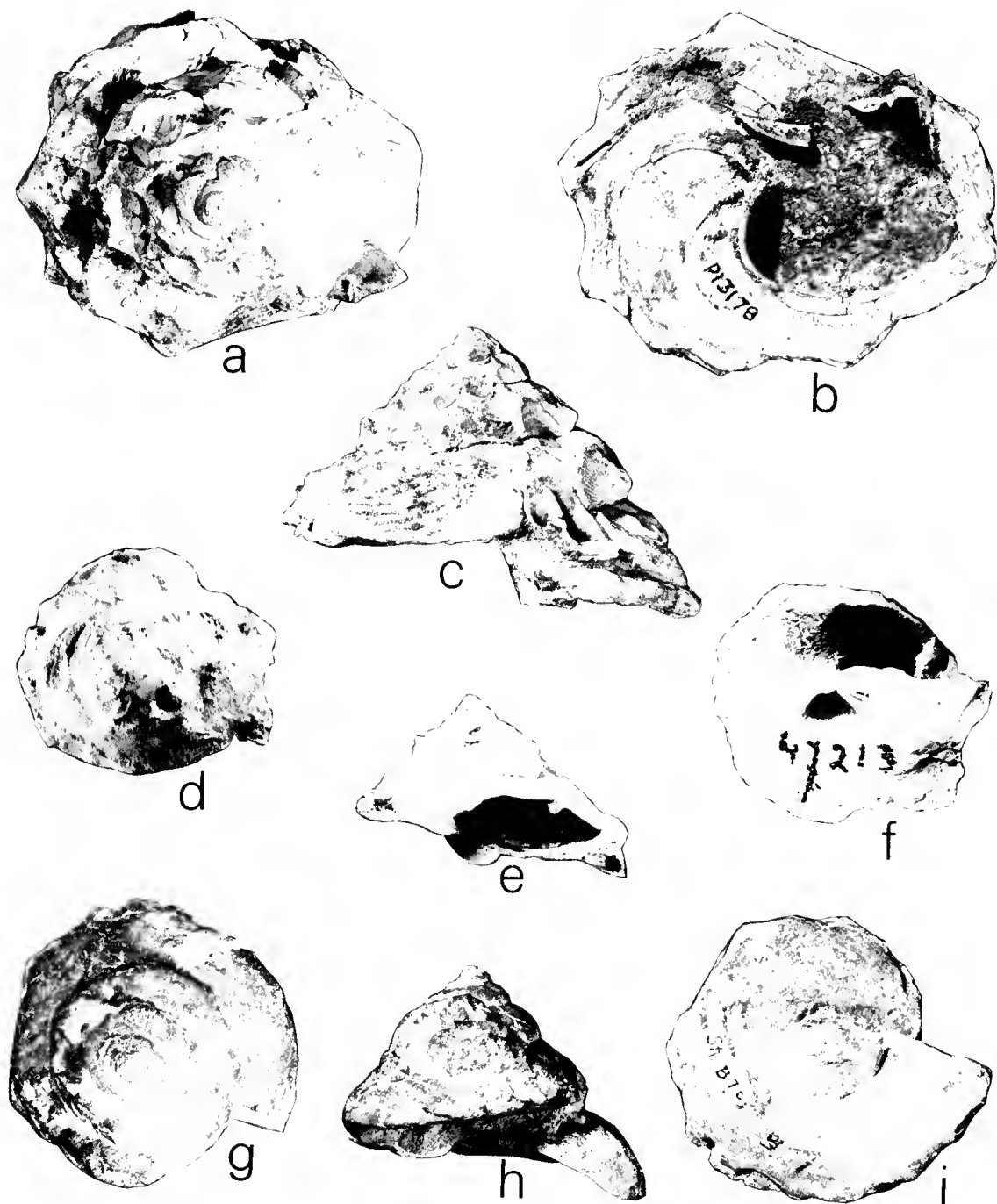


Fig. 18. *Xenophora (Xenophora)* sp. (a-c) Jan Juc Formation, Bird Rock Cliffs, Torquay, Victoria, Australia (NMV, P13178). Diam. 67.2 mm. *Xenophora (Xenophora)* cf. *cerea* (Reeve). (d-f) Near Jogjakarta, Java, Miocene (RGM, 47213). Diam. 22.1 mm. *Xenophora (Xenophora)* sp.: (g-i) Miria Marl, N.W. Carnarvon Basin, Western Australia, Maastrichtian (Bureau of Mineral Resources, Canberra). Diam. 49.5 mm.

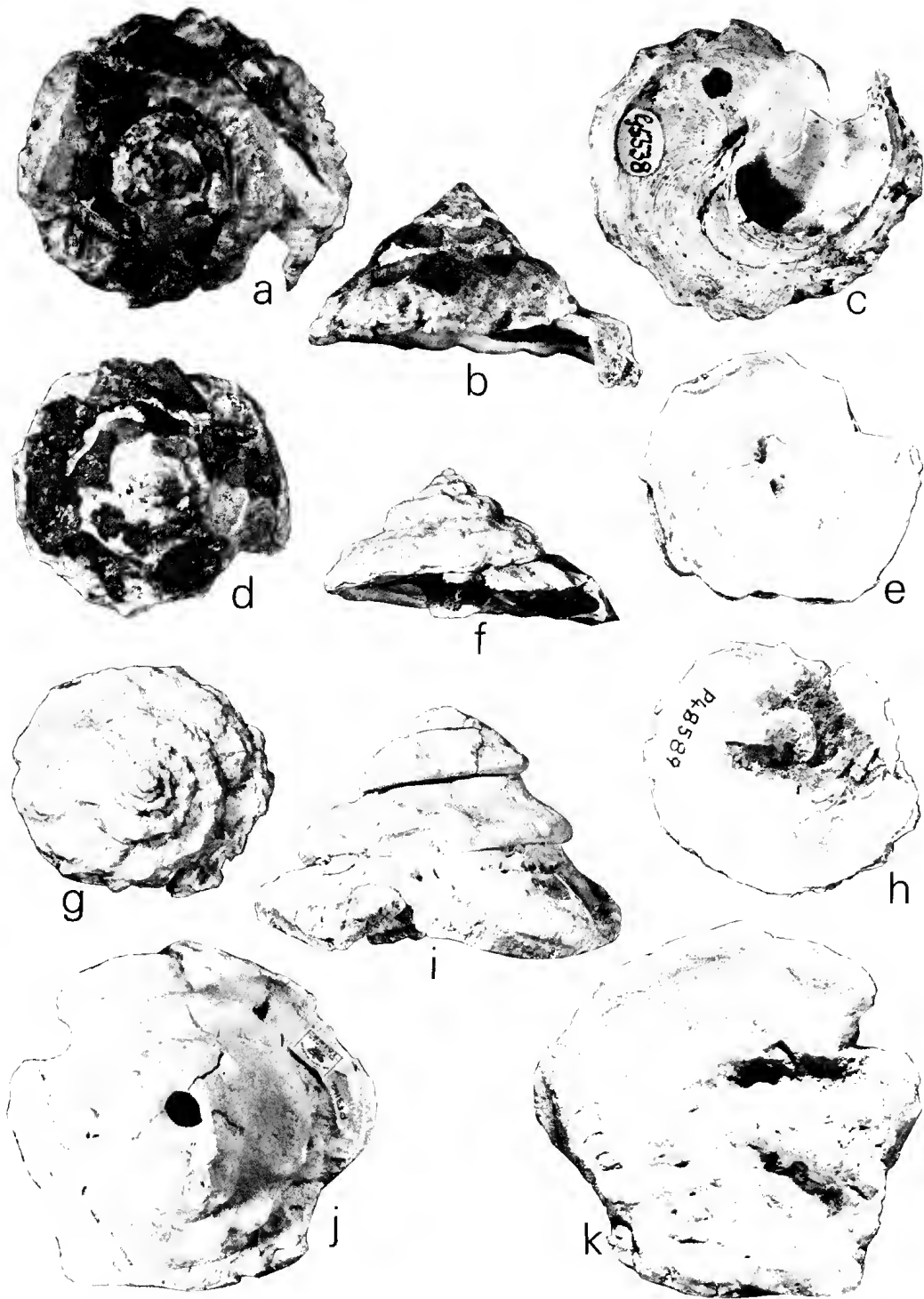


Fig. 19. *Xenophora (Xenophora) tatei* Harris: (a-c) Holotype (BMNH, G.5538). Diam. 44.3 mm. (d-e) Muddy Creek, near Hamilton, Victoria, Australia, Miocene (AMS, C.116800). Diam. 37 mm. *Xenophora (Xenophora)* sp.: (f-h) Cadell Marl, River Murray cliff, 6.4 km. below Morgan, South Australia, Miocene (NMV, P.48589). Diam. 33.5 mm. (i-k) Morgan Limestone, River Murray cliff 0.4 km. above Morgan, South Australia, Miocene (NMV, P.13162). Diam. 101 mm.

Fig. 20 (facing page). *Xenophora (Xenophora) pallidula* (Reeve): (a-c) Holotype (BMNH, 1950.8.28.17). Diam. 71.7 mm. *Xenophora (Xenophora) peroniana peroniana* (Iredale): (d) Off Moreton Bay, S. Queensland, 75-80 m (AMS, C.95218). Diam. 46.7 mm. *Xenophora (Xenophora) mekranensis konoj* Habe: (e) Off Sorsogon, S. end Luzon Is., Philippines (AMS, C.94513). Diam. 47.2 mm. *Xenophora (Xenophora) cerea* (Reeve): (f) Near Michaelmas Cay, Queensland, 46 m (AMS, C.65521). Diam. 54 mm. (g) Off Tosa, Japan (USNM, 346150). Diam. 51.35 mm. *Xenophora (Xenophora) neozelanica neozelanica* Suter: (h) Hauraki Gulf, New Zealand (AMS, C.75861). Diam. 68.2 mm.



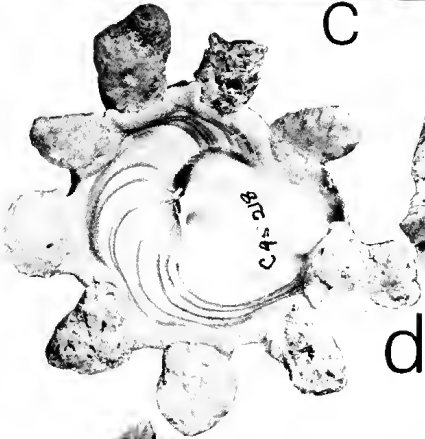
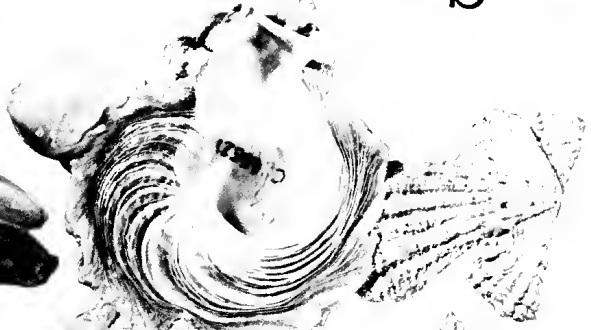
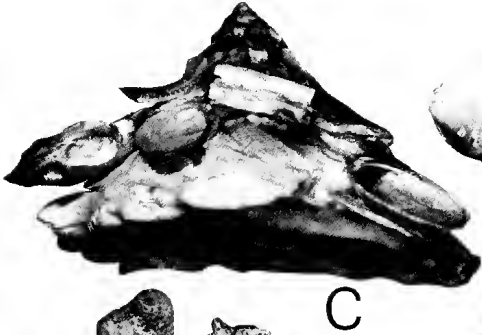
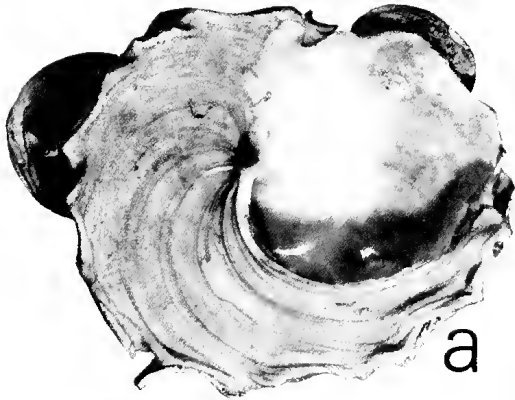




Fig. 21. *Xenophora* (*Xenophora*) *tenuis* Fulton: (a-c) Holotype (BMNH, 1937.7.13.7). Diam. 43.5 mm. *Xenophora* (*Xenophora*) *peroniana peroniana* (Iredale): (d-f) Lectotype (AMS, C.104143). Diam. 46.6 mm. (g-l) Off Fraser Is., S. Queensland, (g-i) 201 m, AMS, C.105519, diam. 40 mm., (j-k) 210-219 m, AMS, C.105514, diam. 31.56 mm. *Xenophora* (*Xenophora*) *peroniana kondoi* n. subsp.: (m-o) Holotype (USNM, 335064). Diam. 42.2 mm.

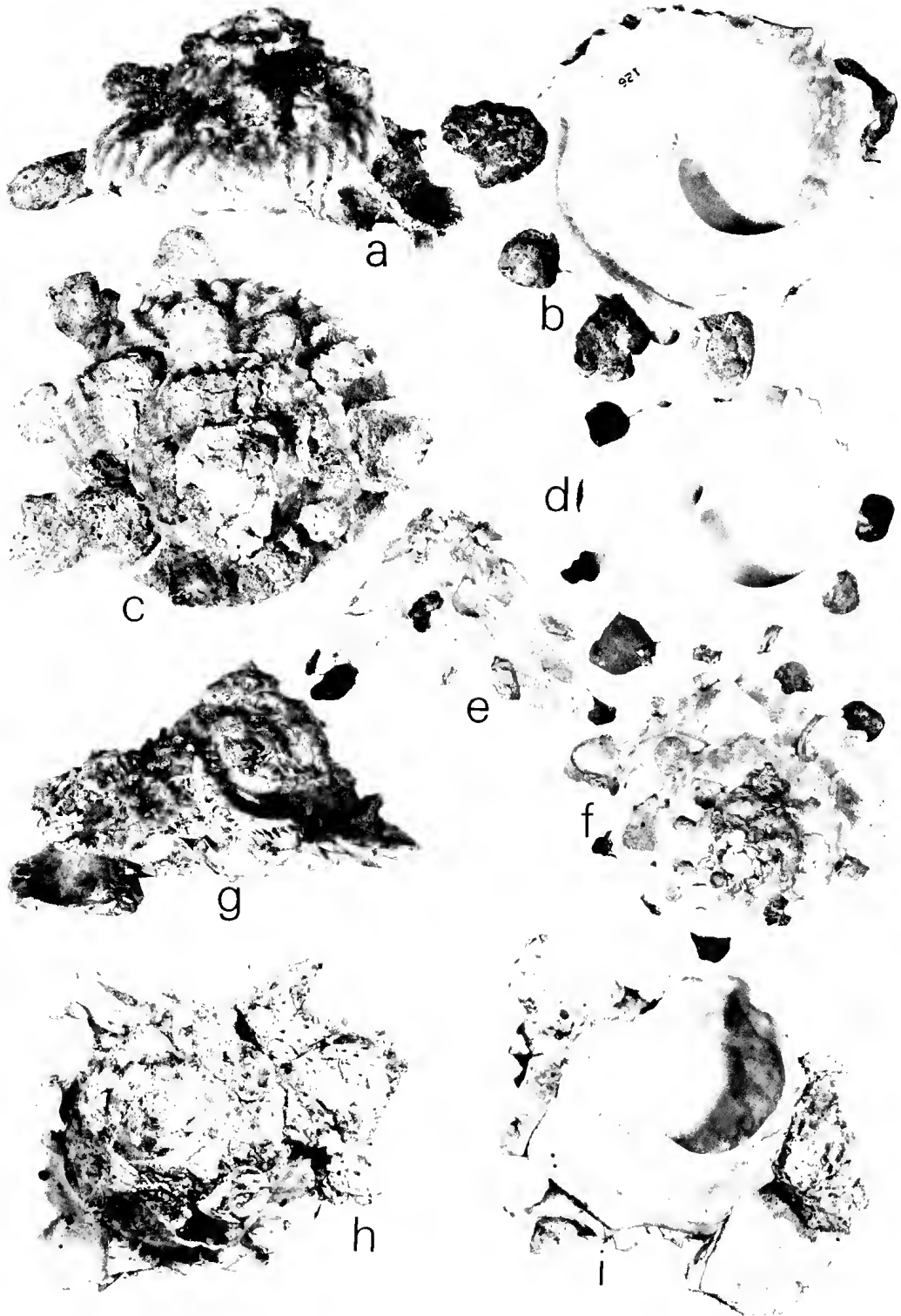


Fig. 22. *Xenophora (Xenophora) granulosa* n. sp. (a-c) Balicasag Is., Bohol, Philippines, 183 m (G. Mallory Colln.). Diam. 63 mm. (d-f) Holotype (NHMP). Diam. 50 mm. *Xenophora (Xenophora) flindersi flindersi* (Cotton & Godfrey): (g-h) Between St. Francis and Smooth Islands, South Australia, 20-30 m (AMS, C.102097). Diam. 49.5 mm.



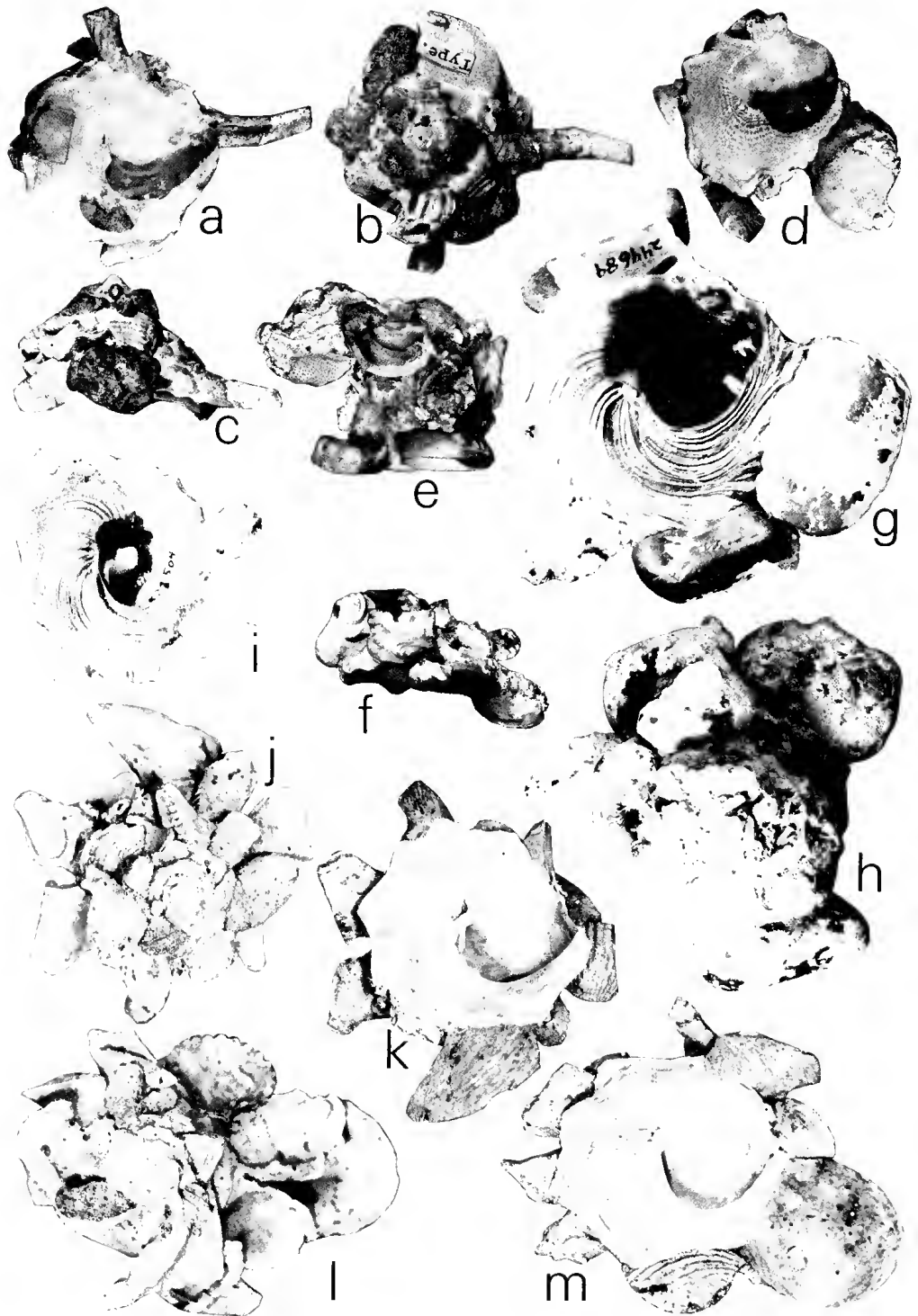


Fig. 23. *Xenophora (Xenophora) cerea* (Reeve): (a-c) Holotype (BMNH, 1950.8.28.19 (a)). Diam. 24 mm. (d-f) Paratype (BMNH, 1950.8.28.19 (b)). Diam. 20 mm. (g, h) Paratype (?) of *Xenophora torrida*. Off Kii, Japan (ANSP, 244689). Diam. 36.8 mm. (i) W. of Jieroru Is., Eniwetok, Marshall Ids (USNM, 582504). Diam. 27.35 mm. *Xenophora (Xenophora) japonica* Kuroda & Habe: (j-m) Paratypes (NSMT). Diam. (j, k) 35 mm, (l, m) 35.5 mm.

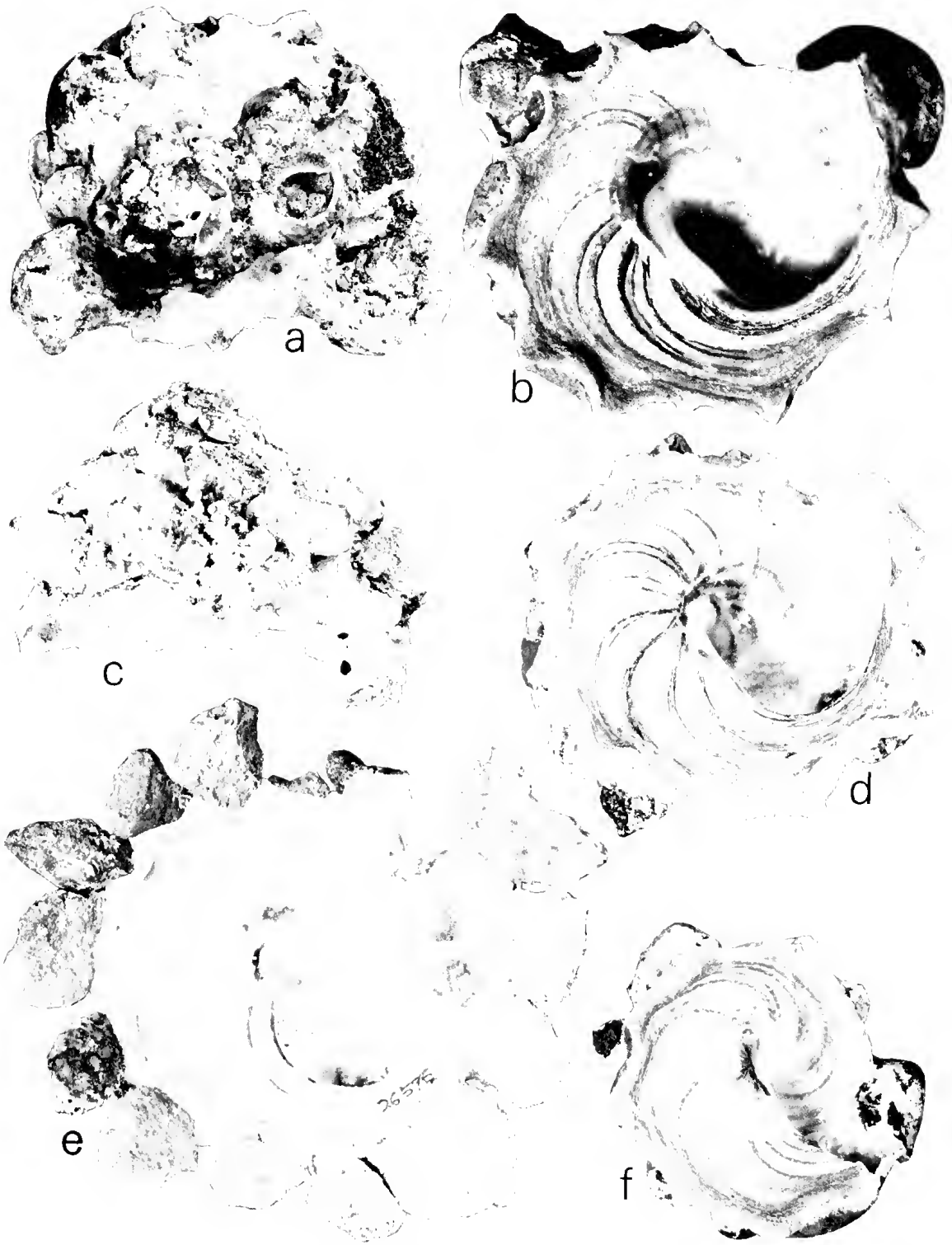


Fig. 24. *Xenophora (Xenophora) neozelanica kermadecensis* n. subsp. (a-b) Holotype (NMNZ, M.F. 30899). Diam. 58.1 mm. (c-d) Paratype (NMNZ, M.F. 22014). Diam. 54.2 mm. (e) Off Raoul Is., Kermadec Ids, 274-219 m (NMNZ, M.F. 26596). Diam. 55 mm. (f) Juvenile paratype (NMNZ, M.F. 22014). Diam. 38.4 mm.



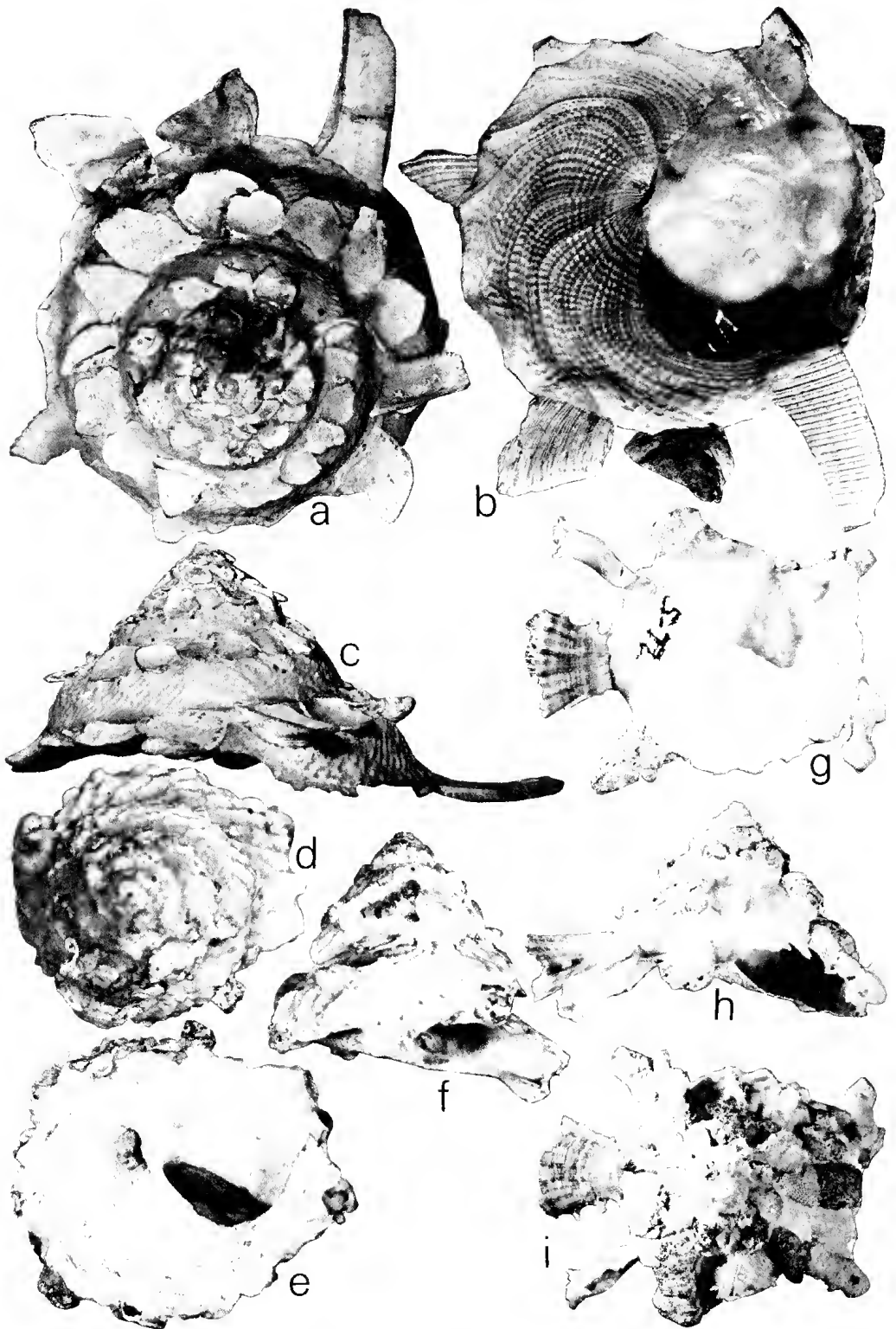


Fig. 25. *Xenophora (Xenophora) corrugata* (Reeve): (a-c) Holotype (BMNH, 1950.8.28.18). Diam. 62 mm. *Xenophora (Xenophora) mekranensis konoii* Habe: (d-f) Holotype (NSMT, 45262). Diam. 54.8 mm. (g-i) W. of Gantheaume Bay, Western Australia (WAM, 5-72). Diam. 37.8 mm.

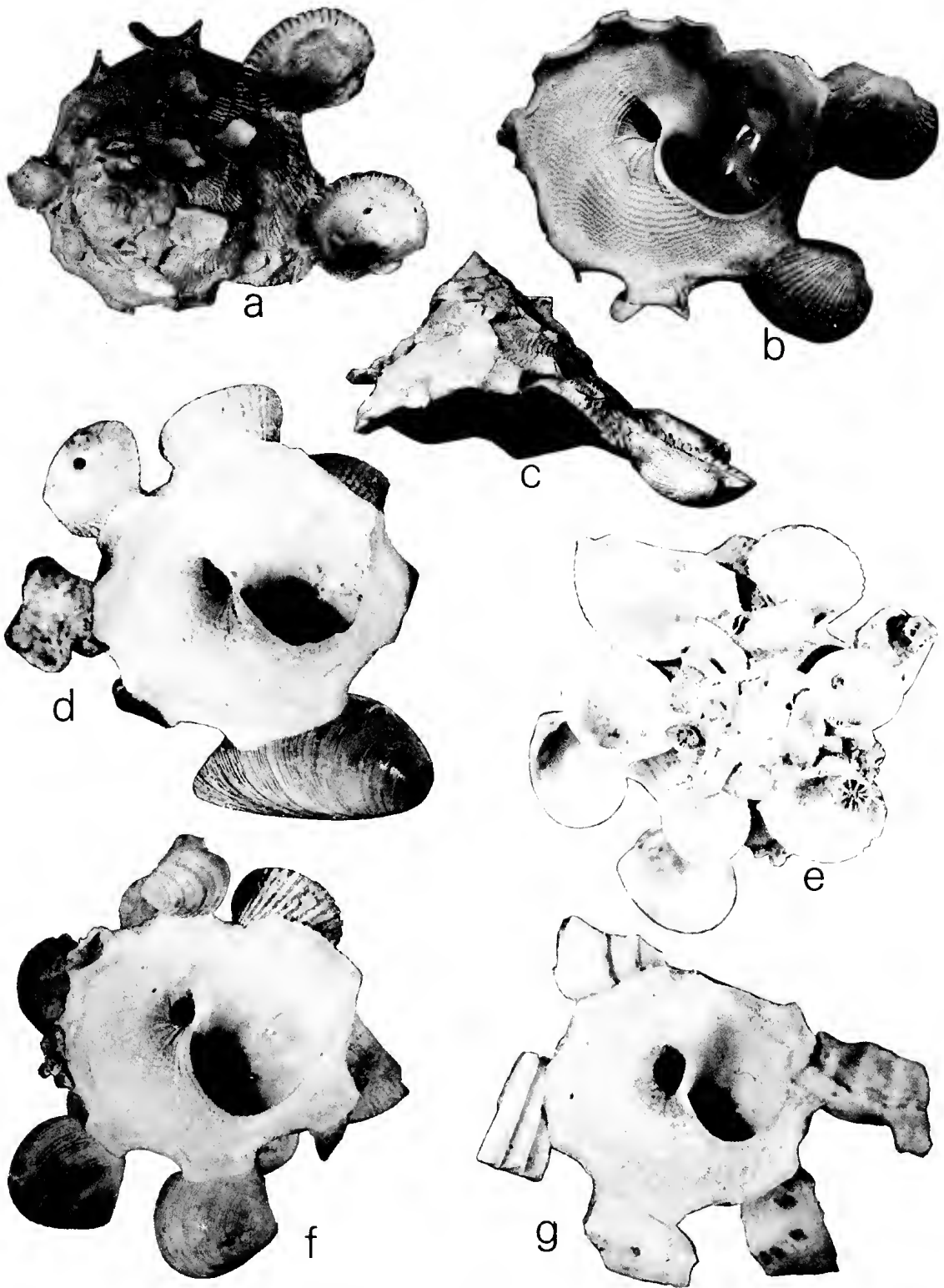


Fig. 26. *Xenophora* (*Xenophora*) *crispa* (König): (a-c) Syntype of *Xenophora cavellieri* Rochebrune (NHMP). Diam. 32 mm. (d-f) Syntypes of *Xenophora mediterranea* Tiberi (NHMP). Diam. (d) 30.7 mm (e-f) 28.7 mm. (g) Holotype of *Xenophora senegalensis* Fischer (NHMP). Diam. 16.7 mm.

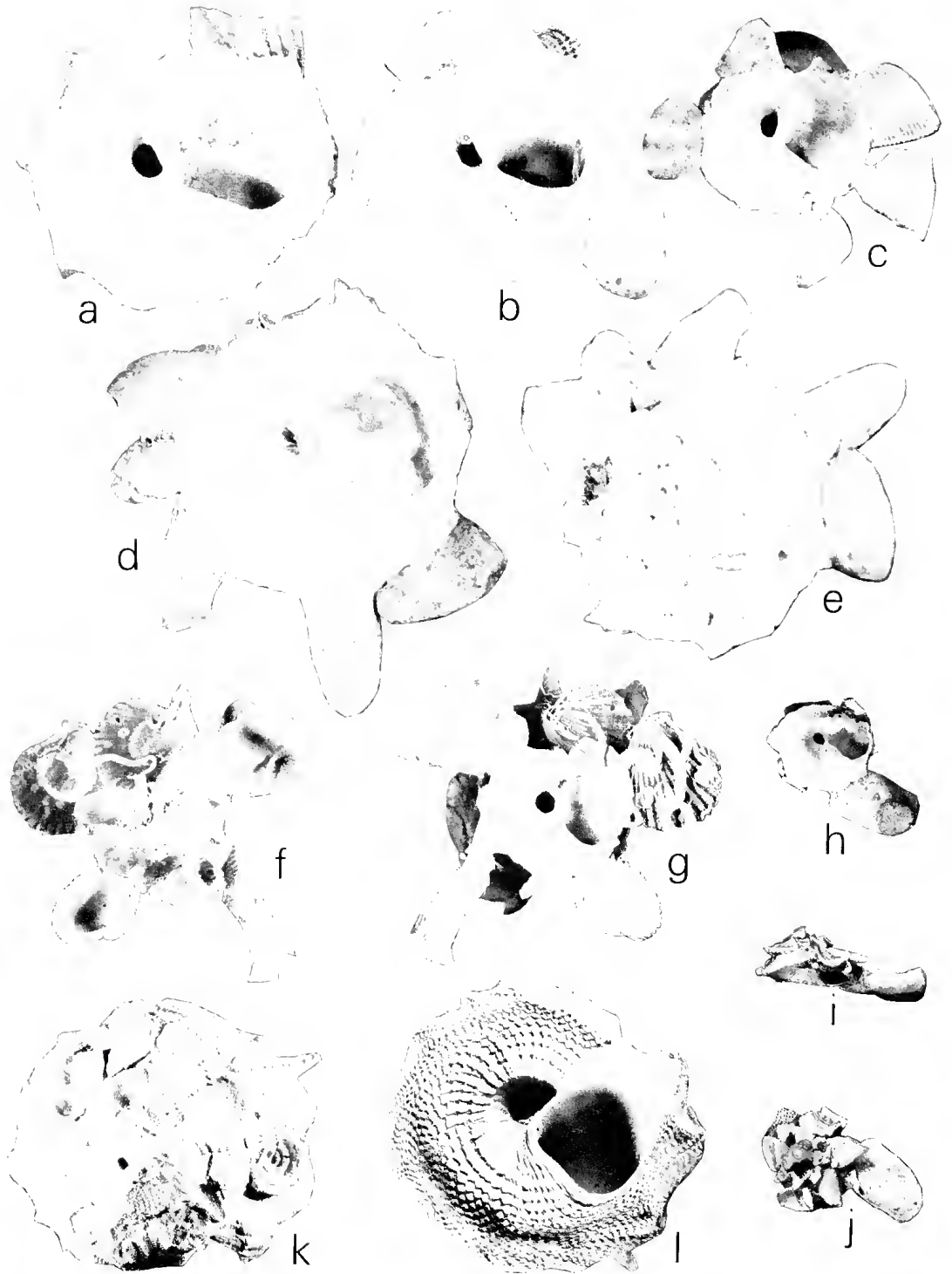


Fig. 27. *Xenophora (Xenophora) solarioides solarioides* (Reeve): (a-e) Syntypes of *Xenophora australis* Souverbie & Montrouzier (NHMP). Dimensions not known. (f-g) Holotype (BMNH, 1953.4.7.47). Diam. 19.1 mm. (h-i) Paratype of *Phorus cereus* Reeve (BMNH, 1950.8.28.19 (c)). Diam. 19.1 mm. *Xenophora (Xenophora) solarioides jezleri* Cox: (k-l) Holotype (Natural History Museum, Basel, H.14390). Diam. 25.0 mm.

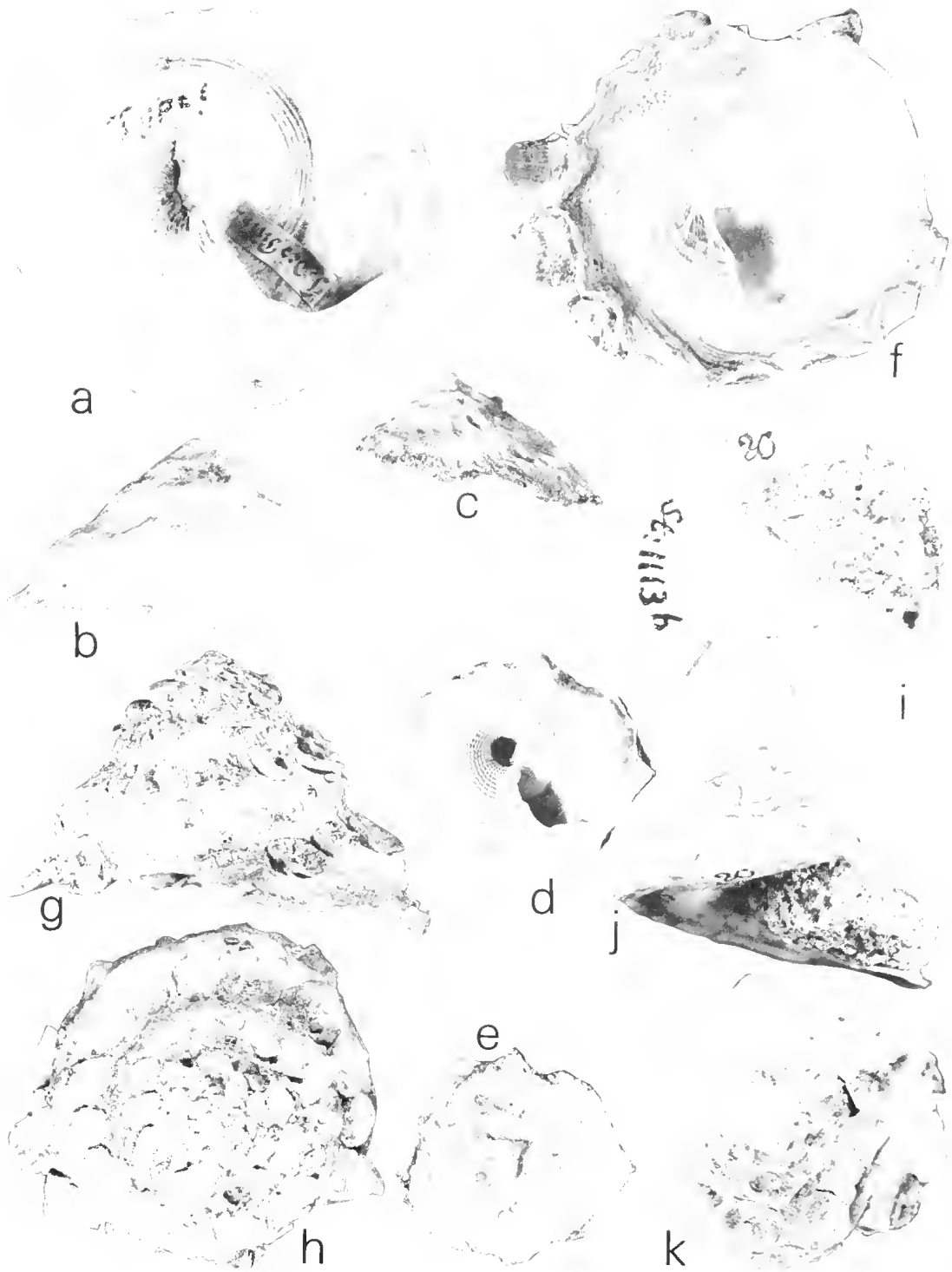


Fig. 28. *Xenophora (Stellaria) lamberti* Souverbie: (a-b) Holotype (Natural History Museum, Bordeaux). Diam. 52.2 mm. (c-e) Ouvéa, Loyalty Ids (Pleistocene) (Doiteau Colln.). Diam. 32.6 mm. *Xenophora (Xenophora) corrugata* (Reeve): (f-h) Bahrain, Persian Gulf (ZMC). Diam. 45 mm. *Xenophora (Xenophora) pallidula* (Reeve): (i-k) Tjkarang, Java (Miocene) (RGM, 11136). Diam. 31.4 mm.



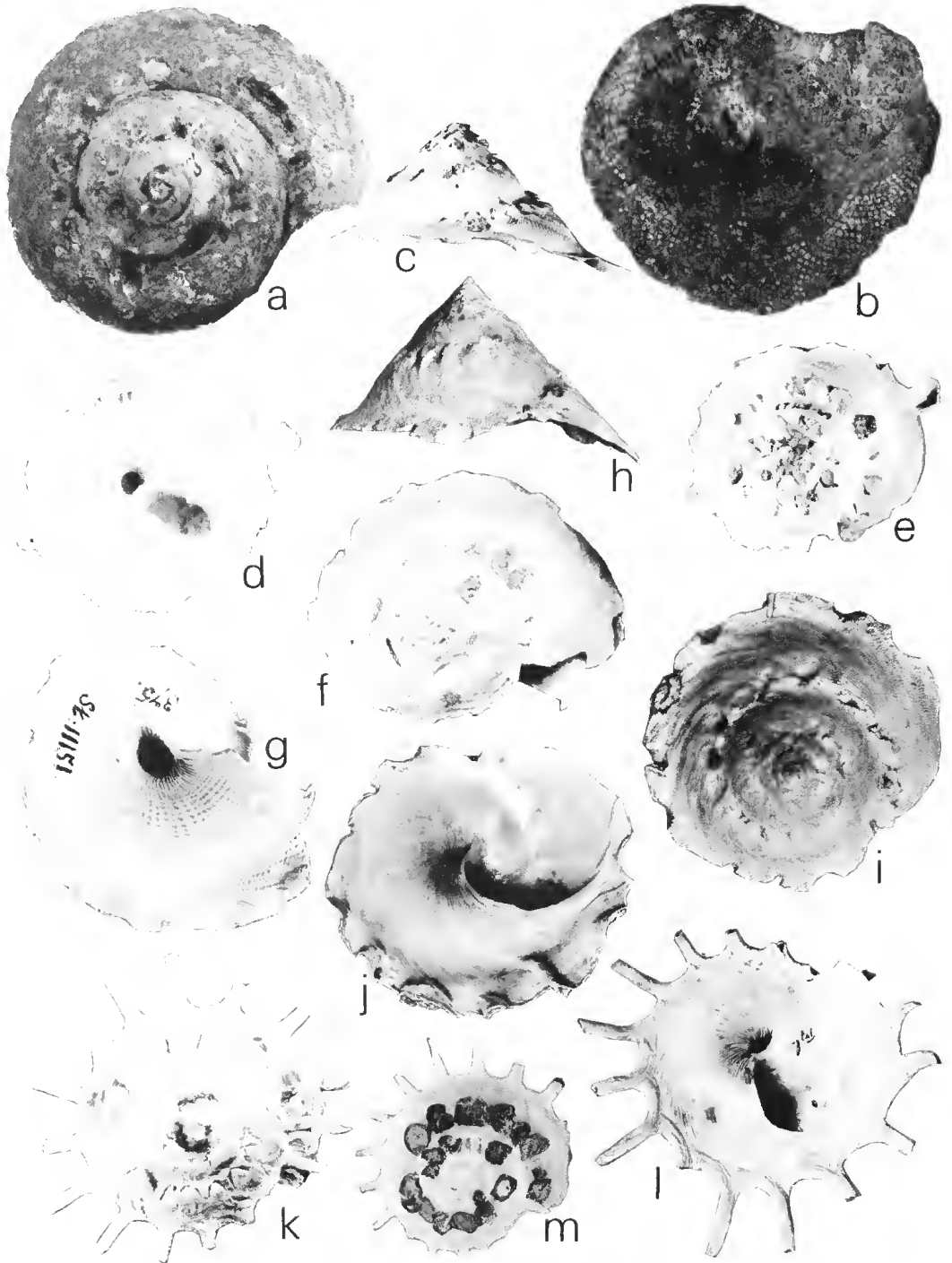


Fig. 29. *Xenophora (Stellaria) chinensis dunkeri* Martin: (a-b) Holotype, Miocene, Java (RGM). Diam. 60.5 mm. *Xenophora (Stellaria) chinensis chinensis* (Philippi): (c-e) Off Dirk Hartog Is., Western Australia (WAM, 1745-69). Diam. 68.9 mm. (f-g) Pliocene, Son dé beds, Java (RGM). Diam. 44 mm. *Xenophora (Stellaria) gigantea* Schepman: (h-i) Holotype (ZMA, 2532). Diam. 98 mm. *Xenophora (Stellaria) solaris* (Linné): (k-l) Nicobar. Original of Chemnitz (1781), figs 1700-1 (ZMC). Diam. 83 mm. (m) 82 m, Kuh-i-Mannar, Persian Gulf (BMNH). Diam. 68.8 mm.





Fig. 30. *Xenophora (Stellaria) testigera digitata* Martens: (a-c) Holotype (EBM, 29316). Diam. 56.3 mm. *Xenophora (Stellaria) testigera profunda* n. subsp.: (d-f) Holotype (BMNH, 19787). Diam. 60.6 mm.

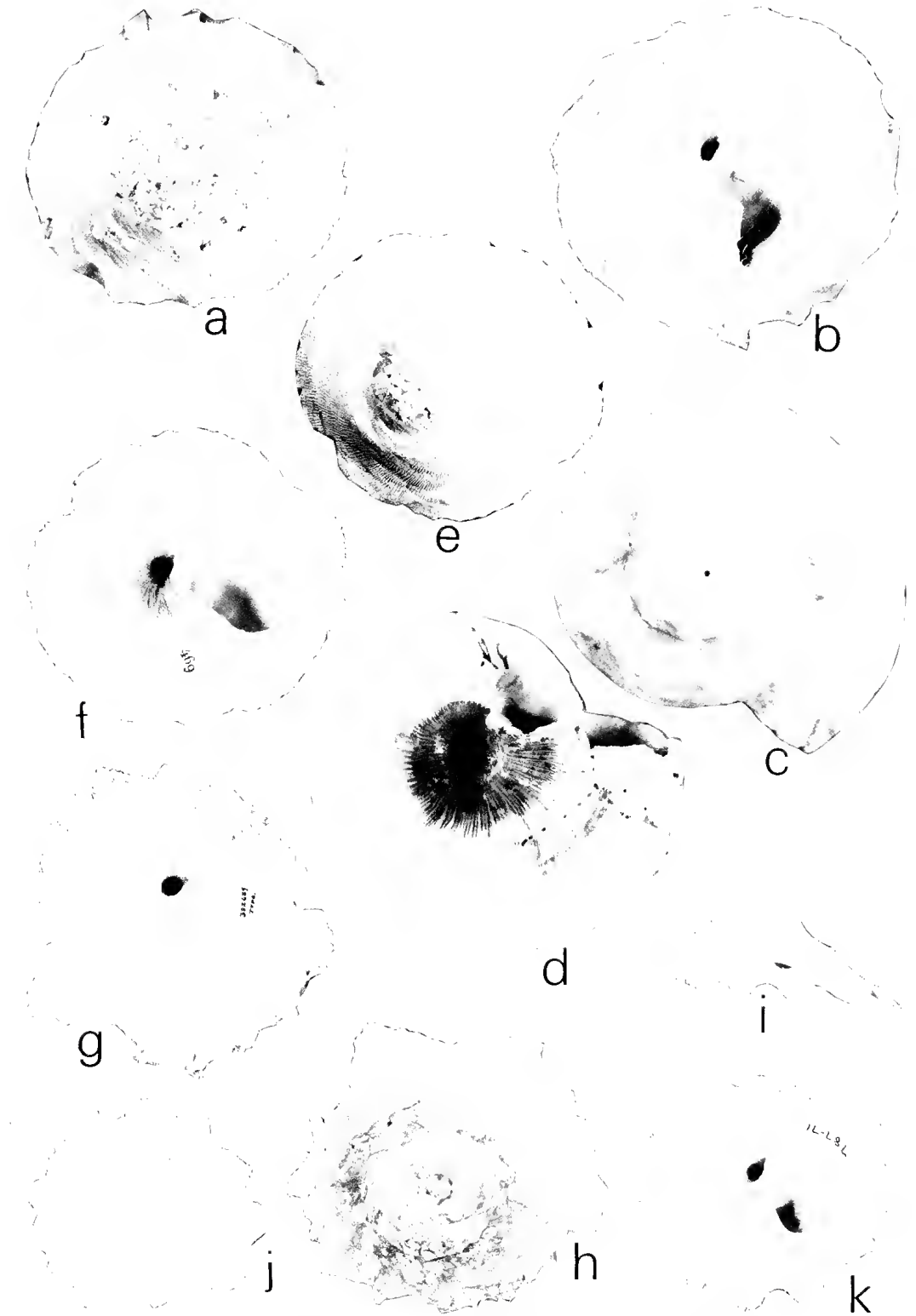


Fig. 31. *Xenophora (Onustus) caribaea* Petit de la Saussaye: (a-b) Syntype (NHMP). Diam. 65 mm. *Xenophora (Onustus) indica* (Gmelin): (c-d) Lectotype (original of Chemnitz, 1781, figs. 1697-8) (ZMC). Diam. 44.7 mm. (e-f) Lectotype of *Xenophora wagneri* Philippi (original of Schubert & Wagner, 1829, figs 4062a, b) (ZMC). Diam. 68.1 mm. *Xenophora (Onustus) longleyi* Bartsch: (g-h) Holotype (USNM, 382689). Diam. 144 mm. *Xenophora (Onustus) exuta* (Reeve): (i-k) Off False Entrance, Western Australia (WAM, 78771). Diam. 63.7 mm.



Fig. 32. Distribution of *Xenophora (Xenophora) conchyliophora* (Born).



Fig. 33. Distribution of *Xenophora (Xenophora) cerea* (Reeve).

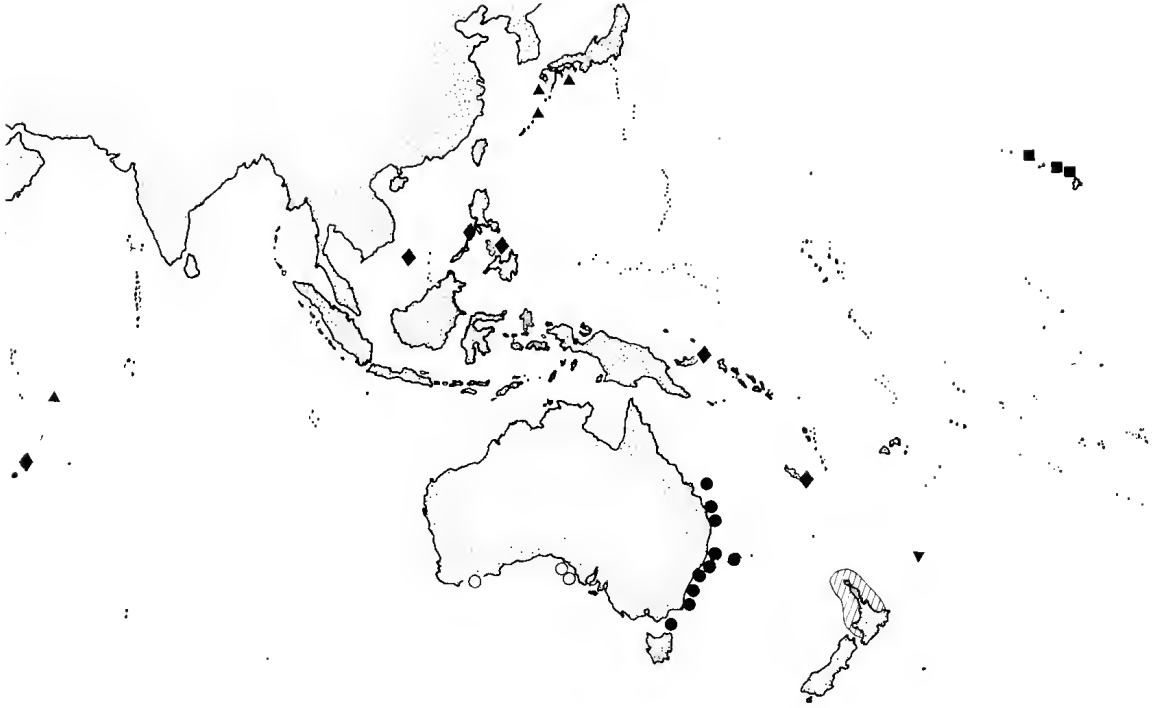


Fig. 34. Distribution of *Xenophora (Xenophora)* species: ● *X. (X.) peroniana peroniana* (Iredale). ■ *X. (X.) peroniana kondoi* n. subsp. ○ *X. (X.) flindersi flindersi* (Cotton & Godfrey). ▲ *X. (X.) tenuis* Fulton. ⊖ *X. (X.) neozelanica neozelanica* Suter. ▼ *X. (X.) neozelanica kermadecensis* n. subsp. ◆ *X. (X.) granulosa* n. sp.

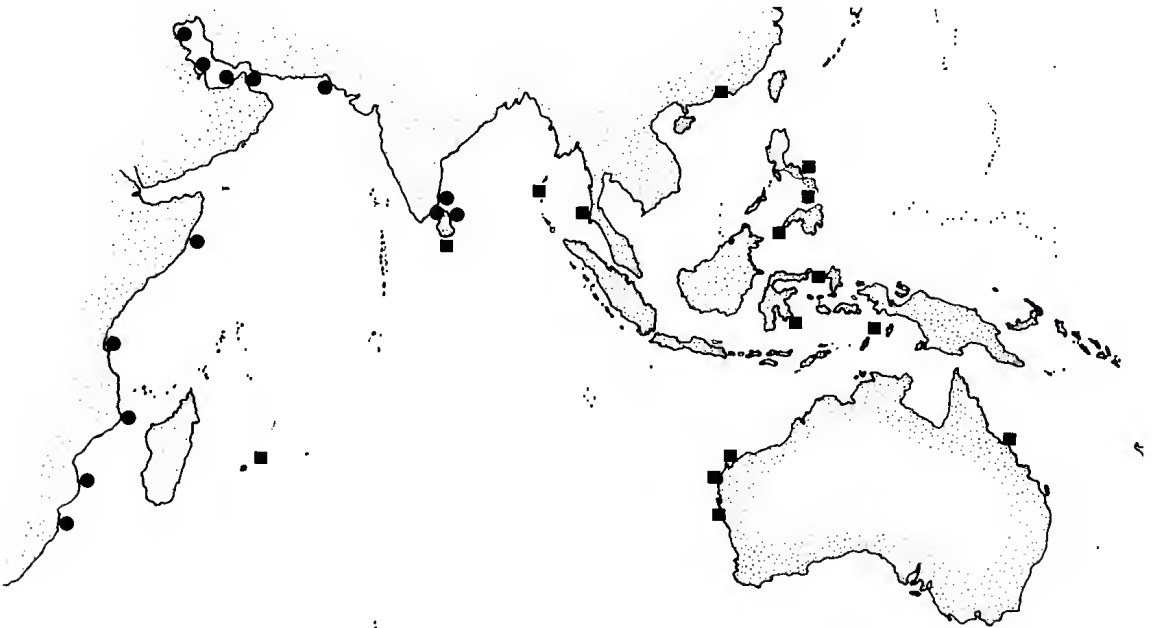


Fig. 35. Distribution of *Xenophora (Xenophora)* species: ● *X. (X.) corrugata* (Reeve). ■ *X. (X.) mekranensis konoii* Habe.

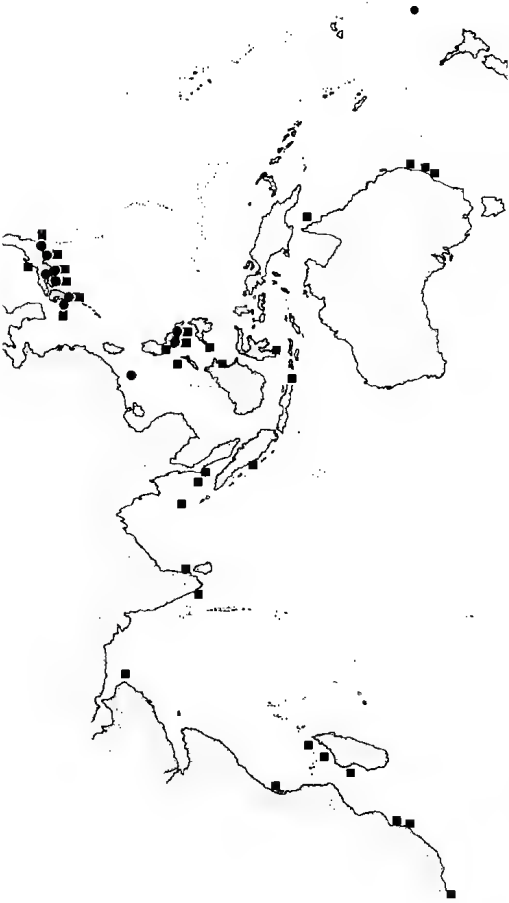


Fig. 36. Distribution of *Xenophora* (*Xenophora*) species: ■ *X. (X.) pallidula* (Reeve). ● *X. (X.) japonica* Kuroda & Habe.



Fig. 37. Distribution of *Xenophora* (*Xenophora*) *solarisoides solarisoides* (Reeve).

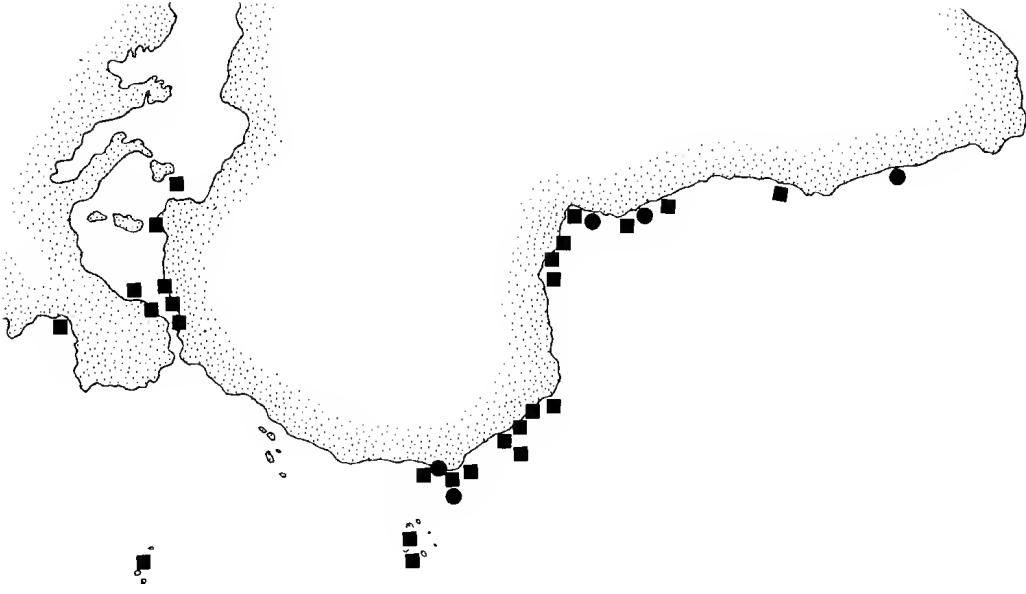


Fig. 38. Distribution of *Xenophora* (*Xenophora*) and *Xenophora* (*Stellaria*) species: ■ *X. (X.) crista* (König). ● *X. (S.) testigera* (*Stellaria*) Martens.





Fig. 39. Distribution of *Xenophora (Stellaria) solaris* (Linné).

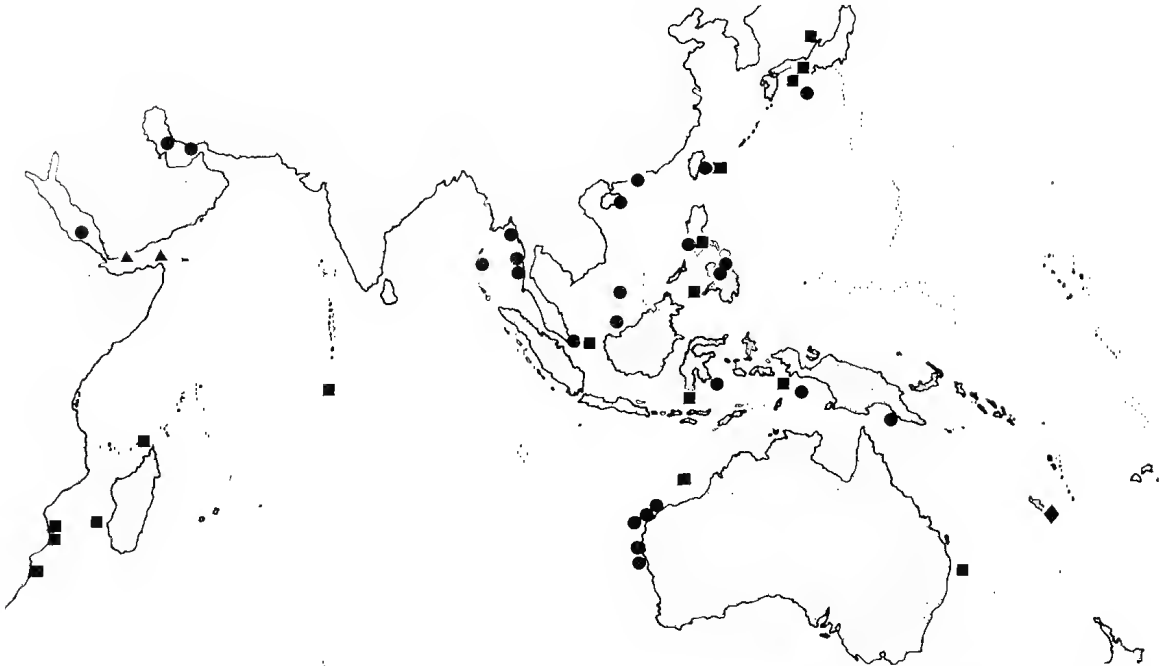


Fig. 40. Distribution of *Xenophora (Stellaria)* species: ● *X. (S.) chinensis chinensis* (Philippi). ■ *X. (S.) gigantea* Schepman. ▲ *X. (S.) testigera profunda* n. subsp. ◆ *X. (S.) lamberti* Souverbie.

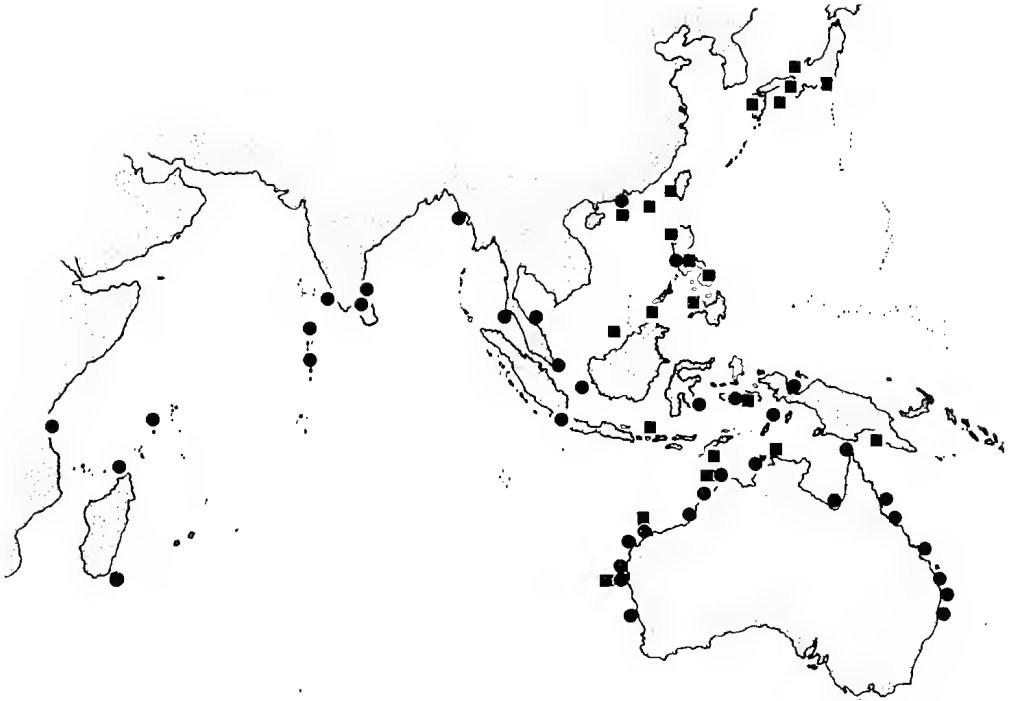


Fig. 41. Distribution of *Xenophora (Onustus)* species: ● *X. (O.) indica* (Gmelin). ■ *X. (O.) exuta* (Reeve).



Fig. 42. Distribution of *Xenophora (Onustus)* species: ■ *X. (O.) caribaea* Petit de la Saussaye. ○ *X. (O.) longleyi* Bartsch.



## INDEX

Species and genus group taxa only are listed. Page numbers in bold type refer to major citations, those in standard type to the main additional references in the text. Minor references to taxa are not listed. Each species name is given the same ending as in its original introduction unless it is a valid Recent species.

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