Distribution and habitats of *Acesta excavata* (Bivalvia: Limidae) with new data on its shell ultrastructure

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Abstract. *Acesta excavata* is the largest known bivalve associated with the *Lophelia pertusa* communities along the northeast Atlantic continental margin, but has also been found along steep cliffs, devoid of bathyal corals, and on more subdued topographies. During the Pleistocene, including the last glacial, *A. excavata* was widespread in the Mediterranean, but is in the Recent fauna known only from four Mediterranean sites. A new possible live-record from the Canyon du Var off Nice is presented. Radiocarbon dating (AMS ^{14}C-method) on an *A. excavata* assemblage from the Strait of Sicily yielded a Late Pleistocene age of 39.9 ka. Biometric parameters indicate that Pleistocene Mediterranean shells achieved about the same maximum sizes as their Recent Atlantic counterparts, but individuals have been slightly smaller on average. The subspecies *Acesta excavata sublaevis* Nordsieck, based on a subfossil juvenile Mediterranean shell, is not considered a valid taxon. Mineralogical composition and ultrastructure of *A. excavata* have been analyzed using thin-sections, Feigel staining, x-ray diffractometry (XRD) and SEM-imaging. Its wide distribution, large size (15 cm) and simple shell architecture makes it a prime candidate for palaeoenvironmental studies in cold-water coral settings.

Keywords. *Acesta,* North Atlantic, Mediterranean Sea, biogeography, ultrastructure, ecology

Introduction

Cold-water scleractinians are the focus of a growing interest in the field of palaeoceanography and palaeoclimatology (Adkins et al. 1998; Mangini et al. 1998). Corals secrete an aragonitic exoskeleton whose growth pattern and geochemical

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composition is complex, making the extraction of suitable climatic signals often technically difficult and not always easy to decipher (e.g., Mikkelsen et al. 1982; Adkins et al. 2002; Risk et al. 2005). There is, therefore, a strong motivation to test additional calcareous organisms co-occurring with cold-water corals, and thus sharing the same ambient environmental conditions. Bivalvia are particularly useful and reliable tracers to reconstruct past attributes of seawater (e.g., Jones et al. 1983; Richardson 2001; Owen et al. 2002). In this respect, *Acesta excavata* Fabricius, 1779 (Fig. 1) is one of the most prominent bivalves that inhabit bathyal cold-water coral communities along the European continental margin. *A. excavata* is expected to be a more reliable environmental recorder than the corals, with a much simpler growth pattern. The margin-wide occurrence in intermediate water masses could provide us with an *in situ* archive.

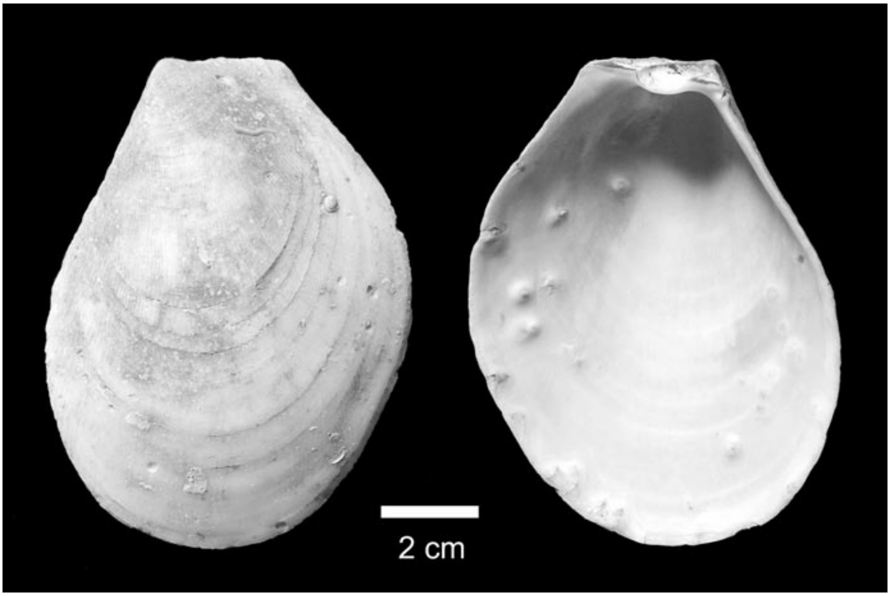

Fig. 1 *Acesta excavata* Fabricius, 1779, from 180 m in Trondheimfjord, Norway. Major growth lines and fine radial ribs sculpture the exterior. Note the attached parasitic foraminifer *Hyrrokkin sarcophaga* and several circular grooves produced by the parasite. The shell interior has a smooth surface. Interior swellings are due to the callus production of *A. excavata*, where *H. sarcophaga* pits had entered the mantle cavity

We propose *A. excavata* as a possible target-species for studies of environmental conditions in cold-water coral settings. This paper summarizes the known distribution of *A. excavata* and its habitats. Herein we provide a biometric analysis and a description of its shell structure, including an examination of its ultrastructure. Our data on shell mineralogy and internal architecture provide a basis for subsequent geochemical examinations.

Taxonomy and biology of *Acesta*

The cosmopolitan genus *Acesta* is represented by more than 30 Recent species, grouped within four subgenera (e.g., Vokes 1963, 1964; Dawson 1995; Coan et al. 2000; Marshall 2001). All of them are epifaunal filter feeders, found in cold-water environments (e.g., Jeffreys 1879; Sowerby 1883; Dall 1902, 1908; Bartsch 1913; Lamy 1930-1931; Madsen 1949; Hertlein 1952; Barnard 1963; Vokes 1963; Kuroda et al. 1971; Coan et al. 2000; Marshall 2001), often associated with bathyal cold-water corals.

The genus *Acesta* comprises larger (~25 cm) species (Lamy 1930-1931), than other genera within the Limidae (*Limaria, Lima*, *Ctenoides, Limatula* and *Limea*) are smaller and, with exceptions, tend to occur mostly in shallower waters (e.g., Coan et al. 2000; Hall-Spencer and Moore 2001; Mikkelsen and Bieler 2003). Limidae live on the surface of seabed sediments or settle various types of hard substrata. They are similar to the Pectinidae in many respects, for both families have species that are active swimmers and that can attach to hard substrata by a byssus (Yonge 1936).

Acesta excavata (Fig. 1) was first described as *Ostrea excavata* from Norwegian fjords in 1779 by Fabricius, a Danish student of the pioneering Swedish taxonomist Carolus Linnaeus. Its current taxonomic position within the phylum Mollusca is shown below, having been transferred to the genus *Acesta* by H. and A. Adams (1858). *Lima solida* Calcara, 1845, *Radula (Acesta) excavata* H. and A. Adams, 1858 and *Lima excavata* Lamarck, 1819 are synonyms of *Acesta excavata* (for details see Vokes 1963), which is the type species for the genus *Acesta*.

Class BIVALVIA Linnaeus, 1758
Subclass PTERIOMORPHA Beuerlen, 1944
Order LIMOIDA Waller, 1978
Superfamily LIMOIDEA Rafinesque, 1815
Family LIMIDAE Rafinesque, 1815
Genus *Acesta* H. and A. Adams, 1858
Species *excavata* Fabricius, 1779

Acesta excavata is a suspension feeder which lives attached to hard substrata and is distributed along the continental shelf-break of the north-eastern Atlantic Ocean (Fig. 2) and during the Pleistocene to Recent within the Mediterranean basin (e.g., Bourcier and Zibrowius 1969), often co-occurring with *Lophelia pertusa* and *Madrepora oculata*. Most specimens for this study were recovered from cold-water coral sites (Fig. 3). Remotely Operated Vehicle (ROV) investigations showed a direct byssal attachment to dead coral frameworks, just below the active growth zone.

Acesta rathbuni (Dawson, 1995) and *A. bullisi* are capable of releasing themselves from their byssus and swimming to more favourable sites (Kohl and Vokes 1994) yet *A. excavata* seems unable to swim actively. Nevertheless, even adult specimens can move easily using their strong byssus (Järnegren 1999).

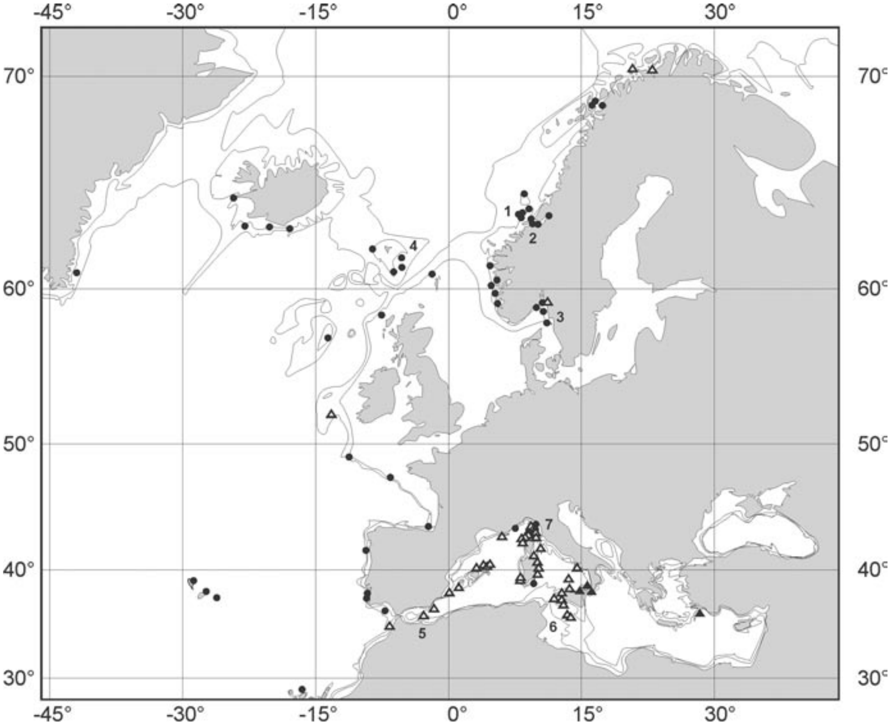

Fig. 2 Distribution of Recent *Acesta excavata* in Europe (black circles). Bathymetry is simplified to the 200 m and the 1000 m depth contour. White triangles indicate submerged sites of subfossil to Late Pleistocene age and black triangles denote uplifted Lower Pleistocene sections on Sicily and Rhodes. Sampling sites covered in detail are: 1 - Sula Ridge, 2 - Trondheimfjord, 3 - Kosterfjord, 4 - Faroe Bank, 5 - Cabliers Bank, 6 - Strait of Sicily, 7 - North Tyrrhenian Sea

Acesta bullisi Vokes, 1963 from the Gulf of Mexico is found attached to large vestimentiferan tubeworms (*Lamellibrachia luymesi*) in chemosymbiotic bottom communities at hydrocarbon seeps (e.g., Boland 1986; MacDonald et al. 1989; Kohl and Vokes 1994). Järnegren et al. (2003) observed an oophagous lifestyle for *A. bullisi*, in addition to its filter feeding habit. This combination is unique in the animal kingdom. *A. bullisi* preys on lipid-rich tubeworm eggs.

Little is known about *Acesta angolensis* Adam and Knudsen 1955, the south-eastern 'neighbour' of *A. excavata*, which inhabits bathyal depths along the west-African continental margin (Boss 1965). *A. angolensis* has its northernmost distribution off north-west Gabon at 439 to 595 m depth, but is more commonly found further south from Pointe-Noire to Moçamedes (pers. comm. R. von Cosel 2003).

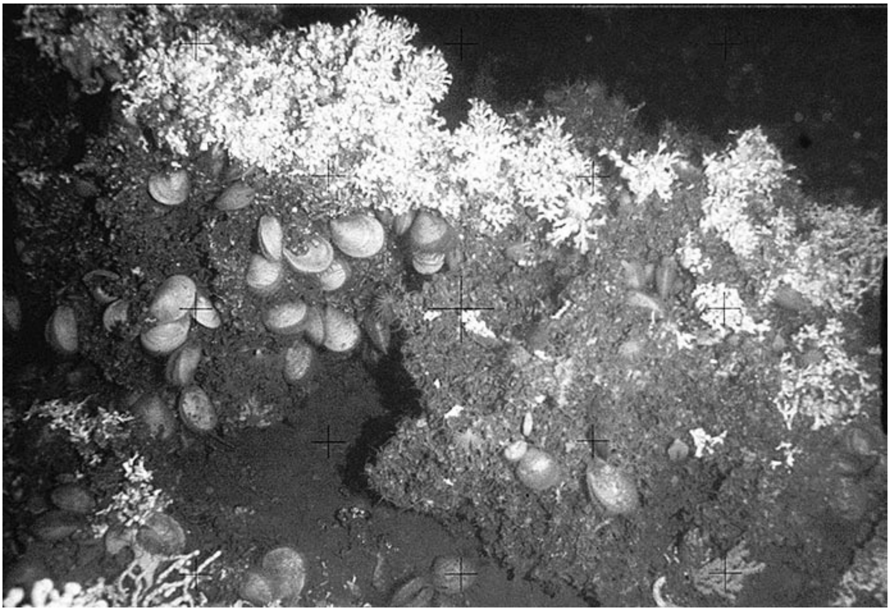

Fig. 3 Haltenpipe Reef cluster, 300 m depth, off Mid-Norway. Dense clusters of large (>10 cm) *A. excavata*, byssally attached to dead coral framework, just below the active growth zone (photo courtesy of M. Hovland, Statoil Company; Hovland and Mortensen 1999)

Description of *Acesta excavata*

The thin white shell, often translucent in juvenile specimens, is roughly oval and higher than wide (Fig. 1). The anteroventral margin is oblique, while a prominent auricle marks the posterior. Adult specimens can reach 20 cm in height and are moderately inflated, strongly inequilateral, but equivalved. The lunular field is excavated, sometimes slightly gaping at the byssal notch.

Many fine radial ribs restricted to the exterior originate from the umbo. Each rib can be traced across the entire shell to its margin. On the medial portion they are often subdued and faint, but again more pronounced towards the valve margin. In anteroventral and dorsal portions the ribs are most prominent, especially on either side of the umbo, in the lunular area and on the posterior auricle. Interspaces between ribs are shallow concave grooves, equally wide as the adjacent costae. The posterodorsal margin shows a distinctly ribbed angular auricle behind the small umbones, while the anterior auricle is reduced.

Major growth lines occur on the exterior side in relatively regular increments (Fig. 1). In large adult specimens (>10 cm) these lines get narrower and are increasingly crowded. Earliest growth lines close to the umbo are often indistinct.

The shiny interior side, in contrast, is smooth with a slight opalescence, only interrupted by the imprints of the posterior muscles. The non-sinuate pallial line is situated close to the valve margin.

The hinge is straight, without teeth, slightly indented by an oblique triangular ligament pit in the middle (Fig. 2). Most of the ligament is restricted to the oblique triangular groove, with narrow lateral extensions onto the actively growing hinge zone. Contact with the valves is partly calcified, in contrast to a black elastic exterior part. The extremely thin periostracum is light brown to brown, often abraded during lifetime on the medial shell portion.

The soft body of the living animal is light orange to white and shows a gaping mantle cavity (Fig. 4), without fused margins and without siphon. Long tentacles, some with eyes, extend from the folded mantle margin (Järnegren 1999). Two muscle imprints are visible on the posterior portion of the shell interior. Usually one large approximately circular imprint is accompanied by a field with dense accumulation of smaller pedal muscle holdfast. This patch is made up of several muscle strings, which can be fused in adult shells. In old shells both muscle attachment areas may form a joint imprint, up to 4 cm in length (1.5 cm wide). The strong foot allows the animal to crawl hinge-first, assisted by strong byssus threads originating from the byssus gland. These fibres exit at the lunular field and allow for a firm attachment to hard substrata. Järnegren (1999) has documented a sex change during the lifetime of *A. excavata*; most specimens from Trondheimfjord (Røberg and Hitra) <9.0 cm were male, while shells >11.5 cm were female.

Fig. 4 *A. excavata* byssally attached to a steep bedrock cliff at 85 m in the Kosterfjord, Sweden. Shells reach 13 cm height (photo courtesy of T. Lundälv, TMBL)

Fossil record of the genus *Acesta*

Taxa attributed to the Limidae can be traced back at least to the Carboniferous (e.g., Coan et al. 2000), while the fossil record of the genus *Acesta* spans the Late Mesozoic and Cenozoic era (e.g., Dall 1900; Clark 1925; Yokoyama 1925; Woodring 1938; Otuka 1940; Kanno 1960, 1971; Vokes 1963, 1964; Aoki 1976; Hickman 1984; Beu and Maxwell 1990; Stilwell and Zinsmeister 1992; Palazzi and Villari 1996; Stilwell and Gazdzicki 1998; Coan et al. 2000). Today more than 30 fossil species are attributed to *Acesta*.

All known Mesozoic *Acesta* localities originate from the southern hemisphere supercontinent Gondwana, encompassing its continental margins. The oldest *Acesta* records are reported from Late Jurassic deposits (Kanjilal 1990) of western India. Early Cretaceous sites are known from New Caledonia (Freneix 1980), southern Chile (Dawson 1995) and India (Kanjilal 1990). Latest Cretaceous to Early Tertiary sections on Seymour Island in Antarctica document the continuous record of *Acesta* across the K/T boundary, represented by *Acesta shakletoni*, *A. seymourensis, A. laticostata* and *A. bibbyi* (Stilwell and Zinsmeister 1992; Stilwell and Gazdzicki 1998).

Lower Oligocene deposits of Austria document early occurrences in Europe with *Acesta szabói* and *A. mittereri* (Löffler 1999). During mid-Tertiary times (especially Miocene) the genus has at least 16 species documented (Vokes 1963). This peak in diversity also marks the onset of its cosmopolitan distribution. Most species are reported from Japan (e.g., Matsumoto 1986), but also from New Zealand (Beu and Climo 1974; Marshall 2001) and from the Pacific side of North America (Moore 1984). According to Sacco (1898) the European *Acesta miocenica* Sismonda, found in Miocene deep-water deposits of Italy and Hungary (Sacco 1898; Báldi 1986), represents potentially a mid-Tertiary ancestor of *Acesta excavata.*

The bathyal, neotectonically uplifted Plio-Pleistocene sections of Rhodes (pers. observ. A. Freiwald) and Sicily (Seguenza 1870, 1880) provide the oldest known *A. excavata* sites. Many occurrences are recorded from Early to Mid-Pleistocene deposits from Sicily and the adjacent southern Italian province Calabria (e.g., Seguenza 1873-1879, 1880; De Stefani 1891; Di Geronimo and Li Gioi 1980; Di Geronimo 1987; Barrier et al. 1996; Palazzi and Villari 1996; Vazzana 1996; Di Geronimo and La Perna 1997).

Apart from those emerged sections, *A. excavata* is also recorded from numerous Late Pleistocene submerged deposits in the western part of the Mediterranean Sea (Fig. 2), often associated with subfossil azooxanthellate scleractinian corals (Segre and Stocchino 1969; Taviani and Colantoni 1979; Corselli and Bernocchi 1990; Bonfitto et al. 1994a, b). *A. excavata* has been recorded so far from the Alboran Sea over the Balearic Sea to the Strait of Sicily (Taviani and Colantoni 1979) and from the Adriatic (Ghisotti 1979). These submerged sites document together with the southern Italian outcrops the frequent fossil (Pleistocene) distribution of the bivalve in the western Mediterranean. Recently dredged hardgrounds (CORTI mission) on the flanks of Cialdi Seamount in the Tyrrhenian Sea have yielded the first submerged example of a micritic limestone containing *A. excavata* (Fig. 5).

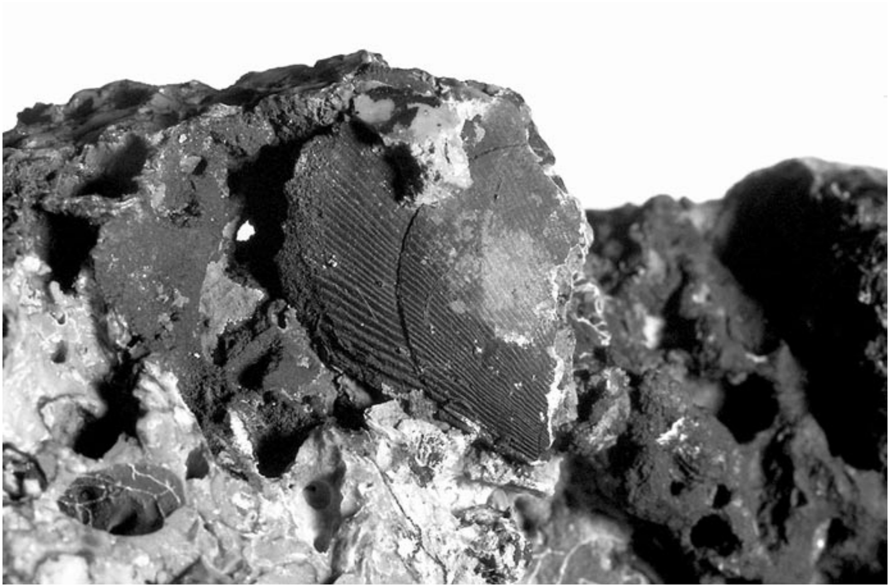

Fig. 5 Pleistocene *A. excavata* from a hardground dredged from Cialdi Seamount (CORTI 86) in the Tyrrhenian Sea (450-1074 m). The pictured fragment is 1.7 cm long, but specimens >10 cm height have been recovered

Emerged Late Glacial to Holocene *A. excavata* have been noted from the glacial isostatically uplifted Norwegian coast (Jeffreys 1879), also together with *L. pertusa* from the Oslofjord (Broch 1922).

Recent distribution of *Acesta excavata*

The Recent distribution (Fig. 2) encompasses the north-eastern Atlantic between Norway and Mauritania (e.g., Sars 1878; Jeffreys 1879; Locard 1898; Friele and Grieg 1901; Kiær and Wollebæk 1913; Madsen 1949; Filatova 1959; Bourcier and Zibrowius 1969; Nordsieck 1969; Poppe and Goto 1991; Mikkelsen and Bieler 2003), including occurrences off southern Iceland (Madsen 1949) and south-western Greenland (Lamy 1930-1931). A record from a fjord setting in south-western Newfoundland (Bay D'Espoir) extends the geographical range to the western Atlantic margin (Haedrich and Gagnon 1991; Gagnon and Haedrich 2003).

At present *Acesta excavata* is a common component of cold-water coral reefs and circalittoral submarine cliffs in Sweden and Norway (Høisæter 1986). The earliest records of *A. excavata* come from Norwegian fjords, which yield the shallowest occurrences at water depths of less than 200 m. Stjernsund in West Finnmark at 70° is the northernmost record for live *A. excavata* (Freiwald et al. 1997). Among the best documented occurrences is the Trondheimfjord, were *A. excavata* is found down to 500 m (Järnegren 1999). Many mid-Norwegian fjords (Grieg 1913; Kiær and Wollebæk 1913; Nordgaard 1929; Dons 1932, 1944; Burdon-Jones and Tambs-Lyche 1960) host the typical deep-water bivalve at relatively shallow depths. The

Swedish Kosterfjord, which is connected to Atlantic waters by an over 500 m deep trough, is inhabited by dense *A. excavata* clusters on steep rock cliffs (Fig. 4) between 65 and 90 m depth (Lundälv 1997).

Apart from the fjord sites, *A. excavata* is distributed all over the relatively deep, glacially influenced Norwegian shelf, between 200 and 350 m (e.g., Sula Ridge; see Freiwald et al. 2002). Further south this species is restricted to the western European shelf-break area. The sites show a rough north-south depth trend, with the shallowest locations at 180 to 380 m on the continental margin off the Faroe Islands (Jensen and Frederiksen 1992; Delongueville and Scaillet 2000) and the deepest sites west of the Strait of Gibraltar (Dautzenberg and Fischer 1897; Hidalgo 1917), off south-western Portugal (1200 m). Southwards *A. excavata* has been scarcely reported from the Moroccan shelf (Reynell 1910; Ghisotti 1979), down to western Sahara (Locard 1898) and Mauritania (Table 1), and from an isolated site off the Ivory Coast (pers. comm. R. von Cosel 2003). Marche-Marchad (1979) reports and figured *A.* cf. *excavata* from 900 m in the Golf of Guinea near Abidjan. Additionally *A. excavata* has also been reported at 3200 m from the Canaries (Dautzenberg and Fischer 1906; Dautzenberg 1927) and between 599 to 1850 m around the Azores archipelago (Dautzenberg 1927).

In the Mediterranean, *A. excavata* was widespread during the last glacial period (Malatesta and Zarlenga 1986) but is currently less successful with only scattered records of live animals (Fig. 2). Early records, like that of Madsen (1949) who was the first to record this species as alive from the Mediterranean, may be questionable since fresh looking shells were often considered as living at that time. Appearances can be deceiving, as fresh-looking shells might be of Pleistocene age. Today there are four reliable reports for live *A. excavata* in the Mediterranean (Ghisotti 1979; Carcassi 1983; Rocchini 1983; Terreni and Voliani 1995), located between 430 and 570 m. Three of those sites are in the northern half of the western Mediterranean, north of Corsica in the Tuscan Archipelago (Fig. 2). The fourth site is located southwest of Sardinia in the Tyrrhenian Sea with a specimen found attached to a thick plastic canvas on a muddy bottom (Terreni and Voliani 1995). Numerous subfossil to fossil sites have been recorded from the western Mediterranean (Table 1) and document the former wide distribution within the basin (e.g., Bourcier and Zibrowius 1969; Taviani 1976; Taviani and Colantoni 1979; Remia and Taviani 2004). Segre and Stocchino (1969) and Colantoni et al. (1970) record fossil *A. excavata* deposits in the Tyrrhenian Sea. Two questionable subfossil sites are recorded from the Adriatic Sea (Ghisotti 1979).

Habitats

The species has an overall depth range report from 40 to 3200 m, but is usually found between 200 and 800 m, bound to intermediate water masses, particularly along the shelf-break area (Fig. 2). Living specimens are reported between 3 and 13°C (e.g., Bourcier and Zibrowius 1969; Ghisotti 1979), while most *A. excavata* sites have a temperature range of 6 to 8°C and salinities of 33.4 to 38.5 ‰ (Malatesta and Zarlenga 1986).

Table 1 Sampling sites of *Acesta excavata* from the North Atlantic and the Mediterranean Sea, which were investigated for this paper. Stations marked with (*) were contributed by H. Zibrowius, indicating further occurrences

Cruise	Station	R/V - ship	Location	Latitude	Longitude	Depth [m]	Preservation
JR-Carbo	JR-111	Johan Ruud	Stjernsund	N 70° 12. 00	E 022° 20. 00	210-280	Recent & subfossil
JH-5-99	4/8	Johan Hjort	Trondheimfjord	N 63° 36. 55	E 009° 23. 13	180-200	Recent & subfossil
POS-228	200-3	Poseidon	Sula Ridge	N 64° 05. 51	E 008° 03. 94	273	Recent
POS-228	215	Poseidon	Sula Ridge	N 64° 06. 53	E 008° 06. 87	250-320	Recent
POS-228	228-JAGO 8	Poseidon	Sula Ridge	N 64° 04. 77	E 008° 01. 71	250-320	Recent
LI-94	162	Littorina	Sula Ridge	N 64° 04. 77	E 008° 01. 71	250-320	Recent
LI-94	163	Littorina	Sula Ridge	N 64° 04. 95	E 008° 01. 63	283-295	Recent
ALK-232	VC-1019	Alkor	Tisler Reef	N 58° 59. 86	E 010° 57. 84	81	Subfossil
ALK-232	GKG-1021-2	Alkor	Tisler Reef	N 58° 59. 86	E 010° 57. 84	81	Subfossil
ALK-232	GKG-1022	Alkor	Tisler Reef	N 58° 59. 88	E 010° 57. 80	91	Subfossil
ALK-232	1051-2	Alkor	Skagerrak	N 59° 05. 85	E 010° 43. 87	120	Subfossil
ALK-232	BG-1053	Alkor	Skagerrak	N 59° 05. 46	E 010° 43. 65	161	Subfossil
ALK-232	BG-1066	Alkor	Skagerrak	N 59° 03. 66	E 010° 44. 25	88	Subfossil
ALK-232	BG-1071-2	Alkor	Skagerrak	N 59° 03. 25	E 010° 44. 56	112	Subfossil
ALK-232	BG-1082-1	Alkor	Djupekrak	N 59° 01. 43	E 010° 52. 01	161	Subfossil
ALK-232	BG-1083-2	Alkor	Djupekrak	N 59° 01. 46	E 010° 51. 98	159	Subfossil
ALK-232	BG-1087	Alkor	Skagerrak	N 59° 05. 02	E 010° 48. 39	130	Subfossil
ALK-232	BG-1092	Alkor	Skagerrak	N 59° 04. 52	E 010° 48. 22	82	Subfossil
ALK-232	BG-1147	Alkor	Skagerrak	N 59° 05. 95	E 010° 48. 34	64	Subfossil
ALK-232	BG-1152	Alkor	Skagerrak	N 59° 05. 83	E 010° 48. 16	91	Subfossil
ALK-232	GKG-1155-2	Alkor	Skagerrak	N 59° 04. 71	E 010° 43. 90	106	Subfossil
TMBL	1	ROV	Kosterfjord	N 58° 88. 00	E 011° 10. 00	85-90	Recent
TMBL	2	ROV	Kosterfjord	N 58° 88. 00	E 011° 10. 00	85-90	Recent
Faroe-1	23-332	(DAFS)	Faroe Bank	N 61° 43. 00	W 005° 54. 00	320	Recent
Procelt I*	K 220	Thalassa I	S-Irish Margin	N 49° 13. 00	W 011° 46. 00	767-840	Recent
Thalassa*	Y-381	Thalassa I	Portugal	N 41° 28. 50	W 009° 14. 10	420	Recent
CYANA*	CY 86-53	Cyana	Canyon du Var	N 43° 63. 00	W 007° 20. 00	<1548	Recent
LM-99	50	Urania	La Gorgona	N 43° 24. 94	E 009° 44. 63	438-536	? subfossil
LM-99	125	Urania	La Gorgona	N 43° 13. 55	E 009° 36. 31	370-374	Pleistocene
CORTI	29	Urania	N Capraia	N 43° 14. 00	E 009° 36. 33	385-399	Pleistocene
CORTI	70	Urania	N Capraia	N 43° 13. 48	E 009° 36. 34	357-402	Pleistocene
CORTI	86	Urania	Cialdi Seamount	N 41° 44. 92	E 010° 32. 68	450-1074	Pleistocene
CORTI	87	Urania	Cialdi Seamount	N 41° 45. 08	E 010° 33. 78	359-495	Pleistocene

Table 1 continued

Cruise	Station	R/V - ship	Location	Latitude	Longitude	Depth [m]	Preservation
CORTI	88	Urania	Cialdi Seamount	N 41° 45. 19	E 010° 34. 65	391-600	Pleistocene
MARCO*	DR-14	Le Suroit	Corsica Margin	N 42° 32. 00	E 008° 31. 80	1175	Pleistocene
MARCO*	DR-15	Le Suroit	Corsica Margin	N 42° 45. 11	E 008° 58. 12	460	Pleistocene
MARCO*	DR-25	Le Suroit	Corsica Margin	N 42° 59. 40	E 009° 10. 90	1265	Pleistocene
MARCO*	DR-30	Le Suroit	Corsica Margin	N 43° 04. 55	E 009° 07. 45	1900	Pleistocene
MARCO*	DR-31	Le Suroit	Corsica Margin	N 43° 04. 54	E 009° 06. 46	1350	Pleistocene
MARCO*	DR-40	Le Suroit	Corsica Margin	N 43° 34. 90	E 009° 25. 50	450	Pleistocene
MARCO*	DR-52	Le Suroit	Corsica Margin	N 43° 45. 50	E 008° 47. 09	900	Pleistocene
SONNE-41*	148DC	Sonne	Eolo Seamount	N 38° 38. 95	E 013° 58. 78	679	? subfossil
CS-96	240	Urania	Strait of Sicily	N 36° 51. 45	E 013° 08. 26	400-767	Pleistocene
CS-96	243	Urania	Strait of Sicily	N 36° 51. 46	E 013° 08. 30	181-634	Pleistocene
CS-96	245	Urania	Strait of Sicily	N 36° 51. 19	E 013° 07. 40	190-435	Pleistocene
COR2	8	Urania	Strait of Sicily	N 36° 51. 43	E 013° 08. 12	181-631	39.9 ka
COR2	39	Urania	Strait of Sicily	N 36° 23. 48	E 013° 15. 17	523	Pleistocene
COR2	46	Urania	Strait of Sicily	N 36° 23. 49	E 013° 15. 18	505	Pleistocene
COR2	53	Urania	Strait of Sicily	N 36° 51. 53	E 013° 06. 29	178	Pleistocene
M-51-1	476 DR	Meteor	Cabliers Bank	N 35° 50. 19	W 002° 09. 57	790-954	Fossil
M-51-1	493 DR	Meteor	SE Cabo de Gata	N 36° 43. 20	W 001° 42. 15	1041-881	Fossil-subrecent
B-74	3	Bannock	SW-Ibiza Channel	N 37° 38. 90	W 000° 01. 40	260-940	Pleistocene
COBAS	43	Urania	S-Ibiza Channel	N 38° 33. 78	E 000° 40. 59	384-715	Pleistocene
COBAS	107	Urania	NE Menorca	N 40° 01. 16	E 004° 23. 62	299-557	Pleistocene
COBAS	109	Urania	NE Menorca	N 40° 01. 14	E 004° 23. 37	341-367	Recent-subrecent
COBAS	115	Urania	NE Menorca	N 40° 02. 43	E 004° 21. 19	344	Pleistocene
MD-04	2804	MarionDufresne	Larache, Marokko	N 35° 17. 45	W 006° 47. 00	550	Pleistocene
(MNHN)*	2	N’Diago	Mauritania	N 19° 04. 00	W 016° 50. 00	425	Recent
ISMAR	-	-	Mauritania	N 19° 00. 00	W 017° 00. 00	600	Recent
(MNHN)*	-	-	Senegal, Dakar	N 14° 30. 00	W 017° 35. 70	240-320	Recent

The most detailed insights into *A. excavata* habitats come from Scandinavian waters (Figs. 3, 4), based on ROV images and submersible observations from several cruises. *A. excavata* is for example common at the 300 m deep Haltenpipe Reef Cluster, on the shelf off mid-Norway (Hovland et al. 1998). Many *A. excavata* are found byssally attached to steep or overhanging hard substrata, especially to *Lophelia* corals and rocks (Hovland and Mortensen 1999). The shells are attached to dead coral skeletons, just below their soft tissue protected active growth zone (Fig. 3). Most *A. excavata* appear to be large (>10 cm height), orientated with the gape of their shells protruding into the water column. They co-occur with the gorgonacean octocorals *Paragorgia arborea* and *Primnoa resedaeformis,* as well as with the actinarian *Protanthea simplex*.

Surveys on the 200 m deep Nord-Leksa *L. pertusa* reefs off western Norway also revealed dense clusters of large (>10 cm) *A. excavata* on vertical to overhanging *L. pertusa* colonies, accompanied by live *L. pertusa*, *Paragorgia arborea* and *Primnoa resedaeformis* as conspicuous associated species (pers. comm. M. Hovland 2003).

Similar observations were possible from submersible (Jago) photographs taken on R/V Poseidon cruise POS 228 to the *L. pertusa* reef complex on the 250 to 320 m deep Sula Ridge (Freiwald et al. 2002). Here large *A. excavata* (up to 13 cm) were attached to vertical faces of dead coral rubble associated with the demosponge *Pachastrella* sp.

A. excavata has been documented at 40 m depth by SCUBA divers in Trondheimfjord, Tautraryggen, mid-Norway (pers. comm. E. Svensen 2003), and from several other sites down to 500 m at the fjord outlet (Hitra). Tautraryggen is at the same time the shallowest known site for the cold-water coral *L. pertusa* and for the bivalve *A. excavata*. Again, *A. excavata* was found attached to live *Lophelia* corals and to vertical faces of dead coral, associated with *Ascidia mentula* forming conspicuous parts of the sessile community.

Recent *A. excavata* from the Mediterranean have been reported attached to hard substrata and were found in the vicinity of dead cold-water scleractinians (*L. pertusa* and *M. oculata*).

ROV investigations from the Swedish Kosterfjord (Fig. 4) revealed a different picture (Fig. 4). *A. excavata* thrives in dense clusters on steep to overhanging bedrock cliffs, in absence of *L. pertusa*. They occur at 65 to 90 m depth with the actinians *Bolocera tuediae* and *Urticina eques*, the tube-dwelling polychaetes *Serpula vermicularis*, *Hydroides norvegica* and *Sabella pavonina*, as well as with encrusting and erect bryozoans *Alcyonidium diaphanum*, and with the ascidians *Dendrodoa grossularia* and *Ascidia* sp. (Lundälv 1997).

A. excavata also occurs in the adjacent Oslofjord (Table 1) on bouldery glacial deposits, as well as on muddy bottoms where dropstones provide hard substrata.

Di Geronimo (1995) reported *A. excavata* from emerged Plio-Pleistocene deposits (Fig. 2) of the Straits of Messina, in the community of "White Corals". The bivalve occurs together with *L. pertusa* and *M. oculata*, all originating from nearby escarpments, later embedded in bathyal marls (Di Geronimo 1987).

Sampling station COR2-56 in the Strait of Sicily in Late Pleistocene muddy sediments at the base (-505 m) of a steep cliff yielded a similar picture. The grab sample contained numerous disarticulated *A. excavata* shells (>200), including at least 64 other macrofaunal taxa within the mixed pelagic to benthic death assemblage. Several organisms that live on hard substrata, like *L. pertusa* and *M. oculata*, the brachiopod *Gryphus vitreus* and the bivalves *Spondylus gussoni* and *A. excavata,* originate from the adjacent cliff.

Epibionts, parasites and endolithic organisms

Acesta excavata valves provide a hard substratum for epibionts. Recent shells often show dense overgrowth of serpulids, bryozoans and sponges, but also scleractinians and saddle-oysters (Anomiidae sp.). Fossil Mediterranean shells were often colonized by the brachiopod *Novocrania anomala*, which produces a typical imprint on the shells.

A. excavata is frequently infested by *Hyrrokkin sarcophaga* Cedhagen, 1994. This parasitic foraminifer also settles on the scleractinian *L. pertusa*, on other bivalves (e.g., *Delectopecten vitreus*), and even on sponges, within cold-water coral settings (Freiwald and Schönfeld 1996). *H. sarcophaga* preferentially uses *A. excavata* and *L. pertusa* as host (Cedhagen 1994). In early ontogenetic stages the foraminifer produces a 0.5 to 1 mm deep and up to 3 mm wide circular groove on the shell surface of *A. excavata* (Fig. 1), usually within the outer calcite zone. Adult foraminifer produce a narrow pit, which penetrates the entire valve and enters the inner soft tissue (Freiwald and Schönfeld 1996). *A. excavata* then forms a callus to close the hole, easily recognized as swelling on the shell interior (Fig. 1). Typical swelling diameter is 5 mm, formed by thin aragonite laminae, enriched in organic matter. More than forty pits have been observed on single valves, often with the parasite still attached in life-position.

A similar relationship is reported from *Acesta angolensis*, which is infested by *Rosalina carnivora* (Todd 1965). *A. angolensis* is the southern 'neighbour' of *A. excavata* and at the same time a closely related species. Both limid bivalves can hardly be distinguished by their biometric parameters (e.g., width and height). The two parasitic Foraminifera *Hyrrokkin sarcophaga* and *Rosalina carnivora* (Marche-Marchad 1979) are also closely related (see discussion in Cedhagen 1994).

The foraminiferan *Hyrrokkin sarcophaga* has not yet been documented from the present day Mediterranean (Cedhagen 1994; Freiwald and Schönfeld 1996). Boring traces preserved in Pleistocene *A. excavata* shells instead suggest that the foraminifer must have persisted in the Mediterranean as well. Unfortunately none of the fossil samples had the parasite still attached. Only a detailed investigation of the trace can consolidate this likely possibility.

Cedhagen (1994) noted that *A. excavata* from the Kosterfjord, although some hundred specimens were collected, had not shown an infestation by *H. sarcophaga*. Samples of *A. excavata* collected during the R/V Alkor cruise 232 to the Kosterfjord and the Skagerrak in November 2003 (Table 1), showed instead traces of the foraminifer at most sampled sites, including Kosterfjord. Both, subfossil to Recent shells were infested.

On older shell portions the periostracum tends to disappear, enhancing early bioerosion during the lifetime of the bivalve. Consequently bioerosion lacks in the youngest shell parts, but becomes increasingly frequent towards the umbonal area. The same pattern can be observed on the hinge plate, where only the youngest part is occupied by the ligament, while the older parts are already slightly affected by boring organisms.

The micro-borings *Orthogonum lineare* and *Saccomorpha clava*, produced by fungi (e.g., *Dodgella priscus*) are the most common ichnotaxa observed in *A. excavata* shells. The macro-boring *Entobia*, produced by sponges like *Cliona,* has been observed on many Pleistocene Mediterranean shells. Traces of boring foraminifers, especially of *Hyrrokkin sarcophaga* are highly abundant on Recent Norwegian *A. excavata* and on Pleistocene material from the Mediterranean.

Materials and methods

Live specimens sampled along the European continental margin, e.g. on the mid-Norwegian shelf or in the Swedish Kosterfjord, and dead specimens (subfossil and fossil) from the Mediterranean Sea, were analysed with various methods. Samples were collected over the years on many cruises (Table 1), supported by the following European research vessels: R/V Bannock, R/V Poseidon, R/V Urania, R/V Johan Hjort, R/V Meteor, R/V Littorina, R/V Lophelia, R/V Victor Hensen, R/V Alkor and R/V Marion Dufresne. Most specimens were obtained with an epibenthic dredge device or by grab sampling (Van Veen grab). Sampling at the Sula Reef site off mid-Norway, involved direct collection with the manned submersible Jago (Freiwald et al. 2002) and the Kosterfjord colonies were documented with ROV. Positions were usually fixed with a differential global positioning system (DGPS).

Over 350 single valves were measured for a biometric analysis. Using a digital calliper, length of the straight hinge line, maximum shell width (parallel to the hinge line) and maximum length (height) along the main growth axes from umbo to margin, as well as single valve inflation and hinge height were measured.

Thin sections were prepared along and across the main growth axes, to study internal architecture and layering of the shell with a high resolution light-optical microscope (Zeiss). Single valves were embedded in a two compound epoxy resin (Araldit and Araldur) to ensure sawing stability.

Some polished slabs were immersed in Feigel's solution for 3 to 4 minutes, resulting in dark staining of aragonitic shell portions. This silver coating leaves calcite unaffected and allows for a quick distinction of major mineralogical zones. Homogenous powder samples were prepared of several interior and exterior shell portions to verify this preliminary mineralogical zonation with x-ray diffractometry (XRD).

Shell ultrastructure was investigated using a Scanning Electron Microscope (SEM). Polished shell sections were etched with 0.1 N dilute hydrochloric acid (HCl) for 30 seconds, then rinsed in deionized water, dried, sputter coated with gold, and photographed under the SEM.

A numeric radiocarbon age from a Mediterranean *A. excavata* (COR2-8) was obtained with the AMS-^{14}C method at the Eidgenössische Technische Hochschule (ETH) in Zurich.

Results

Taxonomy

The subspecies *Acesta excavata sublaevis* Nordsieck, 1969 was established on the photo of a juvenile subfossil specimen from Cassidaigne Canyon off Marseille in the Mediterranean (pers. comm. H. Zibrowius 2004). It is actually the same specimen which is described in Bourcier and Zibrowius (1969) and now stored at the Museum of Natural History in Paris (MNHN). This single valve does not differ in any respect from Recent juvenile *Acesta excavata* Fabricius, 1779 from the North Atlantic and, therefore, the taxon is not considered valid.

Possible documentation of living *in situ Acesta excavata* in the Mediterranean

CYANA-submersible dive CY 86-53 (6th November 1986; SAME-cruise) in Canyon du Var, off Nice (France), photographed *Acesta excavata* on steep canyon walls of conglomerate bedrock (Fig. 6). Still articulated shells with gaping valves occurred on slightly overhanging canyon walls next to solitary scleractinian corals – presumably *Desmophyllum cristagalli*. The 10 cm large shells were either alive or recently dead, being open, but the soft body is not visible on the pictures (pers. comm. H. Zibrowius 2004). The exact depth is unknown, but was shallower than 1548 m.

Radiocarbon dating

A large well-preserved *A. excavata* specimen (COR2-8) from a grab sample in the Strait of Sicily (Table 1) has been radiocarbon dated to 39,960 ± 820 cal yr BP, dating back to the latest glacial period of the Pleistocene. This numeric age is close to the upper age limit of the AMS-^{14}C method and has to be judged carefully. If the numeric age of 39.9 kyr does not correspond to the real value, then it provides at least a minimum age.

Tyrrhenian hardgrounds with *Acesta excavata*

Dredge samples (CORTI 86 to 88) from the steep western and eastern slopes of Cialdi Seamount (Table 1) in the Tyrrhenian Basin have yielded calcareous hardgrounds between 1073 and 450 m (CORTI 86) and between 494 and 358 m (CORTI 87). The rocks contained a high number of fossil *A. excavata* and represent the first known submerged occurrence in lithified Pleistocene deposits (Fig. 5) from steep sediment starved seamount flanks. All rock samples showed a black stained irregular surface with dissolution cavities and partly lithified yellowish brown mud. The interior was built up of micrite containing numerous fossils, dominated by *Gryphus vitreus* and *A. excavata* (~8 cm), associated with *Desmophyllum*

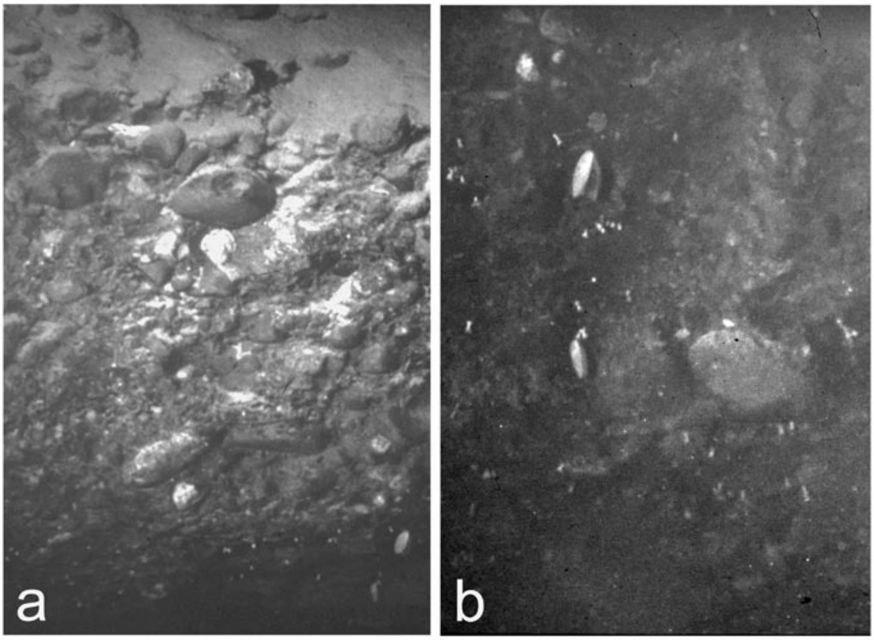

Fig. 6 Pictures from CYANA dive CY86-53 (6th Nov. 1986) in Canyon du Var (<1548 m) off Nice (France) show paired valves of *A. excavata* (**a** - lower right corner, **b** - enlarged), documenting living or recently dead specimens (~10 cm height). The steep conglomeratic bedrock walls are colonized by solitary scleractinians (most likely *Desmophyllum* sp.) (courtesy of H. Zibrowius, modified from IFREMER material)

cristagalli, *Stenocyathus vermiformis*, *Lophelia pertusa* and large oysters. Thin black manganese veneers and irregular seams mark dissolutional horizons. Rock surfaces were densely populated by *Vermiliopsis monodiscus* and *Protula* sp., which occur also as fossils within the rock.

Shell banding and hierarchic growth patterns

Regularly-spaced growth bands on the shell surface are a prominent feature of *A. excavata* (Fig. 1). Growth increments are widest along the main growth axes, and get narrower towards the cardinal area, were they continue as fine ribs on the hinge (Fig. 7). Increments have average widths of 0.3 to 0.5 cm in juvenile shells of around 5 cm height. Older shells, up to 10 cm height, show the widest bands, ranging from 0.4 to 0.9 cm, and measuring 0.6 cm on average. In adult specimens larger than 10 cm, the bands become increasingly narrower (<0.3 cm) and crowded (Fig. 7). The growth band boundaries can be traced as lines across the whole shell. Incomplete and irregular growth bands occur especially where parasitic foraminifers were attached to the valve margins. These ‘false’ rings cannot be traced across the entire shell. Banding of left and right valve is equal, showing the same cyclic patterns and also the same irregularities and incomplete bands in pathologic specimens.

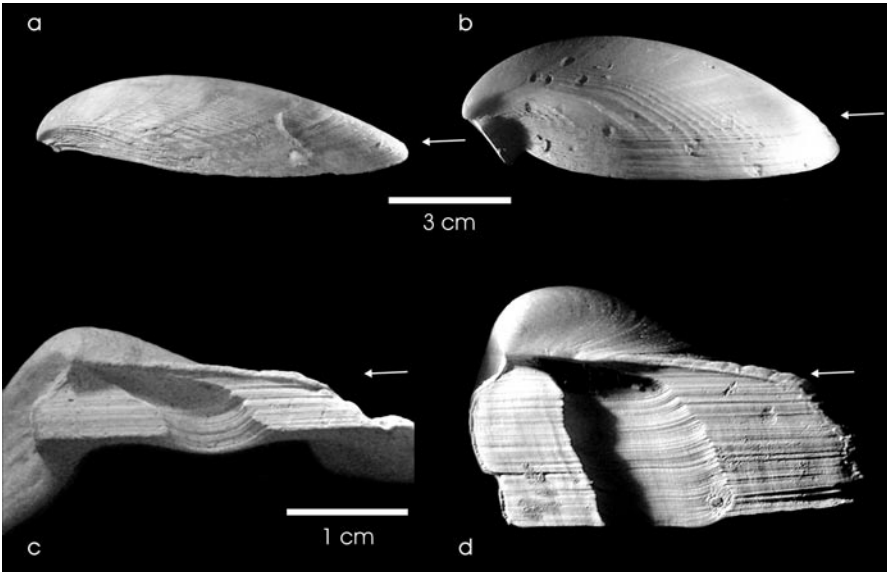

Fig. 7 Shell growth shows two phases. The first phase (**a**), typically up to 10 cm shell height, is marked by a flat shell shape and an oblique ligament pit (**c**). The second phase (arrows) is marked by increased valve inflation and reduced height growth (**b**), while a broad hinge plate is formed (**d**). Samples: JH-5-99 (**a**, **c**) and COR2-39 (**b**, **d**)

Growth increments are clearest on the central portions of large shells (>10 cm). Proximal bands are frequently abraded or faint and hard to recognize, whereas crowded and narrow bands of old shells cannot be accurately counted either. Shells with 10 cm height have typically 18 to 22 bands. These shells, still in their first growth mode, show a raw linear correlation of increment number and height.

Minute banding of parallel, equally wide (<0.4 mm), ribs marks the hinge plate (Fig. 7). Their number corresponds to the number of external growth increments. Shells at the end of the first growth phase, with about 10 cm height, have 18 to 22 hinge lines. The second growth phase produces large arched shells width an extended hinge plate, showing more than 50 hinge lines (e.g., COR2-39). Up to 80 ribs have been counted from Norwegian samples. The maximum number of hinge lines in some Trondheimfjord (Røberg) specimens was in excess of 100 ribs (pers. comm. J. Elvestrand 2003).

Live specimens from one location caught at the same time of the year show a similar degree of growth increment completion. However, exact growth band completion could not be calculated accurately, due to changing band widths during clam ontogeny. Variability of growth ring width, possibly driven by local environmental changes, further prohibited an exact calculation of growth band completion. Relative variation of increment width for the latest 10 growth bands showed a similar pattern for shells from the same location.

Thin-sections revealed hierarchic growth patterns also for the valve interior and especially the hinge shows a rhythmic banding.

Shell growth and allometric changes

Allometric growth shows linear correlations among most biometric parameters (Fig. 8). Shell width correlates linearly especially well with height at an average width/height ratio of 0.77±0.05 (min./max. 0.71-0.90). Older specimens, typically larger than 10 cm (e.g., TMBL 1-4), tend to slightly wider forms with a width/height ratio of 0.83. In these adult shells, the pallial line is retracted a considerable distance (~1 cm) into the shell, resulting in slowed growth ring precipitation. This decrease in growth rate is well depicted by a reduced distance between growth increments on the shell exterior. At this time the valve form changes from a flat cross-section to an increasingly glabrus, arched shape with crowded growth lines (Fig. 7). The onset of the second growth mode is well depicted in the lunular area by the first emplacement of a straight rib. Arched ribs in the excavated lunular area characterize the first growth period. Lunular ribs are parallel in the second growth phase and rapidly increase the valve inflation (Fig. 7).

This changing growth pattern also affects the hinge morphology. In young shells, with sizes of less than 8 to 10 cm the hinge has a strongly oblique ligament groove. At the change of growth modes the hinge reaches a typical width of 3.0 cm and a height of 0.8 cm. Subsequently the shell forms a prominent hinge plate, with the ligament pit approximately centred within the parallel hinge margins (orthogonal to hinge line). Old specimens can reach an inflation of about 3.5 cm and show a prominent hinge plate, with a hinge height of around 1.5 cm and a hinge with of about 3.5 cm.

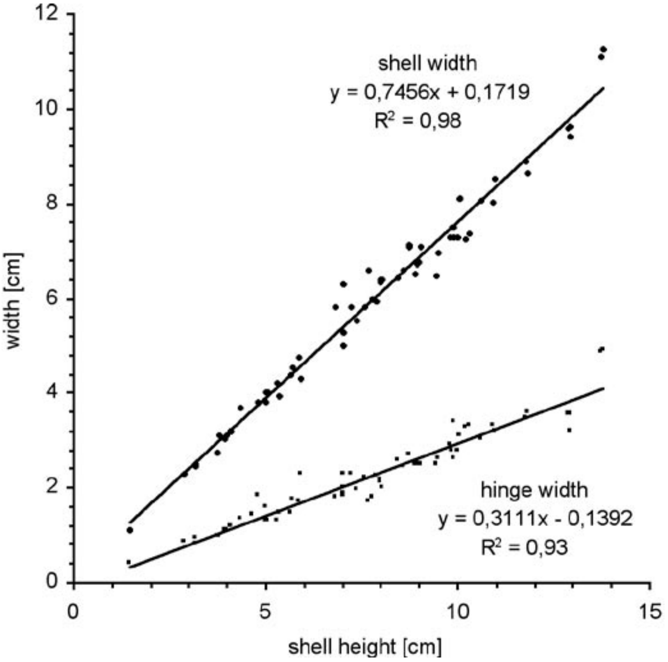

Fig. 8 Linear correlation of shell width *versus* shell height and also linear correlation of hinge width to shell height

Hinge height *versus* hinge width shows similar plots for Recent Atlantic and Pleistocene Mediterranean shells (Fig. 9). The overlap is considerable, although Mediterranean hinges seem to be slightly narrower and start to produce a hinge plate slightly earlier than their Atlantic counterparts. Atlantic shells switched to the second growth mode at a typical height of 10 cm, while Pleistocene Mediterranean shells switch at heights of 8 to 9 cm. The hinge width shows a linear correlation to shell height for Atlantic samples >10 cm (Fig. 8). This morphological relation can be used to reconstruct shell height estimates of Mediterranean populations where often only the hinges are preserved.

Microstructure and shell mineralogy

Polished or broken shell sections show a general subdivision into two layers visible to the naked eye, corresponding to the bimodal mineralogy of *A. excavata* with an outer calcitic and an inner aragonitic layer (Fig. 10). Staining with Feigel's solution of vertical transects along the main growth axes visualized this differentiation. XRD-investigations of powdered shell material from interior and exterior portions confirmed this first mineralogical zonation.

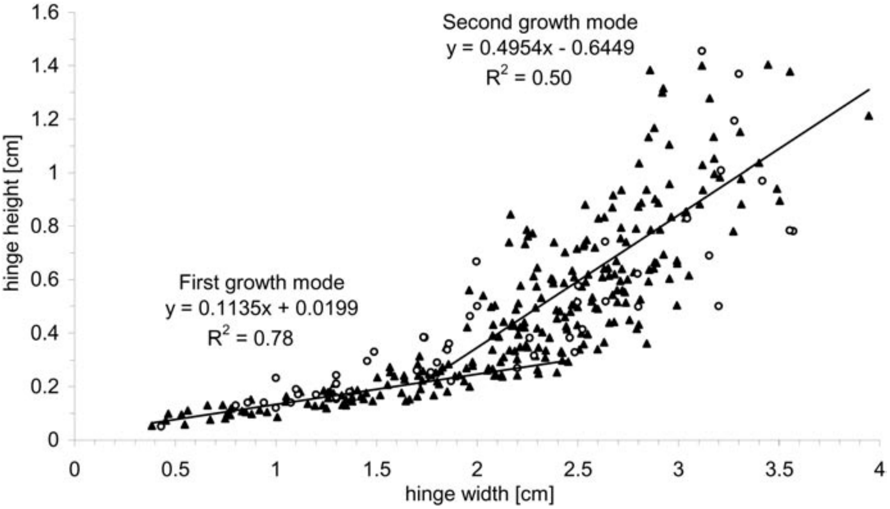

Fig. 9 Hinge width *versus* hinge height for Recent Atlantic *A. excavata* and Pleistocene Mediterranean specimens (triangles) plot in the same field, indicating that fossil Mediterranean shells attained similar sizes as their Recent Atlantic (circles) counterparts. Hinge parameters for shells of the first or second growth mode plot in different fields

Aragonite makes up the entire hinge and the interior valve side (Fig. 10). In the umbonal part of juvenile specimens this aragonitic layer is covered by a thin (<10 %) exterior calcitic veneer, which extends all the way to the valve margins. Along radial transects there is a considerable change in mineralogical proportioning, with the calcitic zone gaining in thickness towards more distal parts. At the pallial line calcite provides about 70 % of the valve over the remaining 30 % of interior

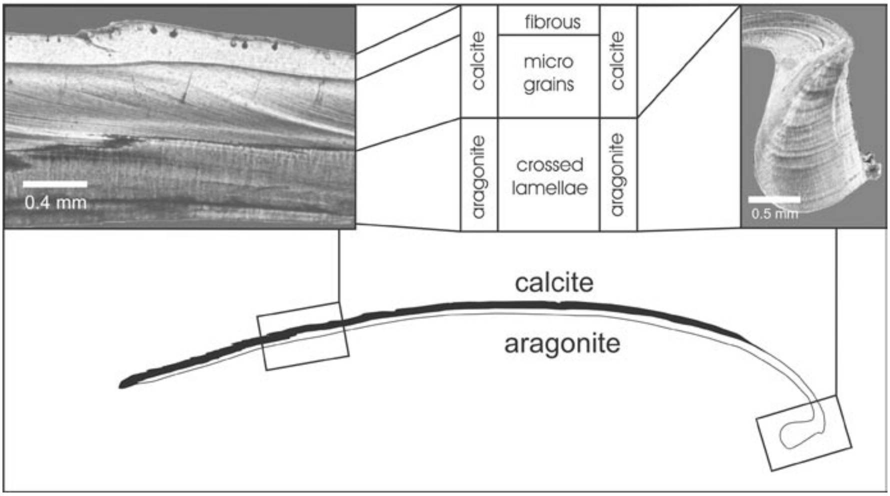

Fig. 10 Shell mineralogy and internal structure. The external calcite is often missing near the umbo

aragonite. The narrow zone (2 to 5 mm) between the pallial line and the margin is entirely formed by calcite. This calcitic zone frequently lacks on the umbonal to central shell portion of adult clams (Fig. 10). Instead intense bioerosion, which penetrates also into the aragonite, often marks this part.

Calcitic outer layer

The calcitic layer is responsible for the thin radiating ribs, which weakly sculpture the shell surface and which are regularly interrupted by growth rings (Figs. 1, 7). The ribs are pronounced towards the anterior and posterior margin of the clam and are least developed in the central portion. In juvenile specimens, the entire shell is covered by ribs. A smooth appearance on the central to umbonal portion in adult shells is due to secondary reduction of the calcitic layer (Fig. 10).

Aragonitic inner layer

The shiny shell interior is made of aragonite layers (Fig. 10). The surface of the interior valve side exhibits a characteristic zebra-fur pattern, which is also visible in shell cross-sections along the growth direction. The aragonitic interior layer shows a fine horizontal banding, with numerous bands close to the umbo and just one layer behind the pallial line. In correspondence to the number of external growth lines there is an equal increase in number of aragonite strata towards older and more proximal shell parts. Each stratum is thinnest in the medial shell part and thickest adjacent to the pallial line. Where the parasitic Foraminifera *Hyrrokkin sarcophaga* penetrated the shell and entered the mantle cavity with its pseudopodia, the mollusc formed a several millimetre thick callus (Fig. 1) of multi-layered aragonite to seal the wound.

Ultrastructure

SEM analysis of polished and slightly etched shell sections has revealed five distinct ultrastructural zones. The calcitic layer exhibits an outer fibrous-prismatic zone (Fig. 11) and a microgranular zone (Fig. 12) below. The aragonitic layer shows mainly a crossed-lamellar structure (Fig. 13), which grades into a radiating crossed-lamellar fashion in the hinge. On the inside of the umbones is a spatially restricted complex crossed-lamellar zone.

Fibrous-prismatic calcite

Thin calcite prisms make up the outermost sublayer of the shell (Fig. 11). They lie subparallel to the outer shell surface, but often inclined up to 20°. Mineralogical c-axes have the same orientation and large areas show synchronous extinction under crossed-nichols. This layer is usually 100 to 150 µm wide, with a well defined boundary against the granular sublayer underneath. Individual prisms reach 50 µm in length and 5 to 10 µm width. The calcite fibres show several forms. Most common are flat, lath-type prisms and rod-type fibres. The longest linear prisms occur on the shell exterior (Fig. 11), which grade inwards into thinner and shorter fibres. Larger prisms often form areas with equally oriented crystals. The broad lath-type prisms attain the largest sizes and show a minute internal banding. SEM-studied shell surfaces show fine prisms that are oriented approximately orthogonal to the closest growth line.

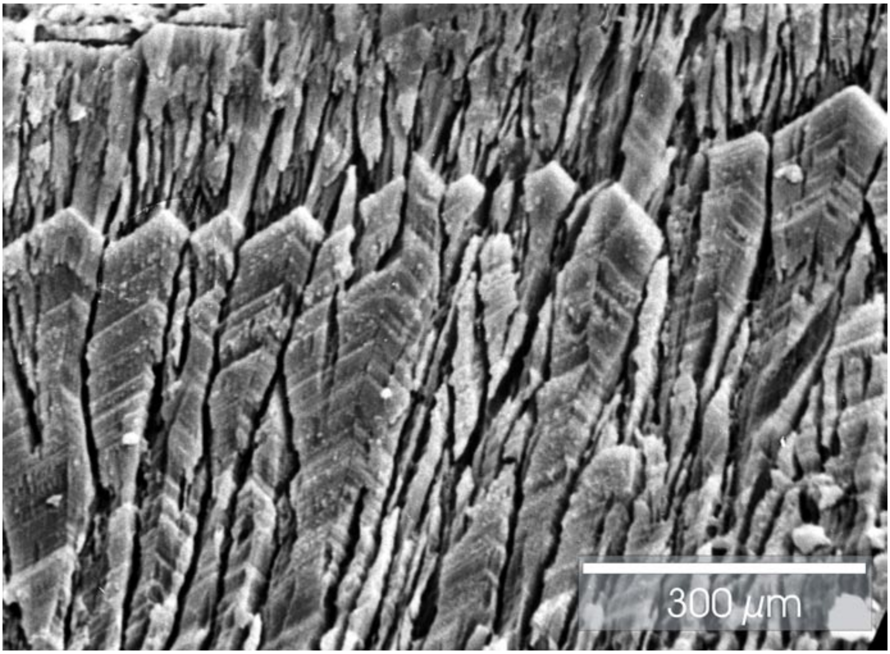

Fig. 11 Surficial SEM image of the exterior fibrous-prismatic calcite layer. The tips of the prisms point in growth direction and mark the boundary of a growth band. The interspaces between the prisms had been filled with intercrystalline organic matrix

Fig. 12 SEM image of the calcitic microgranular layer, situated below the fibrous-prismatic layer. The shape of the granules varies from near spherical to short fibres. The calcitic granules are often arranged in single-grain layers

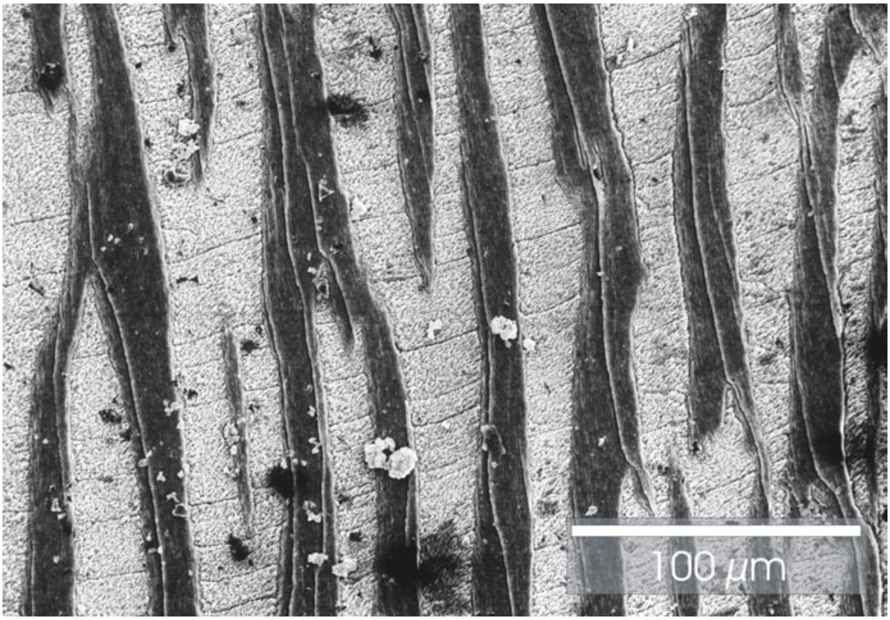

Fig. 13 SEM image of the crossed-lamellar interior aragonite. The first-order lamellae of this ultrastructural and mineralogical unit exhibit a characteristic zebra fur pattern

Microgranular calcite

Light-microscopy on this thickest calcite layer (170 to 250 µm) shows a fine varved appearance. An undulating asynchronous extinction under crossed-nichols is typical for this sublayer. SEM investigations revealed a microgranular ultrastructural zone. Minute calcite granules (Fig. 12), usually less than 1 µm in diameter, comprise 90 % of this sublayer. Irregular globular grains are arranged in monogranular layers, which are inclined against the outer fibrous layer at an angle of 10 to 15°. The lower part shows a shift from almost spherical grains to increasingly elongated particles, which grade inwards into fibrous calcite prisms at the boundary to the aragonitic below. Fibrous calcite is developed closely along the margin towards the aragonitic inner shell material, predominantly in adult specimens. The upper boundary against the outer fibrous-prismatic layer appears very sharp in thin sections, but shows a narrow transition zone under the SEM. This shift of different structure compositions seems to be triggered by the adjacent intercrystalline matrix.

Crossed-lamellar aragonite

Crossed-lamellar aragonite (Fig. 13) builds the interior shell-layer and makes up the entire hinge. Even at thin-section scale crossed-lamellae are visible as repeated vertical zones of extinction under polarized light. Those first-order lamellae (10 to 25 µm wide), which produce a straight to branching zebra fur pattern (Fig. 13), are aligned parallel to the valve outline. The crossed first-order lamellae commence as linear lamellae, but are often branching inward and grade into a radiating pattern in the hinge. SEM images show second-order lamellae within each ‘zebra stripe’, with equal orientation, responsible for the synchronous extinction of a single stripe under crossed-nichols. The second-order lamellae are inclined at an angle of 30 to 45° against the vertical axes of the first order lamellae, resembling a series of inclined books on a shelf board. The lamellae grow in optical continuity, across all internal growth increment boundaries.

Complex crossed-lamellar aragonite

The innermost shell layer, which occurs only on the inside of the umbo and at the hinge, is formed by complex-crossed aragonite lamellae. This ultrastructure zone is thickest (~100 µm) in large shells and is lacking in smaller specimens. Individual lamellae grow in optical continuity to the adjacent crossed-lamellae, starting from a distinct ultrastructural boundary. The first-order lamellae have widths of 15 to 30 µm and branch inward.

Myostracal aragonite prisms

The adductory muscle scar comprises fine aragonite prisms, with a complex layer-wise intertongueing of crossed-lamellar aragonite layers. The overall distribution of this myostracal aragonite is thickest at the muscle scar and thins gradually towards the valve margins. At the muscle scar this ultrastructure unit has a thickness of 150 µm and shows a banded structure, with individual layers of 5 to 15 µm thickness. Typically 10 µm high and wide pyramid-shaped aragonite prisms form these internal bands.

Discussion

The present-day distribution of *A. excavata* is largely bound to the continental margin at depths of 200 m and more (Fig. 2). The depth trend from deep sites (>1000 m) at the Strait of Gibraltar to increasingly shallower localities northwards to the Faroe Islands is likely to be guided by watermass boundaries. Depth range and spatial distribution of *A. excavata* are restricted by temperature (Bourcier and Zibrowius 1969), while salinity does not seem to play a major role. However, the large depth and temperature range of *A. excavata* sites makes it unlikely that these parameters are the singlemost important for the geographical spread of the species.

Depth is certainly not a limiting factor, while 3 and 13°C are the reported extreme temperatures withstood by this bivalve. The extreme depths (Dautzenberg and Fischer 1906; Dautzenberg 1927) reported around the Azores (>1500 to 3200 m) and the resulting lowest temperatures (~3°C) for *A. excavata* have to be regarded with suspicion. Exact depths of dredge samples could not be precisely measured at that time and the deepest records do certainly not refer to living specimens (pers. comm. H. Zibrowius 2004). The continental margin of western Europe and especially the shelf-break are entirely located within this temperature window. Therefore temperature cannot account for the northward 'climbing' of *A. excavata* sites. Western European shelf-break areas are characterized by strong currents, due to the boundary zone of intermediate watermass against deeper water bodies. Plankton from the water column gets enriched along these density boundaries. High levels of nutrients in combination with enforced water circulation allow for thriving cold-water coral ecosystems (Broch 1922) and occurrence of *A. excavata*, which favours similar conditions.

Temperature is though a possible limiting factor in the present day eurythermal Mediterranean Sea, where *A. excavata* seems close to its ecological boundaries, as does the scleractinian *L. pertusa*.

The deepest sites around the Canaries and off Senegal (Table 1), including the isolated record off Ivory Coast, are located in tropical latitudes. Upwelling on the African west coast (Le Lœuff and von Cosel 1998) provides cold watermasses at the continental rise and along narrow shelf edge, allowing for a spread of non-tropical species. The wide distribution gap south of Senegal, between Guinea Bissau and southern Liberia, might be due to the lack of upwelling and could explain this distribution pattern, which is also typical for other northern Bivalvia (Le Lœuff and von Cosel 1998).

Northern guests and oceanographic change

A. excavata was much more widespread during the Pleistocene in the Mediterranean basin (Fig. 2). Several submerged sites indicate a link to the palaeocommunity of 'White Corals' (*sensu* Pérès and Picard 1964) in general. But *A. excavata* does not only occur within mud-covered mound structures, which resemble their present day counterparts in the North Atlantic. The grab samples from the Strait of Sicily indicate that the bivalve also thrived on steep cliffs in absence of the bathyal azooxanthellate scleractinians. These two substrata observed in the Recent North Atlantic sites, cold-water corals and steep bedrock outcrops, occur also in the fossil record. Interestingly enough, the single specimen recorded by Terreni and Voliani (1995) was living on a muddy bottom, although attached to an artificial hard substratum (plastic canvas).

The obtained radiocarbon age of 39.9 kyr from a submerged *A. excavata* site from the Strait of Sicily (Table 1) supports the widespread distribution during the colder periods of the Pleistocene. *A. excavata* joins species like *Arctica islandica*, *Pseudoamussium septemradiatum* and *Mya truncata* as an example of a mollusc with a northern distribution pattern in the present day that spread into the Mediterranean during the last Ice Age and prior glacial periods as a so called 'northern guest' (Segre and Stocchino 1969; Colantoni et al. 1970; Colantoni 1973; Taviani and Colantoni 1979; Malatesta and Zarlenga 1986; Bouchet and Taviani 1992). Nevertheless, there is growing evidence that *A. excavata* is not a pure northern guest, as for example stated in Malatesta and Zarlenga (1986). Instead, the scarce Recent finds indicate that *A. excavata* is capable of surviving in the relatively warm basin at present. Extinct *Lophelia* colonies at North Cabliers Bank, between Spain and Morocco, had revealed an Early Holocene age of 8.5 kyr (±365 yr), which have been dated, using the TIMS U/Th-method (for details see Schröder-Ritzrau et al. 2005). Several *A. excavata* specimens from the same dredge sample indicate that the bivalve might have a similar age. Consequently it could have persisted in the basin throughout the Holocene. There is no doubt that Holocene warming radically diminished the distribution of *A. excavata* in the Mediterranean, which is at present a nutrient-poor isothermal sea with temperatures of around 13°C throughout the bathyal zone. *A. excavata* samples (LM-99-50) from the Tuscan archipelago (Remia and Taviani 2004), northeast of Corsica (Fig. 2), contain pristine shells, accompanied by subfossil valves. Comparing the state of shell degradation with known Late Pleistocene sites makes it likely that those are much younger, possibly latest Pleistocene as co-occurring corals (Remia and Taviani 2004). Shell degradation can only provide hints and further radiometric dating is necessary.

CYANA-submersible pictures from Canyon du Var (Fig. 6), document another possible live-record for *A. excavata* in the Mediterranean Sea (pers. comm. H. Zibrowius 2004). The paired valves hanging from an overhang indicate that the shells were alive or died recently.

Habitats

Marshall (2001) noted that the genus *Acesta* has been found associated with rocky or coral bank facies in deep waters worldwide. Isolated *Acesta* valves have been recorded from sedimentary facies (Vokes 1963); Marshall (2001) considered it likely that at least some of these were byssally attached to hard substrata when alive. Our observations for *A. excavata* from the northeast Atlantic and Mediterranean Sea support and extend these general observations. All photographic records from Norwegian waters suggest a strong link between *A. excavata* and the *Lophelia pertusa* coral sites (Fig. 3) in high biomass saxicolous communities indicating high food availability.

Surveys of *Lophelia*/*Madrepora* coral provinces on the Irish continental margin (Porcupine Seabight) have not recorded *A. excavata* from these habitats, showing that the bivalve is not as strongly linked to the bathyal coral facies as Norwegian surveys would suggest. Instead the smaller *Lima marioni* (Mikkelsen and Bieler 2003) was frequently found byssally attached to *L. pertusa* and *M. oculata* (pers. observ. A. Freiwald). Similarly, living *L. pertusa* and *M. oculata* occurrences in the Tyrrhenian and the Ionian Sea lacked *A. excavata*. This confirms that European cold-water coral facies do not always support populations of *A. excavata*.

Pleistocene submerged sites in the Mediterranean show that steep cliffs have been commonly inhabited by *A. excavata* (COR2-39; Table. 1), similar to the habitats observed in Scandinavian fjords. The steep rugged slopes of Cialdi Seamount in the Tyrrhenian Sea with the recovered *A. excavata* limestone (hardgrounds) provide another example for rock wall habitats (Fig. 5). These rock sites might be in fact more typical for *A. excavata* than the coral sites, where current research is focused. Cialdi Seamount is the first known submerged *A. excavata* occurrence in lithified Pleistocene deposits from a steep sediment starved submarine relief. High number of specimens, often with preserved shell material, document the fossilisation potential of *A. excavata* communities, even in sediment deprived seamount settings. Observations in Canyon du Var provide another record of rock wall habitats (Fig. 6).

Growth rate

Regular spacing of growth increments suggests a rhythmic, possibly annual, control on the shell deposition. Shells collected at different times of the year showed different completions of increments. It cannot be ruled out that increment boundaries are triggered by rhythmic spawning events or changing fluxes in food supply from the water column. First observations though make a seasonal emplacement of growth-increments likely. Thin-sections of the hinge showed a rhythmic internal banding with changing density and different amounts of intercrystalline organic matter. These internal changes were repeated in each ring, making an overriding seasonal control more likely than single events.

Accepting an annual character of the growth increments the shell shows two different modes of growth. The first phase ceases after the deposition of about 18 to 22 increments indicating that the shell reaches a size of about 10 cm within the first 18 to 22 years of its life. The second phase is resolved with possibly annual ribs on the hinge plate, but shows little further size gain (Fig. 7). A typical lifespan of 50 to 80 years, including the first growth phase, is suggested by the number of hinge ribs (pers. comm. J. Elvestrand 2003).

Underwater images from Scandinavia (Figs. 3, 4) all showed that large *A. excavata* live out in the open both on steep rock surfaces (e.g., Kosterfjord and Trondheimfjord) and on cold-water corals of the northeast Atlantic (e.g., Sula Ridge). That smaller *A. excavata* were not visible suggests that they may be cryptic, only moving out onto open areas when they are large enough to be safer from predators. More likely though is a biased size distribution due to the two growth modes (Fig. 7) with an early gain of maximum size during its life time (Fig. 9).

It is possible that the monogranular layers (Fig. 12) of the second calcite layer reflect diurnal deposition of shell calcite, which is also depicted by the banding of individual prisms in the outermost fibrous-prismatic layer.

Biometry

Similar biometric patterns of Pleistocene Mediterranean specimens and Recent Atlantic shells (Fig. 9) indicate that *A. excavata* was thriving under glacial oceanographic conditions in the Mediterranean basin. They show about the same maximum sizes, as their Recent Atlantic counterparts.

Samples from both areas exhibited the abrupt shift between growth modes at around 10 cm height, from flat to more arched valves. The sex change during the lifetime (Järnegren 1999), might account for the abrupt switch between the two observed growth modes. The timing of sex-change from male to female and the change from a flat to a more arched valve seems to take place at the same stage of shell growth.

Ultrastructure

Detailed ultrastructure observations were made in anticipation of isotopic studies that need to be based on a sound understanding of shell structure and composition. The observed structures reflect the characteristics for Limidae, given in Carter (1990), with a fibrous-prismatic outer calcitic layer and a crossed-lamellar interior aragonitic layer. The fine costae on the exterior shell surface (Figs. 1, 7) are exclusively built by the fibrous-prismatic calcitic subzone (Fig. 10). Nevertheless, the sculpture is not guided by the microstructure. The prisms typically run across the costae at an angle, their directions are only equal on the medial shell portion. It is likely that the ribs follow a pattern provided by the precipitating mantle, while the prismatic microstructure follows crystallographic laws. The first-order lamellae of the crossed-lamellar interior aragonitic are oriented commarginal. The exterior fibres and prisms are in every position of the shell orthogonal to the lamellae underneath. This pattern allows for thin shells with a strong architecture, even for large valves.

Aragonitic strata are difficult to count in central portions, since their crossed lamellar ultrastructure shows a syntaxial mineralogical growth across the boundaries of individually deposited layers (Fig. 13). This often makes a distinction of internal growth increments impossible. Therefore the stack of layers cannot be isotopically subsampled for each period precisely, nor would it provide inter-annual resolution.

The calcitic layer has a much simpler growth pattern. Typical growth ring widths on the external surface offer about 0.4 to 1.0 cm of sampling interval per growth increment. The sampling interval in the corresponding aragonitic layer on contrast is usually less than 0.5 mm (best case). It becomes obvious from these growth patterns that only calcitic shell portion with its macroscopic banding is accessible for isotopic sampling with a hand-held drilling device. Based on the observed ultrastructure, we propose an isotopic sampling within the outer calcitic zone of the shell (Fig. 10). The two calcitic zones (fibrous-prismatic and micro-granular) cannot be sampled individually with a hand held drilling device. The resolution of the aragonite is highest in the hinge, where cyclic banding is visible under the microscope, but is not accessible for manual sampling.

Conclusions

Fast growth rate, compared with other organisms containing calcified structures from the same environment, its widespread distribution and its frequent co-occurrence with cold-water corals, make *A. excavata* an ideal sampling object for palaeoenvironmental studies. Moreover, shell architecture is much simpler than in the associated cold-water corals. Its extensive distribution along the northeast Atlantic continental margin and its widespread subfossil to fossil Mediterranean communities will allow for a margin-wide assessment of environmental changes for cold-water coral environments. Both submerged and emergent, uplifted Quaternary fossil occurrences might allow us to extend datasets into the past. We propose that sclerochronology be applied to large limid bivalves to study intermediate and cold waters, as they are large, clearly banded and occur world-wide in bathyal environments of tropical and boreal settings.

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