

Phylogeny and biogeography of pholadid bivalve *Barnea* (*Anchomasa*) with considerations on the phylogeny of Pholadoidea

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The paper examines the systematics, phylogeny and biogeographical history of *Barnea* (*Anchomasa*), which is one of the most abundant and diversified of modern pholadid bivalves. The range of morphology of its distinctive characters and comparisons with other pholadoidean taxa are described in detail. An extensive cladistic analysis based on morphological characters at genus and subgenus levels allowed the inclusion of *B.* (*Anchomasa*) into the phylogeny of Pholadoidea and the establishment of its most appropriate taxonomic position. The analysis confirms that *Barnea* s.s. and *B.* (*Umitakea*) are its closest relatives and that the morphological similarities to other taxa are mainly due to plesiomorphies. The fossil record and the data on the present-day distribution contributed to trace the biogeographical history of *B.* (*Anchomasa*). The present-day biogeography is marked by the disjunct distribution of species. Species are distributed mainly either along the Atlantic and Pacific coasts of the American continent (American group) or in the Indo-West Pacific region (Indo-West Pacific group). Both these groups have distinct morphological features and biogeographical structures. The fossil record and the known geodynamic scenario suggest a relationship of direct derivation between the Indo-West Pacific group and a stock of north-eastern Atlantic to Paratethyan species. This reflects a vicariant event related to the closure of the connection between western Tethys and the Indian Ocean in the middle Miocene. The American group presumably arose from the European stock during the Late Pliocene by dispersal towards the eastern coasts of North America and rapid southward diffusion. A relative differentiation within the American group is probably related to the last phases of emergence of the Panama Isthmus. The cladistic analysis also gives suggestions for the reconstruction of the phylogeny of the superfamily Pholadoidea. It confirms the interpretation of several characters sustained by previous authors. However, it also shows remarkable differences to the previous taxonomic arrangements. Pholadinae includes only taxa having the protoplax and it appears to be the sister-group of a major clade composed mainly of two groups, namely Martesiinae–Jouannetiinae and Xylophaginae–Teredinidae. The Martesiinae are paraphyletic whereas the obligate wood-boring Xylophaginae and Teredinidae form a well-supported monophyletic group.

Key words: Mollusca, Bivalvia, Pholadoidea, *Barnea*, *Anchomasa*, phylogeny, historical biogeography.

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Introduction

The pholadoideans are a group of bivalves specialised for boring into a wide variety of substrates (Turner 1969). Their mode of life clearly reflects on a set of peculiar features of the shell and soft body which has attracted the attention of several authors (see for example Hoagland and Turner 1981 for a list of references and Turner 1998 for a short synthesis). Relevant characters are the truncate foot with discoid extremity adapted for suction and extended out of the shell through a narrow to very wide anterior gape, the outward reflection of the anterodorsal margin of the shell, forming the mostly external attachment area of the anterior adductor muscle, and the simplified hinge structure lacking teeth and with internal ligament small to absent. Other special features (for a list and descriptions see Turner 1969: N705) distinguish the different groups of pholadoideans, e.g., the acces-

sory plates (protoplax, metaplax, mesoplax, hypoplax, and siphonoplax) for supplementary protection of the soft body, and the apophyses acting as structures for the insertion of the pedal muscles.

The major systematic arrangement proposed by Turner (1954, 1955, 1966, 1969) and subsequent authors (e.g., Vokes 1980; Amler 1999), subdivides the pholadoideans into two families, namely Pholadidae Lamarck, 1809 and Teredinidae Rafinesque, 1815. Several authors described their features and mode of life (see references in this paper and in Baker and Padilla 2004). The teredinids (shipworms) are characterised by having a strongly reduced shell and worm-like soft body, the burrow lined by a calcareous tube on which the siphonal retractors are inserted, and pallets closing the tube during the siphons' withdrawal. All the teredinids, apart from very few exceptions (*Kuphus* Guettard, 1770 and possibly some species of the genus *Uperotus* Guettard, 1770; Turner 1998), are obli-

gate wood-borers. In fact, they utilise the wood for food and are provided with a wood-storing caecum in their alimentary apparatus. Furthermore, the presence of bacterial endosymbionts in the gills, allowing the digestion of cellulose, is ascertained in many species (Turner 1998 and references therein). In contrast to the teredinids, the great majority of Pholadidae (piddocks) are filter-feeders, namely the Pholadinae Lamarck, 1809, Jouannetiinae Tryon, 1862, and Martesiinae Grant and Gale, 1931. They bore into inorganic and organic substrates of variable hardness and, occasionally, into waterlogged and decayed wood. A few Martesiinae are almost exclusively wood-borers but they lack the wood-storing caecum and they filter-feed. The Xylophaginae Purchon, 1941 represent the only pholadid group of obligate wood-borers which differ from the other pholadids by living mainly in deep-sea environments.

This paper investigates the subgenus *Barnea* (*Anchomasa*) Leach, 1852, which is one of the most widespread and abundant pholadid taxa, including about fifteen living and fossil species. The taxon has a worldwide present-day distribution. The type species, *Barnea* (*Anchomasa*) *parva* (Pennant, 1777), occurs along the Atlantic coasts of the British Isles and France. A number of species are known from the Indo-West Pacific region and a few other species from the Atlantic and Pacific coasts of the American continent. Detailed analysis shows that the species living along the coasts of the American continent differ from the Indo-West Pacific species in having some distinctive characters (see details below). The present study attempts to understand the origin of that differentiation.

Institutional abbreviation.—MGPD, Geological and Palaeontological Museum of the Department of Geosciences, University of Padua, Italy.

Material and methods

As a first step a morphological analysis at species level was accomplished in order to identify the distinctive characters of *B.* (*Anchomasa*) and their variability, and to compare the subgenus with other pholadoidean taxa. The morphological study is founded on the critical examination of the data available either on the fossil species (Pennant 1777; Sowerby 1818; Dujardin 1837; Wood 1850, 1874; Fischer 1866; Nyst 1878–81; Dolfuss and Dautzenberg 1902; Merklin and Nevevskaya 1955; Zhizhchenko 1959; Glibert 1963; Sakhelashvili 1965; Glibert and Van de Poel 1966; Kennedy 1974; Janssen et al. 1984; Kensley and Pether 1986; Beu and Maxwell 1990; Nevevskaya et al. 1993; Beu 2006; Monari 2008 and references therein) and living species (Say 1822; Hedley 1893; Bartsch 1915; Carcelles 1944; Allan 1950; Nicklès 1950; Turner 1954; Purchon 1955; Phillips et al. 1984; Oliver 1992; Bosch et al. 1995; Ito 1998, 1999; Lamprell and Healy 1998; Poutiers 1998; Turner 1998; Higo et al. 1999; Robba et al. 2002), and on the analysis of the material deposited at MGPD.

A cladistic analysis at genus and subgenus levels was performed to establish the phylogenetic relationships of *B.* (*Anchomasa*) with the other pholadid taxa, to determine the origin of their similarities and differences, and to place the subgenus in the most appropriate taxonomic position. In order to obtain maximally reliable results, the analysis was extended to all the pholadoidean taxa supported by a sufficient amount of available data. The study is based on the rigorous selection of characters and taxa extracted from the contributions of previous authors and from personal observations. In particular, available data come from the following sources: Purchon (1941, 1955, 1987), Clench and Turner (1946), Fitch (1953), Turner (1954, 1955, 1961, 1962, 1966, 1969, 1972a, 1972b, 1998, 2002), Ansell and Nair (1969), Smith (1969), Röder (1977), Turner and McKoy (1979), Hoagland and Turner (1981), Savazzi (1982), Hoagland (1983), Wilson and Kennedy (1984), Okamoto and Habe (1987), Kelly (1988a), Kennedy and Armentrout (1989), Turner and Santhakumaran (1989), Evseev (1993), Pacaud (1998), and Lopes et al. (2000).

Such an extensive analysis provides suggestions also for the interpretation of the phylogeny of the whole superfamily. A discussion of the main results is given below, especially concerning the validity of the current systematic arrangement, the verification of the monophyletic composition of the families and subfamilies, and the significance of the characters of the shell for the reconstruction of the phylogeny of the pholadoideans.

The present-day distribution of *B.* (*Anchomasa*), which reveals the presence of different biogeographical groups, and critically revised data concerning the fossil record are used in relation to the geologic evolution of the regions concerned, allowing the biogeographical history of the subgenus to be elucidated. Finally, the characters distinctive of the different biogeographical groups were employed in a simple cladistic test of the hypotheses of historical biogeography.

Systematics

Suborder Pholadina H. Adams and A. Adams, 1858

Superfamily Pholadoidea Lamarck, 1809

Family Pholadidae Lamarck, 1809

Subfamily Pholadinae Lamarck, 1809

Genus *Barnea* Leach in Risso, 1826

Subgenus *Anchomasa* Leach, 1852

Type species: *Anchomasa pennantiana* Leach, 1852 (a junior synonym of *Pholas parva* Pennant, 1777).

Characters and variability.—According to Turner (1954, 1969), *B.* (*Anchomasa*) belongs to the genus *Barnea* in having a simple (not septate) umbonal reflection and a single, anterodorsal accessory plate represented by the lanceolate, undivided and calcareous protoplax. Moreover, *Barnea* s.s. and *B.* (*Anchomasa*) share the presence of long and thin apophyses

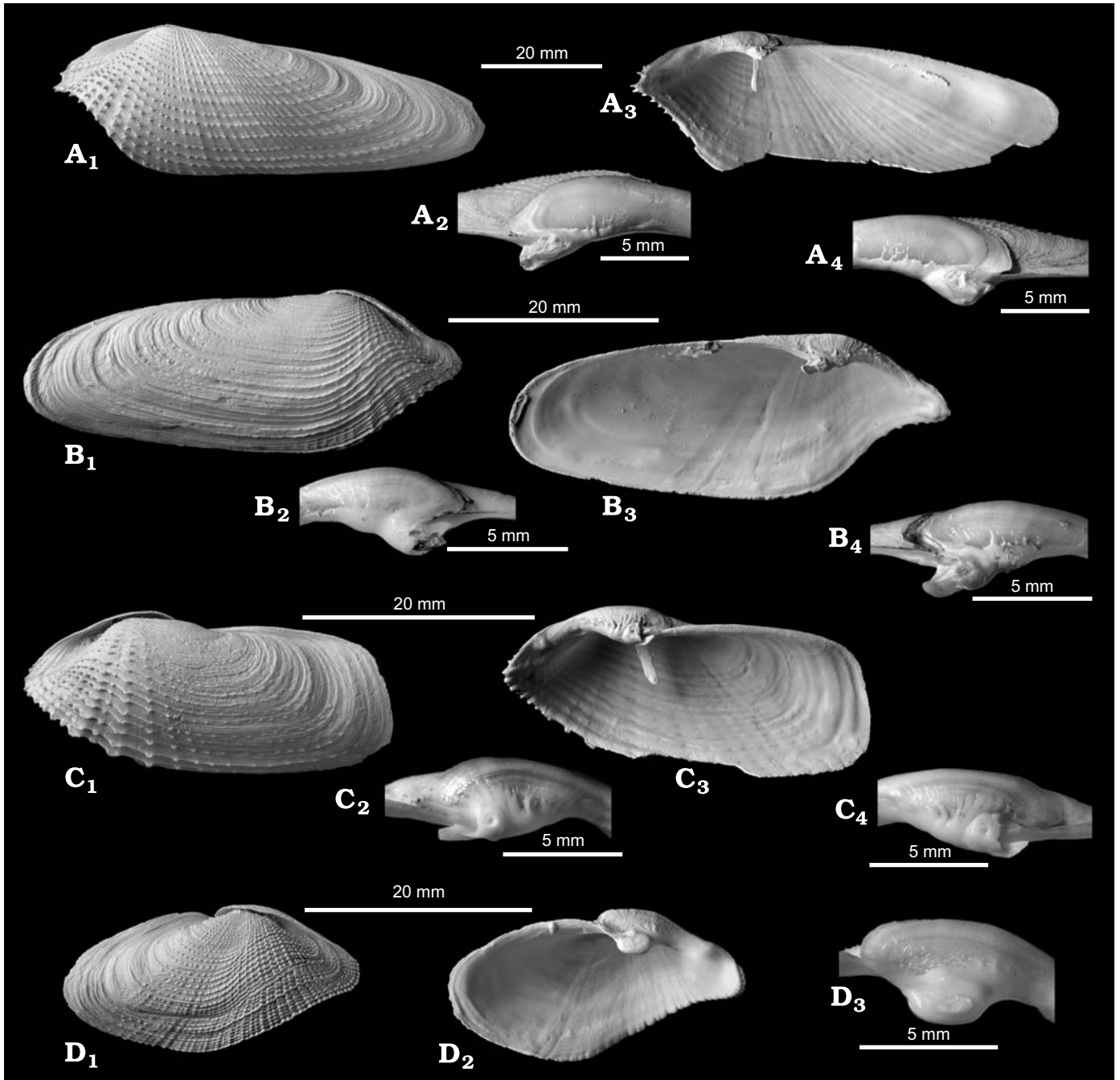


Fig. 1. Variability of pholadoidean bivalve *Barnea* (*Anchomasa*) Leach, 1852. **A.** *Barnea* (*Anchomasa*) *manilensis* (Philippi, 1847), Recent, Natal, Durban Bay, South Africa; MGPD30087b, external view of left valve (A₁), and detail of the umbonal region showing the chondrophore (A₂); MGPD30087a, internal view of right valve (A₃), and detail of umbonal region showing the resilifer (A₄). **B.** *Barnea* (*Anchomasa*) *obturamentum* (Hedley, 1893), Recent, Largs Bay, South Australia; MGPD30089b, external view of right valve (B₁), and detail of the umbonal region showing the resilifer (B₂); MGPD30089a, internal view of left valve (B₃), and detail of umbonal region showing the chondrophore (B₄), apophysis not preserved. **C.** *Barnea* (*Anchomasa*) *truncata* (Say, 1822), Recent, Suffolk County, New York; MGPD30092b, external view of left valve (C₁) and detail of the umbonal region showing the chondrophore (C₂); MGPD30092a, internal view of right valve (C₃) and detail of umbonal region showing the resilifer (C₄). **D.** *Barnea* (*Anchomasa*) *parva* (Pennant, 1777), Recent, Bristol Channel, England; MGPD30091b, external view of right valve (D₁); MGPD30091a, internal view of left valve (D₂) and detail of umbonal region showing the absence of chondrophore (D₃), apophysis not preserved.

(Pacaud 1998). *B.* (*Anchomasa*) differs from *Barnea* s.s. in having a wide pedal gape (Turner 1954, 1969) and, consequently, well-defined prora (sensu Kelly 1988a).

The main characters varying in *B.* (*Anchomasa*) are the general morphology of the shell, the position of the umbo

and the shape of the posterior margin (Fig. 1). In most of the living species, the shape of the shell is elongate to tapered, with length clearly exceeding height. However, in the type species, *B.* (*A.*) *parva* (Fig. 1D), and in some fossil species, such as *Barnea* (*Anchomasa*) *palmula* (Dujardin, 1837) and

Barnea (Anchomasa) dumortieri (Fischer, 1866), the shell is much shorter in the antero-posterior direction. A variably marked radial umbonal-ventral depression of the shell is often present in *B. (A.) parva* (Fig. 1D₁) which is hardly visible or is absent in the other species.

The umbo is variably displaced in anterior position. The outline of posterior margin is lanceolate to subtruncate. A subtruncate posterior margin is usually associated with a wide posterior gape. In contrast, species having a lanceolate posterior part of the shell commonly develop a narrow posterior gape. The pedal gape is always wide and oval in outline. However, the concavity of its margin is slightly variable and, consequently, the prora project to a varying degree. The dorsal condyle, which is formed by the internal protrusion of the umbo below the umbonal reflection, is small to strong. The robustness of the apophyses and their inclination with respect to the direction of the dorsal margin are relatively variable as well. The ornament is composed of radial alignments of imbrications. In most species, they are well-evident in the anterior slope, where they range from few, strong and well spaced, to numerous, dense and relatively feeble. They attenuate towards the posterior part, where they rarely persist.

As described in detail below, the combination of some of these aspects of variability characterizes groups with distinct geographical distribution.

Adults of *B. (A.) parva* lack the chondrophore and ligament (Purchon 1955) (Fig. 1D₃). On the contrary, *Barnea (Anchomasa) manilensis* (Philippi, 1847) shows a prominent chondrophore in the early juvenile left valve becoming a spiny vestigial process in the adult shell (Ito 1998, 1999) (Fig. 1A₄). A small left chondrophore and right resilifer occur also in adult specimens of *Barnea (Anchomasa) obturamentum* (Hedley, 1893) (Fig. 1B₂, B₄), *Barnea (Anchomasa) truncata* (Say, 1822) (Fig. 1C₂, C₄), and *Barnea (Anchomasa) similis* (Gray, 1835) (Suter 1913). Ito (1998) maintained that the left chondrophore, right resilifer and active internal ligament are present in the early post-larval shells of many pholadoideans and these features should be considered as plesiomorphies of the superfamily inherited from bivalves having a chondrophore only in the left valve. According to that author, during the adult growth these structures become vestigial or disappear in many species, but they can also persist in independent lineages by paedomorphosis of the first fibrous ligament. The phylogenetic analysis below confirms the ontogenetic plasticity of the chondrophore, which acts as a highly homoplastic character.

Comparisons.—*Barnea (Anchomasa)* shows similarities with *B. (Umitakea)* Habe, 1952. Turner (1969) considered Habe's subgenus to be a junior synonym of *B. (Anchomasa)*. On the contrary, Vokes (1980) treated *B. (Umitakea)* as a distinct taxon. Evseev (1993) deeply studied the type species, *Barnea (Umitakea) japonica* (Yokoyama, 1920) and compared it with *B. (A.) parva*, mainly based on the data published by Purchon (1955) and Turner (1954). Evseev (1993) listed some details of the anatomy of the soft body, e.g., the long caudal process of the visceral mass, the isometric and compressed ventricle

and the morphology of the midgut, considered to be distinctive characters at supraspecific level. However, these characters are unknown in the other species of *B. (Anchomasa)*. Thus, their supraspecific variability as yet can not be defined.

Ito (1998, 1999) underlined that *B. (U.) japonica* differs from *B. (A.) manilensis* in retaining a prominent chondrophore at the adult stage. As mentioned above, the adult chondrophore in *B. (Anchomasa)* is highly variable and in some species it is slightly less prominent than that illustrated by Evseev (1993) for *B. (Umitakea)*. Differences based on that feature may not be valid to make distinction among these taxa.

B. (Umitakea) differs from *B. (Anchomasa)* in characters of the general shape of the shell. They are evident in comparing the respective type species, although the overall variability of *B. (Anchomasa)* makes the differences less distinct. *B. (Umitakea)* has a much higher shell and the length to height ratio clearly exceeds the field of variability of *B. (Anchomasa)*. The anteroventral margin is slightly concave to slightly convex and, consequently, the prora project less. Moreover, *B. (Umitakea)* has a much wider posterior gape (Evseev 1993).

Barnea (Taiwanobarnea) Wang, 1983, from the late Miocene of Taiwan, shares with *B. (Anchomasa)* and *B. (Umitakea)* the presence of a wide pedal gape and an undivided, calcareous protoplax as a single accessory plate. The degree of the antero-posterior elongation of the shell is intermediate between *B. (Anchomasa)* and *B. (Umitakea)*. However, the moderately prominent prora and the inflation of the anterior region of the shell would indicate closer affinities with *B. (Umitakea)*. Furthermore, according to Wang (1983), the type species, *Barnea (Taiwanobarnea) shihchoensis* Wang, 1983 is very similar to *B. (U.) japonica*, differing in the convex outline of the anteroventral margin and in the absence of a spiny sculpture on the anterior part of the shell. However, as mentioned above, the slightly convex outline of the anteroventral margin is an aspect of the variability of *B. (Umitakea)* as well. Since the differences in the ornament pattern could be not sufficient alone to justify the institution of a distinct subgenus, *B. (Taiwanobarnea)* is strongly suspected to be a junior synonym of *B. (Umitakea)*. These considerations and the lack of information on the internal shell characters determined the exclusion of *B. (Taiwanobarnea)* from the cladistic analysis below.

B. (Anchomasa) is also very similar to *Cyrtopleuropsis* Pacaud, 1998. In fact, the ranges of variation in the shape of the shell, the outline of the anterior area and the ornament are widely continuous among the two taxa. Moreover, as discussed above, the presence of the chondrophore, which Pacaud (1998) included in the diagnostic features of *Cyrtopleuropsis*, is not useful for distinguishing Pacaud's genus from *B. (Anchomasa)*. *Cyrtopleuropsis* differs from *B. (Anchomasa)* in having wide and spoon-shaped apophyses and the posterior slope ornamented by granulations. Accessory plates of *Cyrtopleuropsis* are unknown.

B. (A.) parva has general similarities with *Nipponopholas satoi* Okamoto and Habe, 1987, type species of *Nipponopholas* Okamoto and Habe, 1987 and with the species be-

longing to the genus *Zirfaea* Leach in Gray, 1842. However, in *Nipponopholas* and *Zirfaea* the single accessory plate is represented by the mesoplax. Furthermore, *Zirfaea* has a ventral condyle and an internal umbonal-ventral ridge corresponding to an external sulcus. However, in the fully adult shells of *Zirfaea crispata* (Linnaeus, 1758) these features become reduced (Turner, 1954) and an evident internal radial ridge and ventral condyle are present in the early juvenile shells of *B. (A.) manilensis*, but disappear completely during adult growth (Ito 1999).

Phylogenetic analysis

Characters.—The selection of characters (Appendix 1) started from the analysis of the list at species level made by Hoagland (1983), on which Hoagland and Turner (1981) based their phenetic analysis. Among the characters indicated by these authors, only features showing a sufficiently homogeneous distribution at genus and subgenus levels were considered. Then, the list was upgraded and completed by the inclusion of data coming from other sources (see above for references). Most of the characters are features of the shell and accessory structures. The aspects of the soft body were included mainly to ensure a balanced evaluation of the Teredinidae.

The main constraints are exerted by the scarcity of information on the ontogenetic changes of the selected characters. Furthermore, some aspects of the soft body, which previous authors (e.g., Purchon 1955; Evseev 1993) presumed to be significant at supraspecific level on the basis of comparisons among few species, were excluded from the analysis. These characters lack information on a sufficient number of species and this prevents verification of their validity at genus and subgenus levels.

The definition of morphological terms are mainly those established by Turner (1954, 1955, 1966, 1969, 2002) with the emendation made by Kelly (1988a) suggesting the term “prora” as a replacement for “anterior beak”. In the matrix (Appendix 2), characters depending on the states of other characters are codified as not-applicable (N), but processed as missing data identified by “?”. Autoapomorphies were excluded from the list of characters and the matrix.

Taxa.—Selection of taxa was based on the list of genera and subgenera ascribed by Turner (1954, 1955, 1966, 1969) to the Pholadoidea, with the addition of *B. (Umitakea)*, *Cyrtopleuopsis*, and *Nipponopholas*. Furthermore, *Netastoma* Carpenter, 1864 has been used in place of *Netastomella* Carpenter, 1865 (Vokes 1980: 190). From Turner’s (1969) list, only living and fossil taxa supported by a sufficient amount of information on the selected characters are included in the analysis. Most of the genera added by Vokes (1980) in the list of valid taxa lack that requirement.

As far as the Teredinidae is concerned, several characters indicated by Hoagland and Turner (1981) and Hoagland

(1983) as exclusive to that group were not considered here. Only a number of teredinid genera are included which cover the whole range of morphological diversity in the context of the selected characters. Further inclusions would have added taxa with coding already present in the matrix. For this reason, the relationships among the teredinid genera resulting from the present study may not be indicative of the internal subdivision of the family which should be tested by a more detailed subset analysis.

Outgroup.—The selection of the outgroup is mainly based on the molecular phylogenetic analyses recently presented by Giribet and Distel (2003) and Taylor et al. (2007). Giribet and Distel (2003: 81) found that the family Sphaeriidae Deshayes, 1854 tends to be the sister-group of a clade including the Pholadinae, Xylophaginae, Teredinidae, Myidae Lamarck, 1809, Corbulidae Lamarck, 1818, Dreissenidae Gray, 1840, Mactridae Lamarck, 1809, and Ungulinidae H. Adams and A. Adams, 1857. Moreover, the pholadoideans are polyphyletic and included in a monophyletic group together with the Myidae, Corbulidae, and Dreissenidae (Giribet and Distel 2003: 82). According to Taylor et al. (2007), the Sphaeriidae are the sister-group of a clade composed of Pholadidae, Teredinidae, Dreissenidae, Myidae, and Corbulidae. The Pholadidae and Teredinidae are in paraphyletic relationships. Thus, *Sphaerium* Scopoli, 1777 (Sphaeriidae) was selected as outgroup. In addition, two myoidean taxa were included in the matrix, namely *Mya (Arenomya)* Winckworth, 1930 (Myidae) and *Corbula Bruguière*, 1797 (Corbulidae). The analysis of their characters is mainly based on personal observations and on information contained in the following sources. Data on *Sphaerium* were extracted from Keen and Dance (1969), Castagnolo et al. (1980), Lee (2001), Giribet and Wheeler (2002), and Korniushev and Glaubrecht (2002). Data sources on *Mya (Arenomya)* come from Yonge (1923), Pumphrey (1938), Fitch (1953), Keen (1969), Purchon (1987), and Giribet and Wheeler (2002). Anderson and Roopnarine (2003) and Keen (1969) supplied information for *Corbula*.

Method.—The data matrix is composed of 39 taxa and 47 characters (Appendix 2). A heuristic search, with random addition sequence of 100 replicates and TBR branch-swapping algorithm, was performed employing Paup 4.0b10 (updated version of PAUP 4.0 beta version; Swofford 1998). Characters were treated as unordered and equally weighted, and changes of character states were optimised under both ACCTRAN and DELTRAN conditions. Trees were rooted using the default outgroup (*Sphaerium*). Rooting by inclusion of *Mya (Arenomya)* and *Corbula* into the outgroup produced the same ingroup trees. Then, the analysis by successive approximation reweighting, using characters weighted by maximum values of rescaled consistency index, was performed under the same search setting as that of the unweighted search. The bootstrap method under weighted conditions supplied the support values for clades. The resultant extremely long computational bootstrap time, was reduced by

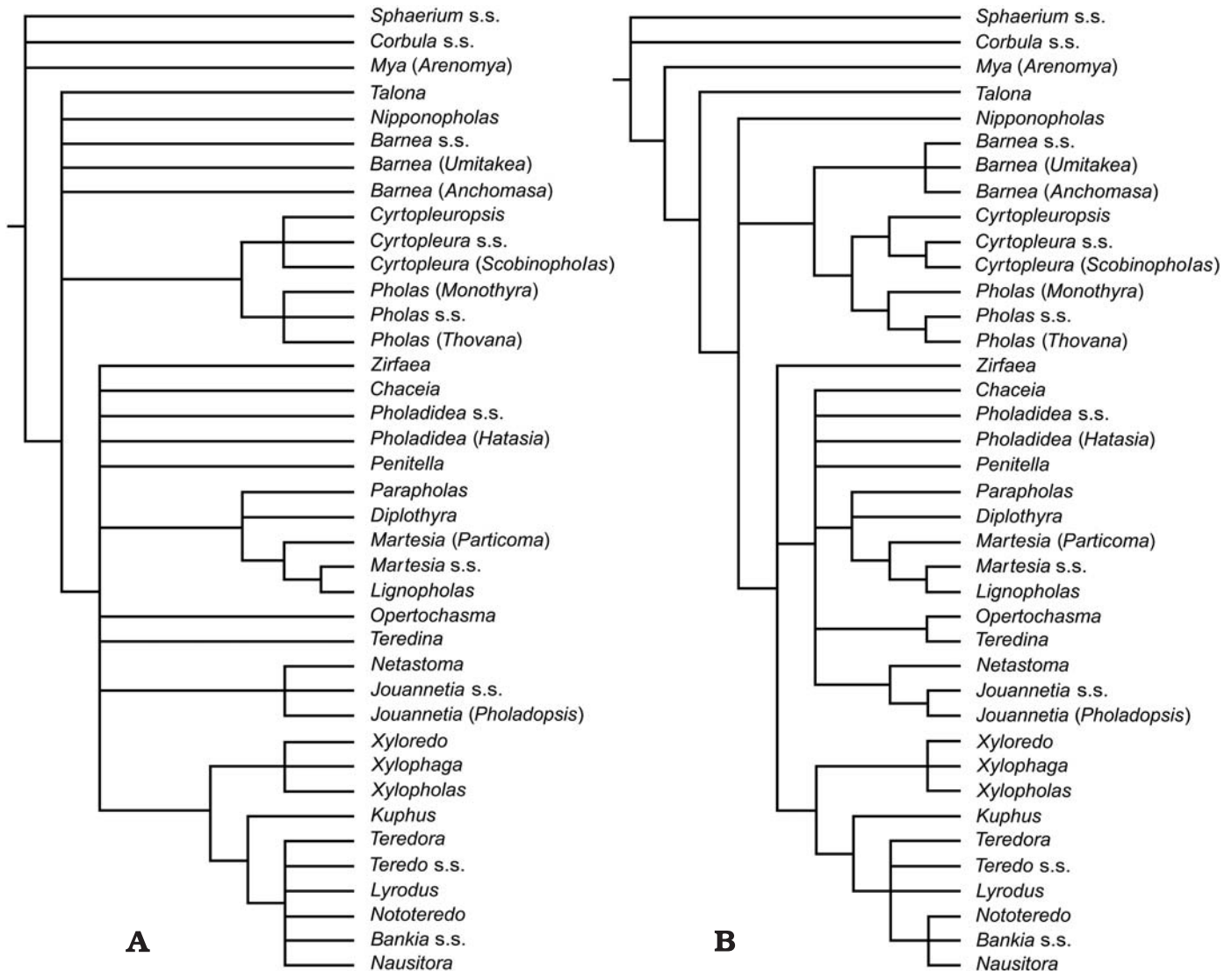


Fig. 2. Phylogeny of Pholadoidea. **A.** Strict consensus tree obtained by heuristic search with unordered and equally weighted characters. **B.** Strict consensus of 173 most parsimonious cladograms retained by successive approximation weighting.

imposing a limit of 1000 replicates and 10000 maximum trees retained per replicate. These constraints were established by increasing gradually both the number of replicate and maximum trees up to the stabilisation of the bootstrap tree and support values.

Results.—The unweighted heuristic search found 3192 maximally parsimonious cladograms [length (L) 96, consistency index (CI) 0.54, retention index (RI) 0.85, rescaled consistency index (RC) 0.46]. The strict consensus is shown in Fig. 2A. The reweighting drastically reduced the number of most parsimonious cladograms. It retained 173 cladograms (CI 0.78, RI 0.94, RC 0.74), all included in the most parsimonious cladograms obtained by the unweighted search. The strict consensus tree (Fig. 2B) retains the ingroup node and all the internal nodes of the unweighted strict consensus tree.

As underlined by Smith (1994), consensus trees are arbitrary and conventional solutions. However, the Majority

Rule consensus tree obtained by the analysis (Fig. 3) corresponds to one of the most parsimonious cladograms. Thus, that cladogram is maintained as the most probable representative of the phylogeny of the superfamily under the assumptions and list of characters here considered.

In contrast with the analyses of Giribet and Distel (2003) and Taylor et al. (2007), the Pholadoidea result to be a monophyletic group. They are organised in clades which partly correspond to the major taxa established by Turner (1954, 1955, 1966, 1969). *B. (Anchomasa)* belongs to a restricted clade of Pholadinae, composed only of taxa sharing the presence of a protoplax (character 24), which is the exclusive synapomorphy of that group. The absence of protoplax in *Talona* Gray, 1842 and *Zirfaea*, taxa ascribed by Turner (1969) to the subfamily Pholadinae, and in *Nipponopholas* determines their exclusion from that clade.

Barnea s.s., *B. (Anchomasa)* and *B. (Umitakea)* form a distinct clade (Fig. 4), although barely supported by the boot-

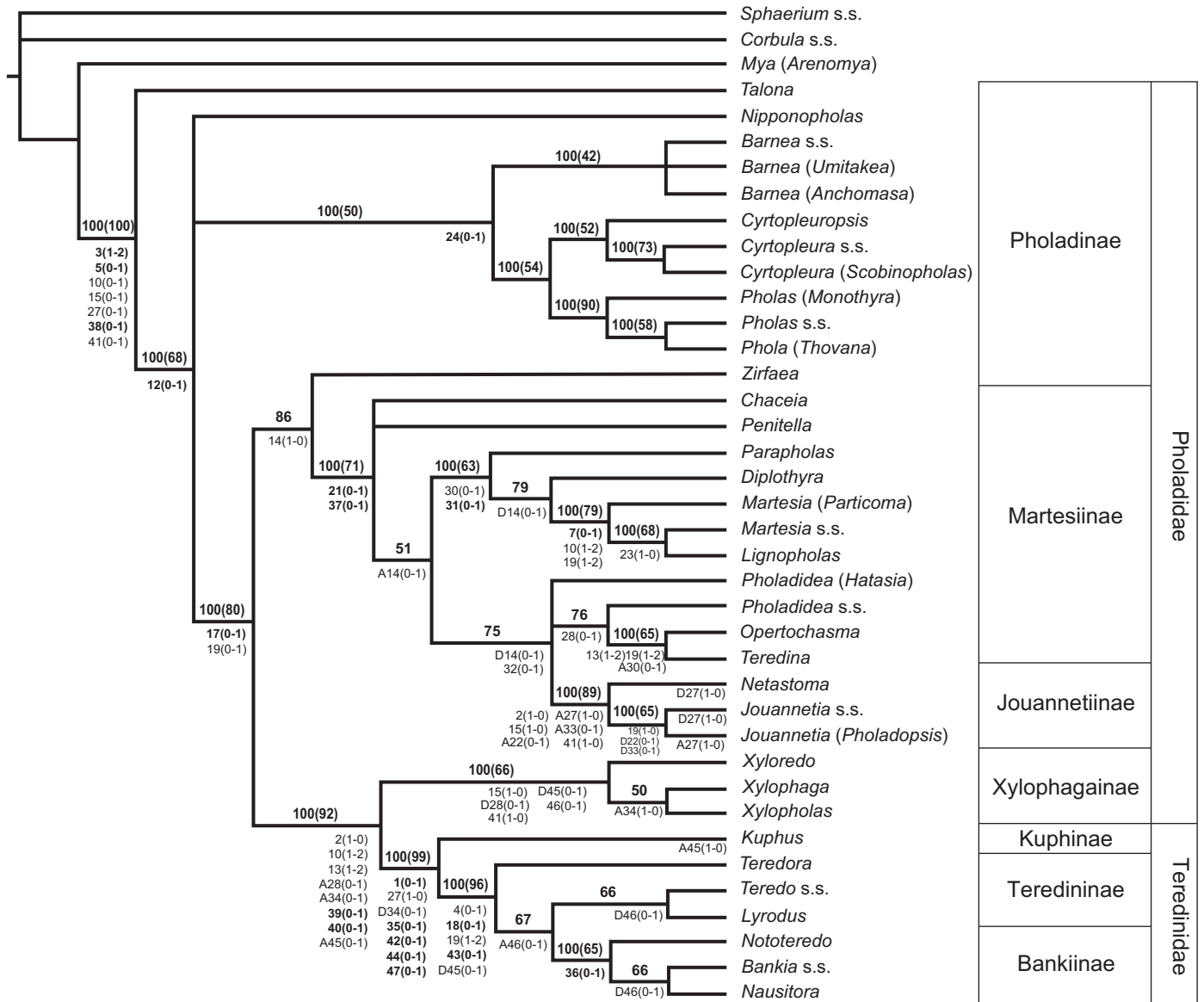


Fig. 3. Phylogeny of Pholadoidea. Most parsimonious tree corresponding to the 50% Majority Rule consensus tree obtained by successive approximation weighting. L 96. Indices under unitary weight conditions: CI 0.54, RI 0.85, RC 0.46. Indices under reweight conditions: CI 0.78, RI 0.94, RC 0.74. Abbreviations: L, length; CI, consistency index; RI, retention index; RC, rescaled consistency index. Numbers in bold indicate the Majority Rule values and, in brackets, the bootstrap support values of the individual nodes. Only bootstrap values higher than 40% are shown. Numbers in smaller type represent the most significant state changes at the respective nodes. Exclusive synapomorphies are in bold. Unambiguous not-exclusive synapomorphies are in normal type. Abbreviations A and D mark the ambiguous changes of character states under ACCTRAN and DELTRAN optimisations, respectively. For changes of character states in the Pholadinae clade see Fig. 4. The classification of Pholadoidea in Turner (1969) is shown besides the tree by comparison.

strap. This is the sister-group of a clade gathering taxa characterised by large, spoon-shaped to spatulate apophyses (character 16), namely *Pholas* Linnaeus, 1758, *Cyrtopleuropsis* and *Cyrtopleura* Tryon, 1862. The arrangement of the Pholadinae clade and the distribution of the character states are in accordance with the suggestions given by previous authors concerning the taxonomic repartition and affinities of the taxa involved. In fact, the *Pholas* clade is consistent with Turner's (1954, 1969) subdivision into three subgenera: *Pholas* s.s., *Pholas (Thovana)* Gray, 1847 and *Pholas (Monothyra)* Tryon, 1862. These taxa share the septate umbonal reflection (character 6), which is an exclusive synapomorphy, and the presence

of a metaplex (character 30). The composition of the *Cyrtopleura*–*Cyrtopleuropsis* clade, gathering taxa with the umbonal reflection free, raised and square at its posterior end (character 8), is in agreement with the suggestions expressed by Pacaud (1998) who recognised close the relationship of *Cyrtopleuropsis* with *Cyrtopleura* s.s. and *Cyrtopleura (Scobinopholas)* Grant and Gale, 1931. Furthermore, each internal clade of Pholadinae contains taxa with a narrow pedal gape besides taxa with a broad pedal gape (character 13). This is consistent with Turner's (1954, 1969) interpretation in attributing subgeneric rank to the shape of the pedal gape in the Pholadinae.

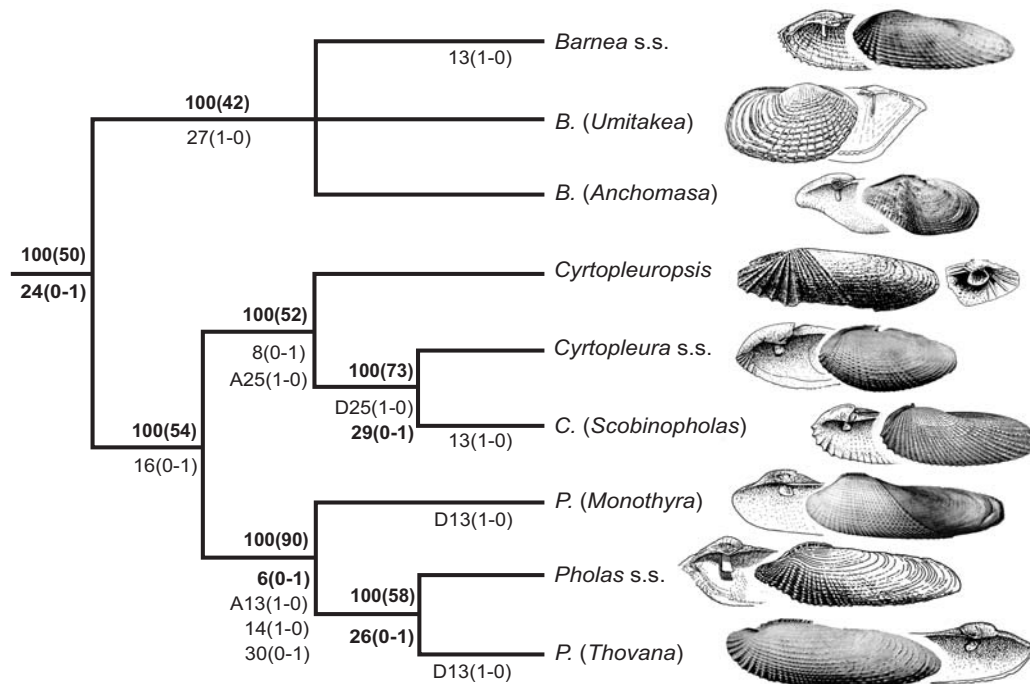


Fig. 4. Detail of the selected cladogram showing the relationships and state changes among the genera and subgenera of the Pholadinae clade. Symbols as in Fig. 3.

Members of the *Barnea* clade are characterised by possessing thin apophyses (character 16) and in lacking the mesoplax (character 27). The presence of a mesoplax is treated as a plesiomorphy of the Pholadoidea that is independently lost in the *Barnea* clade, in *Jouannetia* (*Jouannetia*) DesMoulins, 1828, in *Netastoma*, and in the Tereidinidae. The taxonomic position of *B. (Anchomasa)* as a subgenus of *Barnea* is in accordance with the results of the phylogenetic analysis, although the internal relationships among the taxa composing the *Barnea* clade are not resolved. The analysis shows also that similarities between *B. (Anchomasa)* and *Cyrtopleuropsis*, concerning characters of the general shape of the shell and the presence of a wide pedal gape, are plesiomorphies whereas the spatulate shape of the apophyses is a distinctive character placing *Cyrtopleuropsis* in a different clade within the Pholadinae. The relationships of *B. (Anchomasa)* to *Nipponopholas* and *Zirfaea* are more distant. As mentioned above, both these genera are excluded from the Pholadinae clade by lacking the protoplax. The presence of the umbonal-ventral ridge on the internal surface of the valves (character 17) and the presence of the ventral condyle (character 19) relates *Zirfaea* more closely to the sister-group of the Pholadinae.

Phylogeny of Pholadoidea

Cladistic analysis confirms the interpretation of numerous characters sustained by Hoagland and Turner (1981) and the gross topology of the cladogram recalls that obtained by them (Hoagland and Turner 1981: text-fig. 5, tab. 11) (Fig. 5)

using the characters presumed to be unique and unreversed. In fact, the most consistent characters selected by the reweighting process are indeed those indicated by Hoagland and Turner (1981) as highly significant for the phylogeny of pholadoideans. However, the analysis at genus and subgenus levels shows remarkable differences. These are evident in comparing the structure of the selected cladogram with Turner's (1969) taxonomic arrangement (Fig. 3). Furthermore, it suggests that obscure areas of the phylogeny deserve further research.

Exclusive synapomorphies supporting the ingroup node are represented by the presence of the umbonal reflection (character 5), the position of the umbo located well to the anterior (character 3), the cylindrical shape of the foot with discoid extremity adapted for suction (character 38), and the presence of imbrications on the commarginal ridges of the anterior slope (character 10), changing to fine denticulations in the wood-boring groups. The presence of apophyses (character 15) and the long ctenidia (character 41) are also important characters showing significant reversals in the ingroup (see below).

The subfamilies Pholadinae and Martesiinae (sensu Turner, 1969) are not monophyletic. As described above, a monophyletic group of Pholadinae is exclusively composed of taxa having the protoplax. The Pholadinae clade is the sister-group of a major clade consisting of taxa having the umbonal-ventral ridge (character 17) and ventral condyle (character 19), the latter secondarily lost in *Jouannetia*.

The major clade includes two groups, namely Martesiinae–Jouannetiinae and Xylophaginae–Tereidinidae. The Martesiinae–Jouannetiinae clade is well-supported by two exclusive synapomorphies, i.e., the presence of the

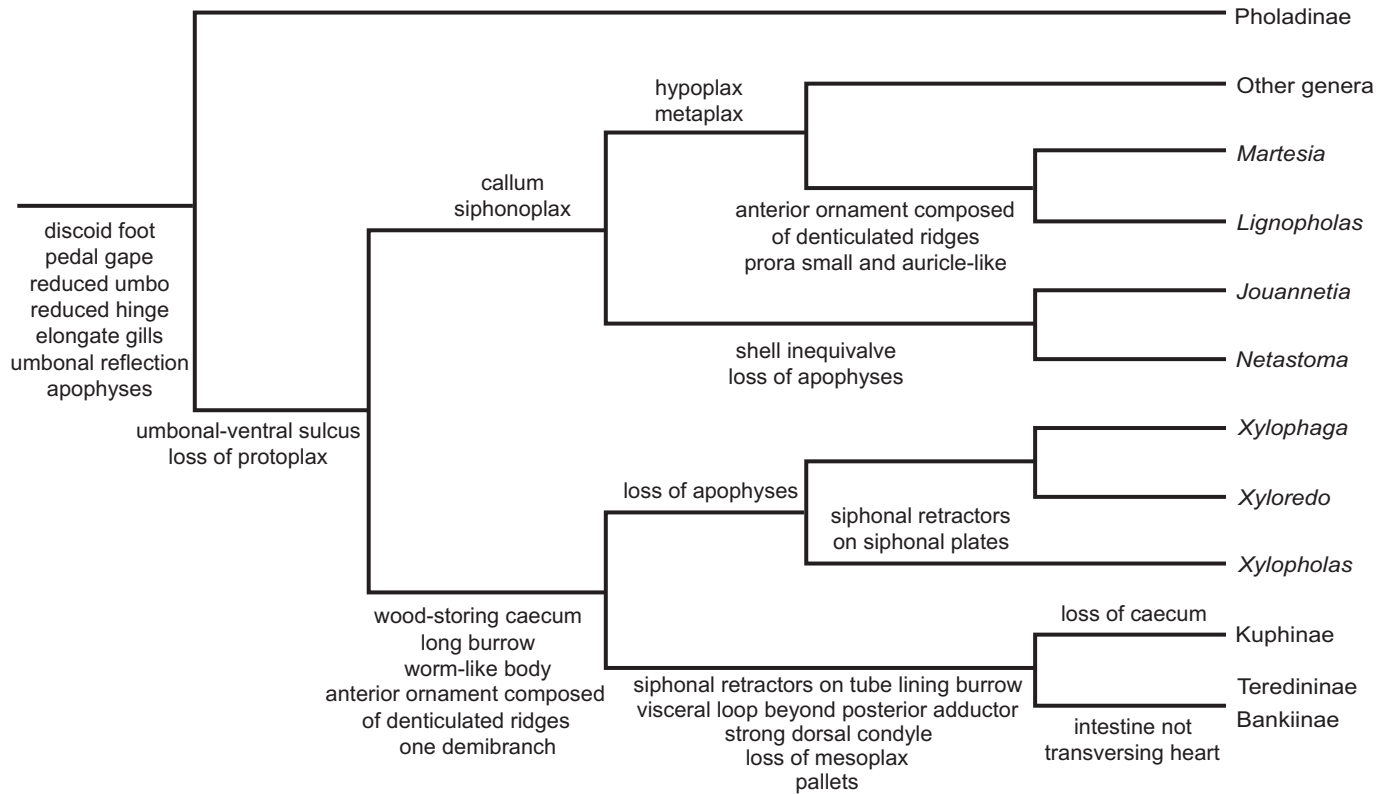


Fig. 5. Phylogenetic reconstruction of Pholadoidea and most significant state changes proposed by Hoagland and Turner (1981: tab. 11, text-fig. 5).

callum closing the pedal gape (character 21) and the consequent atrophy of the adult foot (character 37). However, the Jouannetiinae are monophyletic and well-supported by Majority Rule and bootstrap values, whereas the Martesiinae are paraphyletic. In fact, Martesiinae lack synapomorphies. The states of the characters differentiating the Martesiinae from Jouannetiinae, i.e., the presence of the apophyses (character 15) and the long ctenidia (character 41), are plesiomorphies of the Pholadoidea undergoing reversals in the Jouannetiinae. The Martesiinae–Jouannetiinae clade is subdivided in two main groups, one characterised by the presence of a hypoplax (character 31) and the other, including Jouannetiinae, having the siphonoplax (character 32) as a distinctive character.

According to Haga and Kase (2007), the Xylophagainae are phylogenetically distant from the Teredinidae and, consequently, the symbiosis with xylotrophic bacteria arose independently in these groups. On the contrary, the present study shows that the Xylophagainae and Teredinidae form a well-supported monophyletic group. This corresponds to the results of the molecular analysis made by Giribet and Distel (2003) in which *Bankia* Gray, 1842 is the sister-group of *Xylophaga* Turton, 1822. Thus, the position of Xylophagainae as a subfamily of Pholadidae as proposed by Turner (1955, 1969), is not justified. Exclusive synapomorphies are the gills beyond the posterior adductor (character 40) and composed of a single demibranch (character 39). The Xylophagainae lose the apophyses (character 15) independently from the Jouannetiinae.

The structure of the cladogram here selected is in accordance with Hoagland and Turner's (1981) opinion in showing that the obligate wood-borers originated from the groups boring into inorganic substrates. However, a parallel evolution of the wood-boring adaptation in the Xylophagainae and Teredinidae cannot be excluded. In fact, the wood-storing caecum (character 45), which is commonly considered as the most important character reflecting the ability of wood-boring groups to use the wood for food (Purchon 1941; Hoagland and Turner 1981), is an ambiguous synapomorphy. In ACCTRAN optimisation it is a synapomorphy of the Xylophagainae–Teredinidae group which is secondarily lost in *Kuphus*. This would support a monophyletic origin of the xylotrophy in the pholadoideans. Alternatively, DELTRAN optimisation treats the character as originating independently in the Xylophagainae and in the Teredininae–Bankiinae clades. In this case, the absence of a wood-storing caecum and, possibly, the filter-feeding and mud-boring mode of life of *Kuphus* are plesiomorphies inherited from the ancestors of the obligate wood-boring groups.

Insofar as the origin of the filter-feeding wood-borers is concerned, Ito (1999) and Haga and Kase (2007) maintained that the anterior boring mechanism of the rock- and wood-borers is primary and the groups with ventral boring mechanisms (sand- and mud-borers) evolved later. This hypothesis is supported by the fossil record which testifies that the wood-borers *Opertochasma* Stephenson, 1952 and *Turnus* Gabb, 1864 are the oldest pholadoideans known (Tithonian; Kelly 1988a, 1988b). According to Haga and Kase (2007), the

highly specialised wood-boring groups are the most archaic pholadoideans and the great diversification of the superfamily originated by simplification of the shell morphology. On the contrary, the present analysis indicates that the filter-feeding wood-borers are the most derivative members of two Martesiinae clades. This represents a more parsimonious scenario of the evolutionary pathways of the pholadoideans in which the specialised forms, characterised by a high number of strongly adaptive apomorphies, arose from groups with a more generalist mode of life. As expected, the characters reflecting the adaptation to the wood-boring mode of life, i.e., the finely denticulate ornament of the anterior slope, the small and auricle-like prora giving the shape of an angulate embayment to the wide pedal gape, and the robust ventral condyle (Hoagland and Turner, 1981) developed independently in the Martesiinae clades and in the obligate wood-boring groups. As underlined by Kelly (1988a), the incompleteness of the fossil record and the lack of detailed studies on some problematic taxa do preclude definitive answers.

The biogeographical history of *Barnea* (*Anchomasa*)

Fossil record.—Turner (1969) maintained that the occurrence of *B.* (*Anchomasa*) dates from the Pliocene. However, Kennedy (1993) described *Barnea* (*Anchomasa*) *saularae* Kennedy, 1993 from early Coniacian–Santonian of California, and assigned *Pholas? scaphoides* Stephenson, 1952, from Cenomanian deposits of Texas, to the subgenus *B.* (*Anchomasa*). Kelly (1988a) tentatively ascribed Stephenson's species to *P.* (*Monothyra*), presumably on the basis of the external shell characters. Pacaud (1998) maintained that the general shell shape and the ornament pattern recall also those of *Cyrtopleuropsis*. The Cretaceous species clearly show a simple umbonal reflection (Kennedy 1993). This would exclude their membership of the genus *Pholas*. Insofar as their relationships with *B.* (*Anchomasa*) and *Cyrtopleuropsis* are concerned, the only observable element of comparison is the abrupt interruption of the radial ornament along the line of demarcation of the disc with the posterior slope. This is a characteristic aspect of the ornament pattern of *Cyrtopleuropsis*, whereas it is unusual in *B.* (*Anchomasa*), in which the disappearance of the radial ornament in the posterior part of the shell is commonly gradual. In agreement with Pacaud's (1998) opinion, the genus attribution remains uncertain due to the lack of information on the internal features of the shell, particularly the morphology of the apophyses. The absence of data on the accessory plates of both these species and *Cyrtopleuropsis* is a further element of uncertainty. According to Kelly (1988a), *P.?* *scaphoides* could represent the most ancient fossil record of the subfamily Pholadinae.

The oldest species showing the diagnostic characters of the shell of *B.* (*Anchomasa*) well come from the Miocene deposits

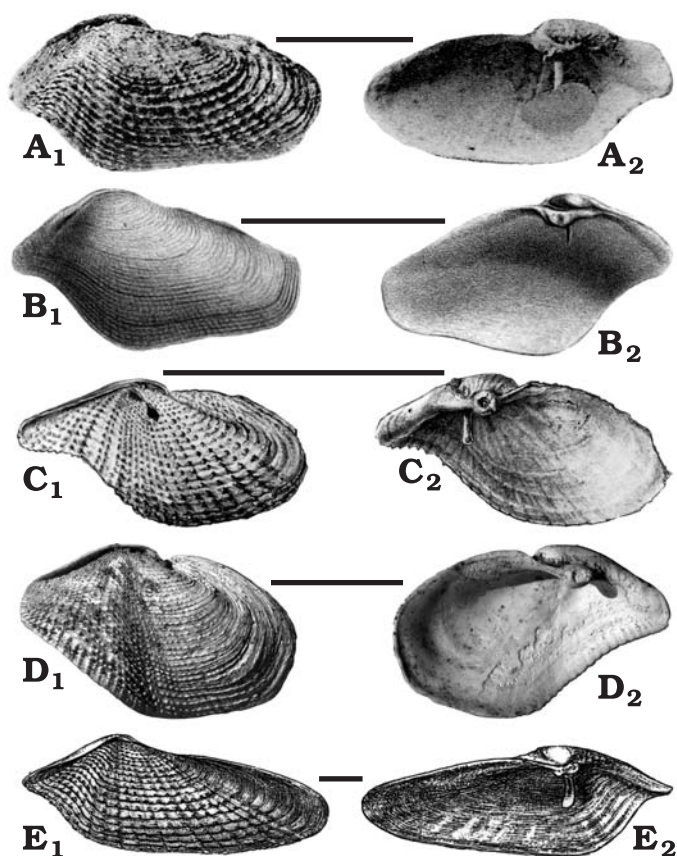


Fig. 6. Fossil species of pholadoidean bivalve *Barnea* (*Anchomasa*) Leach, 1852 belonging to the European stock. **A.** *Barnea* (*Anchomasa*) *palmula* (Dujardin, 1837), from Dolfuss and Dautzenberg (1902: 58, pl. 1: 18–21), Langhian, Touraine, France. **B.** *Barnea* (*Anchomasa*) *dumortieri* (Fischer, 1866), from Fischer (1866: pl. 4: 3, 3a), middle Miocene, Rhone basin, France. **C, D.** *Barnea* (*Anchomasa*) *parva* (Pennant, 1777). **C.** From Janssen et al. (1984: pl. 91: 228a, b), Middle Pliocene, Netherlands. **D.** From Monari (2008: figs. 3a, b), Pleistocene, southern Tuscany, Italy. **E.** *Barnea* (*Anchomasa*) *cylindrica* (Sowerby, 1818), from Wood (1850: 295, pl. 30: 8a, b), Late Pliocene, England. Scale bars 10 mm.

of the Eastern Paratethys and France (Figs. 6, 7). These species constitute an ancient stock that, as explained below, seems to have had great importance for the biogeographical evolution of the subgenus. *Barnea* (*Anchomasa*) *ujratamica* Osipov, 1932 is known from the early Tarkhanian to Konkian (late Burdigalian to early Serravallian in Studencka et al.'s 1998 time correlation chart; earliest Langhian to early Serravallian in Harzhauser and Piller's 2007 time correlation chart) of a Paratethyan area extended from Crimea to Ustjurt (Osipov 1932; Merklin and Nevevskaya 1955; Zhizhchenko 1959; Sakhelashvili 1965; Glibert and Van de Poel 1966; Nevevskaya et al. 1993; Studencka et al. 1998). *B.* (*A.*) *palmula* (Fig. 6A) occurs in the Pontilevian facies of Touraine (Loire basin) (Dujardin 1837; Dolfuss and Dautzenberg 1902; Glibert and Van de Poel 1966) considered to be Langhian in age (Chaix and Cahuzac 2005 and references therein). Doderlein (1862) quoted the presence of the species also in the late Miocene of the northern Apennines (central Italy) but this information

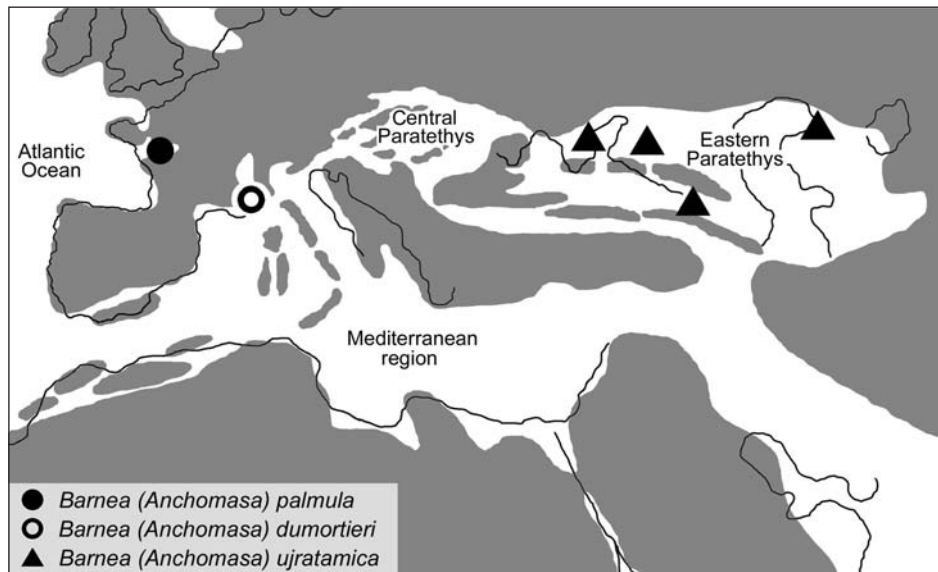


Fig. 7. Palaeogeographical distribution of pholadoidean bivalve *Barnea (Anchomasa)* Leach, 1852 during the middle Miocene. Map redrawn from Rögl (1998), Langhian. See text for sources.

needs confirmation (Sacco 1901). *B. (A.) dumortieri* (Fig. 6B) is another western European species known from middle Miocene marine to fresh-water sediments constituting the uppermost part of the Cainozoic succession of the Rhone region (Fischer 1866; Locard 1878). These sediments should correspond to the Serravallian units of the southern part of the Bresse graben described by Sissingh (1998).

Concerning younger species of the western European region, *Barnea (Anchomasa) cylindrica* (Sowerby, 1818) (Fig. 6E) occurs in the Middle and Late Pliocene of England (Sowerby 1818; Wood 1850, 1874; Glibert and Van de Poel 1966). Nyst (1843) mentioned very poorly-preserved specimens from Cainozoic deposits of Belgium which he doubtfully ascribed to Sowerby's species. *B. (A.) parva* is present in the Middle to Late Pliocene of England (Glibert and Van de Poel 1966; Wood 1874), in the Early to Middle Pliocene of Belgium (Glibert 1963; Nyst 1878–81) (Fig. 6C) and in the Middle Pliocene of Netherlands (Janssen et al. 1984). The presence of the species is quoted also in the Pleistocene of southern Tuscany (central Italy) (Monari 2008) (Fig. 6D). *B. (A.) parva* is the only member of the ancient European stock surviving today.

Insofar as the north-western Atlantic region is concerned, *B. (A.) truncata* occurs in the Pleistocene in South Carolina (Dall 1898). The presence of the species in deposits of the same age on the western coast of South Africa (Kensley and Pether 1986 and reference therein) would contradict Turner's (1954) opinion that the species was recently introduced into western Africa. Moreover, this would indicate that the very wide present-day distribution of *B. (A.) truncata* (see below) was already accomplished in Pleistocene times.

In the north-eastern Pacific area, *Barnea (Anchomasa) subtruncata* (Sowerby, 1834) occurs in the Pleistocene of California (Kennedy 1974).

It is plausible that the specimens on which Noetling

(1901) instituted *Pholas blanfordianus* Noetling, 1901, from the Miocene of the Burma region (Myanmar) and those ascribed by Hayasaka (1969) to *B. (A.) aff. manilensis*, from the Miocene of Tanegashima (south-western Japan), may represent the first occurrences of the subgenus in the western Pacific region. *P. blanfordianus* lacks information on the internal characters of the shell, on the morphology of the umbonal reflection and on the accessory plates, but its general shell shape is close to that of *B. (Anchomasa)*. Its exact stratigraphical position is uncertain. A comparison between the stratigraphical subdivision of the Miocene of Burma made by Noetling (1901) and that currently in use (e.g., Khin and Myitta 1999, Wandrey 2006) permits only to infer that the species comes from the lower to middle Miocene marine and brackish water sediments below the Irrawaddy Group (upper Miocene to Pleistocene). As far as *B. (A.) aff. manilensis* is concerned, the deposits yielding the species belong to the Osaki Formation, i.e., the uppermost unit of the middle Miocene Kukinaga Group (Hayasaka 1969; Kodama et al. 1991; Inoue 2007 and references therein).

The subgenus is certainly present in the late Miocene of New Zealand, with the specimens listed by Gregg (1960) as *Barnea (Anchomasa)* sp. and those listed by Suter (1921) as *B. (A.) similis*, the species living today along New Zealand coasts. Marwick (1931) and Keyes (1972) quoted the subgenus also in Lower Pliocene sediments. Beu and Maxwell (1990) maintained that *B. (A.) similis* is present from the Mangapanian (latest Pliocene) whereas the Early Pliocene specimens belong to a different, undescribed species. However, recently Beu (2006) extensively revised the systematic and stratigraphical data and highlighted the clear morphological continuity between the late Miocene and Recent material. According to Beu (2006), *B. (A.) similis* is a long-ranging species that first appeared in the late Tongaporutuan–Kapitean time span (late Miocene).

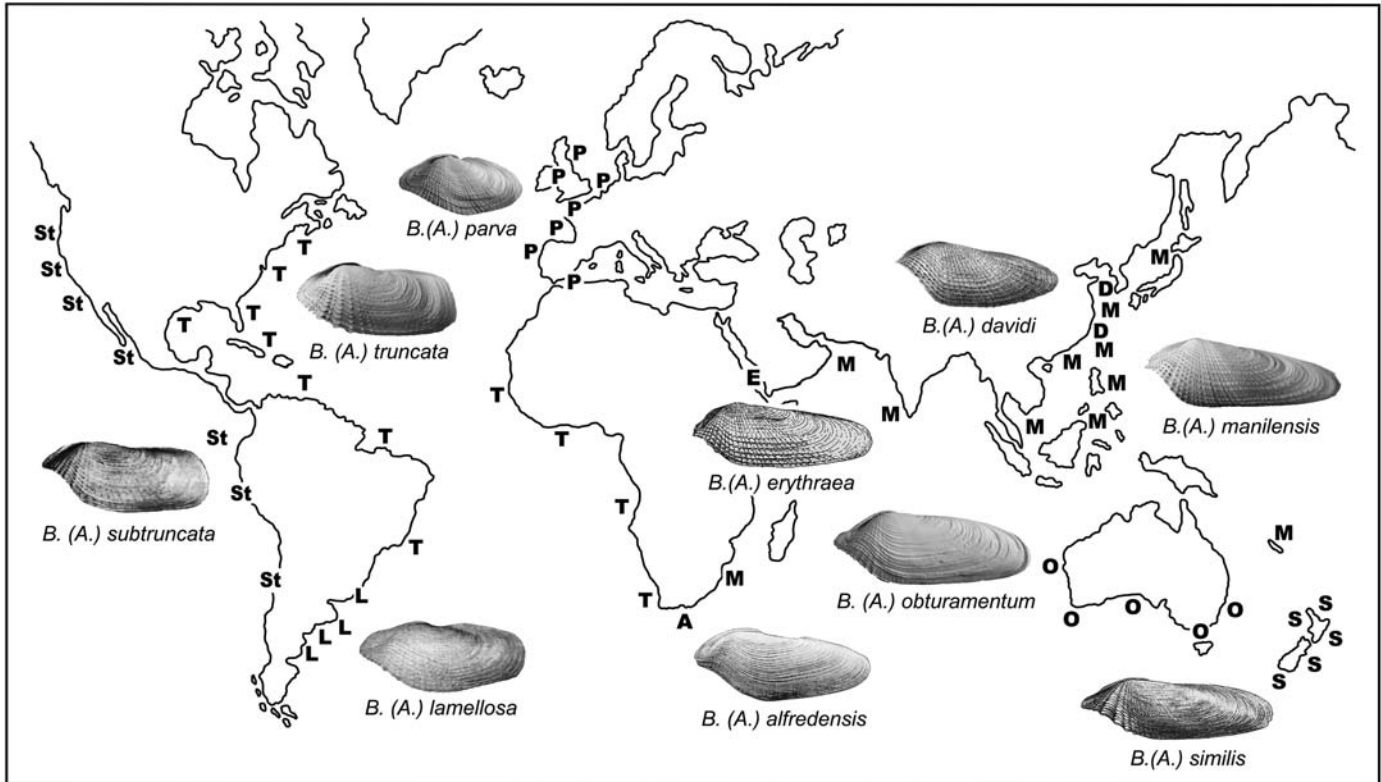


Fig. 8. Present-day geographical distribution of pholadoidean bivalve *Barnea (Anchomasa)* Leach, 1852. See text for sources. A. *Barnea (Anchomasa) alfredensis* (Bartsch, 1915). D. *Barnea (Anchomasa) davidi* (Deshayes, 1874). E. *Barnea (Anchomasa) erythraea* (Gray, 1851). L. *Barnea (Anchomasa) lamellosa* (d'Orbigny, 1846). M. *Barnea (Anchomasa) manilensis* (Philippi, 1847). O. *Barnea (Anchomasa) obturamentum* (Hedley, 1893). P. *Barnea (Anchomasa) parva* (Pennant, 1777). S. *Barnea (Anchomasa) similis* (Gray, 1835). St. *Barnea (Anchomasa) subtruncata* (Sowerby, 1834). T. *Barnea (Anchomasa) truncata* (Say, 1822).

Finally, *B. (A.) manilensis* is quoted in the Pliocene deposits of Japan and Korea (Yokoyama 1920; Kikuchi et al. 1991; Robba et al. 2002).

Biogeographical distribution.—The subgenus *B. (Anchomasa)* has a worldwide present-day distribution, which is particularly accentuated in the western Pacific region (Fig. 8). The type species, *B. (A.) parva*, is diffused along the eastern coasts of the northern Atlantic region, from the British Isles to the Bay of Biscay (see details in Monari 2008) and it is also quoted in the westernmost part of the Mediterranean Sea (Pallary 1900).

Apart from the type species, the global biogeographical pattern of the subgenus shows a disjunct distribution. This consists of two groups of species, here named the “American group” and the “Indo-West Pacific group” having distinctive morphological features. They have distinct biogeographical structures as well, which are revealed by the different ratio between widespread and local species.

The American group is composed of the following species: *B. (A.) truncata*, *B. (A.) subtruncata* and *Barnea (Anchomasa) lamellosa* (d'Orbigny, 1846), sharing the truncate to subtruncate shape of the posterior margin (Fig. 1C). Moreover, the umbo is at almost one third of the shell length and the length/height ratio of the shell is commonly lower than that of

the species of the Indo-West Pacific group. *B. (A.) truncata* and *B. (A.) subtruncata* show a very wide latitudinal distribution. They occur along the Atlantic and Pacific coasts of North and South America, respectively, from the boreal to austral temperate belts (Abbott 1954; Turner 1954; Keen 1958). *B. (A.) truncata* is also quoted along the central and southern Atlantic coasts of the African continent, from Senegal to Cape Twon (South Africa) (Nicklès 1950, 1955; Kensley and Pether 1986). On the contrary, *B. (A.) lamellosa* has a distribution limited to the coasts of Uruguay and Argentina (d'Orbigny 1846; Carcelles 1944; Turner 1954; Scarabino 2003).

The wide distribution of these species is most probably determined by their relatively long planktonic larval life (Turner 1954; Chanley 1965), the capability of adaptation to different types of substrata and a certain tolerance to a wide range of temperature. Moreover, the spatial continuity of the shallow neritic areas along both the Atlantic and eastern Pacific coasts is an important aspect which contributed to greatly increase the dispersal of several marine groups in these areas (see for example Williams and Reid 2004).

The Indo-West Pacific group consists of species having a tapered shell shape, a lanceolate posterior area and the umbo placed well anterior, at almost one fourth of the shell length (Fig. 1A, 1B). *B. (A.) manilensis* is the only widespread species of the Indo-West Pacific group, extending from the

north-eastern coasts of South Africa to Japan (Bernard et al. 1993; Bosch et al. 1995; Poutiers 1998; Higo et al. 1999; Robba et al. 2002). The other relatively numerous species have limited distributions. *Barnea (Anchomasa) davidi* (Deshayes, 1874) occurs from the Bohai Sea to Taiwan (Deshayes 1874; Bernard et al. 1993; Higo et al. 1999). *B. (A.) obturamentum* lives along the southern coasts of Australia, from southern Western Australia to New South Wales and Tasmania (Hedley 1893; Allan 1950; Phillips et al. 1984; Lamprell and Healy 1998; Turner 1998), and *B. (A.) similis* is an endemic New Zealand species (Beu 2006 and references therein). The distribution of *Barnea (Anchomasa) erythraea* (Gray, 1851) is confined to the Red Sea (Oliver 1992). *Barnea (Anchomasa) alfredensis* (Bartsch, 1915) lives along the southernmost coasts of South Africa (Bartsch 1915).

The high local vs. widespread species ratio makes the biogeographical structure of the Indo-West Pacific group clearly different from that of the American group. This pattern is the effect of different factors. Insofar as the western Pacific species are concerned, the radiation involved an area mainly composed of islands and archipelagos fragmenting the continuity of the shallow marine areas (Williams and Reid 2004). Moreover, the Late Cainozoic intense active margin tectonics, and the glacio-eustatic fluctuations (see Stevens 1994 for a synthesis) rendered this area strongly dynamic and contributed to increase the potential of isolation and speciation.

Historical biogeography.—The origin of the disjunct distribution and the paths of radiation and dispersal of *B. (Anchomasa)* are not unequivocally discernible due to the time and space discontinuity of the fossil record. In spite of this, the following hypotheses could be considered which are in the best agreement with the available data.

Lines of evidence suggest relationships of vicariance of the Indo-West Pacific group with the Eastern Paratethyan species as an effect of the dispersion before the closure of the connections between the Mediterranean–Paratethyan area and the Indian region during the Miocene. As a matter of fact, *B. (A.) ujraticum* shows morphological features characterising the species of the Indo-West Pacific group, i.e., a markedly anterior umbo and a lanceolate and elongated posterior area of the shell.

As highlighted by phylogeographical studies (see Williams and Reid 2004 for a synthesis), the Tethyan closure was decisive for the origin of numerous marine Indo-Pacific taxa. Moreover, faunal comparisons (Robba 1987; Piccoli et al. 1991; Piccoli 2002) testify that the wide sea corridors linking these regions (the “Arabian gates” in Vrielynck et al. 1997) became strongly reduced or closed at the end of early Miocene time. Successive temporary connections were robust enough to allow interchanges (Franco 1982; Robba 1987; Piccoli 2002), particularly during the Langhian times (Rögl 1998, 1999; Studencka et al. 1998; Harzhauser and Piller 2007).

According to the fossil record, the appearance of *B. (A.) ujraticum* dates back to the late early Miocene to earliest

middle Miocene time span, whereas the most ancient members of the Indo-West Pacific group probably occur in the late middle Miocene of Japan and, certainly, in the late Miocene of New Zealand. This suggests that the Indo-West Pacific group originated from the Paratethyan species, although data on the occurrence of *B. (Anchomasa)* in the intermediate regions are currently lacking. However, the uncertainties mentioned above, concerning the age of *P. blanfordianus* and its membership of the genus *B. (Anchomasa)*, leave open the possibility that the derivation took place in an opposite direction.

The origin of *B. (A.) erythraea* and its distribution limited to the Red Sea are likely due to the isolation of that area during the Plio-Pleistocene sea-level drops related to glacio-eustatic cycles. In this respect, several authors referred to these events in explaining the endemic distribution of a number of marine taxa in the Red Sea (see Lessios et al. 2001 and references therein). The close similarity of *B. (A.) alfredensis* to *B. (A.) manilensis* could reflect relationships of direct peripatric derivation, although the absence of data in the fossil record leaves the question open currently.

The present-day pattern of distribution suggests two hypotheses for the origin of the American group. The first hypothesis supports its origin from the Indo-West Pacific group in the South African region and its subsequent northward Atlantic radiation. It is mainly based on the geographical sub-continuity of the present-day distribution among the two groups along the South African coasts. However, *B. (A.) truncata*, a species of the American group occurring today also along the southern coasts of western Africa, was already widespread in the Atlantic region during the Pleistocene. This would suggest an older origin for the American group. However, the fossil record testifies that the distribution of the Indo-West Pacific group in pre-Pleistocene times was located far from South Africa.

The second hypothesis seems to be in accordance with the fossil record. It interprets the origin of the American group as from the ancient European stock, presumably during the Late Pliocene, by dispersal towards the eastern coasts of North America followed by a rapid southward diffusion. This hypothesis is supported also by the fact that the North Atlantic species of the ancient European stock have the umbo placed almost at one third of the shell length, which is a feature characterising the American group. *B. (A.) dumortieri* shows the subtruncate posterior margin as well (Fig. 6B).

This consideration, and those discussed above on the origin of the Indo-West Pacific group, would indicate that the morphological differentiation distinguishing the American group from the Indo-West Pacific group arose early within the European–Paratethyan stock.

The close affinities, underlined by Turner (1954), between *B. (A.) truncata* and *B. (A.) subtruncata* most probably reflect relationships of vicariance regulated by the last phases of emergence of the Panama Isthmus. As known (Duque-Caro 1990; Haug and Tiedemann 1998) that area was a stable sea connection until the Middle Pliocene and, before its full

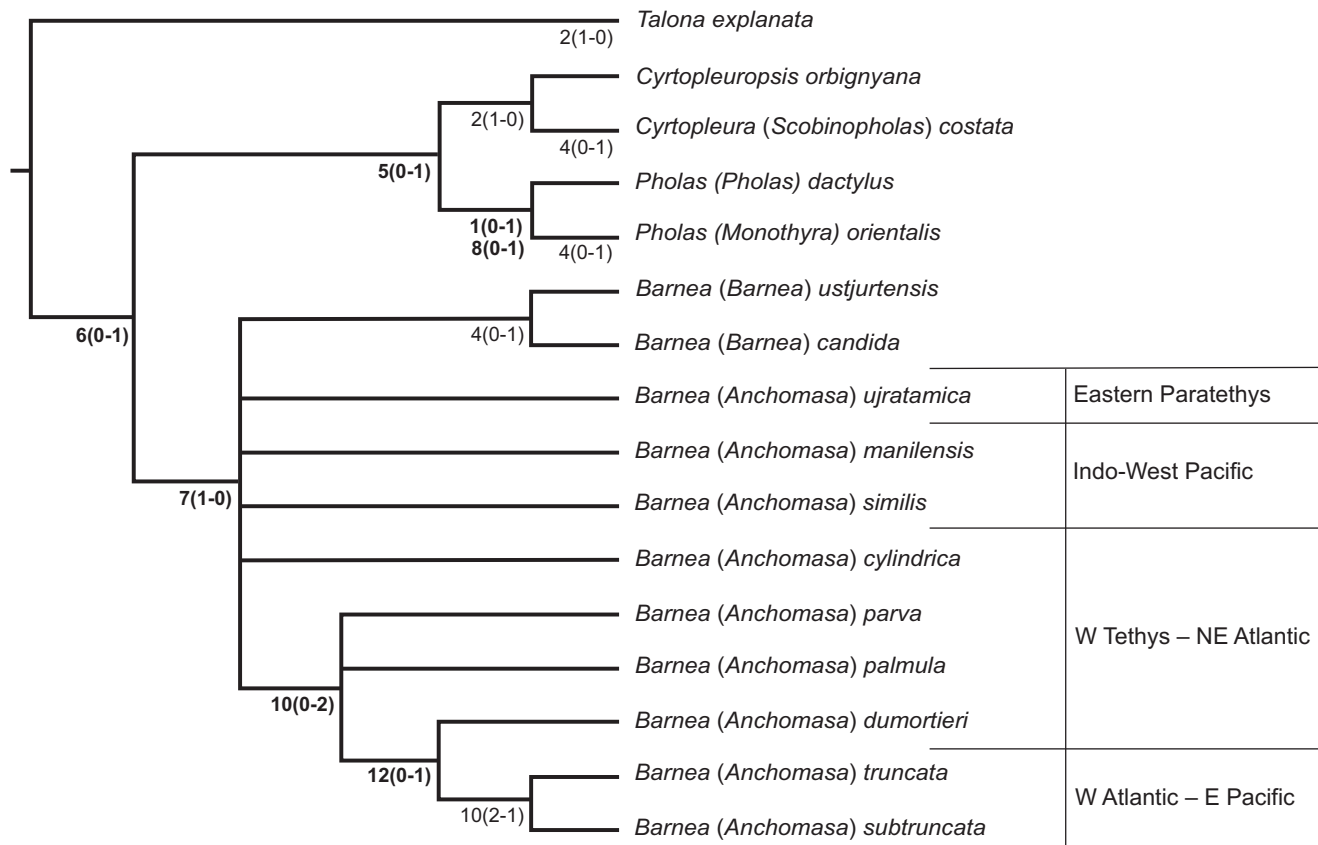


Fig. 9. Cladistic analysis of pholadoidean bivalve *Barnea (Anchomasa)* Leach, 1852 obtained by processing the matrix in Appendix 4. Exhaustive search with constraints enforcing the relationships among the outgroup taxa in order to reproduce the distribution of the supraspecific characters and the topology of the cladogram in Fig. 3. Strict consensus of three most parsimonious cladograms (L 21, CI 0.62, RI 0.74, RC 0.46). Unsupported nodes collapsed. See text for the definition of the cladistic parameters. Symbols as in Fig. 3.

closure in the Late Pliocene it acted as a narrow and shallow seaway for the near-shore faunas (Nesis 2003). During the Early Pleistocene interglacial periods of sea-level rise, brief and intermittent shallow marine connections probably re-established (Beu 2001). The specialisation to mud and peat deposits (Turner 1954) and the relatively restricted geographical distribution of *B. (A.) lamellosa* would indicate its origin by speciation at the southern margin of the expansion of *B. (A.) truncata*.

Phylogeny and historical biogeography

A simple cladistic test of the relationships among the species of *B. (Anchomasa)*, founded on the characters distinguishing the biogeographical groups described above, was performed in order to verify the hypotheses of historical biogeography. The type species of *Talona*, the genus that the phylogenetic analysis of the Pholadoidea indicates as retaining the highest number of plesiomorphies, and the respective type species of *Pholas* s.s., *P. (Monothyra)*, *C. (Scobinopholas)* and *Cyrtopleuroopsis* (Appendix 3), composing the sister-group of the *Barnea* clade, were selected as outgroup.

The analysis was accomplished by forcing closest relationships among the outgroup species in order to reproduce the same topology as that of the cladogram shown in Fig. 3. Moreover, the supraspecific characters (characters 1–8 in Appendix 3) were polarised to ensure the same distribution of their state changes. Two species of *Barnea* s.s. were included, namely *Barnea (Barnea) ustjurtensis* Osipov, 1932, which is one of the earliest representative of the subgenus (early middle Miocene of Eastern Paratethys, Studencka et al. 1998), and the type species *Barnea (Barnea) candida* (Linnaeus, 1758). *B. (B.) ustjurtensis* differs from *B. (B.) candida* in the less strongly anterior umbo and in the slightly less strongly tapered shape of the shell. These aspects can be considered as components of the morphological variation of *Barnea* s.s., as is the case for *B. (Anchomasa)*.

The strict consensus tree (Fig. 9), although highly unresolved due to the very low number of characters involved, demonstrates the close relationships between the European species and the American group. In contrast, *B. (A.) ujraticumica* and the species of the Indo-West Pacific group fall within a polytomic area of the cladogram. Indeed, in the context of the selected characters, the Indo-West Pacific group lacks synapomorphies differentiating it from the Paratethyan species. The comparison between the cladogram and the

(palaeo)geographical distribution of the different species (Fig. 9) clearly illustrates the origin of the present-day biogeographical pattern. During the vicariant event related to the closure of the western Tethys, the Indo-West Pacific group and the Paratethyan species retained the same characters. In the present-day distribution, these characters appear to be exclusive of the Indo-West Pacific group but this is the effect of the disappearance of the Paratethyan species.

The cladogram also clarifies the reasons for the polytomic structure of the *Barnea* clade. In the context of the selected characters, the broad pedal gape is the only feature distinguishing the Indo-West Pacific group and *B. (A.) ujraticumica* from the *Barnea* s.s. species. This is a plesiomorphy of the Pholadinae which changes to a narrow, slit-like pedal gape in *Barnea* s.s. (Fig. 4).

Conclusions

The cladistic analysis based on morphological data indicates that the Pholadoidea are a monophyletic group. The phylogenetic reconstruction, although consistent in some respect with Hoagland and Turner's (1981) cladogram (Fig. 5), suggests a taxonomic arrangement of Pholadoidea different from that proposed by Turner (1969). In detail, a classification of the Pholadoidea should mainly reflect the restricted composition of Pholadinae, the close relationships between Jouannetiinae and Martesiinae and between Xylophaginae and Teredinidae, and the paraphyletic condition of the Martesiinae. Moreover, it should also take into consideration that these groups are members of a major clade which is the sister-group of the Pholadinae clade. The analysis also demonstrated that *Barnea* s.s. and *B. (Umitakea)* are the closest relatives of *B. (Anchomasa)* and compose an unresolved clade within the Pholadinae.

The morphological analysis and the study of the present-day distribution of the species of *B. (Anchomasa)* permitted to identify two biogeographical groups, namely the American and the Indo-West Pacific groups. The fossil record and the known geodynamic scenario suggest relationships of direct derivation between the Eastern Paratethyan species and the Indo-West Pacific group reflecting a vicariant event related to the Tethyan closure in middle Miocene times. The American group originated from the European stock by dispersion towards the western coasts of the northern Atlantic region, probably during the Late Pliocene.

Insofar as the relationships between *Barnea* s.s. and *B. (Anchomasa)* are concerned, the oldest *Barnea* s.s. species are known from the Chokrakian to Konkian (early Langhian to early Serravallian in Studencka et al.'s 1998 time correlation chart; late Langhian to early Serravallian in Harzhauser and Piller's 2007 time correlation chart) of the Paratethyan region (Osipov 1932; Merklin and Nevesskaya 1955; Zhizhchenko 1959; Nevesskaya et al. 1993; Studencka et al. 1998), i.e., just slightly younger than *B. (A.) ujraticumica*. This evidence and the results of the cladistic analysis suggest that *Barnea* s.s.

originated from *B. (Anchomasa)* by the loss of a broad pedal gape, and that the divergence probably began during the early middle Miocene. The presence of at least four species in the middle Miocene of Eastern Paratethys (Studencka et al. 1998) would testify that *Barnea* s.s. underwent a strong and rapid differentiation in that area after its appearance.

Finally, the fossil record and the present-day biogeographical distribution would indicate as plausible the origin of *B. (Umitakea)* from *B. (Anchomasa)* in the western Pacific area. In fact, *B. (Umitakea)* is known from the Pliocene deposits of Indonesia, Taiwan, and Japan (Yokoyama 1920; Evseev 1993; Robba et al. 2002). Today, it is widespread in the western Pacific area, from the Bay of Bengal to Australia and, eastwards, to Japan (Higo et al. 1999; Robba et al. 2002). As mentioned above, *B. (Taiwanobarnea)*, a taxon known from the late Miocene of Taiwan (Wang, 1983), although lacking information on the internal shell characters, shows the closest similarities with *B. (Umitakea)* but also features transitional to *B. (Anchomasa)*. As a matter of speculation, this could suggest that such a derivation arose early, just after the beginning of the dispersion of *B. (Anchomasa)* into the Indo-Pacific region.

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Appendix 1

List of characters and character states employed in the phylogenetic analysis of Pholadoidea.

Shell

1. Size of the shell with respect to the soft body: not reduced (covering at least visceral mass) (0); reduced (covering only the anterior part of visceral mass) (1).
2. Shape of adult valve (length/height ratio): sub-oval, globose (length slightly exceeding to almost equal height) (0); transversally elongated in antero-posterior direction (length clearly exceeding height) (1).
3. Position of umbo: subcentral (0); moderately anterior (1); clearly anterior (2).
4. Posterior slope: not lobed (0); lobed (1).
5. Umbonal reflection: absent (0); present (1).
6. Structure of umbonal reflection: simple (0); with transverse partitions (septate) (1).
7. Funnel-shaped pit below the umbonal reflection: absent (0); present (1).
8. Posterior part of umbonal reflection: adherent to the umbonal region (0); raised and with posterior margin square cut (1).
9. Hinge teeth: present (0); absent (1).
10. Ornament of anterior slope: absent (0); imbrications (1); fine denticulations (2).
11. Periostacal leaves on the posterior slope: absent (0); present (1).
12. Pedal gape: absent (0); present (1).
13. Shape of pedal gape: slit-like (prora not differentiated) (0); broadly lanceolate (prora differentiated) (1); angulated embayment (prora small and auricle-like) (2).
14. Chondrophore on left valve of adult shell: absent (0); present (1).
15. Apophyses: absent (0); present (1).
16. Shape of apophysis: long, narrow (0); large, spatulate to spoon-shaped (1).
17. Umbonal-ventral ridge on the internal surface of the adult valve (corresponding to the external umbonal-ventral sulcus): absent (0); present (1).
18. Dorsal condyle in adult shell: absent to weak (modified umbo) (0); well developed (1).
19. Ventral condyle in adult shell: absent (0); weak (1); prominent (2).
20. Radial sulcus dividing the disc from the posterior slope: absent (0); present (1).

Accessory structures of the shell

21. Callum: absent (0); present (1). The callum develops in taxa

- having pedal gape. Taxa without pedal gape (character 12 state 0) have that character codified as not applicable (N).
22. Development of callum: symmetrical (0); left part more extended and overlapping right part (1).
23. Dorsal extension of the callum: absent (0); present (1).
24. Protoplax: absent (0); present (1).
25. Composition of the protoplax: chitinous (0); calcareous (1).
26. Structure of the protoplax: single piece (0); subdivided in two pieces (1).
27. Mesoplax: absent (0); present (1).
28. Structure of the mesoplax: single piece (0); subdivided in two pieces (1).
29. Posterior area of umbonal reflection modified for reception of mesoplax: no (0); yes (1).
30. Metaplax: absent (0); present (1).
31. Hypoplax: absent (0); present (1).
32. Siphonoplax: absent (0); present (1).
33. Development of siphonoplax: on both valves (0); on right valve only (1).
34. Tube lining burrow: absent (0); present (1).
35. Pallets: absent (0); present (1).
36. Structure of pallets: not segmented (0); segmented (1).

Soft parts

37. Adult foot: not atrophied (0); atrophied (1).
38. Shape of foot: tongue-shaped or hatchet-shaped (0); cylindrical with discoid extremity (1).
39. Gills: two demibranchs (0); single demibranch (1).
40. Position of gills: before posterior adductor muscle (0); beyond posterior adductor muscle (1).
41. Shape of ctenidia: short and wide (0); elongate (1).
42. Loop of visceral mass beyond the posterior adductor muscle: absent (adductor muscles far apart) (0); present (adductor muscles close together) (1).
43. Intestine: transversing heart (0); not transversing heart (1).
44. Position of visceral ganglion: near the ventral side of posterior adductor muscle (0); posterior, at the end of pericardium (1).
45. Wood-storing caecum: absent (0); present (1).
46. Labial palps: large, free at the tips (0); small, not free at the tips (1).
47. Insertions of siphonal retractors: on shell valves (0); on burrow lining (1); on siphonal plates (2).

Appendix 3

Characters and character states employed for a basal phylogenetic analysis of the subgenus *Barnea* (*Anchomasa*).

1. Umbonal reflection: simple (0); septate (1). (character 5 in Appendix 1)
2. Posterior part of umbonal reflection: raised and with posterior margin square cut (0); adherent to the umbonal region (1). (character 8 in Appendix 1)
3. Pedal gape: absent (0); present (1). (character 12 in Appendix 1)
4. Shape of pedal gape: broad (0); slit-like (1). (character 13 in Appendix 1)
5. Shape of apophyses: thin (0); spatulate (1). (character 16 in Appendix 1)
6. Protoplax: absent (0); present (1). (character 24 in Appendix 1)
7. Mesoplax: absent (0); present (1). (character 27 in Appendix 1)
8. Metaplax: absent (0); present (1). (character 30 in Appendix 1)
9. Postero-dorsal granulations: absent (0), present (1)
10. Shape of the shell: tapered (0); moderately low (1); subglobose (2).
11. Position of the umbo: one third of the shell length (0); one fourth of the shell length (1).
12. Shape of posterior part: lanceolate (0); subtruncated (1).

Appendix 4

Data matrix of 16 taxa and 12 characters employed for the cladistic analysis of the subgenus *Barnea* (*Anchomasa*).

| | 111 | | |
|---|--------------|--|--------------|
| | 123456789012 | | |
| <i>Talona explanata</i> | 000?00100100 | <i>Barnea (Anchomasa) parva</i> | 011001000200 |
| <i>Cyrtoleuropsis orbignyana</i> | 00101???1010 | <i>Barnea (Anchomasa) ujraticumica</i> | 011001000010 |
| <i>Cyrtoleura (Scobinopholas) costata</i> | 001111100010 | <i>Barnea (Anchomasa) palmula</i> | 01100???0200 |
| <i>Pholas (Pholas) dactylus</i> | 111011110010 | <i>Barnea (Anchomasa) dumortieri</i> | 01100???0201 |
| <i>Pholas (Monothyra) orientalis</i> | 111111111010 | <i>Barnea (Anchomasa) cylindrica</i> | 01100???0000 |
| <i>Barnea (Barnea) ustjurtensis</i> | 011101000100 | <i>Barnea (Anchomasa) truncata</i> | 011001000101 |
| <i>Barnea (Barnea) candida</i> | 011101000010 | <i>Barnea (Anchomasa) subtruncata</i> | 011001000101 |
| | | <i>Barnea (Anchomasa) manilensis</i> | 011001000010 |
| | | <i>Barnea (Anchomasa) similis</i> | 011001000010 |