

The razor shells of the eastern Atlantic, part 2.*
Pharidae II: the genus *Ensis* Schumacher, 1817 (Bivalvia, Solenoidea)

Rudo VON COSEL

Muséum national d'Histoire naturelle, Département Systématique et Evolution, Unité Taxonomie – Collections, 55, Rue Buffon, F-75005 Paris, France; cosel@mnhn.fr

The razor shells of the genus *Ensis* Schumacher, 1817, from the eastern Atlantic coast are revised. There are six species in total: the native European species *Ensis ensis* (Linné, 1768), *E. magnus* Schumacher, 1817, *E. minor* (Chenu, 1843), and *E. siliqua* (Linné, 1758), the tropical West African species *E. goreensis* (Clessin, 1888) and the introduced species *E. directus* (Conrad, 1843), originally distributed along the northeastern United States and Atlantic Canada and now well-established in Europe between southeastern Norway to the coast of Normandy. It is shown that the well-established name *E. arcuatus* (Jeffreys, 1865) falls into the synonymy of *E. magnus* Schumacher, 1817, and that *E. directus* (Conrad, 1843) and *E. americanus* (Binney, in Gould & Binney, 1870) are conspecific. Furthermore, the names introduced by Van Urk between 1964 and 1984 are placed into the synonymies of their relevant nominate species because of the numerous existing intergrades. The story of the introduction of *E. directus*, now a major element of the marine invertebrate fauna in the southern North Sea and the Channel, is summarized. An identification key to the eastern Atlantic *Ensis* is provided.

Key words: Bivalvia, Solenoidea, Pharidae, *Ensis*, systematics, taxonomy, zoogeography, eastern Atlantic.

INTRODUCTION

In the eastern Atlantic, 23 species of razor shells and jackknife clams (Solenoidea) are known. The Solenidae and the Pharidae other than *Ensis* have been the subject of a previous paper (Von Cosel, 1993); however, because of their complexity and in order not to delay publication too much, the six species of the genus *Ensis* were not included in that work. They are now revised herein.

The *Ensis* species are among the most spectacular and attractive shells in the driftline of European beaches and tourists as well as local shell collectors often pick them up. In some countries *Ensis* are also marketed and consumed. Most species were already treated by Van Urk (1964a, b; 1966; 1971; 1972; 1980; 1984; 1986; 1987) and Von Cosel et al. (1982), but several questions remained open. Moreover, since very recent years, molecular work on some species of *Solen* and *Ensis* was published and is in progress, mostly pushed by increasing commercial fisheries, exploitation and future aquaculture of these species (Fernandez-Tajes et al., 2007; Fernandez-Tajes & Méndez, 2007; J. Vierna, in preparation). This genetic work is essential, because in morphology, the native European *Ensis* show their very close relationship by the existence of occasional intergrades (hybrids) in some species pairs in certain regions of their range. In this paper, an attempt is made to give a synthesis of all facts known to date on the European *Ensis* species complex and also on the impact from the introduced *E. directus* on the native razor shells.

Abbreviations of museums: AMNH, American Museum of Natural History, New York, N.Y., U.S.A.; ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, U.S.A.; BMNH, The Natural History Museum [formerly British Museum

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(Natural History)], London, England, U.K.; CAS, California Academy of Sciences, San Francisco, California, U.S.A.; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MNHN, Muséum national d'Histoire naturelle, Paris, France; RMNH: Nationaal Natuurhistorisch Museum 'Naturalis' (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; SMNH, Naturhistoriska Riksmuseet, Stockholm, Sweden; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington D.C., U.S.A.; ZIM, Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Hamburg, Germany; ZMA, Instituut voor taxonomische Zoologie (formerly Zoologisch Museum), Amsterdam, The Netherlands; ZMC, Universitets Zoologisk Museum, Copenhagen, Denmark.

Other abbreviations: coll., from the collection of; leg., legit, collected by; spm., live-taken specimen; sta., sampling station of a research vessel or field expedition; v., single valve, valves.

KEY TO THE EASTERN ATLANTIC *ENSIS* SPECIES

- 1a. Shells 60 to 130 mm long, slender and markedly curved 2
 1b. Shells 140 to 230 mm long, slender to rather broad, straight to curved 3
 2a. Shell length 50-90 mm, shell narrow to very narrow (l/h ratio 7.5-9), with numerous small spots and speckles; anterior margin truncated. Tropical West Africa
 *E. goreensis*
 2b. Shell length 70-120 mm, shell narrow (l/h ratio 7-8.5), curved but variable in outline, with pinkish transversal bands, also seen on the interior, only few spots, if any; anterior margin rounded. Europe *E. ensis*
 3a. Shells more or less curved to (occasionally) almost straight, narrow to rather broad, 140 to 195 mm long 4
 3b. Shells straight to (occasionally) very slightly curved, moderately narrow, 130 to 230 mm long 5
 4a. Shells narrow (l/h ratio 6.5-8), rather thick, with narrow and rounded pallial sinus (cf. fig. 8) with its innermost point more or less in the middle. Anterior adductor scar distinctly longer than ligament. Whitish, sometimes with partly pinkish *E. magnus*
 4b. Shells rather broad (l/h ratio 5.5-6.5), rather thin, with broad, squarish oblique pallial sinus (fig. 1), with its innermost point at the dorsal corner; anterior adductor scar only slightly longer than ligament; whitish to brownish *E. directus*
 5a. Shells thin to moderately thick, straight; cross-section of posterior gape narrow, with parallel contours of the middle part of rv and lv (Plate 8 k); anterior margin obliquely truncated, with pallial line running (almost) parallel and close to it; periostracum without dark violettish colouration on the postero-dorsal section *E. minor*
 5b. Shells thick and heavy, straight or very slightly curved; cross-section of posterior gape evenly convex (Plate 8 j); anterior margin rounded, with pallial line vertical or slightly inclined, in greater distance to the margin (fig. 15); periostracum with a dark violettish colouration on the postero-dorsal section, often not entirely coinciding with the vertical growth lines (Pls 7 a, 8 b) *E. siliqua*

SYSTEMATICS

Superfamily Solenoidea Lamarck, 1809
Family Pharidae Adams & Adams, 1858
Subfamily Cultellinae Davies, 1935

Genus *Ensis* Schumacher, 1817

Ensis Schumacher, 1817: 143.

Ensatella Swainson, 1840: 365.

Hypogaea Poli, 1791: 29 [partim, name given for soft parts of Solenoidea, Tellinidae and Pholadidae].

Type species (by monotypy). — *Ensis magnus* Schumacher, 1817. Faroe, Shetland, Norway, British Isles and North Sea to Portugal.

With 11 species, from Europe, east coast of North America, West Africa, Southwestern U.S.A, Western Central America, Southern South America (Chile, Patagonia).

Shells from medium-sized (45 mm) to very large (231 mm), very elongate, straight to markedly curved, with almost parallel to parallel dorsal and ventral margins and terminal beaks. Length/height ratio from less than 6 to more than 9, according to species. Anterior margin rounded to truncate or oblique-truncated, posterior margin mostly more or less truncate. Hinge and ligamental area straight or curved upwards.

Interior without anterior and posterior reinforcements. Anterior adductor scar extremely long and narrow, posterior scar short, oval and in a more or less significant distance forward of the posterior pallial line. Pallial sinus very short and broad, rounded or more rectangular to oblique-rectangular. Beaks situated just in front of the anterior adductor scar.

Exterior of valves divided into three zones: an antero-ventral zone with horizontal growth lines, a postero-dorsal zone with more marked vertical growth lines, and a very narrow dorsal zone above the postero-dorsal region with horizontal growth lines. The limits between these zones are sharply marked. Colour of valves variable: entirely white or creamy to whitish with rosy or pink to purplish or more brownish growth lines, zones, spots, streaks or hues. Periostracum usually strong and thick, brownish to olive-greenish or yellowish green, in small tropical species thinner and light olive, folding over the margins of the valves.

Hinge with two vertical and two subhorizontal cardinals in the left valve and one vertical and one subhorizontal cardinal in the right valve. Subhorizontal cardinals longer than in any other Pharidae.

Animal with very short separate fringed siphons, fused at the base and not extendible far beyond the posterior shell margin. Foot very long, strong, laterally compressed and ending in a flattened oblique anterior surface with a surrounding keel, as in all Pharidae. Nervous system well developed. Mantle with a fourth aperture in the middle of the ventral side (see Plate 1 m, n)

For supplementary information to this contribution, with measurements of individual specimens of the various species, see:

www.spirula.nl/publicaties/basteria/supplements/73/B73-VonCosel9-56.pdf.

Ensis directus (Conrad, 1843)

Solen ensis Gould, 1841 (non Linné, 1758) [not seen]; De Kay, 1843: 242, pl. 33 fig. 313.

Solen directus Conrad, 1843: 325-326.

Solen ensis var. *Americanus* Binney in Gould & Binney, 1870: 40-42, fig. 366 (non *Solen americanus* Chenu, 1843, a *Siliqua*).

Ensis americanus (Gould, 1870) — De Bruyne, 2004: 172.

Type material. — A type specimen of *Solen directus* is not listed by Richards (1968), so Conrad's type has to be considered missing.

Type locality. — "Neuse river, below Newbern, North Carolina. Miocene?"

Description. — Shell large (140-150 mm) to very large [over 200 mm; largest specimen according to Clench (1944) 228 mm long and 38 mm broad, European specimens to 187 mm, Vanhaelen (1993)], quite variable, rather flat, thin but strong (younger specimens fragile), nearly straight to conspicuously curved, with nearly parallel margins, only at the posterior end slightly tapering. Length/height ratio 5.5-6.5, but 4 in dwarf specimens. Anterior margin well rounded, posterior margin vertically to obliquely truncated, margin slightly convex with rounded corners. Dorsal margin weakly to markedly concave, occasionally nearly straight, hinge and ligamental area bent upwards. Ventral margin weakly to conspicuously convex. Broadest part of the valves in the middle or just behind the middle.

Cross section of posterior gaping moderately narrow, prolonged-oval. A dorsal view of the closed valves shows that the last 4-5 cm of the posterior part of the valves are gradually more and more compressed towards the posterior end.

Anterior adductor scar moderately short, at the anterior end narrow, broadening considerably towards posterior, with the end more or less rounded, straight to very slightly curved, pointing towards the postero-ventral corner or the posterior half of the ventral margin. Posterior adductor scar prolonged-oval, situated at a distance of $\frac{1}{2}$ its length or less before the pallial sinus, sometimes in adult specimens only at a distance of 2-5 mm. Anterior pallial line slightly concave, descending vertically or weakly forward, at a distance equal or slightly less than the distance ventral pallial line - ventral margin, then bending abruptly backwards. Ventral pallial line below the anterior adductor scar straight, at its end slightly concave. Pallial sinus short and broad, truncated, obliquely square, with its innermost point at its upper part directly below the dorsal pallial line.

Exterior with irregular growth lines and some very strongly marked growth stages. Colour of valves whitish to creamy, with pale brownish to violet growth zones on the postero-dorsal part of the valves, merging one into another, sometimes being nearly unicoloured, on the interior usually only faintly showing through. Inside of anterior margin, ventral part of the valves and posterior margin often tinged with brownish violet.

Periostracum strong, brownish green, on the postero-dorsal part with the vertical growth lines pale grey.

Distribution. — Western Atlantic: East coast of North America from Labrador to Virginia, probably more southward. Eastern Atlantic: SE-Norway (Oslofjord westward to Kristiansand) NE-Skagerrak, Kattegat southward to Zealand (Sejrø Bay, Isefjord), Swedish west coast from Koster Islands to Laholmsbukten, Western Baltic Sea southward to the Bay of Lübeck. North Sea coast from N-Denmark (Skagen) to Belgium, French coast southward to Normandy (Calvados), east coast of the Cotentin Peninsula. North Sea coast of England: Sussex, Norfolk, Lincolnshire, the Wash, Humber estuary.

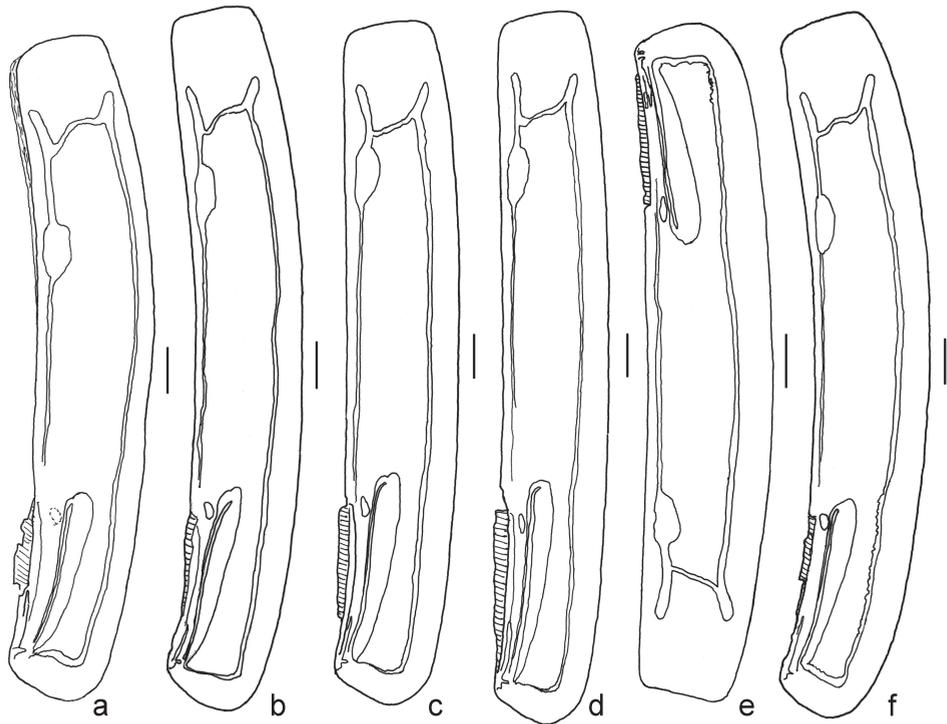


Fig. 1. *Ensis directus* (Conrad, 1843). a-f, half schematic drawings of the insides of valves. a, St. Johns, Newfoundland, coll. J. Vierna; b, Amrum, North Frisian Islands, Germany, 1983, MNHN; c, Schiermonnikoog, Netherlands, March 1986, MNHN; d, same locality (the last two with almost straight shell); e, Graye-sur-Mer, Calvados, France, Sept. 2006, MNHN (note the vertical anterior pallial muscle scar and compare with Van Urk, 1972: 136, fig. 2); f, same locality, MNHN (note the well curved shell and the more forward placed posterior adductor scars). Scale 10 mm

Material examined (sole numbers refer to empty shells) — Eastern Atlantic: SWEDEN: Saltö, Koster Islands, Bohuslän, leg. Hansson, ix.1986 (SMNH/<10, slightly dwarf, short and distorted); Boviken on Hamburgö Is., Bohuslän, leg. C. Schander, vii.1994 (MNHN/2; >30v.). DENMARK: Gammelgab, between Nymindegab and Henne Strand, leg. Sturm, 3.vii.1982 (ZIM/>10 and v.); Blavands Huk, leg. Zunk, 26.v. and 11.ix.1982 (ZIM/>20); Skallingen, leg. Zunk, 21.v.1982 (ZIM/>5 juv.); Off Romø Is., 55°9'N 8°17'E, 13 m, 31.viii.1981 (Biol. Anstalt Helgoland/about 50 juv. spms.). GERMANY: Sylt, North Frisian Is., between List and Westerland, leg. Münzing & Von Cosel, x.1981, 16. iii. & 25.viii.1982 (ZIM/>30); Amrum, North Frisian Is., leg. Bieler (ZIM/>10); Amrum, Knipsand beach, leg. Mühlenhardt-Siegel, ix.1983 (MNHN/13; 1v); Tümlauer Bucht and Westerheversand, Eiderstedt Peninsula, 20.v.1982, leg. Rühm (ZIM/<10); off Cuxhaven, trawled, iii.1982 (ZIM/2 spms., fresh dead); NW of Grosser Vogelsand and Elbe estuary, >30 juv. spms., v.1979 - viii.1982 (not preserved, for details see Mühlenhardt-Siegel & al., 1983); Jade estuary, trawled, leg. Dörjes, iii.1982 (ZIM/>10); Jade estuary, NW of Maifeldsteert, 53°32.54'N 08°11.51'E, 3,6 m, dredged R.V. "SENCKENBERG", leg. Türkay, 16.v.1987 (SMF/1 spm.); Norderney, East Frisian Is., north side beach, leg. Leja, 1982 (MNHN/20); off Borkum, East Frisian Islands, 53°45,01'N 06°30,0'E, 23-24 m, dredged R.V. "SENCKENBERG", leg. Türkay and Dörjes, 21.iv.1986 (SMF/1 spm.).

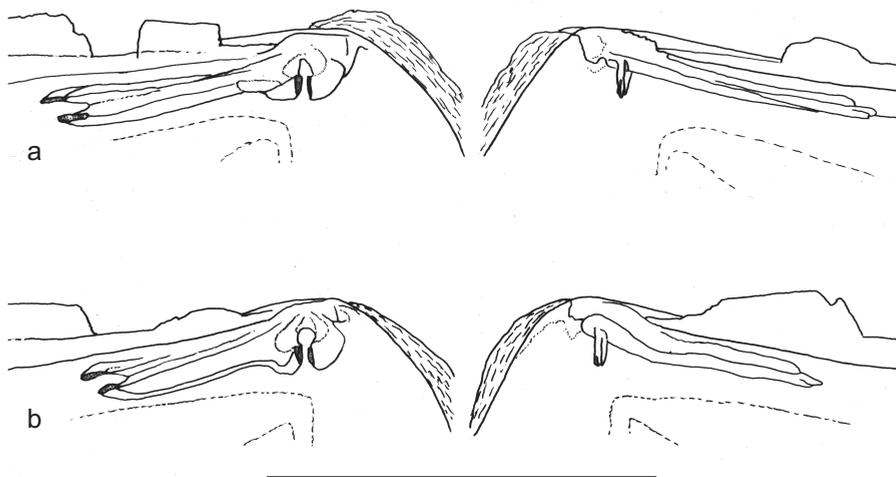


Fig. 2. *Ensis directus* (Conrad, 1843). Noordwijk – Katwijk, Netherlands, Feb. 1989, MNHN. Close-up view of hinge teeth. **a**, shell length 101 mm; **b**, shell length 86.5 mm. Scale 10 mm.

NETHERLANDS: Schiermonnikoog, leg. De Boer, x.1985 & 31.iii.-iv.1986, (MNHN/17; >100 juv.; 123v.); Terschelling, km 8, leg. Moolenbeek, v.1986, (MNHN/4, 3v.; ZMA/>10); Noordwijk - Katwijk, leg. Von Cosel, 18.ii.1989 (MNHN/91, 10v.; SMF/<20); Noordwijkerhout, leg. B. & R. von Cosel 1.viii.2008 (SMF/>20); Rhine Delta, 51°28.2'N 3°12.3'E, 10 m, R/V "SENCKENBERG", leg. Türkay, 9.vii.1988 (SMF/6). BELGIUM: off Zeebrugge, 51°25.5'N 3°0.09'E, 19 m, trawled R/V "SENCKENBERG", leg. Türkay, 10.vii.1988 (SMF/4). FRANCE: Dunkerque Plage, leg. Y. Müller, 1990 (MNHN/3, 1v.); Quend-Plage, Somme, Picardie, leg. Noel, 1.iv.2007 (MNHN/12, 2v.); Cayeux-sur-Mer, Somme, Picardie, on pebble beach, leg. Von Cosel, 25.iv.2009 (MNHN/13, 10v.); same locality, leg. Noel, 20.x.1998 (MNHN/1v.); La Brèche de Bisson, Graye-sur-Mer, Calvados, leg. Noel, 21.ix.2006 (MNHN/3). ENGLAND: Brancaster, North Norfolk, leg. P. Dansey, 27.xii.1999 (MNHN/5).

Western Atlantic: CANADA: Carleton, Gaspé, leg. ten Houten, 1935 (ZMA/1); St. Johns, Newfoundland (J. Vierna/10 spm). UNITED STATES: Old Orchard Beach, Maine (CAS/3); Prospect harbour, Washington County, Maine, leg. Bogart, 21.vii.1974 (AMNH 180082/7); Boston, Massachusetts (SMNH/3); Duxbury Beach, Massachusetts, leg. Pannekoek, 22.viii.1935 (ZMA/6); Plymouth, Massachusetts (RMNH/2); W-shore, Eastham Flats, Eastham, Cape Cod, Massachusetts, leg. Brooks, 1935 (ZMA/3); Sippewisset, Cape Cod, leg. Pannekoek, 23.viii.1935 (ZMA/2); Chatham, Pleasant Bay, Cape Cod (RMNH/4); Gay's Island, "M.E." (most probably Martha's Vineyard) (RMNH/2); Butterwoods, Rhode Island, leg. Johnson (RMNH/2); Fire Island, Moriches Bay, Long Island, leg. Taxson, 9.i.1962 (AMNH 105143/7); Far Rockaway Bay, Long Island, leg. Gwyer (AMNH 34267/4); Barren Island, Brooklyn (Rockaway Inlet), New York, leg. Jacobson, iii.1946 (RMNH/4 juv.); Staten Island, New York (ZMA/1); Corson's Inlet, Cape May, New Jersey, leg. Fowler, 1909 (RMNH ex ANSP/7, 3v.); Brown Point - Pleasant Point, Long Island Sound, Connecticut, leg. Ross, 2.xii.1962 (AMNH 100361/>5); Seashore State Park, Princess Anne County, Virginia, leg. Old, winter 1953 (ZMA/2).

Biotope. — In fine and clean sand, current-swept (Wolff, 2005), but also in silty sand, from low tide mark to about 30 m, most common in the sublittoral of the Wadden Sea and the estuaries (Nehring & Leuchs, 1999). At its arrival in Europe the species found its eco-

logical niche unoccupied, and it spread very rapidly, colonizing lower intertidal sand flats and offshore sand banks in high density. Moreover, the natural predators in their original biotope on the American east coast, e.g. the naticid snail *Polinices heros* (Say, 1822) and the nemertean worm *Cerebratulus lacteus* (Leidy, 1851) (see McDermott, 1976) are not present in Europe. As a consequence, mass growing and then mass dying of the razor shell was frequently observed (for details see below; Von Cosel et al., 1982; Mühlenhardt-Siegel et al., 1983). The recent discovery of the large and voracious predator gastropod *Rapana venosa* (Valenciennes, 1846) in the southern North Sea off the Netherlands coast near Scheveningen and mid-way between the English and the Belgian coast (Nieweg et al., 2006) may give hope that the situation changes. Although it is possible that *Rapana venosa*, once well established in the region, may feed on commercial bivalves such as *Mytilus edulis*, *Crassostrea gigas* and *Cerastoderma edule*, the very common *Ensis directus* may also represent a good prey for *Rapana* (see Nieweg et al., 2006, also for the history of the introduction of *Rapana venosa* at other places). Moreover, commercial exploitation of *E. directus* in Europe (Fernandez-Tajes & Méndez, 2007) may also contribute to control the populations of this introduced species.

Larval biology. — The earliest larvae of *E. directus* measure 92 x 78 µm (Loosanoff & Davis, 1963: 119), the smallest of them were 80-85 µm long. The umbos appear “in larvae only 115 µm in length and” are “well developed in larvae 135 µm long” (Loosanoff & Davis, 1963). The settling length is from 210 to 270 µm, depending on environmental conditions. A larger size of the smallest larvae, 140 x 120 µm, is given by Sullivan (1948). The larvae are “light in colour”, and just before reaching settling size they get “a purple cast...along the edge of the larval shell” (Loosanoff & Davis, 1963). Loosanoff et al. (1966: figs 48, 49) give figures of different development stages from the early straight-hinge to the final metamorphosis stage. The cited authors observed a duration of the free swimming larval phase of 10 to 27 days, the shortest period (10 days) at a water temperature of 24°C. The larval period coincides well with the duration of a cargo ship’s voyage between the U.S. east coast and the North Sea.

Remarks. — *Ensis directus* is easily distinguished from the European *Ensis* by the form of the pallial sinus which in *E. directus* has its innermost point at its upper part directly below the dorsal pallial line, whereas in the European *Ensis*, that point is situated more ventrally, almost in mid-shell height (see drawings). The other American species examined (*E. macha* Molina, 1782; *E. minor* Dall, 1899) and the species of the Panamic-Pacific faunal Province (*E. myrae* Berry, 1954; *E. californicus* Dall, 1899; *E. tropicalis* Hertlein & Strong, 1955) have this same feature. Furthermore, the valves of *E. directus* are somewhat thinner for the size and more brittle. Molecular research on *E. directus* in comparison to the native *Ensis* is under work by J. Vierna (La Coruña). He showed that the genetic distance between American *Ensis* species and the eastern Atlantic species is greater than between the European species themselves (Vierna, personal communication, Dec. 2008), a fact which coincides with morphology.

Van Urk (1972: 135) separates the Recent form of this species from the Miocene form originally described as “*Solen directus*” by Conrad and leaves Conrad’s name for the fossil form only. Van Urk treats the Recent specimens under the name *Ensis americanus* (Binney, 1870) without noticing that the name *Solen americanus* is preoccupied by Chenu (1843); he mentions several differences between the Miocene and the Recent form which, according to him, could justify a separation: the fossil form reaches only 10 cm and is straight, the impression of the pallial line parallel to the anterior margin is vertical in the fossil form, whereas in the Recent form it is slightly pointing towards anterior. At least the greater part of these differences cited by Van Urk falls within the variation of the Recent form: among the examined Recent material from Europe there exist several half-grown and adult

straight specimens (Pl. 1 i; fig. 1 d) which coincide with the specimen figured by Van Urk (1972: 163, figs 2, 3) as well as specimens with vertical impression of the pallial line at the anterior margin (fig. 1e). Although Van Urk (1987a, b) insists in separating the fossil and the Recent form without giving further explanation and referring to an unpublished study, I continue uniting them under Conrad's name. After examination of several hundreds of specimens from many European localities, Severijns (2002: 67) came to the same conclusion. If the two forms would finally be separated, Binney's name *Solen americanus* could not be employed because of homonymy.

After only 30 years in Europe, *Ensis directus* is now a firmly established member of the European mollusc fauna as one of the most successful invaders. On the German North Sea coast, it has become "one of the ecologically most important invertebrate animal species" (Türkay, 2008, therein more references). It has already achieved a considerable variability in form and size, from markedly curved to straight, even with convex dorsal margin (see also figures in Severijns, 2002). Dwarf, shorter specimens were often encountered where ecological conditions seemed to be less favourable. A few small specimens of an unidentified *Ensis* recorded from tidal flats near Terschelling already in 1977 may probably have been *E. directus* (Beukema & Dekker, 1995) but this cannot be confirmed. An *Ensis* specimen positively identified as *E. directus* was first recorded on June 6, 1979, in the German Bight on a position north of the ELBE I lightship (a specimen of 47 mm length) (Von Cosel, Dörjes & Mühlenhardt-Siegel, 1982). Three years later, adult specimens were found along the whole North Sea coast of Germany and the Danish coast north to Henne Strand (Jutland).

From August 1982 onward, the species was also found on the Dutch coast, first on the West Frisian Islands, where empty shells were washed ashore on the sea side and live specimens collected in the Wadden Sea (De Boer & De Bruyne, 1983; Essink, 1984, 1985). In 1983, shells were found on the beaches of Terschelling, Ameland and Schiermonnikoog (De Bruyne & De Boer, 1984), and 1984 on the beaches of IJmuiden and Zandvoort (Essink, 1986a, b). In 1984, a live specimen was collected off Texel (Swennen, 1984), and in the Western Wadden Sea, live specimens of the 1984 recruitment were found at 7 localities (Essink & Tydeman, 1985). In 1986 and 1987, shells were encountered on the beaches of Scheveningen, Kijkduin, Terheyde and Hoek van Holland (Van Urk, 1987a). In August 1988, shells were dredged off the Rhine delta and off Zeebrugge (this paper). A short summary of the occurrence of *E. directus* on the Dutch coast is given by Wolff (2005).

The Belgian coast was reached most probably already in 1985, the first shells with length of 105 and 113 mm were found in April 1987 on the beach at Oostduinkerke and Zeebrugge (Kerckhof & Dumoulin, 1987; 1988a, 1988b). The species continued its way to the Channel and towards the coasts of France, where the first specimens were found at the Belgian-French border in February 1988 (Y. Meyer, personal communication; Kerckhof & Dumoulin, 1988a). On July 29th, 1988 the first shells were observed on the beach of Malo Terminus east of the beach of Dunkerque (Y. Meyer, personal communication, material of 1990 in MNHN) and 1991 at Gravelines (near Calais) (Dauvin, personal communication). In February 1992, a population was found well established with the southwestern limit at the western harbour of Dunkerque (Luczak et al., 1993). In November 1992, the species was found at Sangatte and Blériot-Plage, Calais (Severijns & Vanhaelen, 1994; Severijns, 2002). In July 1993 followed records from the beaches of Boulogne and Le Touquet (Severijns & Gilles, 1993), one month later at Berck-sur-Mer; it is presumed that the species lives there since mid 1991 (Severijns, 2002).

On the French shore, *E. directus* advanced further southwestward along the coast of the Département du Nord, and the Baie de Somme was attained in about mid 1992, the first record from there dates from June 1994 (Severijns, 1999, 2002). Two years later, *E.*

directus was recorded from Ault (Somme) by fully grown specimens, it had arrived there about mid 1993 (Severijns, 2002). I received an adult valve which was collected on 29 October, 1998 on the beach of Cayeux-sur-Mer in Somme (Picardie). The species continued its migration towards the SW and most probably reached the coast of Calvados by mid-1996. The first record in the eastern Bay of Seine between Le Havre and Antifer was 1998 (Dauvin et al., 2007). Then the species was found in August 1999 in Villers-sur-Mer, near Deauville, and from 2001 onwards, numerous populations were found in Seine Bay during surveys by the Wimereux Marine Station (Dauvin, personal communication; Dauvin et al., 2007). Severijns (2002) records *E.directus* from the mouth of Orne river (Merville/Franceville) in August 2000, and the same author (Severijns, 2004) records it from Ouistreham, on the western shore of the Orne estuary, in October 2001 (complete shells up to 148 mm length). From the size, Severijns calculates 1996 as the year of settling. The first record (March 2002) from the beaches of the Allied landing in Normandy in 1944 came from Colleville-Montgomery Plage (first settling also 1996). The next record there was from Utah Beach near La Madeleine Monument, in August 2002, with an almost record size specimen of 182 mm length. On Omaha Beach, more eastward, the species was only found one year later, in August 2003. The actual westernmost known locality is Le Gaugins (St. Marcouf), 13 km W of Madeleine, also from August 2003. The first settling of *E. directus* in front of the landing beaches is assumed to be in 1997 (Omaha Beach) and 1998 (Utah Beach) (Severijns, 2004). It cannot be excluded that, due to currents, the Cotentin peninsula may be a mayor obstacle for a dispersal further southwestward of *E. directus*.

The species also crossed the Channel, and in 1989 it was first recorded from the North Sea coast of England at Holme-next-the-Sea, Norfolk (Howlett, 1990) and was found 1993 at Sutton-on-Sea, Lincolnshire (Dansey, 1998); it continued towards the Humber River (Dansey, 1998; Essink in Eno et al., 1997;) where it is also now established (J. Light, personal communication). *E. directus* is also very common in The Wash where it was first found in Titchwell in May 1993 (Severijns, 2002) and where it is exploited commercially (Essink in Eno et al., 1997; Palmer, 2004). Just eastwards, near Brancaster, a very large specimen of 164 mm was found in Dec 1999. - To the West on the English Channel coast, the species has reached Newhaven Harbour, Sussex; fresh shells were found there in February 1998 (J. Light, personal communication) and Rye Bay (Palmer, 2004).

In the north, *E. directus* has now populated both sides of N-Jutland (Essink, 1986) and in Sweden the Koster Islands, Bohuslän and furthermore all along the Swedish West coast, with records from the Göteborg area (Warén, personal communication) and Malmö (Severijns, 2002). In the Kattegat it spread out southward to Sejrø Bay and the Isefjord, both on the North coast of Zealand (Rasmussen, 1996, see there for details). The species has also passed the Fehmarn Belt in the Baltic Sea and small (60 mm) but rather broad specimens, still with rests of the soft parts, were found in autumn 1993 on the beach near Grömitz marina in the Bay of Lübeck (Gürs et al., 1993).

European specimens of *Ensis directus* have not yet attained the size of some specimens from the US east coast: the largest European shell known to me reaches 184 mm and was found at Oostduinkerke (Belgium) (Severijns, 2002; a still larger shell of 187 mm was recorded by Vanhaelen, 1993, also from Belgium), whereas American specimens may grow longer than 200 mm. On the Dutch coast, the largest specimen with almost 170 mm length was taken at Schiermonnikoog, whereas the numerous shells collected by the author on two occasions on the beaches around Noordwijk and Katwijk are distinctly smaller (120-140 mm), the largest shell measures 155 mm only.

A specimen from St. Johns, Newfoundland, Canada, measures 170 mm (incl. periostracum), has a very thick shell and is estimated to be more than 20 years old (Pl. 1 l). The

maximum size of the species along the U.S. east coast is surely variable in certain limits according to ecological features and to populations, as is the case in Europe e.g. with *Ensis minor*. We cannot yet say how the maximum size of *E. directus* in Europe will develop in the future and with further dispersal, and we also do not know how far and with what speed the species will continue its dispersal north and south of its actual range. For the German Bight population, a maximum shell length of 166.8 mm was calculated using the Bertalanffy method (Mühlenhard-Siegel et al., 1983), a figure which well coincides with the "normal" size of fully grown specimens on the European coast (see also Severijns, 2002 and 2004).

Ensis ensis (Linné, 1758)

Solen ensis Linné, 1758: 672.

Hypogaea falcata Poli, 1791: 18, Index: 5, pl. 11 fig. 14.

Ensatella europaea Swainson, 1840: 365.

Solen ensiformis Locard, 1886: 371 [proposed conditionally, not valid].

Ensis phaxoides Van Urk, 1964: 39-42, pl. 2 figs 7, 8.

Ensis sicula Van Urk, 1964: 42-44, pl. 3 fig. 11.

Type material. — There are three specimens, without number and locality data, in the Linnean collection, London (Van Urk, 1964, fide Dance). Dodge (1952) mentions one specimen in the Linnean collection, which "bears no identification". Van Urk (1964) selected "the shell figured by Lister (the only reference in the 10th edition of Linnaeus' *Systema Naturae*)" as lectotype. Linné refers to Lister's *Historiae animalium angliae* ("List. angl. app. T 2, fig. 9"); however, the copy of 1678 in MNHN has no appendix. The figure in question is most probably that reproduced later in Lister (1687) (pl. 410 fig. 257A). A probable syntype has been found in the Linnean collection at Uppsala (73.0 × 9.0 mm, no locality), the other specimen in the lot is *E. minor* (Chenu).

The holotype and numerous paratypes of *E. phaxoides* Van Urk are in RMNH (for details see Van Urk, 1964), one paratype is in ZMA.

The holotype and paratypes (3 sh., 3 v.) of *E. sicula* Van Urk are in RMNH. The holotype has a slightly chipped right valve and a posteriorly partly broken left valve.

Type localities. — *Solen ensis*: "M. mediterraneo. Anglico". *Ensis phaxoides*: Katwijk, Netherlands, on beach, 3.x.1954. *Ensis sicula*: Beach near Floria, 15 km W of Istanbul, Turkey, 2.iv.1959.

Description. — Shell medium-sized (90-125 mm long and 15 mm broad), thin and quite fragile, very variable, moderately to conspicuously curved, tapering posteriorly. Length/height ratio 7-9. Anterior end rounded, posterior end obliquely truncated. Dorsal margin slightly to markedly concave, very rarely nearly straight, hinge and ligamental area curved upwards. Ventral margin strongly convex. Broadest part of the valves situated near or just behind the middle.

Cross section of posterior gape very narrow. A dorsal view of the closed valves shows that the posterior parts of the valves are gradually more and more laterally compressed, thus diminishing considerably the posterior gaping.

Anterior adductor scar very long and slender, straight, occasionally slightly curved (in Mediterranean specimens shorter), broadening towards posterior, with rounded posterior end. Posterior adductor scar small, oval, situated in a distance of its own length (fig. 3d) to slightly more than 1½ its length (fig. 3a) before the pallial sinus. Anterior pallial line at a distance smaller or equal to the distance ventral pallial line - ventral margin, then curving abruptly backwards. Ventral pallial line below the anterior adductor scar almost straight. Pallial sinus short, variable, rather narrow and more or less V-shaped, with

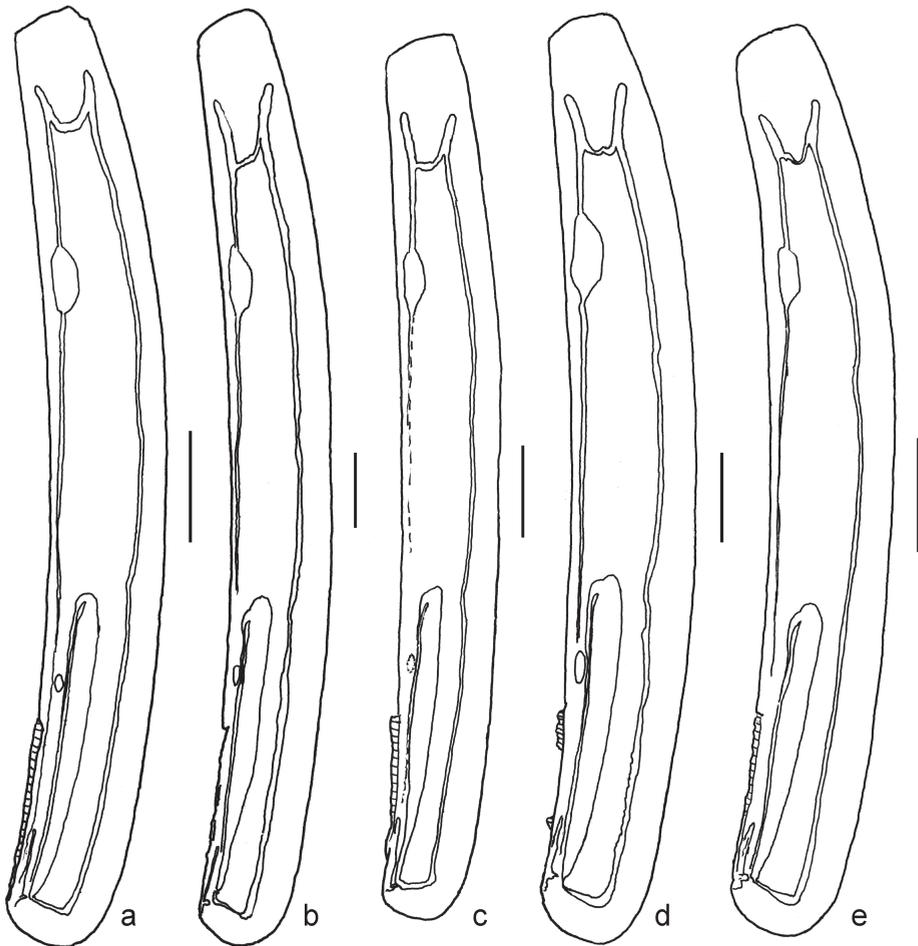


Fig. 3. *Ensis ensis* (Linné, 1758). a-e, half schematic drawings of the insides of valves. a, Læsø, N-Kattegatt, 1960, Ockelmann; b, Schiermonnikoog, Netherlands, Nov. 1985, MNHN; c, Laredo, Cantabria, Spain, Feb. 1988, MNHN; d, Houlgate, Calvados, France, Nov. 1969, MNHN (note the similarity to *E. phaxoides*); e, paratype of *Ensis phaxoides* Van Urk, 1964, Katwijk, Netherlands, Aug. 1961, RMNH. Scale 10 mm

rounded end (e.g. figs 3e, 4c, 4g), sometimes with inner extremity on the upper part (figs 3b, 4a, 4e).

Exterior with irregular growth lines, some of them well marked. Colour of valves whitish to creamy with reddish brown to violet growth lines, bands and zones, from very faint to marked, occasionally obsolete. Mediterranean specimens appearing pale violet, with dense regular vertical growth bands on the postero-dorsal half. Interior white or pattern showing through, especially in Mediterranean specimens. Antero-ventral part besides the horizontal lines with small points and speckles. Periostracum brownish green to yellowish green, in Mediterranean specimens slightly more transparent.

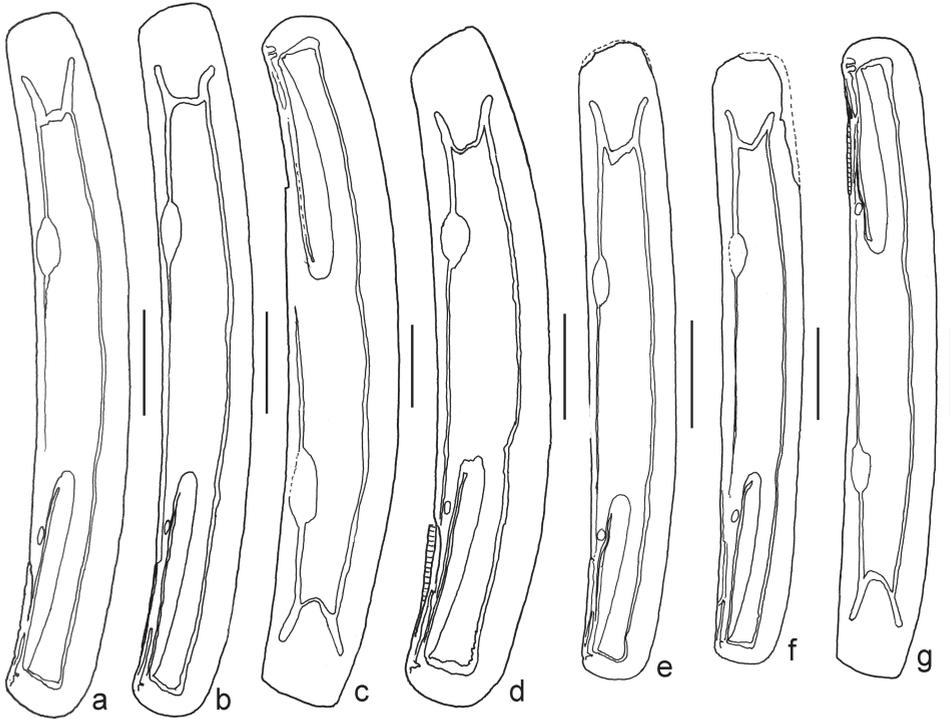


Fig. 4. *Ensis ensis* (Linné, 1758). a-g, half schematic drawings of the insides of valves. a, La Franqui, Roussillon, France, May 1987, MNHN; b-c, same locality, MNHN; d, Salerno, Italy, 1874, SMNH; e-g, paratypes of *Ensis sicula* Van Urk, 1964, Marmara Sea, beach near Florya, 15 km W of Istanbul, April 1959, RMNH (note the rather straight shells with noticeably forward placed posterior adductor scar). Scale 10 mm.

Animal creme-white, with pale red-brown foot (Holme, 1951).

Distribution. — Skagerrak, Kattegat southward to northern entrance of Øresund, British Isles, North Sea, eastern Atlantic coast south to Agadir, Morocco, throughout the Mediterranean, Black Sea. A record from "Finmarken, 15.v.1968" (in SMNH) needs confirmation.

Material examined. — SWEDEN: Saltö, Koster Islands, Bohuslän, 3-15 m, leg. Warén (SMNH/>5 v.); Fjällbacka, Bohuslän, leg. Warén (SMNH/1 subfossil postglacial v.). DENMARK: Læsø Island, N-Kattegat, 8-20 m, leg. Ockelmann, 1960 (MNHN/1); Skagen (no details) (ZIM/<5); Løkken, Skagerrak, leg. Baumgarten, x.1959 (ZIM/ >10); Hirtshals, 56°50'N 5°10'E, 30 fms (SMNH/old coll). GERMANY: Spiekeroog, East Frisian Is., leg. Baumgarten, 1962 (ZIM/5); Baltrum, East Frisian Is., leg. Von Cosel, vii.1955 and 1956 (SMF/<5); N of Helgoland 22-24 m, leg. Türkay, 13.viii.1984 (SMF/4 spm); Norwegian Channel, "Entenschnabel", 42 m, leg. Türkay, 13.viii.1984 (SMF/1 spm.). NETHERLANDS: Schiermonnikoog, km 7-11, leg. De Boer (MNHN/5; 4 v.); Terschelling, km 12-16. leg. Dijkstra, vii.1985 (MNHN/5); Terschelling, km 8, leg. Moolenbeek, v.86 (MNHN/11, 5v.); Scheveningen (no details)(SMNH/1); North Sea, 54°30'N 2°32'E, 21 m; 52°50'N 3°47'E, 27 m, trawled, R/V "AURELIA", 3.ix.

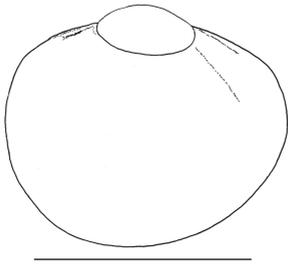


Fig. 5. *Ensis ensis* (Linné, 1758). Larval shell with protoconch I and II, 383 x 317 μm , Hirsholmen, N-Kattegat 10. July 1983, leg. Ockelmann, after an original sketch by K. Ockelmann. Scale 300 μm .

and 15.x.1975 (RMNH/3, 1 v.). SCOTLAND: Carnoustie, E-coast, NE of Dundee, leg. B. & R. von Cosel, 11.x.1987 (MNHN/<5); E. coast of Firth of Forth, leg. B. & R. von Cosel, 8.-10.x.1987: Gosford Bay, (MNHN/1; 10v.), Aberlady Bay (MNHN/4v.), Gullane Bay (MNHN/1; 10v.), North Berwick (MNHN/1v.); Saltcoats, Firth of Clyde, W-coast, leg. B. & R. von Cosel, 6.-7.x.1987 (MNHN/1, 4v.). ENGLAND: Liverpool, coll. Staadt, (MNHN/1); Shell Bay, Studland, Dorset, leg. Staadt, 1922 (MNHN/3). WALES: Swansea, coll. Schmierer (SMNH/1). ATLANTIC FRANCE: Berck-sur-Mer, Pas-de-Calais., leg. Von Cosel, 23.v.1987 (MNHN/9; 10 v.); Berck-sur-Mer, Pas-de-Calais, leg. Bouchet, 1991 (MNHN/3, 17 v.); Trouville, Calvados, coll. Soyer, 1965 (MNHN/1); Villers s. Mer, Calvados (MNHN/7); Houlgate, Calvados, leg. Bouchet, 1.xi.1996 (MNHN/4, 1v.); Houlgate - Langrune, Calvados, coll. Arnoul (MNHN/1); St-Honorine-des-Pertes, Calvados, leg. Noel, 20.ix.2006 (MNHN/1); Colleville, Seine-Maritime, coll. Brasil, 1904 (MNHN/2v.); Cabourg - La Hôme, Calvados, leg. B. & R von Cosel, 9.viii.1987 (MNHN/25, 65v.); Lion-sur-Mer - Riva Bella, Calvados, coll. H. Fischer (MNHN/5, 2 v.); Cherbourg, Manche, coll. Petit (MNHN/2); Granville, Manche, coll. Bourguignat 1870 (MNHN/1, 2v.); St. Brieuc, Côtes-du-Nord, coll. Arnoul, 1892 (MNHN/9); Binic, Côtes-du-Nord, leg.. Chérière, viii.1964 (MNHN/23; 2v.); Porsguen, near Plougastel, Finistère, leg Gofas, 1976 (MNHN/10, 5v.); Morgat, Finistère, fine sand, at extreme low tide (aequinoctial spring tides), leg. Von Cosel, 21.iii.1984 (MNHN/1spm.); Douarnenez, Finistère, coll. Soyer (MNHN/2, 1v.); Quiberon, Morbihan, coll. Bourguignat, 1872 (MNHN/1, 2v.); Le Croisic, Loire-Atlantique, coll. Locard, 1892 (MNHN/1); Bassin d'Arcachon, Gironde, Banc d'Arguin, leg. Salvat, 1961 (MNHN/1). ATLANTIC SPAIN: Laredo, Cantabria, leg. Von Cosel & Gofas, 7.ii.1988 (MNHN/131, 48v.); El Portil - El Rompido, W of Huelva, leg. Van Urk, iii.1974 (RMNH/4v.); Cadiz - Algeciras, leg. Van Urk, iii.1974 (RMNH/4v.). PORTUGAL: Sagres, Ponta de Baleeira, 17-23 m, leg. Mission Algarve, v.1988 (MNHN/2v.). MOROCCO: Agadir, leg. Theilken, iii.1973 (MNHN/1v.); Tetouan, coll. Buchet (MNHN/1, 1v.). ALGERIA: Oran., coll. Locard, 1892 (MNHN/1). TUNISIA: Radès, near Tunis, leg. Vidal, 1985, (MNHN/2). SLOVENIA: S. Giovanni i Pelago, Istria, leg. Koch, 1901 (SMNH/1). ITALY: Salerno, coll. G. Lovén, 1874 (SMNH/>5); Sicily: Agnone Bagni, Bay of Catania, 37°19.0'N 15°06.1'E, leg. Mission Sicile Orientale, vii.1990 (MNHN/1juv., 20v.); Sicily: Vendicari, 36°46'N 15°06'E, leg. Mission Sicile Orientale, vii.1990 (MNHN/8v.); Sicily: Acitrezza, Capo Mulini, 37°34.5'N 15°11.9'E, 60-90 m, leg. Mission Sicile Orientale, vii.1990 (MNHN/1v.). MEDITERRANEAN FRANCE: Marseille, Bouches-du-Rhône, coll. Locard, 1892 (MNHN/1); Fos-sur-Mer, Bouches-du-Rhône, coll. Bourguignat, 1872 (MNHN/3v.); Port-Camargue, Languedoc, leg. Gofas, viii.1976 (MNHN/2); Le Grau du Roi, Gard, Plage Boucanet, leg. Von Cosel, 28.ix.1999 (MNHN/5, 71v.); Sète, Hérault, coll. Locard, 1892 (MNHN/2); La Franqui, Roussillon, leg. Von Cosel, 2.v.1987 (MNHN/5, 105v.), x.1987 (MNHN/14, 107v.); Etang de Leucate, at the canal to the sea, leg. Gofas, iv.1999 (MNHN/<5). MEDITERRANEAN SPAIN: Rincon de la Victoria, Malaga, Andalucía, on sand, 1-5 m leg. Gofas, ix.1994 (MNHN/2v).

Biotope. — In sandy bottom, mostly fine sand, with not more than 16% silt (Holme, 1954: 155), usually offshore from 10 to about 60 m, but occasionally also at extreme low tide, exposed only during peak tides. The species is confined to more or less sheltered

areas, where it often co-occurs with *Chamelaea striatula* (da Costa, 1778), *Donax vittatus* (da Costa, 1778), *Tellina fabula* Gmelin, 1791, *Gari fervensis* (Gmelin, 1791), *Mactra corallina cinerea* Montagu, 1808 and *Lutraria lutraria* (Linné, 1758) (Holme, 1954).

Larval biology. — The protoconch I (fig. 5) measures about 140 x 105 µm, the settling size (protoconch II) has, like in *E. magnus*, 300-400 µm. The larval shell is more convex than that of *E. magnus* (see there) and rather pale and not as coloured as in the former. It is estimated that *E. ensis* remains also about 3-5 weeks in the plankton (Ockelmann, personal communication, 16.Dec.1987). The observations have been made on larvae caught in the northern Kattegat on July 10, 1983, by K. Ockelmann. Holme (1954: 165) reared larvae of *E. ensis* to metamorphosis. The planktonic phase lasted one month at a water temperature of 13-15°C. The settling size was 290 µm.

Remarks. — Like most *Ensis* species, *E. ensis* is very variable in shell outline, curvature and size, which led Van Urk (1964) to the distinction of two further species, *E. phaxoides* Van Urk, 1964, from the Netherlands and Belgian coast and *E. sicula* Van Urk, 1964 from the Marmara Sea (Turkey). The form *E. phaxoides* (fig. 3e) is broader, somewhat shorter and posteriorly more tapering, with the ventral margin more curved. The posterior adductor scar is situated somewhat closer to the pallial sinus. However, already Van Urk admits that he is "still unable to fix precisely the limits of the species, more especially as far as the young and immature material concerned" (1964: 41). Among the extensive material in RMNH of both forms (several hundred lots), there is a smooth transition between the forms *ensis* and *phaxoides*. Besides the Netherlands and German coast specimens, *phaxoides*-like shells come also from Cabourg, Houlgate and Berck-sur-Mer, Northern France.

The form *E. sicula* (fig. 4e-g) is smaller, shorter and less curved than typical *E. Ensis*. It resembles more a miniature *E. magnus*, but is shorter and looks like more straight specimens of this, the posterior adductor scars are placed still more forward than in *E. ensis* and *E. magnus*. It is most probably a local form in the Marmara Sea and is placed herein in the synonymy of *E. ensis* in spite of its slightly different form seemingly somewhat more homogeneous. More material and molecular work is needed for determining its final status. Mediterranean *Ensis ensis* in general have a slightly less tapering anterior and posterior part, the posterior margin being broad and more oblique with sharper corners. The shells are often somewhat shorter than Atlantic specimens (fig. 4d) and are coloured typically violet; the posterior adductor scar is situated at a distance of its own length (fig. 4d) to 1½ that distance from the pallial sinus, or still more forward. Specimens from Laredo (Spain) (Pl. 2 i-k) on the south coast of the Bay of Biscay are quite close to the Mediterranean form in shape of the posterior end and the arrangement of the colour bands on the postero-dorsal part, but they are more slender. Some specimens from Brittany (Finistère) look similar (Pl. 2 g,h).

Placed in the *Ensis phaxoides* is here considered a variation which is linked with the "nominal" form with all kinds of intergrades. Hence that nominal taxon is placed in the synonymy of *E. ensis*.

Ensis goreensis (Clessin, 1888)

Solen goreensis Clessin, 1888: 34, pl. 13 fig. 4.

Type material. — The collection Clessin was deposited in the Museum für Naturkunde Stuttgart but nearly totally destroyed in World War II, among which most probably the type material of *S. goreensis*.

Type locality. — Gorée, Senegal, West Africa.

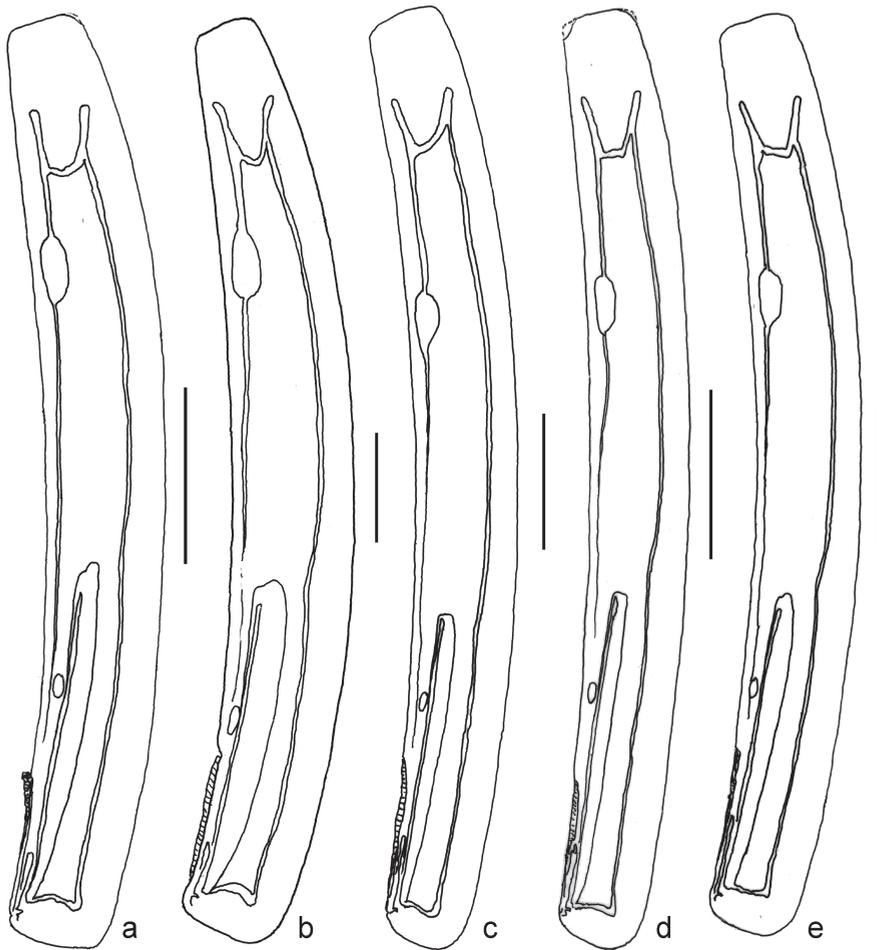


Fig. 6. *Ensis goreensis* (Clessin, 1888). a-e, half schematic drawings of the insides of valves; a, Nouadhibou, Mauritania, Miss. Gruvel 1908, MNHN; b, off Casamance, Senegal, 10-20 m, 1987, MNHN; c, shelf of Guinea, W of Ouendi, 9°54' N 16°01,5' W, 39 m, May 1988, SEDIGUI sta 443 CH, MNHN; d, shelf of Guinea, 9°54' N 15°25' W, 25 m, May 1988, sta. 455 CH, MNHN; e, Ile Banié, Gabon, 2-6 m, 1985, MNHN. Scale 10 mm.

Description. — Shell small (50 mm) to medium-sized (90 mm long and 10 mm broad), thin and fragile, almost always strongly curved (rarely less, fig. 10 g), dorsal and ventral margin nearly parallel or posteriorly slightly tapering. Length/height ratio 7-9.3. Anterior margin rounded-truncated with well rounded corner, posterior margin truncated and slightly convex. Dorsal margin markedly concave, ventral margin conspicuously convex. Hinge and ligamental area curved upwards only corresponding to the line of concavness of the dorsal margin. Broadest part of the valve slightly in front of, in or behind the middle.

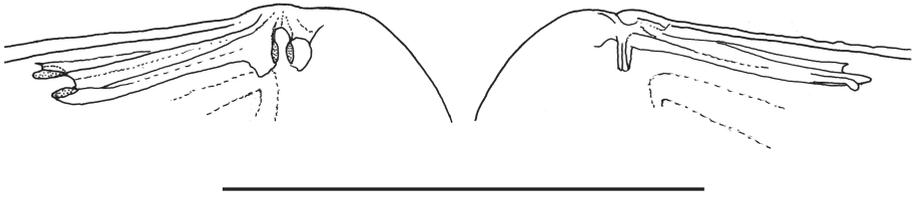


Fig. 7. *Ensis gorensis* (Clessin, 1888). Close-up view of hinge teeth of a specimen from Mauritania, 19°00'N 16°30'W, MNHN. Scale 5 mm.

Cross-section of posterior gape lens-shaped and narrow. A dorsal view of the closed valves shows that the posterior parts of the valves are only very gradually more and more compressed towards the posterior end.

Anterior adductor scar long and very slender, weakly curved, slightly broadening posteriorly, with rounded end. Posterior adductor scar very small, rounded-oval, situated in a distance of 1½-2 to 2½ times its length in front of the pallial sinus. Anterior pallial line descending more or less vertically, at a distance a little less than the distance ventral pallial line - ventral margin, slightly concave, then curving abruptly backwards. Ventral pallial line below the anterior adductor scar straight, at its end weakly concave. Pallial sinus short, truncate, with the innermost point in the middle, upper or lower half.

Exterior with fine irregular growth lines. Colour of valves whitish to pale rosy violet with few weakly marked to numerous well marked brownish red to violet vertical growth zones and bands on the postero-dorsal part, and numerous small points and spots on the antero-ventral and the dorsal part of the valves, on the interior showing through. Periostracum yellowish green and thin.

Animal with a very long foot, which is white with pale brown on the tip and the first 15 mm.

Distribution. — Tropical West Africa from the southern part of West Sahara (Rio de Oro, 22°N; Levy, 1975) to southern Angola (Lucira); Cape Verde Islands.

Material examined: — MAURITANIA: Port Etienne (now Nouadhibou), Mission Gruvel 1908 (MNHN/1; 1v., fragm.); Mauritanian continental shelf 17°42'-20°30' N and 15°06'-17°18'W, 15-38 m, R/V N'DIAGO, leg Richer de Forges, 1981 (MNHN/12 lots with 11 spms, 4 sh. & 3 v.). CAPE VERDE ISLANDS: W of Boavista, 16°01'N 23°00'W, 45 m, R/V "CALYPSO"- sta. 75, 25.xi.1959 (MNHN/1v). SENEGAL: Baie de Rufisque, 18-20 m, Mission Gruvel, 3.iv.1909 (MNHN/2v., >20fragm.); between Rufisque and Hann, 6-9 m, Mission Gruvel (MNHN/some broken v); Gorée - Thiaroye, 15 m, sand + gravel, leg. Thorsson, 2.iii.1952 (ZMC/2 fragm.); Dakar, SW of Madeleines, 48 m, leg. Marche-Marchad, 15.ix.1953 (MNHN/1, 4v.); off Cap Manuel, 18 m, leg. Marche-Marchad, 1. iii. 1957 (MNHN/11v., 10fragm.); Baie de Gorée, leg. Marche-Marchad (MNHN/1spm., 1v.); Baie de Gorée, leg. Leung Tack, 1983 (MNHN/1; 1v.); Baie de Gorée, 5-10 m, leg. Pin, 1987 (MNHN/4); off Casamance, 10-20 m, leg. Pin (from shrimpboat), 1987 (MNHN/11); Casamance, upper continental shelf 12°30.4'-13°05.6' N 17°02.4'-17°29.9' W, 22 m, sandy bottom, 19-45 m, R/V "LOUIS SAUGER", leg. Von Cosel, 15-28.iii.1988 (MNHN/14 lots with 1 spm., 25v., 38 fragm.). GUINEA (Conakry): Guinean continental shelf between the Compony Banks and the border to Sierra Leone, 9°03'-10°36'N 13°06'-16°10'W, sandy bottom, 15 and 50 m, Cruises SEDIGUI I and II, R/V "ANDRÉ NIZERY", leg. Von Cosel, iv.-v. & x.-xi.1988 (MNHN/16 lots with >50 sh. and v.). LIBERIA: 5°06'N 9°34'W, 78 m, R/V "ATLANTIDE" sta. 60, 9.i.1946 (ZMC/<5 broken v.). COTE D'IVOIRE: Grand Bassam, 5°07'N 3°22'W, 20 m, Guinean Trawling Survey, R/V "LA RAFALE", leg. Cherbonnier, 21.iii.1964 (MNHN/1 broken v.); Abidjan region (no precision) R/V "REINE POKOU"; leg. Le Loeuff (MNHN/1v.). GABON: Ile

Banié, north of Cap Esterias, 2-6 m, leg. Bernard, 1985 (MNHN/2); Port-Gentil, 0°43'S 8°47.5'E, leg. Chevalier, 1980-89 (MNHN/1 v.). ANGOLA: Ponta do Mussulo, Luanda., leg Gofas, 1984 (MNHN/1 fragm.); Palmeirinhas, Luanda, 15-20 m, muddy sand, leg. Gofas, ii.1987 (MNHN/1 spm.); Ilha de Luanda, 120 m, leg. Gofas, 1982 (MNHN/1v.); Baía de Corimba, Luanda, 10-20 m, leg. Gofas, 1982 (MNHN/1v.); Baía de Lucira, Moçâmedes, 10-20 m, leg. Gofas, 1982 (MNHN/1 broken v.).

Biotope. — In fine sand, mixed sand, moderately coarse sand and sandy bottom with calcareous algae, mostly offshore between 5 and 80 m, but occasionally shallower.

Remarks. — Like the other eastern Atlantic species of *Ensis*, *E. goreensis* is very variable in size and length/height ratio, and also so in degree of curvature and of posterior tapering. The specimens from Mauritania and Senegal including Casamance (Pl. 3 a-i) are somewhat shorter (L/H ratio 7-8) than the prevailing very slender specimens (L/H ratio 9 [8.7-9.3]) from the tropical zone proper (Guinea and southward, see Pl. 3 j-g), the posterior adductor scar in the northern specimens is placed more posteriorly (fig. 6a, b). If placed side by side, specimens from Casamance or the Dakar region on one side and the slender specimens from the Guinean continental shelf on the other side, one might think that two different species may be involved. However, the presence of presumed intermediates and the lack of much more and freshly collected material do not allow further conclusions, and for the moment, *E. goreensis* is treated as one very variable species. It is the only tropical Eastern Atlantic *Ensis* species; it is separated from the next northern species, *E. ensis* (Agadir, Morocco), by a distance of 1200 km. From *E. ensis* it can be distinguished by its more slender shell and the peculiar small dark violet spots, dots, points and mottlings on the antero-ventral section of the shell. The anterior margin in general is less rounded than in *E. ensis*.

Nothing is known about the larval biology, but from the distribution pattern it can be concluded that the free-swimming larval phase lasts more than two weeks.

Ensis magnus Schumacher, 1817

Ensis magnus Schumacher, 1817: 143, pl. 14 fig. 1a, b.

Solen ensis major Chenu, 1843: pl. 3 fig. 2, 2a, b, e.

Solen ensis var. *magna* Forbes & Hanley, 1848: pl. 14 fig. 2 (this form not in text therein).

Solen siliqua var. *arcuata* Jeffreys, 1865: 19.

Ensis ensis auct., non Linné, 1758.

Ensis siliqua auct., non Linné, 1758.

Ensis arcuatus var. *ensoides* Van Urk, 1964: 31-33, pl. 1 fig. 6.

Ensis arcuatus var. *norvegica* Van Urk, 1964: 33-35, pl.3 fig. 10.

Type material. — The specimen figured by Chemnitz (1782: pl. 4 fig. 29) has been selected as the lectotype of *Ensis magnus* by Van Urk (1964: 29) because he did not find "the holotype ... in the Copenhagen collection", nor could H. Lemche "give any...information about it".

The shell figured as *Solen ensis major* by Chenu (1843) is a typical *E. magnus* form with a length of 192 mm (figure), thus reaching almost the maximum size of the species. This specimen is selected here as lectotype since we do not know if the author had other specimens at hand.

The holotype and one paratype of *Solen siliqua* var. *arcuata* are in USNM (No. 171127), Jeffreys collection, illustrated in Van Urk (1964) (see also Warén, 1980: 49).

The holotype of *E. arcuatus* var. *ensoides* Van Urk, 1964, and several paratypes are in RMNH.

The holotype and several paratypes of *Ensis arcuatus* var. *norvegica* Van Urk, 1964, in Trondheim Museum, Norway (for details see Van Urk, 1964).

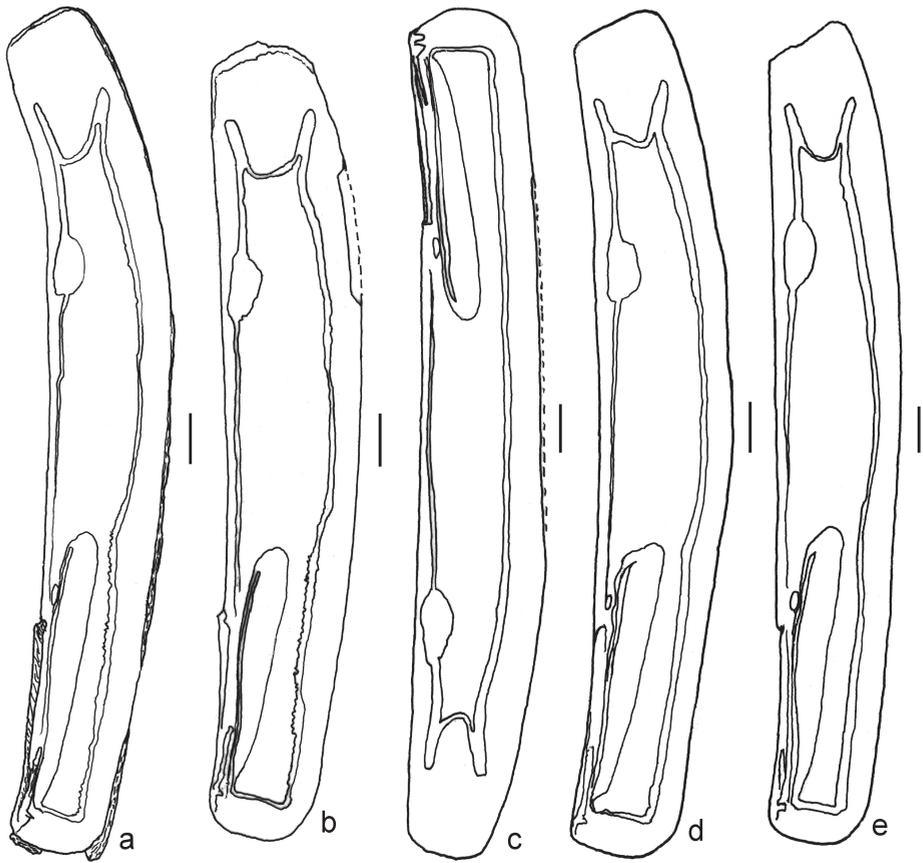


Fig. 8. *Ensis magnus* Schumacher 1817, “*magnus*” form from Faroe and Norway, **a-e**, half schematic drawings of the insides of valves; **a**, Høyvik, Faroe, 18 m, Sept. 1993, MNHN; **b**, same locality; **c**, typical specimen of a 19th Century collection, labelled “*E. magnus*”, no locality but most probably from Faroe, SMF ex Zool. Inst. Marburg; **d**, holotype of *Ensis arcuatus* var *norvegica* Van Urk, 1964, Storfosen, Orlandet, Norway, May 1941, Trondheim Museum; **e**, same locality, Trondheim Museum. Scale 10 mm.

Type locality. — “Norwegen, Ferröische Eylanden” (Chemnitz, 1782: 46), restricted to Faroe by Van Urk (1964: 29).

Description. — Shell large (140-150 mm) to very large (160 to almost 200 mm long and 27 mm broad), considerably variable in shape, size and thickness; thin but strong to moderately thick, slightly to conspicuously curved, but occasionally almost straight to straight. Length/height ratio 6,5 - 8. Anterior margin rounded or more or less obliquely truncated with well rounded ventral corner. Posterior margin obliquely truncated, slightly convex, with rounded corners. Dorsal margin usually slightly to markedly concave, sometimes straight or even convex (the so-called “*magnus* form”), hinge and ligamental area curved upwards. Ventral margin always moderately to conspicuously convex. Broadest part of the valves situated in the middle or within the posterior half.



Fig. 9. *Ensis magnus* Schumacher 1817, **a-d**, half schematic drawings of the insides of valves; **a-c**, “*magnus*” form from other localities (note the straight shells with broader posterior part typical for the “*magnus*” form); **a**, Silver Strand, Galway, Ireland, May 1985, MNHN; **b**, Berck-sur-Mer, Pas-de-Calais, France, May 1987, MNHN; **c**, Laredo, Cantabria, Spain, Feb. 1988, MNHN; **d**, *Ensis arcuatus* var. *ensoides* Van Urk, 1964, specimen close to the type specimen figured by Van Urk, 1964, Berck-sur-Mer, Pas-de-Calais, France, May 1987, MNHN. Scale 10 mm.

Cross section of posterior gaping narrow, with in the middle nearly “parallel” posterior margins. A dorsal view of the closed valves shows that the last 4 cm of the posterior part of the valves are gently curved towards the middle horizontal axis thus diminishing considerably the posterior gaping.

Anterior adductor scar long to very long and slender, straight or very slightly curved (in the forms *magnus* and *norvegica* somewhat shorter and broader), more or less broadening posteriorly, generally with an obliquely truncated end, pointing towards the postero-ventral corner of the valve. Posterior adductor scar small, rounded-oval to oval, situated at a distance of slightly less its own length or its own length (mostly *magnus* form) to $1\frac{1}{2}$ its length before the pallial sinus. Anterior pallial line weakly concave, descending vertically (90°) or slightly towards posterior, rarely slightly towards anterior, at the same

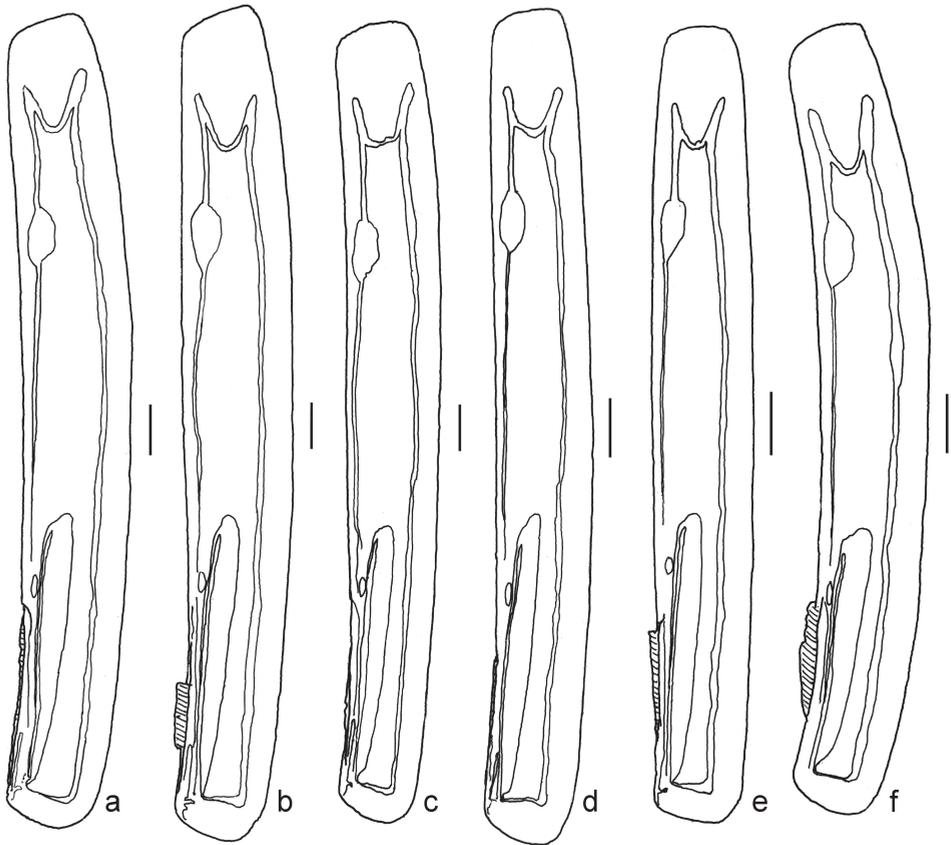


Fig. 10. *Ensis magnus* Schumacher 1817, "arcuatus" form, a-f, half schematic drawings of the insides of valves; a, Stavanger, Norway, 1983, ZMA; b, Sand-Voe, North Mainland, Shetland Is., June 1976, SMF; c, Silver Strand, Galway, Ireland, May 1985, MNHN; d, Schiermonnikoog, Netherlands, March 1986, MNHN; e, Berck-sur-Mer, Pas-de-Calais, France, May 1987, MNHN; f, Penthièvre, Baie de Quiberon, France, March 1987. Scale 10 mm

distance to the anterior margin as the ventral pallial line to the ventral margin, then turning sharply backwards. Ventral pallial line below the anterior adductor scar straight or very slightly concave. Pallial sinus short and narrow, variable, rounded or truncate, its innermost tip mostly at the middle or near its upper part.

Exterior with often quite pronounced growth lines and growth zones. Colour of valves whitish to creamy, with reddish brown to purplish violet growth lines, bands and zones, Inside white with the outside pattern more or less showing through. Interior of specimens from the more southern part of its range often conspicuously tinged with reddish brown, violet or occasionally pink, especially near the ventral margin and the posterior end. Antero-ventral part besides the horizontal lines with small points and speckles.

Periostracum strong, greenish brown to brown, on the zone with the vertical growth lines often darker, but there mostly eroded.

Animal creme white, with foot of the same colour.

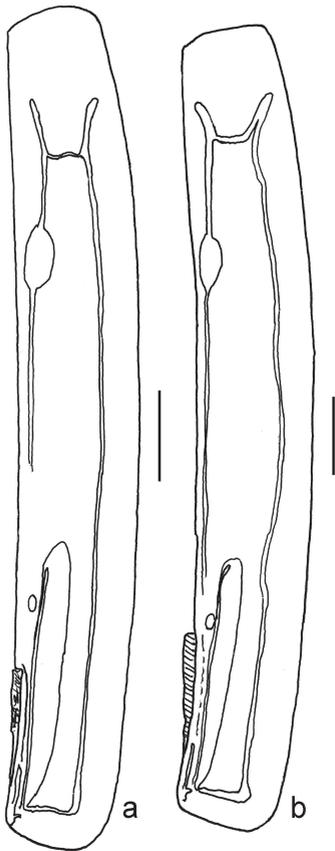


Fig. 11. *Ensis magnus* Schumacher 1817, Mediterranean form, a-b, half schematic drawings of the insides of valves; a, Tanger, Morocco, 1971, MNHN; b, La Franqui, Roussillon, France, May 1987, MNHN. Scale 10 mm

Distribution. — Island (Oskarsson, 1982: 311-313). Norway north to Finmarken (Tromsø, Bodø and Lofoten) (M. Sars, 1851: 165; G.O. Sars, 1878: 80; Sparre Schneider, 1885: 89). Sweden southward to northern Kattegat, scarce in southern Kattegat. Faroe Islands, Shetlands, Orkney, British Isles, North Sea, Atlantic coast to Portugal, North Morocco (Tanger) and the Alboran Sea (Tetouan; Fuengirola) (Van Urk, 1984). The species seems to be very rare in the Mediterranean where a few specimens are only known from localities on the coast of the Golfe du Lion.

Material examined. — FAROE ISLANDS: between Kaldbak and Kaldbakbottnur, ix.1993, leg. Schander (MNHN/1, 1v.); Kaldbakbottnur, 8.ix.1993, leg. Schander (MNHN/2 spm. fresh dead); entrance to Nolsø Harbour, 15-20 m, 20.ix.1993, leg. Schander (MNHN/1); Høyvik, outside Torshavn, 18 m, sand, strong currents, 24.ix.1993, leg. Schander (MNHN/36, 4v.; SMF/2). NORWAY: Finmarken (no precise loc.) (SMNH/3, 2 v.); Finmarken (no precise loc.), old coll., perhaps from Sars (SMNH/3); 1 km ESE of Alstahaug (66°N), in shallow water in a protected bay, sandy bottom, leg. Ahlner, 13.vi.1953 (SMNH/2); Fevag, Trondheimsfjord, leg. Warén (SMNH/1, 4v.); Lyapollen, Trondheimsfjord, leg. Odhner (SMNH/6, 1v.); Munken, near Oerland, mouth of Trondheimsfjord, leg. Dons, 1942 (Trondheim Museum/2, 6v.); Storfosan, Oerland, mouth of Trondheimsfjord, leg. Dons, v.1941 (Trondheim Museum/1); Inntian, just outside Trondheimsfjord, leg. Dons, 27.v.1937 (Trondheim Museum/1v.); Heggdalen, Trondheim, leg.

Dons, 13.vi.1927 (Trondheim Museum/1); Sistranda, just outside Trondheimsfjord, 25.iii.1943 (Trondheim Museum/2); Lyngholmfaera, Storfosen, Oerland, mouth of Trondheimsfjord, 20.iv.1942 (Trondheim Museum/holotype *E. arcuatus*. var. *norvegica*); Eggholmen, Raunefjord, S of Bergen, 60°16'33"N 5°13'3"E, in sandy bay, 0.50 m, after very strong frost, partly with dead animal, leg. Warén, 1969 (SMNH>20; MNHN/19.); Lieholmarne, Korsfjord, S of Bergen, leg. Warén, 1971 (SMNH/>10); Haugesund, SW-Norway, leg. Wittrock, viii.1865 (SMNH/1); Frederikshalde, Oslofjord (SMNH/1). SWEDEN: Tjärnö, Langholmen W-side, Koster Islands, Bohuslän, sandy bottom, 3-20 m, leg. Warén (SMNH/<5); Saltö, Koster Is., 3-15 m, leg. Warén (SMNH/<5); Fjällbacka, Bohuslän, leg. Warén SMNH/<10 subfossil post-glacial v.); Raö, S of Göteborg (SMNH/2); Bonden, Gullmar Fjord, 58°12.7'N 11°19'E, 18-25 m, leg. Vierna (coll. Vierna/2). DENMARK: Anholt Island, Kattegat, leg. Muchardt, vi.1933 (SMNH/2, 9v); Læsø Island, Kattegat, 8-20 m, leg. Ockelmann, 1960 (MNHN/8); Grenen, Skagen, leg. Warén (SMNH/1); Hirtshals, leg. Warén (SMNH/1); North Sea, 56°50'N 5°10'E, 30 fms. (SMNH/1v.). GERMANY: Baltrum and Juist, East Frisian Is., leg. Von Cosel, 1955-57 (SMF/>5). NETHERLANDS: Schiermonnikoog, km 7 - 11, leg. De Boer, 17. xi. 1985 (MNHN/9, 6v), .iii. and iv.1986 (MNHN/5, 2v.); Terschelling, km 8, leg. Moolenbeek, v.1986 (MNHN/11); Terschelling, km 12-16, leg. Dijkstra, vii.1985 (MNHN/3); Egmond aan Zee, leg. Moolenbeek, v.1987 (MNHN/29, 25v.); Katwijk-Noordwijk, leg. Von Cosel, 18.ii.1989 (MNHN/8, 18v.). SCOTLAND: Carnoustie, NE of Dundee, E-coast, leg. B. & R. von Cosel, 11.x.1987 (MNHN/1); Firth of Forth, E-coast, leg. B. & R. von Cosel, 8.-10.x.1987: Gosford Bay (MNHN/1, 2v.), Aberlady Bay (MNHN/3, 4v.), Gullane Bay, (MNHN/9v.); Firth of Clyde (no precision), W-coast (Glasgow Museum/1 [183 mm long]); Saltcoats, Firth of Clyde, leg. B. & R. von Cosel, 6.-7.x.1987 (MNHN/3); Dawarr Is., Campbeltown, W-coast, leg. Williams, coll. Staadt (MNHN/2); Sand-Voe, N-Mainland, Shetland Islands, leg. Türkay, 26.iv.1976 (SMF/1); Orkney Islands (no precise locality), RMNH/5). ENGLAND: Brancaster, North Norfolk, leg. Dansey, 27.xii.1999 (MNHN/1); Folkestone, leg. Warén (SMNH/<10v.); Shell Bay, Studland, Dorset, coll. Staadt (MNHN/2; 4v.); Liverpool, coll. Staadt (MNHN/5). IRELAND: Silver Strand, W of Galway, Galway Bay, leg. Von Cosel, 24.v.1985 (MNHN/37, 38v.). ATLANTIC FRANCE: Dunkerque, Pas-de-Calais, coll. Locard 1892 (MNHN/1); Berck-sur-Mer, Pas-de-Calais, leg. Von Cosel, 23.v.1987 (MNHN/>300 & v.); Baie d'Authie and Ault, Somme, Picardie, coll. Staadt (MNHN/22); Cayeux-sur-Mer, Somme, Picardie, on pebble beach, leg. Noel, 20.x.1998 (MNHN/1 v.) Le Havre, Seine-Maritime (MNHN/3); Villers s. Mer, Calvados coll. Locard, 1892 (MNHN/2); Houlgate, Calvados, leg. Bouchet, 1.xi.1996 (MNHN/18); Cabourg, Calvados, coll. Bourguignat, 1872 and Locard, 1892 (MNHN/12); Cabourg - La Hôme, Calvados, leg. B. & R. von Cosel, 9.viii.1987 (MNHN/116, 33v.); form "var *ensoides* Van Urk": MNHN/4, 11v.); Ile de Tatihou, St. Vaast-La Hougue, Manche, leg. Noel, 2004-2009 (MNHN/22 [in 4 lots]); Cherbourg, Manche, coll. Locard, 1892 (MNHN/1); Pirou, Manche, leg. students' excursion UPMC Paris, 18.ii.2003 (MNHN/9); Pointe d'Agon, Granville, Manche, leg. Noel, 7.iii.2008 (MNHN/4); Granville, Manche, Plage Donville, leg. Von Cosel, 7.x.1999 (MNHN/42, 12v.); Ile Chausey, Manche, leg. Noel 8.iii.2008 (MNHN/1); Cancale, Ille-et-Vilaine (MNHN/9); St. Malo, Ille-et-Vilaine, leg. H. Fischer, 1901 (MNHN/5); Dinard, Côtes-du-Nord, leg. Von Cosel, 13.ii.1982 (MNHN/16, 3v.); Binic, Côtes-du-Nord, coll. Staadt (MNHN/5); Roscoff, Finistère, in sand banks of fine and mixed sand, some situated between rocky areas, extreme low tide (aequinoctial peak tides), leg. Von Cosel, 16.-21.iii.1984 (MNHN/<5 spm.); Concarneau, Finistère, leg. Noel, 12.v.2006 (MNHN/1); Penthièvre, Morbihan, Quiberon Bay side, leg. B. & R. von Cosel, 29.iii.1987 (MNHN/13, 1v.); off Port-Haliguen, Baie de Quiberon, 5-10 m, leg. Vidal, vii.1987 (MNHN/14, 13v.); Golfe de Morbihan, leg. Bouchet, 1977 (MNHN/1); Plouharnel, Morbihan, leg. Vidal, iii. 1986 (MNHN/3); Le Croisic, Loire-Atlantique, coll. H. Fischer (MNHN/3); La Baule, Loire-Atlantique, coll. H. Fischer (MNHN/1); Pornichet, Loire-Atlantique, coll. Locard, 1892 (MNHN/2); Les Sables d'Olonne, Vendée, coll. Locard, 1892 (MNHN/1); Ile de Ré, Charente-Maritime, coll. Locard, 1892 (MNHN/1); Ile d'Oleron, Charente-Maritime, coll. Locard, 1892 (MNHN/1). ATLANTIC SPAIN: Laredo, Cantabria, leg. Von Cosel & Gofas, 7.ii.1988 (MNHN/2, 2v.); 5 km NNE-wards of Cabo Finisterre, La Coruña, Galicia, leg. Warén (SMNH/1); Playa de Samil, Ria de Vigo, Pontevedra, Galicia., leg. Navarro (ZIM and SMF/<5); El Portil - El Rompido, W Huelva, leg. Van Urk, 17.ix.1974 (RMNH/1v.); Conil de la Frontera, S of Cadiz, leg. Gofas, 1978 (MNHN/1, 1v.). PORTUGAL: Lagoa de Obidos, N of Peniche, leg.

Von Cosel, viii.1982 (SMF/<5); Figueirinha, Setubal, leg. Gofas, vi.1988 (MNHN/3, 2v.); Praia da Peninsula de Troia, S of Setubal., leg. Bouchet, iv.1987 (MNHN/3); Canal of Olhão, Ria Formosa, Algarve, leg. Bouchet & Lozouet, vi.1988 (MNHN/1); Fuzeta, Algarve, lagoon, 8.viii.1982, leg. B. & R. von Cosel (SMF/1v.). MOROCCO: Tanger, leg. Gofas, 1971 (MNHN/2); Tetouan, coll. Buchet (MNHN/1). MEDITERRANEAN FRANCE: Mouth of Etang de Leucate, Roussillon, leg. S. Gofas, iv.1999 (MNHN/10); La Franqui, Roussillon, leg. Von Cosel, 25. and 31.x.1987 (MNHN/2); Le Grau du Roi, Gard, Plage Boucanet, leg. Von Cosel, 28.ix.1999 (MNHN/2).

Biotope. — In moderately fine sand, “mixed” sand and coarse sand, in part with shell debris, also coarse muddy sand (Holme, 1954), from extreme low tide (sand banks) to about 50 m. Off the German and Netherlands coast and northward, the species is only found offshore from about 8-10 m downwards. It lives in coarser sand than *E. siliqua*: near Roscoff (north coast of Brittany) I did not find it within populations of this latter species, but just next to them in a separate population. It occurs together with *Dosinia exoleta* (Linné, 1758) and *Tellina donacina* Linné, 1758 (Holme, 1954: 146). The species lives generally in sheltered areas and does not tolerate much wave exposition (Holme, 1954: 159-60). According to De Bruyne (2004: 172), during the last years, fresh dead specimens have become rarer on Netherland beaches after storms than before; it seems that the species might have withdrawn from the nearshore parts of its biotope, perhaps because of the invading of *E. directus*; however, more offshore, *E. magnus* is still regularly encountered.

Larval biology. — The protoconch I measures about 140×105 µm, the settling size (Protoconch II) is about 300-400 µm. The larval shell is anteriorly rather pointed, larval shells and freshly settled juveniles are yellowish brownish. There is no exact figure known how long the larvae are planktonic, it is estimated that they remain 3-5 weeks in the plankton, but there can be a delay in the larval phase when the veligers do not find adequate biotopes at once. These observations (as well as those on *E. ensis* and *E. siliqua*) have been made by K. Ockelmann on plankton and freshly settled juveniles caught in the northern Kattegat over shell gravel bottom with some sand in July 1983 (K. Ockelmann, personal communication 16.xii.1987).

Remarks. — *Ensis magnus* is a very variable species, and it has been treated under several name combinations throughout the literature. In modern publications it was usually separated into two species: the common and widespread *Ensis arcuatus* (Jeffreys, 1865) and the “true” *Ensis magnus*, cited only from the Faroe Islands and from Norway. In older literature it was frequently put together with *Ensis ensis* (Linné, 1758) under that name, as well as in popular identification books. The name *arcuatus* was used after Jeffreys only by Winckworth (1932), and he raised it to specific rank without any comments. Only Holme (1951) documented the separation of *E. ensis* and *E. arcuatus*, describing in detail the diagnostic characters and later on also the ecological differences (Holme, 1954).

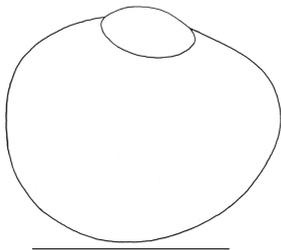


Fig. 12. *Ensis magnus* Schumacher 1817. Larval shell with protoconch I and II, 415 × 338 µm, Hirsholmen, N-Kattegatt, 10. July 1983, leg. Ockelmann, after an original sketch by K. Ockelmann. Scale: 300 µm

Within *E. arcuatus*, Van Urk (1964) distinguished two further "forms" besides *E. magnus* and *E. arcuatus*, viz. *E. arcuatus* var. *ensoides* Van Urk, 1964 (Pl. 4 j; fig. 9 g) with a tapering posterior part resembling *Ensis ensis* but larger, and *E. arcuatus* var. *norvegica* Van Urk, 1964 (fig. 8d) with a large and well curved shell, similar to some specimens from Faroe.

If typical specimens of all these different or morphs, inclusive of the "true" *E. magnus*, are put side by side, they are in fact distinguishable in a few to several characters. However, thorough examination of material from the whole distribution area in most European museums as well as extensive field work by myself and other colleagues did not reveal any stable characters which would justify a separation on species or subspecies level in any of these cases. Also the identification of specimens in RMNH by Van Urk himself are in several cases controversial and not clear. Within the vast distribution area of the species, the different morphs may in some aspects be characteristic for certain regions, but these areas are not isolated, they touch each other or overlap, and intermediate forms between each morph are common, making a clear separation of these impossible. There does not exist any place where two or more morphs co-occur without any intergrade.

The most outstanding example is "*E. magnus*" vs. "*E. arcuatus*". The typical "*magnus* form" has a rather straight or slightly curved shell with a characteristically broader posterior part and therefore a more or less markedly convex posterior part of the ventral margin, behind the vertical midline (Pl. 4 a; figs 8 b,c). This form was recognized only from the Faroe Islands and Norway, until Van Urk (1980: 91) reported it from the Netherlands coast near Scheveningen, where a few specimens and fragments were found in dredge spoil together with the common *arcuatus* form. From this, Van Urk concluded that these are two sympatric species, and he continued separating them (Van Urk, 1980; 1984). However, it resulted that the "*magnus*" form is quite widespread within the distribution area of *E. magnus*. Among the more than 200 fresh shells and valves of *E. magnus* collected by me on the beach of Berck-s.-Mer, French Channel coast, on May 23, 1987, three morphs could be distinguished: a well curved, colourful form which is typical e.g. for specimens from more westward situated areas (Normandy, Brittany), a less curved (closer to the type lot) and less coloured, often nearly white, form which is very common in the southern North Sea and the eastern part of the Channel, and the typical straight to slightly curved and posteriorly broader *magnus* form, nearly identical to some Faroe specimens, but slightly smaller. These are only the extremes, and numerous intergrades between these three forms cannot be assigned to one or the other form and demonstrate that *E. magnus* and *E. arcuatus* finally cannot be separated. Also the distance between the posterior adductor scar and the pallial sinus, according to Van Urk a diagnostic feature within the *E. magnus/arcuatus* complex, is extremely variable in this and other populations. In the Faroe Islands themselves, specimens show a high variability and degree of curvature (see below).

Another supporting argument for uniting *E. magnus* and *E. arcuatus* is the fact that K. Ockelmann (personal communication) found in the Northern Kattegat the planktonic larvae of three species only: *E. ensis*, "*E. arcuatus*" and *E. siliqua*. If *E. magnus* would be a separate species, it should have most probably a different larva, and in this case, four different larvae should have been found. With an assumed duration of the planktonic phase of about three weeks and more for *Ensis* in that region, the larvae of specimens at least from the Trondheim region, Norway, and possibly also from Faroe can well, at least occasionally, be transported into the Northern Kattegat during periods of favourable currents, and they certainly would have been taken by K. Ockelmann during his regular sampling operations.

It can be assumed that a larval transport (gene flow) from a nearby coast (Shetlands, Scotland, Norway,) to the Faroe Islands takes place more or less often and that at several

occasions larvae reached the islands, encountered favourable conditions, settled and built up a population which still exists. The extensive sampling in the Faroe Islands carried out by Ch. Schander in September 1993 finally show that a typical, only slightly curved “*magnus* form” as mentioned above, distinguished by Van Urk and shown on fig. 8c does not exist; there is a considerable variability as in other localities, although in the Faroe population, contrary to Van Urk’s statement, very strongly curved specimens dominate (see Pl. 4 b-f; fig. 8 a). Moreover, Faroe specimens often tend to be somewhat more irregular than those from other regions, perhaps due to probably coarser or irregular sediment. As in other *Ensis* species, northern specimens (Faroe, Norway, Scotland, northern North Sea) grow somewhat larger than southern specimens (Netherlands and France southward).

Also the other forms, *ensoides* Van Urk and *norvegica* Van Urk, are linked to the *arcuatus* form and the so-called *magnus* form by all kinds of intergrades and are considered ecological forms. Already Van Urk himself (1966: 13) admits that concerning *E. magnus* and *E. arcuatus* “there seem to be equally good arguments for uniting the two into one variable species”. In general, one should note that most of Van Urk’s names have to be considered “informal” variety names without nomenclatural value.

Among the vast material of *E. magnus* collected in the Galway region on the West coast of Ireland, two specimens were found having similarities to *E. minor* (see fig. 15h), although that species was not found there (the closest known locality for *E. minor* is Cardigan Bay on the NW coast of Wales). The specimens are as straight as *E. minor* and have a markedly obliquely truncated posterior margin; however, the anterior part is slightly curved upwards like in *E. magnus*, the valves are thick-shelled and more slender than average *E. minor*. It cannot be fully excluded, that these are hybrids.

The few known Mediterranean specimens of *E. magnus* might come from an isolated population in the Golfe du Lion in the western Mediterranean; there are no other records yet known. The specimens are smaller and broader in relation to length (Pl. 4 p-t; fig. 11), with typical “Mediterranean” pinkish violet colour, otherwise they are curved and fit well into the *arcuatus* form. Two small specimens from Tanger (Morocco) have a similar appearance. *Ensis sicula* Van Urk, 1964 (see under *E. ensis*, figs 4e-g) is also similar to these morphs.

Ensis minor (Chenu, 1843)

Solen siliqua minor Chenu, 1843: Solen, pl. 3 fig. 3, 3a.

Ensis siliqua auct., non Linné, 1758.

E. minor var. *subarcuata* Van Urk, 1964: 27, pl.1 fig. 5.

Type material. — The specimen figured by Chenu is a typical Mediterranean specimen and is not to be confounded with *E. siliqua*. It is selected here as lectotype since we do not know if the author had other specimens at hand; the whereabouts of this specimen are unknown.

Type locality. — Chenu’s *Solen* plates are not accompanied by a text. As a consequence, the whereabouts of the lectotype are unknown. Since the type locality is linked to the holotype by definition, it cannot be indicated. However, the very good quality of Chenu’s figure, and the form and size (on illustration 119 mm) of the figured specimen lead to the conclusion that it originates from the population in the Golfe du Lion in the western Mediterranean.

Description. — Shell medium-sized (110-120 mm) to large (175 mm long and 27 mm broad), thin but strong to quite thick (northern specimens), straight, only exceptionally slightly curved. Length/height ratio 5.5-7.5, beaks terminal. Anterior margin obliquely truncate to vertically truncate, posterior end always oblique and truncate, with rounded

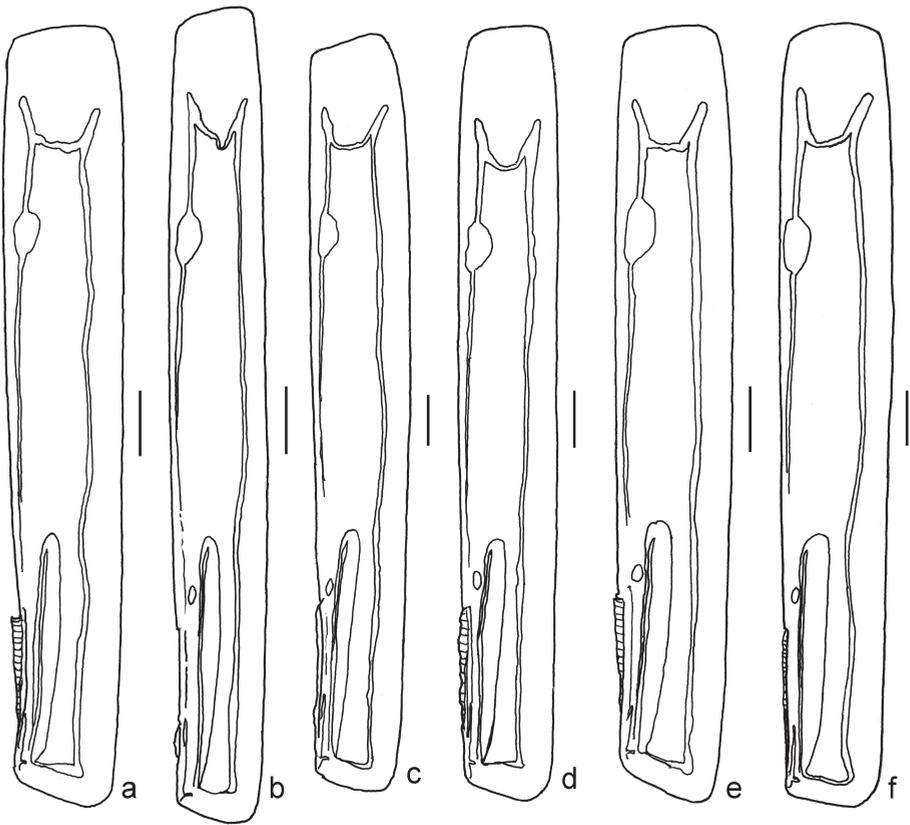


Fig. 13. *Ensis minor* (Chenu, 1843). a-f, half schematic drawings of the insides of valves; a, La Franqui, Roussillon, France, May 1987, MNHN; b, Tanger, Morocco, Dec. 1971, MNHN; c, Praia Alagoa, Monte Gordo, Algarve, Portugal, April 1987, MNHN; d, same locality, MNHN; e, Terschelling, Netherlands, May 1986, MNHN; f, Shell Island, Cardigan Bay, NW-Wales, U.K., April 1999, MNHN. Scale 10 mm

corners. Dorsal margin normally slightly convex or straight, often in its posterior part markedly convex, very rarely in its middle part or its posterior part somewhat concave. Hinge and ligamental margin not or very slightly curved upwards. Ventral margin centrally straight or weakly convex, in its anterior and posterior part more or less convex, in some specimens from the Netherlands markedly convex. Broadest part of the valves situated just behind the middle or on the posterior half.

Cross section of posterior gaping narrow, with in the middle nearly "parallel" posterior shell margins (Pl. 8 k). A view of the closed valves from dorsal shows that the last 3-4 cm of the posterior part of the valves are gradually more and more laterally compressed, along the middle horizontal axis, thus diminishing considerably the posterior gaping. Occasionally one of the valves slightly twisted so that the valves do not close along the whole ventral margin.

Anterior adductor scar long, straight or very weakly curved, anteriorly narrow to relatively broad, broadening more or less towards its rounded posterior end and pointing

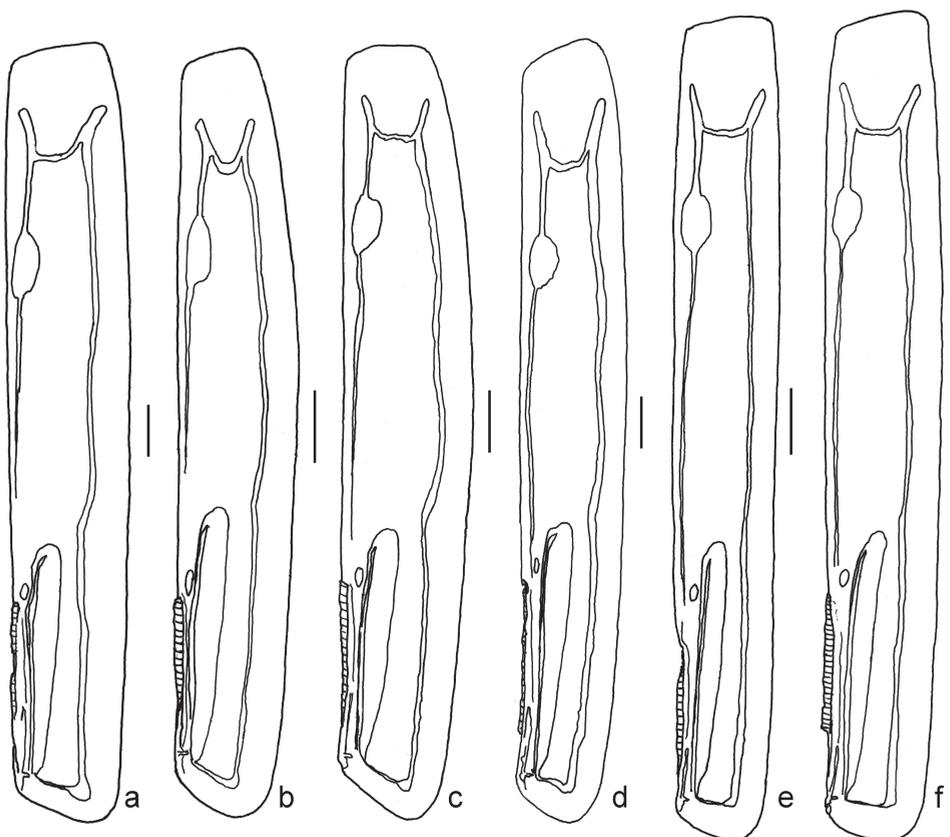


Fig. 14. *Ensis minor* (Chenu, 1843) and intergrades. a-f, half schematic drawings of the insides of valves; a, *E. minor*, Shell Bay, Studland, Devon, England, 1922, MNHN; b, *Ensis minor* var *subarcuata* Van Urk, 1964, holotype, Scheveningen, Jan. 1960, RMNH; c, *E. minor* var *subarcuata* Van Urk, Oostvoorne, Netherlands, July 1958, SMF; d, "hybrid" *E. minor* × *E. magnus*, Silver Strand, Galway, Ireland, 1985, MNHN; e, "hybrid" *E. minor* × *E. siliqua*, Fort Penthièvre, Quiberon, Morbihan, France, 1987, MNHN; f, "hybrid" *E. minor* × *E. siliqua*, same locality, MNHN. Scale 10 mm.

towards the middle of the posterior margin or the postero-ventral corner of the valve. Posterior adductor scar oval, moderately large and situated at a distance of its own length to 1½-2 times its length before the pallial sinus. Anterior pallial line descending vertically (90°) or inclined towards anterior, parallel to the anterior margin and quite close to it, sometimes slightly concave, then turning sharply backwards. Ventral pallial line more or less parallel to the ventral margin, slightly concave below the anterior adductor scar and its end. Pallial sinus short, broad, with more or less rounded inner extremity, this innermost tip at the upper part or in the middle.

Exterior with irregular growth lines which are usually very pronounced at the last 1-1.5 cm before the posterior margin. Limit between the antero-ventral part with horizontal growth lines and the postero-dorsal part with vertical growth lines well marked with a shallow depression. Antero-ventral part of the surface divided by another very slight but

well marked narrow and straight depression running anterior to the growth line limit from the umbonal area to the ventral margin and ending there in adult specimens about 0.5-1 cm behind the middle of the valves; sometimes it is visible only as a discontinuity in the colour of the horizontal growth lines (see e.g Pl. 5 d)

Colour of valves whitish to creamy, with reddish brown to purplish growth lines and zones, on the inside more or less showing through, especially in specimens from the southern part of the range. Besides the dense horizontal lines antero-ventral parts with small points and speckles. Mediterranean specimens with growth zones and bands coloured vividly violet to purple, visible on inside and outside of the valves.

Periostracum greenish brown and glossy, on the vertical growth lines only slightly darker but usually eroded.

Distribution. — British North Sea coast from the east coast of Scotland (Firth of Tay mouth) to North Yorkshire, Southern England, the Netherlands, and the Channel; European Atlantic coast from the NW part of Wales (Cardigan Bay) southward to North Morocco and throughout the Mediterranean. Not in Scandinavia and the eastern and southeastern North Sea. Only during the 1920's the species had been positively recorded along the Netherlands coast (fide De Bruyne, 2004: 171); in the following years it became more common and was found living in shallow water inshore. However, during the last decades the number of live-collected specimens and of fresh shells dwindled but it is not sure if this is due to the invasion of *E. directus*, which occupies the same biotope; this phenomenon had started already before the arrival of *E. directus* (fide De Bruyne, 2004).

Material examined. — NETHERLANDS: Schiermonnikoog, km 5-10, leg. De Boer, 31.iii.1986 (MNHN/1v); Terschelling, km 8, leg. Moolenbeek, v.1986 (MNHN/1); Zandvoort, leg. De Bruyne, 13.iii.1989 (MNHN/1); Scheveningen, leg. d'Ailly, 6.viii.1909 (SMNH/2); Oostvoorne, beach and tidal flats, leg. Von Cosel, vii.1958 (before construction of Europoort) (MNHN/9). SCOTLAND: Carnoustie, NE of Dundee, E-coast, leg. B. & R. von Cosel, 11 x.1987 (MNHN/2, 3v.); Firth of Forth, E-coast, leg. B. & R. von Cosel, 8.-10.x.1987: Aberlady Bay, eastern Point (MNHN/8, 20v.), Gosford Bay (MNHN/19, 8v.), Gullane Bay (MNHN/3, 10v.), North Berwick (MNHN/7, 3v.). ENGLAND: Saltburn on Sea, North Yorkshire, leg. N. Dansey, v.2000 (MNHN/3); Brancaster Golf Course, North Norfolk (The Wash, southern shore), leg. Reineck, 1967 (SMF/2); Brancaster, North Norfolk, leg. P. Dansey, 27.xii.1999 (MNHN/6); Folkestone, leg. Warén (SMNH/2, 2v.); Shell Bay, Studland, Devon, leg. Staat, 1922 (MNHN/20; 8v.); Exe River, Devon, leg. Warren, 1881 (MNHN/1). WALES: Shell Island, near Harlech, Cardigan Bay, North Wales, leg. P. Dansey, 4.iv.99 (MNHN/7). ATLANTIC FRANCE: Dunkerque, Pas-de-Calais, leg. Warén, (SMNH/3, 1v.); Douarnenez, Finistère, coll. Soyer (MNHN/3); Concarneau, Finistère, coll. Locard, 1892 (MNHN/1); Penthièvre, Morbihan, Quiberon Peninsula, Atlantic side, near Fort Penthièvre, leg. B. & R. von Cosel, 29.iii.1987 (MNHN/8, 10v., and some hybrids *E. minor/E. siliqua*); Le Pouliguen, Loire-Atlantique, coll. Staat (MNHN/2); La Baule, Loire-Atlantique, leg. H. Fischer, 1907 (MNHN/5, 1v.); Pornichet, Loire-Atlantique, coll. Locard, 1892 (MNHN/1); Banc du Bûcheron, Ile de Ré, Charente-Maritime, fine sand at low tide, leg. Tardy & Von Cosel (Atelier Ile de Ré), v.1996 (MNHN/9, 3v.); Plage de la Loge, Ile de Ré, Charente-Maritime, leg. Tardy & Von Cosel (Atelier Ile de Ré), v.1996 (MNHN/27, 89v.); Ile d'Oleron, Charente-Maritime, coll. Locard, 1892 (MNHN/1v); Arcachon, coll. Locard, 1892 (MNHN/2); Banc d'Arguin, mouth of Bassin d'Arcachon, Gironde, leg. Von Cosel, ix.1975 (MNHN/11, 55v.), Hendaye, Pyrénées-Atlantiques, coll. Locard, 1892 (MNHN/2). ATLANTIC SPAIN: San Sebastian, Guipuzcoa, Pais Vasco, Playa "La Concha", leg. Staat, 1935 (MNHN/2); Laredo, Cantabria, leg. Gofas, 11.xi.1987, Von Cosel & Gofas, 7.ii.1988 (MNHN/25, 28v.); 5 km ENE of Cabo Finisterre, La Coruña, Galicia, leg. Warén (SMNH/>10 and v.); Playa de Samil, Ria de Vigo, Pontevedra, Galicia, leg. Rolan (SMF/<5); Conil de la Frontera, S. of Cadiz, leg. Warén (SMNH/6v.). PORTUGAL: Praia da Peninsula de Troia, S of Setubal, leg. Bouchet, iv.1987 (MNHN/39, 86v.); Praia de Alagoa, W of Monte Gordo, Algarve, leg. Bouchet, iv.1987 (MNHN/30, 14v.); Vila Real de Sto. Antonio, Algarve, leg. Warén (SMNH/<10).

MOROCCO: Tanger, Grande Plage, leg. Gofas, 28.xii.1971 (MNHN/21); Tetouan, coll. Staadt (MNHN/6, 2v.); Melilla, coll. Staadt (MNHN/1). ALGERIA: Arzew, E of Oran, coll. Locard, 1892 (MNHN/1), coll. Pallary (MNHN/4). TUNISIA: Radès, near Tunis, leg. Vidal, 1985 (MNHN/2); Carthago, intertidally, leg. Bouchet & Warén, 1982 (SMNH/2). GREECE: Cape Zosten, Swedish Exp. to Greece, iv.1934 (SMNH/2); Kalanaka, Gulf of Messinias, leg. Jaux (MNHN/2); Skhinias, near Marathon, leg. Gofas, iv.1988 (MNHN/2, 2v.). ITALY: Trieste, coll. Westerlund (SMNH/<10); Venice, Lido, coll. H. Fischer, 1908 (MNHN/4); Sicily (no prec. loc.), coll. Caron, 1836 (MNHN/<5v.); Naples, coll. Petit (MNHN/2); Naples, leg. d'Ailly, 25.ii.1913 (SMNH/2); Cape Misenum, Gulf of Naples, leg. Dick, iv.1939 (SMNH/2); Viareggio, leg. Machandt, 1939 (SMNH/2v.). MEDITERRANEAN FRANCE: Cannes, Alpes-Maritimes, coll. d'Orbigny (MNHN/3); Fréjus, Var, mouth of Argens river, leg. Roussel, 21.ii.2007 (MNHN/4); Porquerolles, Iles d'Hyères, Var, coll. Locard, 1892 (MNHN/1); Marseille, Bouches-du-Rhône, coll. Locard, 1892 (MNHN/3); Les Martigues, Bouches-du-Rhône, coll. Locard, 1892 (MNHN/1); Port Camargue, Bouches-du-Rhône, leg. Gofas, ix.1976 (MNHN/2); Le Grau du Roi, Gard, Plage Boucanet, leg. Von Cosel, 28.ix.1999 (MNHN/20, 19v.); Sète, Hérault, coll. Locard, 1892 (MNHN/3, 1v.); Cap d'Agde, Hérault, Plage St. Martin, leg. Chevalier, viii.1967 (MNHN/4); La Franqui, Roussillon, leg. Von Cosel, 2.v.1987 (MNHN/58, 18v.); Ajaccio, Corsica, coll. Locard, 1892 (MNHN/1); Calla di Rena, Gulf of Porto Vecchio, Corsica, leg. F. & C. Monniot, 25.vii.1988 (MNHN/1). MEDITERRANEAN SPAIN: Benalmádena-Costa, Malaga, Andalucia, leg. Gofas, 1991 (MNHN/22, 14v.); Rincon de la Victoria, Malaga, Andalucia, on sand, 1-5 m, leg. Gofas, ix.1994 (MNHN/29, 12 juv.); 5 km SW of Algeciras, Andalucia, leg. Warén (SMNH/2, 6v.).

Biotope. — In fine sand from low tide to more offshore, in the northern part of its range normally only subtidal. At Ile de Ré, Atlantic France, the species was also found above spring low tide mark; at this place, it remains covered only during neap tides.

Remarks. — *Ensis minor* is characterized and distinguished from *E. siliqua* (see next entry) by its straight shell, the more or less obliquely truncate anterior and posterior margins, the narrow cross-section of the posterior gaping with subparallel to parallel shell margins, the greater distance of the posterior adductor scar to the pallial sinus and the position of the anterior pallial line close to the anterior margin. The typical dark portion on the postero-dorsal periostracum present in *E. siliqua* is absent in *E. minor*. The species is less variable than *E. ensis* and *E. magnus*, there is only one "form" separated by Van Urk: *E. minor* var. *subarcuata* Van Urk, 1964 (Pl. 6 b; figs 14 b-c), which seems mostly to occur locally along the Netherlands coast but is also found elsewhere: among the very large specimens from the east coast of Scotland (Firth of Forth) some may tend to this form (fig. 6 b). It has a markedly convex ventral margin and a straight dorsal margin with posterior taper, but otherwise the characters of *E. minor*. Van Urk (1964: 27) admits that it is "linked with the typical form by intermediates".

The population from the east coast of Scotland is quite uniform but we do not know if there is a distribution gap somewhere on the British North Sea coast; isolated records exist from North Yorkshire and from eastern-England (The Wash) the next southern records being those of the Netherlands. The Scottish specimens are larger and heavier than any other *E. minor*, they differ also in the very short distance between the posterior adductor scar and the pallial sinus, less than the length of the scar. All other characters, however, are without doubt those of *E. minor*, especially the posterior part with the very strongly marked and close-set growth stages and the narrow cross section of the gape at the end of the valves, the colour with violet zones and the anterior pallial line close and parallel to the anterior margin. There are no intergrades with the sympatric *E. siliqua*. The close-set growth stages are without doubt annual rings and indicate that the species in this region becomes quite old, up to 10-14 years. The difference between the two species in eastern Scotland had already been pointed out in a short bionomic study by S.M. Smith

(1970). In the specimens from North Yorkshire, the distance between posterior adductor scars and pallial sinus is about the length of the scar, the same with the specimens from Cardigan Bay, NW Wales.

Ensis minor is the most common *Ensis* in the Mediterranean. Specimens from there, especially those from the eastern Mediterranean, are on the average smaller than Atlantic specimens, only specimens from the Golfe du Lion may reach almost similar size, they are more thick and solid than the eastern specimens, and the growth rings indicate a presumable age of about 6 to 9 years. The species is more vividly coloured than many Atlantic specimens.

Ensis minor was frequently treated under the name *E. siliqua* or as a subspecies of that taxon; however, along the Atlantic coast the two species occur sympatrically with only very few possible intergrades which occasionally were found at the south coast of Brittany (Pl. 8 f-k) and also a few at Ile de Ré, Charente Maritime. They are looking superficially like *E. minor* but mostly have the rounded posterior cross-section of *E. siliqua* (Pl. 8 e) Only molecular research will elucidate this. Some *E. magnus* from the west coast of Ireland (Galway area) are quite close to *E. minor*, but nevertheless they can be assigned to *E. magnus* without doubt (Pl. 4 m). *E. minor* itself has not been found in that area.

There is nothing known about the larval biology, and larvae have not been found by K. Ockelmann in the N-Kattegat.

Ensis siliqua (Linné, 1758)

Solen siliqua Linné, 1758: 672.

Solen novaculus Montagu, 1803: 47-48.

Solen ligulus Turton, 1822: 81-82.

Solen siliquosus Locard, 1886: 372 [proposed conditionally].

Nomenclature and type material. — In Linné's *Solen siliqua* both *Ensis minor* and *E. siliqua* are involved, according to Linné's references. According to Van Urk (1964: 22), the material present in the Linnean collection in London belongs to *E. minor*. The specimen in the Linnean collection in Uppsala, which is not mentioned by Van Urk, is also *E. minor*. Based only on the London material and Linné's references, Van Urk selected the specimen figured by Lister (1678: 192, pl. 5 fig. 37) as lectotype "since it is doubtful on which material Linnaeus based his *Solen siliqua*" (Van Urk, 1964: 22). This figure shows a specimen with rounded anterior end, which is *E. siliqua*.

Type locality. — "Oceano Europaeo", restricted to Scarborough, Great Britain, the locality of Lister's specimen, by the selection of the lectotype.

Description. — Shell large (150 mm) to very large (230 mm long and 38 mm broad), more or less thin but strong, occasionally quite thick and heavy, straight to weakly curved, length/ height ratio 6 – 7.5. Anterior end rounded-truncate to slightly oblique, posterior end obliquely truncate, very weakly convex, with rounded corners. Dorsal margin straight, slightly concave or very slightly convex, hinge and ligamental area only very slightly curved upwards if at all. Ventral margin generally more or less convex, in its middle part sometimes nearly straight, but not always parallel to the dorsal margin: broadest part of the shell in the middle or the posterior half, occasionally near the posterior end.

Cross section of posterior gaping oval. A dorsal view of the closed valves shows that the posterior parts of the valves are only very slightly laterally compressed along the middle horizontal axis, and that the posterior gape has nearly the same diameter as the rest of the shell.

Anterior adductor scar long, straight anteriorly narrow and broadening posteriorly,

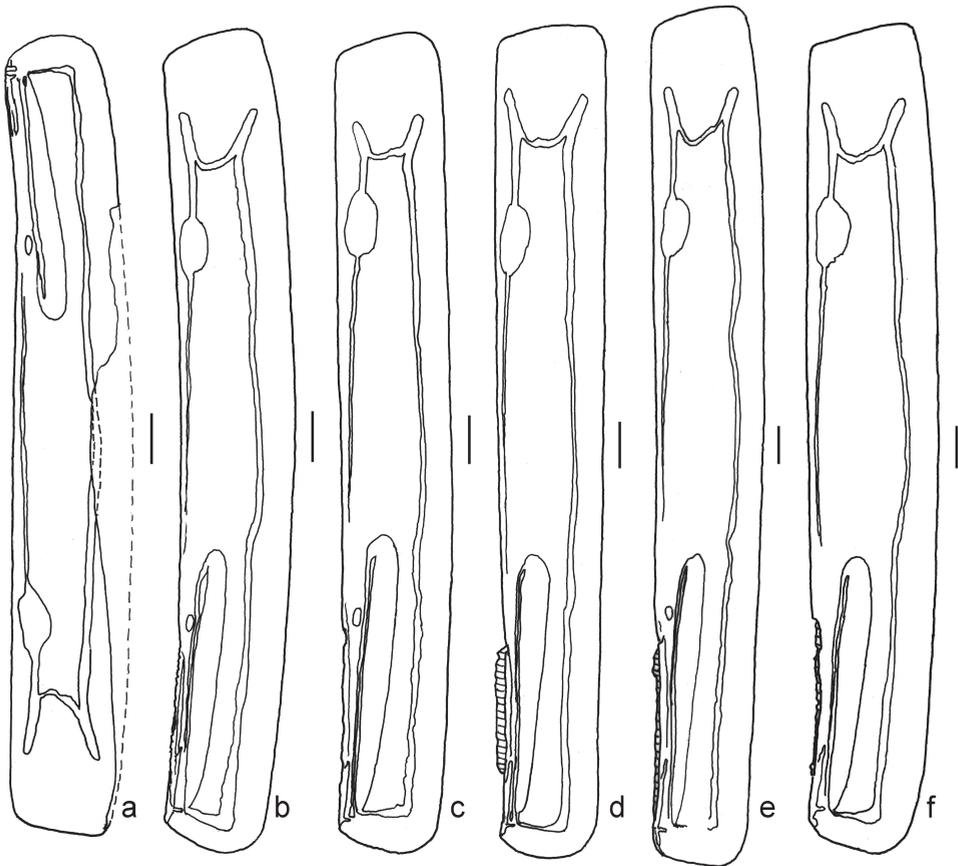


Fig 15. *Ensis siliqua* (Linné, 1758), half schematic drawings of the insides of valves; a, Meia Praia, Lagos, Algarve, Portugal, April 1964, SMF; b, Morgat, Finistère, France, 1984, MNHN; c, Terschelling, Netherlands, July 1985, MNHN; d, Schiermonnikoog, Netherlands, April 1986, MNHN; e, Doggerbank, Great Silverpit, Aug. 1976, ZMA; f, St. Andrews, Scotland, Sept. 1986, MNHN. Scale 10 mm

rounded at its posterior end, pointing towards the middle or the lower half of the posterior margin or the postero-ventral corner. Posterior adductor scar oval, quite large, and situated at a distance nearly equal or less than its own length before the pallial sinus. Anterior pallial line descending vertically (fig. 15c, g) or slightly towards anteriorly, more or less parallel to the "general slope" of the convex anterior margin and in a distance usually less than the distance ventral pallial line - ventral margin, then curving sharply backwards. Ventral pallial line more or less parallel to the ventral margin, below the anterior adductor scar straight and horizontal, at its end slightly concave. Pallial sinus short and narrow to moderately broad, with its innermost tip in the middle or frequently near the upper part but not in the upper corner.

Beaks situated in front of the anterior adductor scar. Ligament very strong.

Exterior with irregular growth lines. Umbonal scar in certain northern specimens occasionally eroded.

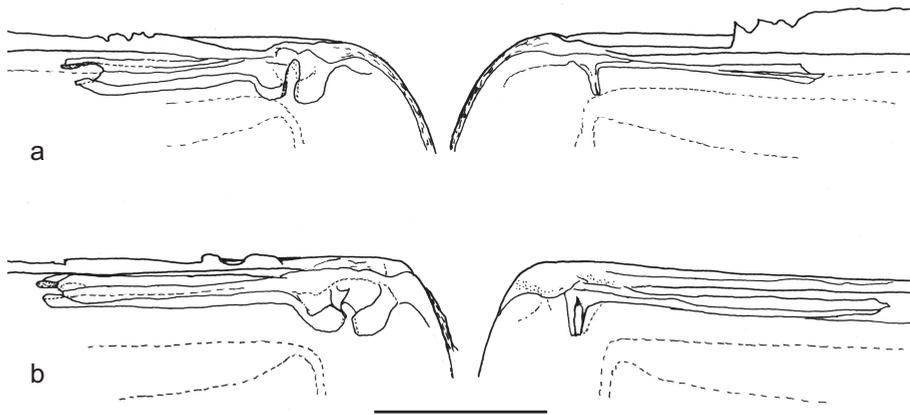


Fig. 16. *Ensis siliqua* (Linné, 1758). Port Haliguen, Baie de Quiberon, Morbihan, France, 5-10 m, July 1987, MNHN. Close-up view of hinge teeth. **a**, shell length 200 mm; **b**, shell length 203 mm. Scale 10 mm.

Colour of valves whitish to creamy, with reddish brown to violet irregular growth lines and zones, on the inside more or less showing through, specially in specimens from the southern part of the geographical range. Otherwise interior white. Antero-ventral part occasionally with tiny reddish points and speckles, not very dense and only visible on the earlier (more dorsal) part of the valves. Ventral part and posterior end of more southern specimens sometimes more or less intensively tinged with violet.

Periostracum very strong, glossy, greenish brown, on the postero-dorsal part with a light to dark brown radial ray or zone which more or less coincides with the area of vertical growth lines and which, in fully grown specimens often ends posteriorly in a few to several narrow rays or may become totally obsolete. In juvenile and subadult specimens but also adults, this dark zone may not always be developed.

Animal cream-white, with foot of same colour.

Distribution. — Norway (Trondheimsfjord), Skagerrak, northern part of Kattegat, North Sea, British Isles, European Atlantic coast south to Spain (Galicia) and Portugal (Algarve, rare). Not in the Mediterranean. Records from Faroe are not confirmed.

Material examined. — NORWAY: Munken, near Oerland, mouth of Trondheimsfjord, leg. Dons, 1942 (Trondheim Museum/1 chipped v); Roaldsanden, near Alesund, leg. Bjorlykke, 1936 (Trondheim Museum/1 large fragm. of a sh. 33 mm broad). DENMARK: Læsø Island, N-Kattegat, leg. Ockelmann, 1960 (MNHN/1); Grenen, Skagen, leg. Warén (SMNH/7, 2v.); Løkken, Jammerbucht, Skagerrak, leg. Baumgarten, x.1962 (ZIM/1v.); Hirtshals, leg. Warén (SMNH/1 broken v.). GERMANY: Spiekeroog, East Frisian Is., leg. Baumgarten, 1962 (ZIM/1v.); Baltrum, E-Frisian Is., leg. Von Cosel, vii.1955 and 1956 (SMF/2v.). NETHERLANDS: Schiermonnikoog, leg. De Boer, 29.iii.-4.iv.1986 (MNHN/6, 20 juv.v.); km 7-11, leg. De Boer, x. and 17.xi. 1985 (MNHN/50, 49 juv., 1v.); Schiermonnikoog, leg. De Bruyne, vi.1977, MNHN/2); Terschelling, km 12-16, leg. Dijkstra, vii.1975 (MNHN/3); NE-Doggerbank, 55°35.0'N 4°24.0'E, trawled, leg. Türkay, v.1977 (SMF/3); Doggerbank, Grand Silverpit, leg. Buizer, 19.viii.1976 (ZMA/2); Doggerbank, 55°01.04'N 02°0.0'E, 28 m; 54°26.2'N 2°16.8'E, 24-32 m, dredged R/V. "SENCKENBERG", leg. Türkay, 20.iv.1986 and 14.vii.1988 (SMF/1, <10 fresh dead spm.); Southern Doggerbank, 20-25 fms, leg. Anderson, 1934 (SMNH/10). SCOTLAND: Back, Harris, Hebrides, leg. Warén (SMNH/1, 3v.); Firth of Clyde (no precision), W-coast (Glasgow Museum/1 [231 mm long]); Saltcoats, Firth of Clyde, leg. B. & R. von Cosel, 6.-7.x.1987 (MNHN/35+24 juv, 31v.+7 juv.); Carnoustie, NE of Dundee, E-coast, leg. B. & R. von

Cosel, 11.x.1987 (MNHN/11, 7v.); St. Andrews, E-coast, leg. Marshall, 7.ix.1986 (MNHN/3); Firth of Forth, E-coast, leg. B. & R. von Cosel, 8.-10.x.1987 (MNHN/10); Gosford Bay (MNHN/37, 15v.), Aberlady Bay, eastern part (MNHN/16, 27v.), Gullane Bay (MNHN/9; 6 juv., 12v.), North Berwick (MNHN/2, 3v.). NORTHERN IRELAND: Strangford Lough, SE of Belfast, donated Fernandez-Tajes. ix.2007 (MNHN/17 lv. of 22 spms, used for DNA.). IRELAND: W coast, Clew Bay, Mayo County, leg. Bail, 1988 (MNHN/1). ENGLAND: Bournemouth, leg. May, coll. Staadt MNHN/1); Studland, Dorset, leg. Staadt, 1922 (MNHN/3); Weymouth, coll. Retout (MNHN/1); Exe River, Devon, leg. Warren, 1881 (MNHN/1); Sandy Bay, Exmouth, Devon, leg. Wimbleton, ii.1991 (MNHN/1); Paignton, Devon, leg. Von Cosel, x.1960 (SMF/<5); Hayle, Cornwall, leg. Von Cosel, x.1960 (SMF/<5 and v.); Carne Beach, Gerrans Bay, Cornwall, leg. P. Dansey, 11.viii.1999 (MNHN/1). FRANCE: Dunkerque, Pas-de-Calais, coll. Locard, 1892 (MNHN/1); Baie de Dinan, Côtes-du-Nord, coll. Locard, 1892 (MNHN/1); Ile Ste. Ane, Pempoul, S of Roscoff, Finistère, sand flat, low water (spring peak tides), leg. Von Cosel, 16-21.iii.1984 (MNHN/3 spm., 21, 11v.); Morgat, Finistère, beach and in fine sand at extreme low tide (aequinoctial peak tides), leg. Von Cosel, 20.iii.1984 (MNHN/11, 50 juv. and subadult spms., 3v.); Fort Penthièvre, Morbihan, Quiberon Peninsula, Atlantic side., leg. B. & R. von Cosel, 29.iii.1987 (MNHN/48, bay side: 1); Quiberon, Plage de Conguel, fine sand, extreme low tide (aequinoctial peak tides), leg. B. & R. von Cosel, 28 iii.1987 (MNHN/1spm., 37, 51v.); Plouharnel Océan, Morbihan, leg. Vidal, iii.1986 (MNHN/2); off Port-Haliguen, Baie de Quiberon, 5-10 m, leg. Vidal, vii.1987 (MNHN/8, 9 v.); Le Pouliguen, Loire-Atlantique, coll. Jousseume (MNGN/4); La Baule, Loire-Atlantique, coll. H. Fischer (MNHN/2); Pornichet, Loire-Atlantique, coll. Locard, 1892 (MNHN/1); Les Sables d'Olonne, Vendée, coll. Locard, 1892 (MNHN/2); Banc du Bûcheron, Ile de Ré, Charente-Maritime, leg. Tardy & Von Cosel (Atelier Ile de Ré), v.1996 (MNHN/1 spm., 9, 3v.); Plage de la Loge, Ile de Ré, Charente-Maritime, leg. Tardy & Von Cosel (Atelier Ile de Ré), v.1996 (MNHN/7, 1v.); Ile d'Oleron, Charente-Maritime, coll. Locard, 1892 (MNHN/1). SPAIN: Laredo, Cantabria, leg. Gofas, 11.xi.1987 (MNHN/2); 5 km ENE of Cabo Finisterre, La Coruña, Galicia, leg. Warén (SMNH/2, 3v.); Playa de Samil, Ria de Vigo, Pontevedra, Galicia, leg. Rolan (ZIM and SMF/<5). PORTUGAL: Praia de Peninsula de Troia, S of Setubal, leg. Bouchet, iv.1987 (MNHN/1); 5 km E of Cape Sagres, Algarve, leg. Warén (SMNH/3, 4v.); Meia Praia, Lagos, Algarve, leg. Von Cosel, iv.1964 (SMF/1v.).

Biotope. — In clean fine sand without mud or silt from low tide mark to about 50 m, also on open coasts. In France (Brittany) and England locally abundant in sandbanks which are only exposed at peak tides. In more northern places (for example E-coast of Scotland) living subtidally only. Off the German and Netherlands coast the species is found only offshore, e.g. on the Doggerbank; in the German Bight becoming uncommon.

Larval biology. — The protoconch I is considerably smaller than that of the two other northern *Ensis* species, it measures only about 110×85 µm, but the settling size (Protoconch II) is also about 300-400 µm (fig. 17). These settling sizes refer only to the larvae found in the northern Kattegat. The shells of the *E. siliqua* larvae and of freshly settled juveniles are dorsally distinctly lilac. Like in the two other *Ensis* species, the duration of the planktonic phase is estimated at three to five weeks. The larvae were caught in the northern Kattegat on July 10., 1983 (K. Ockelmann, personal communication, 16.xii.1987). In the Plymouth area, South England, larvae are released in March/April and disappear in May (Lebour, 1938). The smallest larvae had a shell length of 100 µm and the largest one, still with velum 350 µm. It is not known, however, if in Lebour's observations also larvae of *E. minor* were involved.

Remarks. — *Ensis siliqua* is the largest *Ensis* and also the largest species of all Solenoidea. It can reach a length of over 23 cm (one specimen from "Clyde" in the Glasgow Museum and the already cited one collected by me in the Firth of Forth measure 23.1 cm each) and a shell height of nearly 4 cm. Within the northern part of the distribution area they frequently reach in some regions 21.5-22 cm, whereas in more southern regions (Gulf of Biscay, Galicia) such large specimens are quite rare, the average length

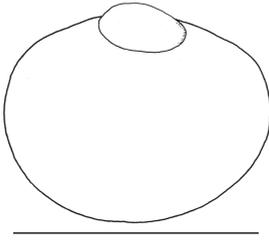


Fig. 17. *Ensis siliqua* (Linné, 1758). Larval shell with protoconch I and II, 326 x 261 μm , Hirsholmen, N-Kattegat, 10. July 1983, leg. Ockelmann, after an original sketch by K. Ockelmann. Scale 300 μm .

being 18-20 cm. The next largest *Ensis* is *E. macha* (Molina, 1782) from southern Chile and southern Argentina; this species reaches 22 cm in length, but can be considerably broader than *E. siliqua*, up to 5 cm (a specimen in BMNH measures 210x41 mm).

Ensis siliqua is variable in shape, curvature and length/height ratio (fig. 15), but there are no "forms" which are predominant in certain regions, as in *E. magnus* and *E. ensis*. Short and broad specimens occur together with longer and more slender ones. However, the proportion of very broad specimens is higher in the northern part of the distribution area (Scotland, fig. 15f). Furthermore, *E. siliqua* is characterized by the clean white interior, only occasionally, a violetish hue is present near the posterior or ventral margin. The valves are normally straight but there are occasionally markedly curved specimens (Pl. 8 a). Juvenile shells are thin and delicate, whereas fully grown specimens may become extremely thick and heavy for a solenacean.

In some localities of the French Atlantic coast in southern Brittany (e.g. Penthievre – Quiberon, Pl. 8 f) and southward to the coast of Charente Maritime (Pl. 8 g) and Vendée, occasional intermediate forms between *E. siliqua* and *E. minor* may occur; however, such intergrades were not found at any other place where *E. minor* and *E. siliqua* live sympatrically. These intermediate forms seem to occur only where *E. siliqua* and *E. minor* are about equally common like in the Quiberon area. However, the biotopes of both species seem to be slightly different, because at certain places such as Ile de Ré (Charente Maritime), *E. minor* is the preponderant species, whereas of *E. siliqua* only very few specimens and few shells were encountered. At Morgat near Brest and on the coast of northern Brittany (e.g. the Roscoff area) only *E. siliqua* was found. More towards the North and further northeastward towards Belgium and the Netherlands, the depth preferences diverge: *E. minor* occurs in more shallow water (just under low tide mark down to several metres), whereas *E. siliqua* remains restricted to subtidal depth, from about 10 m to 35 m and deeper.

DISCUSSION

With its four autochthonous species and the many "varieties", the genus *Ensis* without doubt has now its distribution centre in European waters. This is also supported by the fossil record: besides *E. arcuatus* and *E. ensis*, Van Urk (1971) lists four more fossil and now extinct species from the Netherlands and Europe: *E. complanatus* J. Sowerby, 1844, *E. degrangei* Cossmann & Peyrot, 1909, *E. rollei* Hörnes, 1870 and *E. waltonis* Van Urk, 1971 [nom. nov. for *E. ensiformis* J. Sowerby, 1844, non Conrad, 1843] It is a rather young genus, the fossil record in Europe goes back only to the Mid-Tertiary (Lower Miocene). The northwestern Atlantic representant, *E. directus*, has been described from material which most probably is Miocene (Conrad, 1843). Van Urk (1972) lists three more species from the

region which are from the Pliocene and now extinct: *E. altenensis* Van Urk, 1972, *E. ensiformis* (Conrad, 1843) and *Ensis* spec.

There are currently 11 living species of *Ensis* known worldwide; besides the five native eastern Atlantic species there are at least two species on the east coast of North America, three on the American Pacific coast from California to Panama and the already mentioned *E. macha* on the southern tip of South America from southern Chile to Patagonia.

The taxa retained in this paper as species are in general easily discernible. However, as shown in the vast iconography herein, each species is very variable in shell outline, arrangements of adductor scars, pallial line and pallial sinus, length-height ratio and degree of curvature. For example the distance innermost extremity of the pallial sinus to posterior margin vs. total valve length can be quite variable. This variability goes so far that occasionally species may still form intergrades, and the several names proposed for European *Ensis* are the evidence for this. Presumable intergrades were found in some regions, e.g. between *E. minor* and *E. siliqua* on the south coast of Brittany and along Charente Maritime (Ile de Ré), between *E. minor* and *E. magnus* (= *arcuatus*) on the west coast of Ireland, and between *E. ensis* and *E. arcuatus* on the Netherlands coast. On other localities, no intermediates between species were found. It is also to note that in the Mediterranean, where three *Ensis* species occur, *E. magnus* and *E. ensis* are often shorter and broader than their Atlantic counterparts, especially *E. magnus* often shows this shorter form. *E. minor*, the most common *Ensis* in the Mediterranean, varies from small, long and slender (southern and eastern Mediterranean) to larger and occasionally shorter and heavier in the northwestern Mediterranean, especially the Golfe du Lion.

On the contrary, after the invasion of *E. directus* in European waters, intergrades between this and the native European species have never been found. That leads to the assumption that the distance between *Ensis directus* and the European species is larger than between the European species themselves. Moreover, within the native eastern Atlantic species, the probable intergrades in part mentioned above, still leave many questions open, and molecular genetic analyses are imperatively necessary not only to prove the assumption that *E. directus* and all other American species have a greater distance to our native *Ensis* than the natives among themselves. In morphology, one key character is the form of the pallial sinus which in the American species always is broad and "trapez-shaped" with its deepest point on the dorsal side just under the dorsal limb, whereas in the eastern Atlantic species, the sinus is narrower and more or less rounded, with its deepest point more towards the middle. The first molecular results confirm the greater distance of the European species to *E. directus* (Fernandez-Tajes, personal communication); additional research is performed by J. Vierna.

The distribution areas of the European species of *Ensis* are mostly overlapping, and there are very few areas which are populated by only one or two species. However, the four species occur in different biotopes, that means each species has a slightly different combination of grain size and depth preference and probably also water temperature preference; these factors also vary according to where the population is living within the distribution area of each species. During the 22 millions of years of existence in the area, the European *Ensis* have thus found a stable balance between their populations, and the competition between the species is minimized. The last thirty years, however, have shown that the introduced *E. directus* has disturbed this balance permanently. In the northern part of their European distribution area (e.g. Denmark, Germany and the northern part of the Netherlands), *E. directus* found an ecological niche which was almost unoccupied by the native *Ensis*: the lower intertidal and shallow subtidal parts of the vast flats of fine sand or muddy sand in the Danish, German and Dutch Wadden Sea. More southward, on the

Belgian and French coast, where the native razor shells live more and more shallower, up to low tide mark from Brittany peninsula towards the south, a strong competition takes place, and, according to Severijns (2002), on the Belgian coast, *E. magnus* (= *arcuatus*) and *E. minor* "seem to have disappeared since a few years"; however, *Solen marginatus* seemed not to be affected by the arrival of *E. directus* (Severijns, 2002; own observations in April 2009 of the beach drift in Cayeux-sur-Mer, Somme). On the beaches between Boulogne and the Somme, Severijns (2002) observed a diminishing of *E. magnus* (= *arcuatus*) in the last years, but further southward, the number of native *Ensis* and of *Solen marginatus* on the beaches did not change during the last five years. Nevertheless, the competition between *E. directus* and the native razor shells may become still more vigorous, when the more southward *E. directus* proceeds. Moreover, in contrast to the original biotope on the American East coast, where the species is predated by large carnivorous snails such as *Polinices heros* and *Busycon* spp. and the nemertean *Cerebratulus lacteus*, there are no such predators on the European coast. So it is no surprise that the population density of *E. directus* in Europe is, at least regionally, much higher (Mühlenhard-Siegel et al., 1983) than that of our indigenous *Ensis* species. The result of this were and still are repeated mass mortalities of *E. directus* of all sizes during unfavourable conditions (e.g. too dense population and/or exceptionally cold weather in winter with ice). Nevertheless, it seems that, because of the more extreme climatic conditions at the east coast of North America, *Ensis directus* can better withstand such conditions than our European *Ensis*, and survive in spite of occasional mass extinctions. Moreover, this fact may be a reason why in the northern part of their distribution area, our native *Ensis* do occur only subtidally, beyond the influence of ice, whereas from Brittany southward, they are regularly found at low tide.

The only other very large *Ensis* species, *E. macha* from southern South America, is a relict; in shell shape and muscle scar arrangement it looks close to *E. directus* and the other American species. Also the three species from the West coast of America have to be placed in this category.

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Plate 1. *Ensis directus* (Conrad, 1843). a-b, Norderney, East Frisian Islands, Germany, 1982, MNHN; a, 108.4 mm; b, 98.2 mm; c-d, Boviken, Hamburgö Isl., Sweden, July 1994, MNHN; c, 148.9 mm; d, 151.8 mm; e, Noordwijkerhout, Netherlands, Aug. 2008, MNHN, 154.0 mm; f-g, Schiermonnikoog, Netherlands, March 1986, MNHN, 166.8 mm; h, Graye-sur-Mer, Calvados, France, Sept. 2006, MNHN, 158.7 mm; i-j, almost straight specimens; i, Quend-Plage, Somme, France, April 2007; j, Boviken, Hamburgö Isl., Sweden, July 1994, MNHN; k-n, St. Johns, Newfoundland, Canada, Sept. 2007, coll. Vierna; k, 140 mm; l, 163 mm; m, dorsal and ventral view with soft parts; n, close-up of fourth aperture.

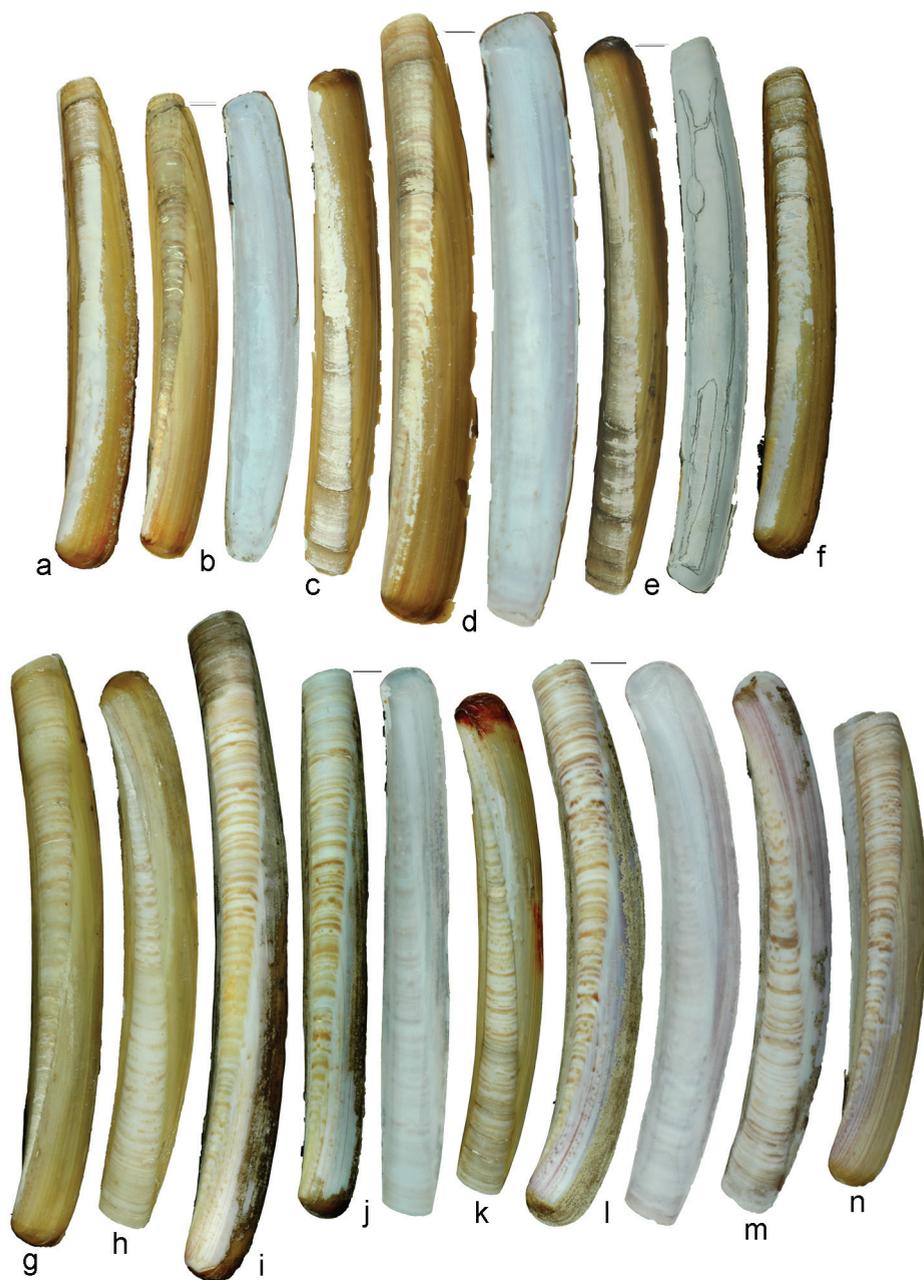


Plate 2. *Ensis ensis* (Linné, 1758). a-d, Berck-sur-Mer, Calvados, France, May, 1987, MNHN; a, 109.4 mm; b, 107.7 mm; c, 116.8 mm; d, *Ensis arcuatus* var *ensiformis* Van Urk, 1964, 135.5 mm (in comparison with *E. ensis*); e-f, Schiermonnikoog, Netherlands, Nov. 1985, MNHN; e, 127.4 mm; f, 103.4 mm; g-h, Porsguen, near Plougastel, Finistère, France (no date), MNHN; g, 99.5 mm; h, 92.7 mm; i-k, Laredo, Cantabria, Spain, Febr. 1988, MNHN; i, 112.3 mm; j, straight specimen, 91.4 mm; k, 82.8 mm; l-n, Mediterranean specimens, Le Grau du Roi, Gard, France, Sept. 1999, MNHN; l, 93.6 mm; m, 89.4 mm; n, 78.3 mm.



Plate 3. *Ensis goreensis* (Clessin, 1888). **a-m**, specimens from Senegal; **a-e**, off Casamance, 10-20 m, from fishermen, 1987, MNHN; **a**, 91.7 mm; **b**, 90.3 mm; **c**, 85.1 mm; **d-e**, 83.9 mm; **f-g**, Casamance, 13°05.6'N/17°02.4'W, 19 m; **f**, 49.2 mm, March 1988, MNHN; **g**, 39.6 mm; **h-i**, SW of Madeleines, 48 m, Sept. 1953, MNHN, 62.0 mm; **j-q**, specimens from the shelf of Guinea; **j-m**, W of Cap Verga, 10°15'N 15°56'W, 26 m, Oct. 1988; **j**, 86.1 mm; **k**, 76.5 mm; **l**, 70.5 mm; **m**, 65.1 mm; **n**, W of Foulaya, 10°18'N 15°53'W, 21 m, Oct. 1988, MNHN, 88.7 mm; **o**, W of Konebomby Island, 9°48'N 15°18'W, 28 m, May 1988, MNHN, 73.0 mm; **p-q**, W of Rio Yomponi, 12°24'N 15°02'W, 23 m, Oct. 1988, MNHN; **p**, 78.1mm; **q**, 66.8 mm.

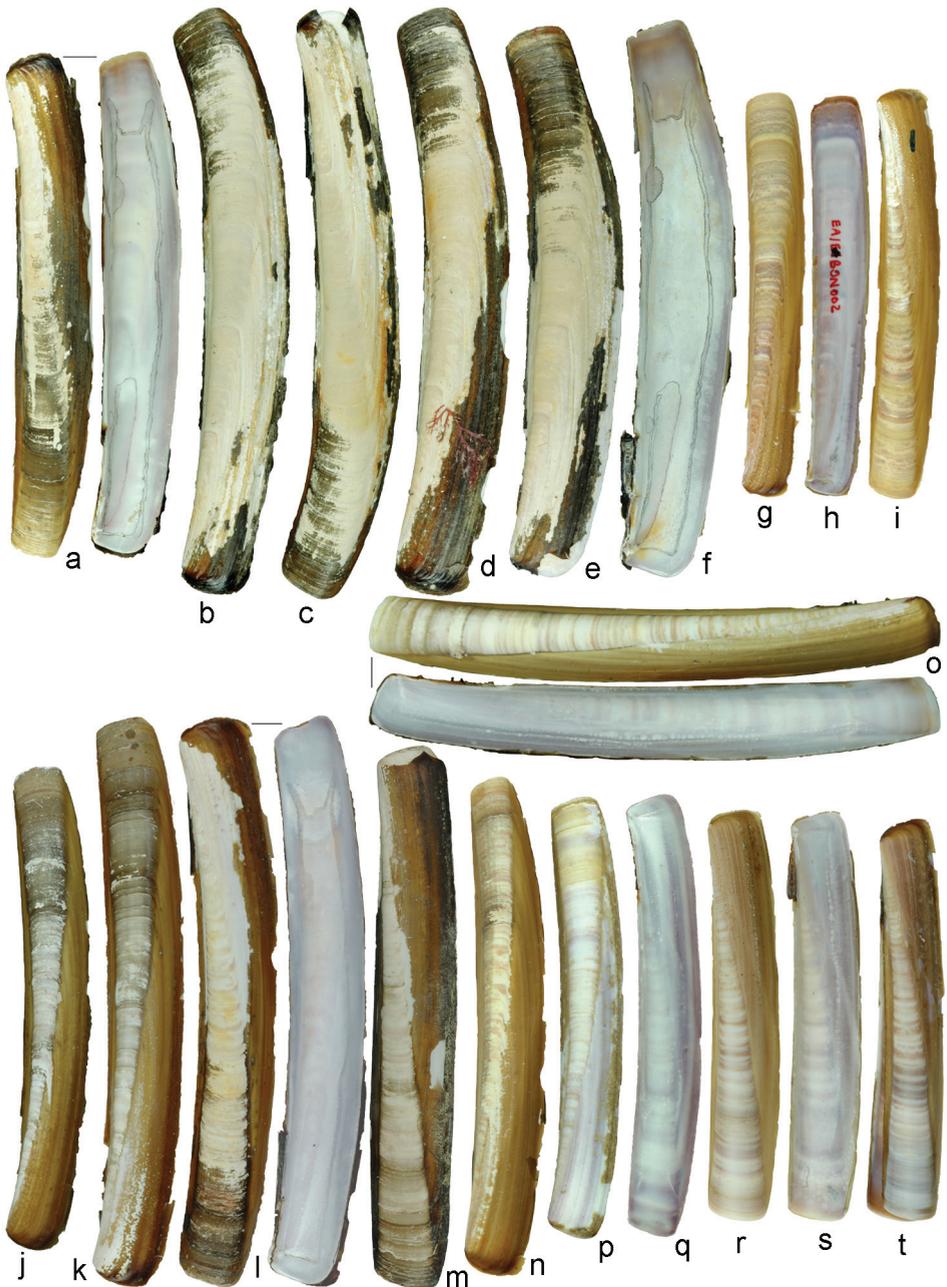


Plate 4. *Ensis magnus* Schumacher, 1817. a-f, Specimens from Faroe Islands, the type locality. Only a is of the typical rather straight “*magnus*” as known from older material. Høyvik, outside Thorshavn, Faroe Islands, 18 m, leg. Schander, 18. Sept. 1993, MNHN; a, 146.5 mm; b-c, 169.6 mm; d, 168.7 mm; e-f, 159.4 mm; g-n, Bonden, Gullmar Fjord, Sweden, 58°12.7'N 11°19'E, 18-25 m, coll. Vierna; g-h, 115 mm; i, 117 mm; j, Concarneau, Finistère, France, May 2006, MNHN, 128.2 mm; k-l, Dinard, Côte du Nord, France, Feb. 1982, MNHN; k, 152.7 mm; l, 149.4 mm; m, Silver Strand, W of Galway, Ireland, 24. May 1985, MNHN. This straight specimen resembles a very slender *E. minor* apart from the slightly upward-bent anterior fourth; n, *Ensis arcuatus* var. *ensoides* Van Urk, 1964, Berck-sur-Mer (see Fig. 9d), o, Laredo, Cantabria, Spain, Febr. 1988, MNHN, 140.2 mm; ►



Plate 5. *Ensis minor* (Chenu, 1843). **a-h**, typical specimens from the Mediterranean; **a-b**, Fréjus, Var, mouth of Argens river, Feb. 2007, MNHN; **a**, 73.5 mm; **b**, 62.3 mm; **c-d**, Skhinias near Marathon, Greece, April, 1988, MNHN; **c**, 88.5 mm; **d**, 84.0 mm; **e-g**, La Franqui, Roussillon, France, Oct. 1987, MNHN; **e**, 136.6 mm; **f-g**, 130.8 mm; **h**, Radès, near Tunis, 1985, MNHN, 89.7 mm (note the broader posterior part, especially in spm. e).

◀ **p-t**, Mediterranean specimens with comparatively short shells; **p-q**, La Franqui, Roussillon, France, Oct. 1987, 104.4 mm; **r-t**, entrance of Etang de Leucate, Roussillon, France, April 1999, MNHN; **r-s**, 96.6 mm; **t**, 94.0 mm.

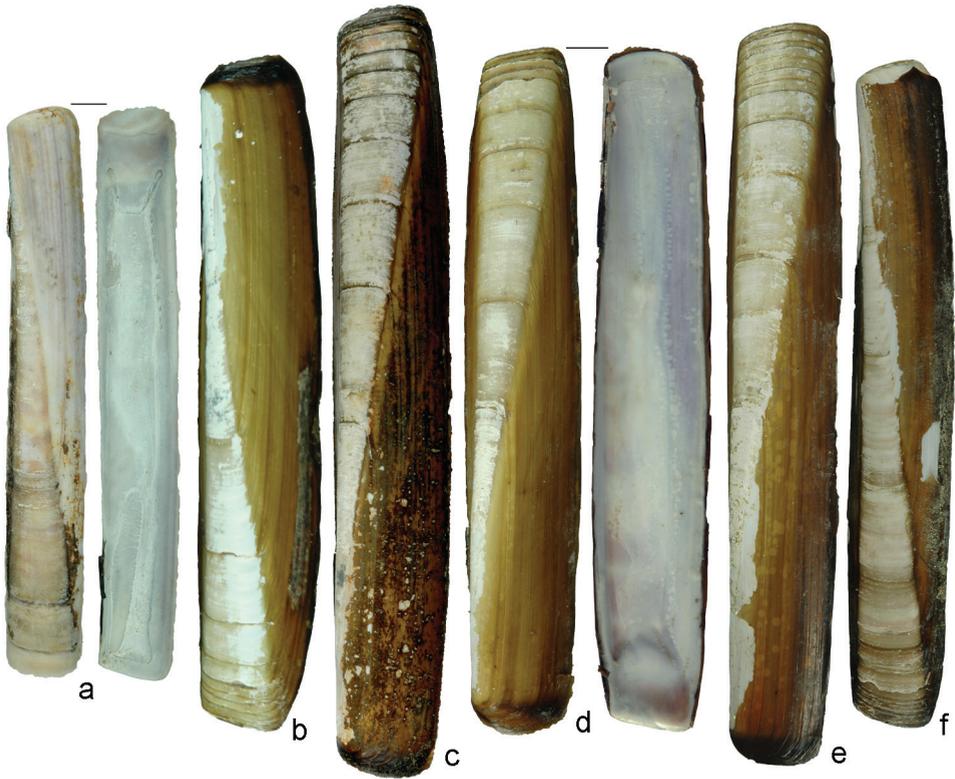


Plate 6. *Ensis minor* (Chenu, 1843). Atlantic specimens. a, Schiermonnikoog, Netherlands, March 1986, MNHN, 127.1 mm; b, specimen close to form "*subarcuata*" Van Urk, Gullane Bay, E-Scotland, Oct. 1987, MNHN, 152.3 mm; c-e, Gosford Bay, E-Scotland, Oct. 1987, MNHN; c, 176.2 mm; d, 153.9 mm; e, 167.7 mm (note the numerous strong growth rings near the posterior margin, which would mean an age of 10-12 years); f, same specimen of *E. magnus* as on Plate 4 m for direct comparison.



Plate 7. *Ensis siliqua* (Linné, 1758). a, Strongford Lough, Northern Ireland, Sept. 2007, MNHN; 216.9 mm; b-d, Carnoustie, E-Scotland, Oct. 1987; b, 217.4 mm; c, 213.9 mm; d, 193.6 mm; e, Læsø Island, N-Kattegatt, Denmark, no date, MNHN, 143.8 mm.



Plate 8. *Ensis siliqua* (Linné, 1758) and "hybrids" of *E. minor* x *E. siliqua*. **a-e**, *E. siliqua*; **a**, Plaque de la Loge, Ile de Ré, Charente Maritime, France, May 1996, MNHN, 168.2 mm (note the curved valves); **b**, Quiberon, Bay side, Morbihan, France, March 1997, MNHN, 154.1 mm; **c-d**, Schiermonnikoog, Netherlands, June 1977, MNHN, typical specimens with more or less postmortal colouration occasionally washed up from deeper subtidally on the beaches of the southern North Sea islands; **c**, 197.9 mm; **d**, 184.8 mm; **e**, Camaret-sur-Mer, Finistère, France, 1986, MNHN, 121.8 mm. **f-i**, "Hybrids" *E. minor* x *E. siliqua*; **f**, Port Penthièvre, Morbihan, France, MNHN, 147.4 mm; **g**, Plaque de la Loge, Ile de Ré, Charente Maritime, France, May 1996, MNHN, 169.3 mm; **h-i**, Anse de Martray, Ile de Ré, Charente Maritime, France, May 1996; **h**, *E. siliqua*, 151.2 mm; **i**, *E. minor*, 136.6 mm, but both with a few subtle characters of the other species; **j**, posterior view of specimen h, showing the typical cross-section of *E. siliqua*; **k**, posterior view of specimen i, showing the typical cross-section of *E. minor*.