# The presence of the genera Talochlamys and Hinnites (BIVALVIA: PECTINOIDEA: PECTINIDAE) in West Africa 

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#### Abstract

Summary: Four species of PECTINIDAE from the West African waters are discussed, three of them belong to the genus Talochlamys, namely T. abscondita (P. Fischer, in Locard, 1898), T. multistriata (Poli, 1795), T. pusio (Linnaeus, 1758) and one to the genus Hinnites, H. corallinus (Sowerby I, 1827).


## Abbreviations used in the descriptions:

H: height (dorsal-ventral); L: length (anterior-posterior); LV: left valve; RV: right valve.
BMNH: British Museum (Natural History) (now: The Natural History Museum), London.
FN: Private collection of Frank Nolf, Oostende, Belgium.
KBIN: Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium.
LSL: Linnean Society of London.
MNHN: Muséum national d'Histoire naturelle, Paris.
PEMARCO: Pêche maritime du Congo.
R/V: research vessel or trawler converted for research purpose.

## Glossary of morphological terms

Adductor muscle: muscle, commonly one or two, connecting two valves of a shell, tending to draw them together.
Adductor scar: impression on interior of a shell where adductor muscle was attached.
Anterior: direction parallel to cardinal axis more nearly approximating to that in which mouth of animal faces.
Antimarginal: shell sculpture concentric with margin.
Auricle: earlike extension of dorsal region of a shell commonly separated from body of the shell by notch or sinus.
Basal margin: edge of a shell opposite hinge, i.e., ventral margin.
Beak: nose like angle, located along or above hinge margin, marking point where growth of the shell started; the tip of each valve; the oldest part of the shell.
Byssal gape: opening between margins of shell for passage of byssus.
Byssal notch: indentation below anterior auricle of right valve for passage of a byssus or protrusion of the foot.
Byssus: bundle of hair like fibres (silky threads) by which temporary attachment of a bivalve to other objects can be made.
Cardinal area: the region of the shell between the beaks and the hinge margin.
Cardinal axis: imaginary straight line along which two valves of a shell are hinged.
Chondrophore - chondrophore pit: excavation (pit) for attachment of internal ligament.
Commarginal ( $=$ new term for concentric): with direction on part of surface of shell under consideration determined by former position of the shell margin.
Commissure: line of junction of two valves.
Concentric: with direction coinciding (parallel) with that of growth lines.
Costa: moderately broad and prominent elevation of the surface of a shell, directed radially or otherwise.
Ctenolium: comb like row of small teeth on lower side of byssal notch.
Depth: the distance measured from the outer surface of the left to the outer surface of the right valve, when the shell is closed.
Disc, disk: in pectinoid shells, rounded part of the valve except auricle and lunule.
Equilateral: the condition when the growth of the shell on either side of the beaks is symmetrical or almost so.
Equivalve: the condition when the valves of a shell are similar in shape, size or sculpture.
Fasciole: a small band; a distinct band of colour.

Gape: the space left between the valves when the adductor muscles are fully contracted.
Growth line: a fine concentric line formed after a period of growth of the shell.
Growth stages: approximately concentric lines about the beaks indicating a cessation of growth at varying times, for some reason or another, but often annually, and superimposed upon the whole sculptural pattern.
Height: distance measured from the top straight down to the lower margin of the valve.
Hinge: the dorsal region of the shell along which the valves meet and where interlocking teeth may hold them together, these may sit directly on the hinge line or on an infolding of it called the hinge plate.
Hinge line: part of shell bordering dorsal margins and occupied by or close to hinge teeth and ligament.
Inequilateral: the condition when the growth on either side of the beaks is asymmetrical.
Inequivalve: the condition when the valves of the shell are not alike in size, shape or sculpture.
Inflated: strongly convex.
Lamella: thin plate.
Left valve: valve lying on left-hand side when the shell is placed with anterior end pointing away from observer and commissure vertical, the hinge being uppermost.
Length (= width): distance between two planes perpendicular to cardinal axis and just touching anterior and posterior extremities of shell.
Ligament: horny elastic structure joining two valves of a shell dorsally and acting as spring causing to open when adductor muscles relax; either external (a tensilium) or internal (a resilium) in a pit or chondrophore (a resilifer).
Lirae: fine raised lines or fine grooves on the shell surface, ornamented with sharp, raised threads, marked with parallel grooves or ridges; threadlike sculpture.
Longitudinal: direction parallel to that of cardinal axis.
Lunule: a depressed area present in some bivalves, situated in front of the beaks, in one, or both valves, generally set off from the rest of the shell by a change in sculpture or colour.
Muscle scar: impression on interior of shell marking former place of attachment of a muscle.
Oblique: most extended in direction neither parallel nor perpendicular to cardinal axis, but intermediate between these.
Ontogeny: sequence of different stages of growth.
Orbicular: circular.
Pallial line: line or narrow band on interior of a valve close to margin, marking line of attachment of marginal muscles of mantle.
Pallial region: marginal region of the shell interior adjacent to pallial line.
Pallial sinus: an indentation in the pallial line forming line of attachment of siphonal retractor muscles, always with its opening in the posterior half of the shell and sometimes whith its lower margin confluent with part of the pallial line.
Plica: fold or costa involving entire thickness of the wall of a shell.
Posterior: direction parallel to cardinal axis more nearly approximating to that in which anus faces and exhalant current is discharged.
Posterior area: part of surface of valve posterior-to-posterior edge.
Posterior ridge: ridge passing over or originating near umbo and running diagonally towards posteroventral part of a valve.
Posterodorsal margin: margin of dorsal part of a shell posterior to beaks.
Primary riblet: on shell with riblets of different orders of strength, riblet that appears early in ontogeny and remains stronger than those appearing later.
Radial: direction of growth outward from the beak at any point on surface of a shell, commonly indicated by direction of costa or other element of ornamentation.
Resilifer: recess or process for attachment of internal ligament.
Resilium: internal ligament.
Rib: moderately broad and prominent elevation of surface of a shell, directed radially or otherwise; same as costa.
Riblet: rather narrow linear elevation of the surface of a shell, subsequently being part of the microsculpture; same as costella.
Right valve: valve lying on right-hand side when shell is placed with anterior end pointing away from observer and commissure vertical, the hinge being uppermost.
Sculpture: regular relief pattern present on surface of many shells.
Secondary riblet: on a shell with riblets of different orders of strength, riblet that appears somewhat later in ontogeny than primary ones and remains weaker than these remain.

Squamose: bearing scales.
Stria: narrow linear furrow or raised line on surface of a shell.
Submargin: one of the dorsal edges of disc or body of a shell, adjoining lower border of auricle.
Surface ornament: regular relief pattern present on the surface of many shells.
Thread: narrow elevation of the surface of a shell.
Transverse: direction perpendicular to that of cardinal axis in plane of the valve margins.
Umbo: the surface of the valves immediately behind the beaks, normally convex (many authors treat beak and umbo as synonymous).
Umbonal angle: in pectinoid shells the angle of divergence of umbonal folds.
Valve: one of the calcareous structures (two in most bivalves) of which a shell consists.
Ventral: pertaining to or located relatively near to region of shell opposite hinge, where valves open most widely.
Width: = length.


Inside of the right (lower) valve


## The genus Talochlamys in West Africa

## Genus Talochlamys Iredale, 1929

Talochlamys Iredale, 1929 (as a subgenus of Mimachlamys). Type species (by original designation): Chlamys famigerator Iredale, 1925 [= Pecten pulleineanus Tate, 1887]. Recent, New South Wales, 91127 m.

Diagnosis: Byssally attached and cemented member of the Chlamydinae. Rather inflated, weakly convex, solid to fragile, inequivalve, equilateral to inequilateral, elongate, about 40 mm in height; with irregularly arranged, primary radial ribs, flanked with irregularly commenced secondary riblets; granulated microsculpture in preradial stage, presence of intercalated commarginal lirae in early stages and antimarginal striae throughout, more prominent laterally; shagreened microsculpture commonly lacking; auricles unequal, byssal notch deep, byssal fasciole rather broad, ctenolium well developed.

Distribution: Oligocene to Recent (Beu, 1995). Indo-West Pacific and eastern Atlantic. Living littoraly to bathyal depths.

# Talochlamys abscondita (P. Fischer, in Locard, 1898) 

(Plate I, Figs 1, 2; Plate II, Figs 3-6)
Hinnites ? absconditus P. Fischer, in Locard, 1898: 408, pl. 18 figs 9-11. Syntypes: MNHN (not registered);
"Talisman" 1883 stn 103, Cape Verde Islands, Santo Antao Island, 225 m (S. Gofas, in litt.).
Hinnites ? absconditus var. submutica [sic] P. Fischer, in Locard, 1898: 409.
Pecten (Hinnites) absconditus; Nicklès, 1955.
Chlamys (f. acc. Hinnites) abscondita, Adam, 1960: 1-10, pl. 1 figs 1-4, pl. 2 fig. 1.
Hinnites absconditus; Lucas, 1980: 6, fig.; Gofas et al., [1986]: 110, fig. 46a.
"Hinnites" absconditus; de Boer, 1988: 190, figs 67, 68.
Hinnites absconditus; Rolán \& Ryall, 1999: 75.
Description: Shell up to about 70 mm in height, thin, elongate, inequivalve. Valves nearly equally convex, inequilateral. Juvenile Talochlamys-stage to about 30 mm high; adult growth stage distorted. Right valve cemented to hard substrate. Auricles unequal in size, distorted laterally; umbonal angle about $85^{\circ}$.

Juvenile stage: About $18-30 \mathrm{~mm}$ in height and length, equivalve and rather equilateral, sculptured with 15-18 fine primary radial ribs, secondary and even tertiary intercalating ribs resulting in a total of $80-90$ at the end of the regular stage. All these ribs are finely squamose, irregularly arranged and closely spaced. On the right valve, they are rather equal, but on the left valve, the primary and some secondary ribs are much stronger than the others and at the end of the regular stage, some twenty ribs are dominating.
In both valves the interstitial space is finely but irregularly striated at a microscopic level. In this antimarginal microsculpture, striations become concentric and stronger at the anterior and posterior edges.
The anterior auricle is slightly more developed than the posterior auricle. Scaling of ribs is similar to scaling in the valves. The auricles of the left valve are rather unequal, the anterior one being longer than the posterior auricle.

Cemented stage: From this irregular stage on, starting with the fixation of the right valve, the shell becomes very different, distorted and inequivalve. Generally, the right valve is cemented onto a rock, another shell or sometimes onto the right valve of the same species. The shell becomes convex and loses its radial ornamentation, forming large very irregularly spaced lamellae. These concentric lamellae completely surround the regular shell and even reach the auricles or the umbo.
The left valve is less convex, rather oblate, sometimes partially concave, often rather inequilateral and always higher than long. The scaling of the young valve continues in the irregular stage, but the ornamentation of the ribs suddenly becomes stronger. Some twenty radial ribs are larger than the intermediate ribs (5-6). The principal ribs are irregularly scaled, prominent lamellae alternating with small ones.
Auricles with 8-10 radial riblets and antimarginal microsculpture (not on anterior auricle of right valve), commarginal sculpture on anterior auricle of left valve in early growth stage.

Hinge line straight. Byssal notch in juvenile stage rather deep, in adult stage distorted with lamellae.
The chondrophore pit is triangular, narrow and slightly inclined backwards. In old shells, the cardinal area sometimes becomes very high, resulting in a very long and narrow chondrophore pit.
The internal part of the right valve is whitish, rather pink in the middle and near the edge. The left valve is more reddish inside. The outside of the right valve is yellowish and the left valve is creamy and irregularly coloured with reddish brown rays.

Distribution: Tropical eastern Atlantic from the Cape Verde Islands and along the Atlantic coast of Africa from the Gulf of Guinea ( $4^{\circ} 44^{\prime}$ N.) southwards to northern Angola ( $8^{\circ} 30^{\prime} \mathrm{S}$.) (Waller, 1993: 202).

Habitat: Living sublittorally (100 to 200 m range) to bathyal depths, usually cemented to hard substrates.

Remarks: Former authors placed the present species in Hinnites, but the juvenile stage ('free living' or byssally attached) has morphological characters similar to those of Talochlamys. The adult (cemented) stage has no macro- or microsculpture, but only deformed developed shell material.
According to Waller (1993: 203), living members of this species from West Africa are but a relict of a similar species from the Pliocene of Italy and the Miocene of Belgium: "Hinnites" ercolanianus (Cocconi, 1873). The ancestor of this species is considered to be "H." brussoni (de Serres, 1829) from the Burdigalian of southern France (Roger, 1939). Waller's opinion is not respected here because of a lack of fossil material.
W. Adam ${ }^{1}$ compared the recent West African species with "Hinnites" ercolanianus (Cocconi, 1873) from the Miocene and the Pliocene of Europe. The original description ${ }^{2}$ of the fossil shell was based on a left valve from marl (Cassola, Italy), whereas F. Fontannes ${ }^{3}$ described the right valve of a specimen found in the marl of Saint-Restitut (Drôme, France). M. Glibert ${ }^{4}$ mentioned this species from the Miocene (Anversien) of Belgium. W. Adam thinks there is only little difference between the right valve of the recent species and the fossil shells from the Miocene of Belgium.
However, according to W. Adam, there is an important difference in the left valve of both Miocene and recent shells. Fossil shells from the Anversien possess radial ribs, which are equal unlike the recent specimens. There is no sudden change in the ornamentation because the scales in the irregular stage stay small. Fossil species from the Pliocene of Italy tend to be very variable according to Sacco ${ }^{5}$, one form (var. subdistorta Sacco) being very similar to the Miocene material from Belgium whereas another form (var. pseudocrispa Sacco) has the same strong sculpture as in recent shells from West Africa.

As most authors are not convinced of the complete similarity of Talochlamys abscondita and "Hinnites" ercolanianus, both species are here regarded as being different.

Talochlamys multistriata (Poli, 1795)
(Plate IV, Figs 14-20; Plate V, Figs 21-27)
Ostrea multistriata Poli, 1795: 164, pl. 28 fig. 14. Lectotype: the shell figured by Poli (1795: pl. 28 fig.14), designated by Waller (1993: 213); Sicily, Italy.
Pecten tinctus Reeve 1853: species 106, pl. 26 fig. 106. Lectotype: BMNH 1981247/1, designated by Waller (1993: 213); locality unknown.
Pecten effulgens Reeve 1853: species 156, pl. 33 fig. 156. Lectotype: BMNH 1993039/1, designated by Waller (1993: 213)); locality unknown.
Pecten textilis Reeve 1853: species 174, pl. 35 fig. 174. Lectotype: BMNH 1993040/1, designated by Waller (1993: 213); locality unknown.
Pecten multistriatus (Poli), Bucquoy et al., 1887: 104.

[^0]Chlamys multistriata (Poli), Roger, 1939: 165.
Chlamys multistriata; Lucas, 1979: 10, figs
Chlamys (Chlamys) multistriata; de Boer, 1988: 187, fig. 108; Wagner, [1991]: 29, text-fig. 16.
Chlamys multistriata; Barash \& Danin, 1992: 250, fig. 268.
Crassadoma multistriata; Waller, 1993: 212, figs 5a, 5d, 5g, 6c-j (synonymy, data on type series).
Chlamys (Chlamys) multistriata; Zenetos, 1996: 81, map 25.
Chlamys (Chlamys) multistriata; M.C. Consolado Macedo et al., 1999: 395, figs
Crassadoma multistriata; Rolán \& Ryall, 1999: 75.
Talochlamys multistriata; Dijkstra \& Kilburn, 2001: 300, figs 38-39.
Description: Byssate, non-cemented shell of small size (less than 40 mm in height), usually 15-20 mm , longer than wide, inequivalve and inequilateral. Right valve slightly more convex than left one. Auricles very unequal; umbonal angle about $80^{\circ}$. Left valve with about 50-60 ribs of which two thirds are distinctly more pronounced. Right valve always with a few (about 5) ribs more than the left valve, all ribs almost equally pronounced and irregularly arranged, closely spaced and provided with scaly ribs and riblets. Fine grooves in between the ribs. Anterior auricle of LV with 7-10 spinous radial riblets; on posterior auricle 5-7 fine spinose radial riblets. Anterior auricle of RV with 4-7 scabrous radial ribs; on posterior auricle finer and more spinose riblets.
Hinge line straight, somewhat sloping near postero-dorsal margin. Byssal fasciole broad; byssal notch rather deep. Ctenolium broad with 5-8 prominent teeth on suture. Resilium triangularly elongate.
Colour very variable, principally red to brown, sometimes orange, purple, white or yellow with maculations or zones. Colour pattern consisting of 7-9 radial reddish brown bands, each 2 or 3 more close set to each other.

Distribution: Talochlamys multistriata has an enormous latitudinal range, occurring from the Brittany coast of France southward into the Mediterranean Sea, and then southward along the African coast to southernmost South Africa. The species occurs throughout the Mediterranean as well as in Madeira, the Canary and Cape Verde Islands and in the central Atlantic Ocean at St. Helena. It is even present along the southern and southeastern coast of Africa to southern Mozambique in the Indian Ocean (Waller, 1993: 214).

Habitat: T. multistriata lives byssally attached to rocks and hard objects or amongst coral rubble from below low tide level to at least 100 m in normal marine environments. Dead shells have been dredged from bathyal depths (700-930 m).

Morphological variation: The only significant geographic variation in Talochlamys multistriata occurs along the Atlantic and Indian Ocean of southern Africa, where specimens tend to have narrower umbonal edges and correspondingly higher height to length ratios (about 1.34). Some authors consider these narrow forms to be a distinct species, Chlamys tincta (Reeve, 1853). The two forms, however, overlap in shell narrowness and are identical in shell microsculpture.

A few authors thought that Talochlamys multistriata becomes cemented in the northern part of its range along the Atlantic coast of France. Therefore, they treated this species as a synonym of Talochlamys pusio (Linnaeus, 1758). Waller (1993: 213) was not able to substantiate intergradation of these taxa. Bucquoy et al (1887: 104) noted the presence of both regular and distorted forms of $T$. multistriata in samples from Brest (France). Shell distortion in the absence of cementation is not a diagnostic feature, because it occurs in many independent lineages of byssate, nestling chlamydoid pectinids. In T. multistriata, distortion is common among many specimens in the Atlantic, as well in the northern as in the southern part of its range. Pre-cemented Talochlamys pusio, however, can generally be distinguished in the same size range using identification tools mentioned in this paper.

Comparison: Talochlamys multistriata closely resembles its western counterpart, Caribachlamys sentis (Reeve, 1853), in shell shape and colour. The umbonal region of T. multistriata is more inflated and less flattened than that of $C$. sentis, and the byssal fasciole of $C$. multistriata has a deeply incised groove whereas that of $C$. sentis does not.

This species can be distinguished from Mimachlamys varia (Linnaeus, 1758) by the formation of secondary ribs in between the primary ribs all over the left valve. The larger number of ribs, its distinctly smaller size, more close set squamae on the ribs, and the anterior auricles being generally larger in respect to the posterior auricles are discriminating characters too. Anterior auricles are 2.002.34 times larger than the posterior ones. In M. varia, anterior auricles are 1.88-2.14 times larger.
T. multistriata mainly differs from Talochlamys pusio (Linnaeus, 1758) in lacking cementation and foliated-calcite umbonal transgressions throughout ontogeny. In T. pusio, cementation begins at shell heights between about 12 and 25 mm . The pre-cementation growth stage of $T$. pusio closely resembles shells of $T$. multistriata of the similar size. Even at this early stage, however, the two species can be distinguished by two features. First, in T. multistriata, there is no transgression of foliated calcite from the hinge region ventral ward across the region inside the pallial line at any stage of growth. In mature shells of $T$. pusio, this foliated calcite may extend ventrally at least to the level of the top of the adductor scar. Second, the beak of the left valve of T. multistriata has only weak microsculpture, particularly near the distal margin of the preradial stage. Microsculpture at this same stage is stronger in T. pusio, consisting of distinct, generally discontinuous antimarginal striae and pits. Juvenile specimens of $T$. pusio often show traces of distortion in a rather early stage of their ontogeny, and squamae are less developed and abundant.
In T. pusio, anterior auricles are only 1.31-1.46 larger than posterior ones.
Remarks: The present species has an enormous latitudinal range. However, the reported records of southern Mozambique (Waller, 1993: 214) could belong to Laevichlamys deliciosa (Iredale, 1939) (Dijkstra \& Kilburn, 2001).
In literature, T. multistriata and T. pusio are often mixed up (Waller, 1993: 214). Recently Waller (1993: 214) considered both as distinct species of Crassadoma. Dijkstra \& Gould (2002), however, are convinced that morphological characteristics of both species are more similar to those of Talochlamys: similar intercostal commarginal lamellae in early ontogeny and antimarginal microsculpture throughout. Crassadoma has prominent intercostal commarginal lamellae throughout and lacks antimarginal microsculpture in non-cemented stage.
Talochlamys multistriata and Talochlamys pusio can be considered as two distinct species in the eastern Atlantic: T. multistriata being a non-cementing species and T. pusio a cementing representative of the genus Talochlamys.

## Talochlamys pusio (Linnaeus, 1758)

(Plate VI, Figs 28-33; Plate VII, Figs 34-38; Plate VIII, Figs 39-42; Plate IX, Figs 43-47)
Ostrea pusio Linnaeus, 1758: 698, no. 169; Dijkstra, 1999: 417, fig. 4c-f. Lectotype: LSL (not registered), designated by Waller (1993: 215); "O. australiore". Waller (1993: 215) designated a new locality: northeastern Atlantic.
Pecten pusio (Linnaeus), Pennant, 1777, pl. 61, fig. 65.
Ostrea miniata Born, 1778: 88; 1780: 104, pl.7, fig. 1.
Pecten distortus Da Costa, 1778: 148, pl. 10, figs 3, 6.
Ostrea sinuosa Gmelin, 1791: 3319.
Pecten spinosus Brown, 1827, pl. 33, fig. 8.
Pecten irregularis Deshayes, 1832: 273.
Hinnites isabellae Macgillivray, 1843: 203, 225.
Pecten crotilus Reeve, 1853, species 150, pl. 33, fig. 150.
Hinnites distortus; Lucas, 1980: 4, figs
Chlamys (Chlamys) distorta; de Boer, 1988: 187, figs 60-63.
Chlamys (Hinnites) pusio; Rombouts, 1991: 25, pl. 9 fig. 5.
Hinnites (Hinnites) distortus; Wagner, [1991]: 32, text-fig. 17.
Hinnites distortus; Poppe \& Goto, 1993: 65, pl. 9 fig. 8a-b.
Crassadoma pusio; Waller, 1993: 215, figs 5b, 5e, 5h, 6k, 61 (synonymy, data on type series).
Chlamys (Hinnites) distorta; Gómez Rodríguez \& Pérez Sánchez, 1997: 174, illustr.
Chlamys distorta; M.C. Consolado Macedo et al., 1999: 393, figs
Description: Cemented shell of moderate size, up to about 60 mm in height, higher than wide, solid; juvenile valves slightly equally convex, adult valves distorted, right valve usually cemented to hard substrates and more convex than left one in free living specimens; inequivalve, inequilateral, auricles unequal in size, umbonal angle about $80^{\circ}$. Both valves with 60-80 irregularly arranged, closely spaced, spinous radial riblets present at distal margin of mature shells. Microsculpture of commarginal lamellae in early growth stage and antimarginal striae, both in interstices. The anterior auricle of the right valve has 5 ribs, the left valve $6-9$ ribs. The hinge line is straight, somewhat declined on posterior side, byssal notch rather deep, active ctenolium present.
Inner surface of valves with small foliated-calcite transgression in umbonal region, seldom extending past level of dorsal edge of adductor in mature shells. Colour variable, creamy, yellowish, orange or brown. Pattern consisting of a basic colour with flames of zigzag lines of a different colour.

Distribution: Common throughout the British Isles from the Orkney Islands to Cornwall and extending across the North Atlantic as far westwards as southwestern Iceland; present along European coasts from northern Norway southward to Spain and Portugal. Present in the Azores and apparently rare in the westernmost Mediterranean (Waller, 1993: 216). The southernmost record is $33^{\circ} 24^{\prime} \mathrm{N}$. (material of the R/V 'Vanneau'). Findings from Morocco to Ivory Coast are probably unreliable and may prove to be juvenile specimens of $T$. abscondita or T. multistriata.

Habitat: In general, all individuals within populations of Talochlamys pusio seem to become cemented after a certain stage of ontogeny has been reached. The early growth stage of $T$. pusio is byssate on hard objects, particularly rocks or shells, later becoming cemented onto hard substrates by the edges of the right valve. The height of right valves at the time of their cementation to the substrate varies from about 12 to about 25 mm . Depth records for specimens collected alive range from just below low tide level to about 100 m , but records of 900 m (Dijkstra, 2002) are also known.

Morphological variation: The height of right valves at the time of their cementation to the substrate varies from about 12 to 25 mm . There is no evidence for geographic changes in the height at first cementation or in the frequency of cementation within samples. In general, all individuals within populations of $T$. pusio seem to become cemented after a certain stage of ontogeny has been reached (Waller, 1993: 215). The presence of small foliated-calcite transgressions in the umbonal region of both valves is consistent, independent of geographic trends. However, foliated calcite in the umbonal region can be absent, for instance if specimens are attached to floating objects, coarse microsculpture in the pre-radial stage of the left valve is always present.

Remarks: Juveniles of T. pusio and T. multistriata are hard to distinguish and are often confused (Waller, 1993: 215). Whereas T. pusio has pointed and grooved squamae, T. multistriata has blunter and smoother squamae. The shells of $T$. pusio are generally more elongate and slightly distorted in a rather early stage. Refer to the section on T. multistrata for comparative details. Mimachlamys varia (Linnaeus, 1758) has a distinctly lower number of ribs, which are also coarser in outline, without secondary riblets.
T. pusio differs from T. abscondita and Hinnites corallinus of the eastern Atlantic in being of smaller maximum size and having less extensive foliated calcite inside the pallial line. The prominent commarginal lirae present between ribs in the early ontogeny of $T$. pusio are lacking in both other species.
The early Chlamys stage of $H$. corallinus differs from those of the other two cementing species in having ribs that begin late, following an extensive pre-radial area having antimarginal striae in a uniform sweeping pattern.
The Chlamys stage of $T$. abscondita differs from that of $T$. pusio in having a distinctive microsculpture in rib interspaces. This consists of antimarginal striae of highly irregular trends, probably a vestige of the shagreened microsculpture present in the ancestry of this species. T. pusio lacks shagreened microsculpture.

## The genus Hinnites in West Africa

## Genus Hinnites Defrance, 1821

Type species: Ostrea crispa Brocchi, 1814. Fossil, Pliocene, Italy.
Diagnosis: Cemented member of the Chlamydinae in late stages; prominent antimarginal microsculpture and no shagreened microsculpture.
Early stage with very weak and smooth irregular radial ribs and few riblets or threads in each interspace; in cemented stage numerous coarse, irregular, wavy ribs and radial ribs being unequal in size, one in every five being more developed; concentric lamellae prominently present all over the shell surface, developing a sculpture as in Spondylus; auricles unequal, byssal notch nearly absent.

Distribution: Recent. Only one species worldwide known. Southeastern Atlantic (Angola). Living littorally to sublittoral depths.

## Hinnites corallinus (Sowerby I, 1827)

(Plate X, Figs 48, 49; Plate XI, Figs 50-52; Plate XII, Figs 53-55; Plate XIII, Figs 56, 57;<br>Plate XIV, Figs 58, 59; Plate XV, Figs 60-63; Plate XVI, Figs 64, 65; Plate XVII, Figs 66, 67)

Chlamys corallina Sowerby I, 1827
Hinnites spectabilis von Cosel \& Gofas, 1984
Chlamys (Hinnites) corallina; Rombouts, 1991: 24, pl. 9 fig. 2.
Hinnites corallinus; Ardovini, R. \& Cossignani, T., 2004: 271.
Synonymy: In 1984, von Cosel and Gofas described a new cemented pectinid species, Hinnites spectabilis, which they reported as living along the southern part of the coast of Angola. Their description and illustrations leave no doubt that this is the same as the southwestern Atlantic species H. corallinus. Later on von Cosel examined the type specimen of Hinnites corallinus G.B. Sowerby I, 1827, originally said to come from East Africa, and determined this being the same species that he and Gofas (1984) had described as new. The East African locality is apparently in error (Waller, 1993: 203).

Description: Shell large, up to 160 mm (collection F. Swinnen, Lommel, Belgium), strong and moderately heavy, irregularly shaped according to the substrate, but generally more or less circular and, if only with small area attached, of similar height and width. Young regular "Chlamys" stage of the valves ca. $16-25 \mathrm{~mm}$ high and broad, with 20-30 very weak and smooth irregular radial ribs, and 1-4 riblets or threads in each interspace, part of these riblets becoming additional 'regular' ribs in the later irregular growth stage. Sculpture becoming obsolete towards the umbo. In adult specimens outside of upper (left) valve generally with numerous coarse, irregular, more or less wavy ribs (about 50 near the ventral margin) and irregular concentric growth lines. Radial ribs normally unequal in size, one in every 4-6 being more developed, some of the intercalated smaller ribs gradually catching up in size towards the ventral margin in the later growth stage. Surface of lower (right) attached valve depending on the contact with the substrate: with irregular concentric lamellae when attached to or overlying the substrate, with radial ribs like the upper valve on the free growing parts. Ears more or less distorted, byssal gape very shallow and hardly visible and without function in fully-grown specimens. Interior with large adductor scar within a comparatively small area surrounded by the pallial line. Hinge strong, hinge line straight or irregular, depending on the form of the substrate. Right valve slightly larger than left valve, especially in fully attached specimens.
Exterior colour of valves bright orange to deep violet or brick red. Interior yellowish, whitish with reddish stain of adductor scar or with a deep violet sector, or nearly entirely deep violet. Inner margin with an approximately $5-10 \mathrm{~mm}$ broad orange to brick red, reddish brown or purple zone; in the lower valve additional narrow deep violet fringe of about 3 mm directly along the ventral margin, in the upper valve the reddish zone is nearly entirely obscured by the violet colour of the interior, leaving only the narrow deep violet fringe along the ventral margin visible. Dark violet stain also along the hinge line. Unattached part of the outer surface of adult specimens heavily incrusted with barnacles, polychaete tubes, oysters or smaller specimens of $H$. corallinus, when the specimens are growing on exposed parts of the substrate.

Distribution: While the deep water (100-200 m) species Talochlamys absconditus (P. Fischer, in Locard, 1898) lives from the Cape Verde Islands to Punta do Dande, Luanda, Angola ( $8^{\circ} 30^{\prime \prime} \mathrm{S} .13^{\circ}$ E.), the littoral-sublittoral ( $0-25 \mathrm{~m}$ ) species H . corallinus is restricted to a much smaller area, from Mussulo Bay, South of Luanda, Angola ( $8^{\circ} 55^{\prime} \mathrm{S} .13^{\circ} 5^{\prime} \mathrm{E}$. $)^{6}$, to Praia Amelia, Namibe, the former Moçâmedes, Angola ( $15^{\circ} 15^{\prime} \mathrm{S} .12^{\circ} 5^{\prime} \mathrm{E}$.). This is a rather restricted area, but not as narrow as mentioned by von Cosel \& Gofas (1984) in their description of the erroneous Hinnites spectabilis [= Hinnites corallinus (Sowerby I, 1827)]. In fact, the distribution areas of both species do not overlap, but are adjacent. The range of Hinnites corallinus seems to coincide with the so-called 'tropical-subtropical transition zone', which is still influenced by the Benguela Current, causing a permanent upwelling with cold, clear and nutritive water. The absence of more southern records may be a consequence of virtually inexistent data on the Namibian coast, due to for instance insufficient scientific research.

Habitat: Infralittoral, from extreme low tide to a depth of about 25 m , attached to hard substrate exposed either to light, or in crevices or under rocks, in moderately calm and very clear water. Locally, specimens are abundant but most are attached by the entire lower valve and are difficult to remove.

[^1]Remarks: The early Chlamys stage of Hinnites corallinus off Angola is similar to the one in Laevichlamys multisquamata (Dunker, 1864) from the Caribbean Sea, but differs in having more prominent and persistent first order radial plicae and in having less numerous secondary intercalated radial ribs.

Hinnites corallinus can be compared with Crassadoma gigantea (Gray, 1825) (syn. Pecten multirugosus Gale, 1928), from the West coast of North America, which attains an equal size or grows even larger. The sculpture of $C$. gigantea is somewhat different. It consists of strongly scaled ribs, every $3^{\text {d }}$ to $5^{\text {th }}$ rib being stronger throughout the whole surface, whereas in $H$. corallinus the ribs are coarser and become equal-sized towards the ventral part of fully adult specimens.
The valves of $C$. gigantea are generally higher than wide, whitish inside, with a deep purple stain at the hinge area, in $H$. corallinus the valves are broader and have characteristic colours.

Talochlamys absconditus (P. Fischer, in Locard, 1898) is smaller; its upper valve has 15-20 more delicate scaly radial ribs, with 2-6 fine threads in each interspace. The lower (attached) valve only has heavy concentric lamellae, the radial ribs being more or less restricted to the 'regular' juvenile stage. In contrast to $H$. corallinus, the sculpture of the free-swimming stage of $T$. absconditus is visible throughout its whole surface in both valves. T. absconditus is light brownish, with the interior of the upper valve always stained pinkish to reddish; the lower valve is whitish inside, sometimes with some light pink and red colour.

The cemented species Hinnites corallinus (G.B. Sowerby I, 1827) can be considered as a probable descendent from Laevichlamys. In turn it may prove to be the same as the presumably extinct type species of the genus Hinnites, namely $H$. crispus (Brocchi, 1814), mainly known from the Mediterranean Pliocene. Following is a synopsis of the arguments of Waller (1993: 203):

- The pattern of rib introduction looks like that present in Laevichlamys, where rib interspaces are filled by the repeated medial intercalation of new radial costae. Furthermore, auricular shapes, the dorsal margin of the right anterior auricle extending prominently above the hinge line and the posterior margin of the posterior auricle exhibiting a convex outline tending to form an oblique angle with the hinge, indicate a close relationship to L. squamosa (Gmelin, 1791). Some specimens of H. corallinus show the minute net of white pigment lines that is common in species of Laevichlamys and look-alikes.
- The macro- and microsculpture of the Chlamys stage of Hinnites corallinus is remarkably similar to that of the type species of Hinnites. The latter is H. crispus (Brocchi, 1814), a fossil described from the Pliocene of Italy. The fossil species tends to be larger and to have a thicker shell than the living one, but there are broad similarities in form as well as in sculptural detail. It is possible these species may be synonymous, in which case the living West African specimens are but a relic of a previously more broadly distributed species.

- If it is true that Hinnites crispus is derived from an ancestral species in the genus Laevichlamys, then the fossil record of $H$. crispus tends to support the idea that Laevichlamys did not enter the Atlantic by westward dispersal across the proto-Mediterranean. This is because the oldest specimens of H . crispus are not known from the Mediterranean but from the Atlantic side of France (Roger, 1939). H. crispus has been reported from the late Miocene of Austria, Hungaria and Bulgaria and it did not become widely distributed in the Mediterranean until the Pliocene, at which time it also extended as far as the British Isles (Roger, 1939). Roger (1939) thought that the species persisted into the late Pleistocene (Sicilian) in the western Mediterranean based on specimens from the Alpes-Maritimes region of France. Unfortunately, there is no Miocene or Pliocene fossil record of H. crispus (or H. corallinus) in southern Africa, nor is there any fossil record of a preceding free-living Laevichlamys in the eastern Atlantic.
- The fossil record of the Caribbean species, Laevichlamys multisquamata, is not any older than Pleistocene.
A reasonable interpretation of this evidence is that a species of advanced Laevichlamys had entered the eastern Atlantic from the Indian Ocean by late Miocene time via a route around southern Africa. A derivative of this species adopted a cemented mode of life, evolved into true Hinnites, dispersed into the Mediterranean through its western portal after the end of the Miocene, and nearly became extinct during the late Pliocene and early Pleistocene climatic cooling that profoundly affected the early Pliocene fauna of the Mediterranean (Raffi et al, 1985). If the extant Hinnites corallinus is indeed synonymous with $H$. crispus, then the species survives today in refuges along the West African coast. It seems likely that another ancestor of Laevichlamys dispersed to the tropical Western Atlantic and evolved into Laevichlamys multisquamata during the Pleistocene. This species has no geminate sister species in the eastern Pacific because it originated in the tropical western Atlantic region after the closure of connecting seaways.

|  | T. abscondita | T. multistriata | T. pusio | H. corallinus |
| :---: | :---: | :---: | :---: | :---: |
| Dimensions | H: max. 70 mm | H: max. 40 mm , usually $15-20 \mathrm{~mm}$ | H: max. 60 mm | $\mathrm{H}: 160 \mathrm{~mm}$ |
| Morphology | - elongate; <br> - right valve cemented to substrate | - elongate; <br> - non-cemented shell | - higher than wide; <br> - cementation begins at shell heights between $12-25 \mathrm{~mm}$ | - broader than wide: more or less circular - cemented shell |
| Sculpture | - juvenile stage: 15-18 fine primary ribs and $80-90$ secondary and even tertiary ribs at end of regular stage; <br> - cemented stage: right valve convex with large, concentric, very irregularly spaced lamellae; - left valve convex partially concave; ornamentation of ribs becomes suddenly stronger; some 20 radial ribs are larger than the intermediate ribs (5-6) | - auricles very unequal: anterior auricles at least 2 times larger than the posterior ones; <br> - inside: no transgression of foliated calcite from the hinge region ventral ward into the region inside the pallial line in any stage of growth; <br> weak microsculpture in the beak | - anterior auricles only 1.3-1.4 times larger; - microsculpture in pre-cementation stage is stronger than in $T$. multistriata; juvenile specimens show traces of distortion and squamae are less developed and abundant | - coarse irregular ribs becoming equal-sized towards ventral part of fully adult specimens; - byssal gape hardly visible; <br> - large adductor scar |
| Colour | - interior: whitish in RV; more reddish in LV; <br> - outside: RV is yellowish; LV cream, with reddish brown rays | - very variable: generally red to brown, sometimes orange, purple, white or yellow with maculations or zones; <br> -7 to 9 radial reddish brown bands | - variable: cream, yellowish, orange or brown; <br> - pattern with flames of zigzag lines of a different colour | - bright orange to deep violet or brick red; - interior yellowish with reddish stain and a deep violet sector along the ventral margin and the hinge line |

Table 1: Concise comparison between the four described scallops

Comparison between different similar scallops according to W. Adam ${ }^{7}$


Fig. 1. T. abscondita (P. Fischer, in Locard, 1898): a. RV: intercalation of ribs; b. LV: intercalation of ribs.
Fig. 2. 'Hinnites' ercolanianus (Cocconi, 1873): a. RV: intercalation of ribs; b. LV: intercalation of ribs. Fig. 3. Crassadoma gigantea (Gray, 1825): a. RV: division of ribs; b. LV: intercalation of ribs.


Fig. 4. Talochlamys multistriata (Poli, 1795): a. RV: division of ribs; b. LV: intercalation of ribs.
Fig. 5. Talochlamys pusio (Linnaeus, 1758): a. RV: division of ribs; b. LV: intercalation of ribs.
Fig. 6. Mimachlamys varia (Linnaeus, 1758): a. RV: division of one rib; b. LV: intercalation of one rib.

[^2]Distribution of West African species belonging to the Genera Talochlamys and Hinnites


Talochlamys abscondita (P. Fischer, in Locard, 1898):
Talochlamys multistriata (Poli, 1795):
Talochlamys pusio (Linnaeus, 1758):
Hinnites corallinus (Sowerby I, 1827):
$\qquad$
$\qquad$
$\qquad$

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## Plate I

Talochlamys abscondita (P. Fischer, in Locard, 1898) Ambriz, Angola.
Attached to cold-water coral Lophelia pertusa (Linnaeus, 1758). Trawled by fishermen (PEMARCO). 1967.

Collection FN.
Fig. 1 LV: H. 63.8 mm L. 53.1 mm . Fig. 2 RV: H. 50.9 mm L. 48.3 mm .



Plate II. Fig. 3. Talochlamys absconditus (P. Fischer, in Locard, 1898) Ambriz, Angola. Attached to coldwater coral Lophelia pertusa (L., 1758). Trawled (PEMARCO). 1967. Collection FN. LV: H. 41.1 mm L. 37.2 mm; Fig. 4. T. absconditus Angola. Trawled. Collection J. Verstraeten (Belgium). Juvenile specimen. LV: H. 19.0 mm L. 17.0 mm . Fig. 5. T. absconditus. Microsculpture of LV, juvenile stage. Fig. 6. T. absconditus. Microsculpture of LV, cemented stage.


Plate III. Fig. 7. Talochlamys multistriata (Poli, 1795). Corse, France. Dived at a depth of 20 m . Collection FN. LV: H. 37.8 mm L. 35.0 mm ; Fig. 8. Idem. RV; Fig. 9. T. multistriata. Taranto, Italy. Trawled. Collection FN. LV: H. 21.1 mm L. 18.1 mm ; Fig. 10. T. multistriata. Cambrils, Spain. Trawled. Collection FN. LV: H. 29.0 mm L. 23.4 mm; Fig. 11. T. multistriata. Port de Sóller, Balearic Islands, Spain. Trawled. April 1971. Collection FN. LV: H. 21.7 mm L. 17.0 mm ; Fig.12. T. multistriata. Iles de Frioul, Marseille, France. Trawled at 25 m . August 1963. Collection FN. LV: H. 18.5 mm L. 15.6 mm ; Fig. 13. T. multistriata. Iles de Frioul, Marseille, France. Trawled at 25 m. August 1963. Collection FN. LV: H. 23.9 mm L. 18.8 mm .


Plate IV. Fig. 14. Talochlamys multistriata (Poli, 1795). Branco Island, Cape Verde Islands. Dredged by Yacht 'Chazalie'. 9 November 1895. Collection Ph. Dautzenberg, KBIN. LV: H. 14.1 mm L. 11.8 mm ; Fig. 15. T. multistriata. Santa Cruz, La Palma, Canary Islands. Dived at 8 m in harbour. 1970. Collection FN. LV: H. 21.3 L. $\mathbf{1 7 . 2} \mathrm{mm}$; Fig. 16. Idem. LV: H. 16.6 mm L. 13.7 mm ; Fig. 17. Idem LV: H. 28.5 mm L. 23.1 mm ; Fig. 18. Idem. LV: H. 17.1 mm L. 14.0 mm ; Fig.19. Idem. LV: H. 22.5 mm L. 19.7 mm ; Fig. 20. Idem. LV: H. 24.4 mm L. 19.3 mm .


Plate V. Fig. 21. Talochlamys multistriata (Poli, 1795). Off Luanda, Angola. Dredged at a depth of 40 m . March 1982. Collection FN. LV: H. 23.8 mm L. 17.6 mm ; Fig. 22. T. multistriata. Moita Seca, Angola. Trawled by fishermen (PEMARCO). 1973. Collection FN. LV: L. 14.6 mm L. 11.5 mm ; Fig. 23. Idem. V: H. 20.1 mm L. 14.6 mm ; Fig. 24. Idem. LV: H. $23.9 \mathrm{~mm} \mathrm{L}$.18.8 mm ; Fig. 25. T. multistriata. Buffels Bay, Cape, Republic of South Africa. At base of large seaweed, at low tide. November 1980. Collection FN. LV: H. 12.3 mm L. 9.6 mm; Fig. 26. T. multistriata. Jeffreys Bay, Cape, Republic of South Africa. 20 May 1979. Collection FN. LV: H. 18.0 mm L. 14.9 mm ; Fig. 27. T. multistriata. Arrecife, Lanzarote, Canary Islands. Under rock at low tide. 25 May 1971. Collection FN. LV: H. 14.1 mm L. 11.3 mm.


Plate VI. Fig. 28. Talochlamys pusio (Linnaeus, 1758). Skye, Scotland, U.K. Trawled. August 1992. Collection FN. LV: H. $38.5 \mathrm{~mm} \mathrm{L}$.32.9 mm ; Fig. 29. Idem. RV: H. 38.5 mm L. 32.9 mm ; Fig. 30 . Idem. LV: H. 40.2 mm L. 33.3 mm ; Fig. 31. Idem. RV: H. 40.2 mm L. 33.3 mm ; Fig. 32. T. pusio. 7 miles east of Island of Man, Irish Sea. Trawled among Modiolus modiolus (L., 1758) at a depth of 64 m. April 1982. H. 32.0 mm L. 27.0 mm ; Fig. 33. T. pusio. St. George's Channel, Rep. of Ireland, U.K. Trawled at 50 m . LV: H. 23.9 mm L. 24.5 mm .


Plate VII. Fig. 34. Talochlamys pusio (Linnaeus, 1758). Cap de la Hague, Normandy, France. Trawled. In niches of piece of limestone at 50 m . Collection FN. LV: H. 25.7 mm L. 22.8 mm ; Fig. 35. Idem. RV: H. 25.7 mm L. 22.8 mm ; Fig. 36. Idem. LV: H. 21.1 mm L. 18.4 mm ; Fig. 37. Idem. RV: H. 25.2 mm L. 22.8 mm ; Fig. 38. Idem. LV: H. $\mathbf{3 7 . 7} \mathbf{~ m m ~ L . ~} \mathbf{3 0 . 7} \mathrm{mm}$


Plate VIII. Fig. 39. Talochlamys pusio (Linnaeus, 1758). Ile Callot, Finistère, Brittany, France. Under rock at extreme low tide. August 1997. Collection FN. LV: H. 42.0 mm L. 38.6 mm; Fig. 40. Idem. RV: H. 42.0 mm L. $\mathbf{3 8 . 6} \mathrm{mm}$; Fig. 41. Idem. LV: H. $\mathbf{4 0 . 0} \mathrm{mm}$ L. 36.6 mm ; Fig. 42. Idem. RV: H. $\mathbf{4 0 . 0} \mathbf{~ m m ~ L . ~} \mathbf{3 6 . 6} \mathbf{~ m m}$.


Plate IX. Fig. 43. Talochlamys pusio (Linnaeus, 1758). Ile Callot, Finistère, Brittany, France. Under rock at extreme low tide. August 1997. Collection FN. LV: H. $27.8 \mathrm{~mm} \mathrm{L}$.25.3 mm ; Fig. 44. Idem. LV: H. $\mathbf{3 0 . 8} \mathbf{~ m m ~ L . ~}$ 30.5 mm (specimen with 3 valves); Fig. 45. Idem. LV: H. $22.5 \mathrm{~mm} \mathrm{L}$.20.3 mm ; Fig. 46. T. pusio. São Miguel, Azores. 1895. Trawled by Capt. Chaves. Collection Ph. Dautzenberg, KBIN. LV: H. 17.2 mm L. 15.3 mm ; Fig. 47. Idem. RV: H. 17.2 mm L. 15.3 mm .


Plate X. Fig. 48. Hinnites corallinus (Sowerby I, 1827). Mussulo Bay, off Luanda, Angola. Dived at a depth of 22-25 m. 26 September 1994. Collection F. Swinnen (Belgium). LV: H. 152 mm L. 159 mm ; Fig. 49. Idem. Microsculpture of LV, adult stage.


Plate XI. Fig. 50. Hinnites corallinus (Sowerby I, 1827). Mussulo Bay, off Luanda, Angola. Dived at a depth of 22-25 m. 26 September 1994. Collection F. Swinnen (Belgium). RV: H. 152 mm L. 159 mm ; Fig. 51. Idem. Microsculpture of RV, juvenile stage; Fig. 52. Idem. Microsculpture of RV, adult stage.








[^0]:    ${ }^{1}$ Adam, W., 1960. Mededelingen K.B.I.N., Deel XXXVI, nr.20. A propos de Chlamys (f. acc. Hinnites) abscondita (P. Fischer, 1898) de la Côte Occidentale de l'Afrique, 1-10.
    ${ }^{2}$ Cocconi, G. 1873. Enumerazione sistematica dei Molluschi miocenici e pliocenici delle Provincie di Parma e di Piacenza. Mem. Acc. Sci. Bologna, s. III, T. III: 1-372.
    ${ }^{3}$ Fontannes, F. 1879-1882. Les Mollusques pliocènes de la vallée du Rhône et du Roussillon. II. Acéphales des formations marines et saumâtres. Lyon-Paris.
    ${ }^{4}$ Glibert, M. 1945. Faune Malacologique du Miocène de la Belgique. I. Pélécypodes. Mém. Mus. r. Hist. nat. Belg., 103: 1-266.
    ${ }^{5}$ Sacco, F. 1897. I Molluschi dei terreni terziarii del Piemonte e della Ligura. Parte XXIV (Pectinidae). Torino. 74 pp.

[^1]:    ${ }^{6}$ collection F. Swinnen (Lommel, Belgium)

[^2]:    ${ }^{7}$ Mededelingen K.B.I.N., Deel XXXVI, nr.20. A propos de Chlamys (f. acc. Hinnites) abscondita (P. Fischer, 1898) de la Côte Occidentale de l'Afrique, 1-10.

