

THE LOST APORRHAIIS SPECIES FROM THE ITALIAN PLIOCENE: *A. PERALATA* (SACCO, 1893) (GASTROPODA: CAENOGASTROPODA)

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Abstract Three Early – Middle Italian Pliocene aporrhaid species are redescribed on the basis of material from the Siena and Radicofani basins (central Italy). Two of them, *Aporrhais pespelecani* (Linnaeus, 1758) and *Aporrhais uttingeriana* (Risso, 1826), are well known but the third, *Aporrhais peralata* (Sacco, 1893), has been almost completely overlooked despite its probable widespread distribution in the Italian Pliocene. This species, characterized by peristome with large parietal callus, long adapical digitation, thick laminar abaxial lip with three short digitations and short abapical digitation, is distinct from other Euromediterranean Pliocene to Recent species. However problems remain with specimens of *Aporrhais serresiana* (Michaud, 1828) having a wider lip and shorter digitations. The latter were formerly assigned to a different species, *Aporrhais macandreae* Jeffreys, 1867, but are now considered conspecific with *A. serresiana*, though re-analysis of their taxonomic status by modern approaches would be useful. *A. peralata* is distinct from these specimens by virtue of its more delicate axial sculpture, more obtuse spire and larger abaxial lip with shorter digitations.

Key words *Aporrhaidae*, taxonomy, systematics, nomenclature, distribution.

INTRODUCTION

Three species of aporrhaid, a small relict group of marine infaunal gastropods now occurring in continental waters of the Atlantic Ocean and Mediterranean Sea (Roy, 1994), are reported from the Italian Pliocene: *Aporrhais pespelecani* (Linnaeus, 1758), *Aporrhais serresiana* (Michaud, 1828) and *A. uttingeriana* (Risso, 1826) (Sacco, 1893; Ruggieri, 1971; Marquet *et al.*, 2002).

Major past contributions to the taxonomy, phylogeny and biogeography of Euro-Mediterranean Neogene fossil species were made by Sacco (1893, 1894) and Ruggieri (1971). Sacco (1893: 27-28; 1894: 154-156) claimed that two distinct groups existed since the Miocene: one having wide subfoliose digitations with coarse granular ornamentation including only *A. pespelecani* ("*Chenopus pespelecani* group"); the other having narrower quasi needle-like digitations with finer granular ornamentation including *A. serresiana* and *A. uttingeriana* ("*Chenopus serresianus* group"). According to Sacco, the *C. pespelecani* group included littoral and shallow water forms which, though characterized by wide variability, belonged to only one species known since the Miocene, whereas the *C. serresianus* group included mainly deep water forms characterized by less variability but which could be assigned to a number of species. According to Sacco, *C. meridionalis*, the

most ancient of them, gave rise to *C. uttingerianus* during the Late Miocene, a species which became widespread and common in the Early Pliocene and disappeared at the end of the Pliocene. During the Piacenzian, a third species, *C. serresianus*, evolved from *C. uttingerianus*; initially it co-existed with its parental species and then replaced it, surviving until the Recent.

Ruggieri (1971) regarded the scenario delineated by Sacco (1893, 1894) as valid but requiring corrections and additions. In fact, due to desiccation of the Mediterranean Sea in the Messinian (an event unknown to Sacco), Mediterranean Pliocene marine fauna was not derived from the Miocene fauna but from that of the Atlantic Miocene. Re-colonization of the Mediterranean by the Atlantic fauna would explain the sudden appearance of *A. serresiana* (a typical inhabitant of deep water) in the Early Pliocene. This species was erroneously regarded by Sacco as a rare entity, simply because he mainly studied fauna of shallow facies where it does not occur.

Ruggieri made many major changes, despite the fact that he considered Sacco's scenario valid. He assigned small-sized specimens from the Late Miocene, attributed by Sacco to varieties of *A. pespelecani*, to *A. alata* (Eichwald, 1830) a species which, according to Ruggieri, gave rise to *A. pespelecani* in the Mediterranean and *A. serresiana* in the Atlantic in the last part of the Miocene. In the same period, *A. uttingeriana* gave rise to another species, *A. thersites* (Brives,

1897), characterized by a thick columellar callus, in the Mediterranean. *A. thersites*, which Ruggieri regarded as guide fossil of the Sahelian, became extinct together with other Mediterranean aporrhaid species during the Messinian crisis at the end of the Miocene. At the beginning of the Pliocene, three species of aporrhaid species re-colonized the Mediterranean: two (*A. pespelecani* and *A. serresiana*) survived until the Recent, and the other (*A. uttingeriana*) became extinct in the Calabrian (and not at the end of the Pliocene as claimed by Sacco).

In the last few years, taxonomy, faunistics, palaeontology and biogeography of the aporrhaid species have been the subject of specific papers (von Cosel, 1977; Lozouet & Maestrati, 1987; Kronenberg, 1991; Solsona *et al.*, 2001; Marquet *et al.*, 2002) or tackled in the context of faunal reports (Malatesta, 1974; Janssen, 1984; Baluk, 1995; Wienrich, 2001; Landau *et al.*, 2004). These papers show that the systematics and evolution of Neogene aporrhaid species are surely much more complex and uncertain than Sacco (1893, 1894) and Ruggieri (1971) thought.

The present paper is devoted to a "lost" species, *A. peralata* (Sacco, 1893), overlooked despite its widespread distribution in the Italian Pliocene. This species is redescribed and compared with the two other well recorded *Aporrhais* species of the Italian Pliocene: *A. pespelecani* and *A. uttingeriana*.

TAXONOMY, SYSTEMATICS AND NOMENCLATURE OF THE EUROMEDITERRANEAN APORRHAIIDS

Most of the authors assign the Euromediterranean Recent aporrhaid species to the genus *Aporrhais* Da Costa, 1778 (type species *Aporrhais quadrifidus* Da Costa, 1778, by monotypy; *A. quadrifidus* is a junior synonym of *Strombus pespelecani* Linnaeus, 1758) (cf. Sabelli *et al.*, 1990-92; Giannuzzi Savelli *et al.*, 1997; Bouchet *et al.*, 1998; Marquet *et al.*, 2002). North West Atlantic species are usually assigned to the genus *Arrhoges* Gabb, 1868 (type species: *Rostellaria occidentalis* Beck, 1836) (cf. Roy, 1994; Solsona *et al.*, 2001), sometimes regarded as a subgenus or junior synonym of *Aporrhais* (cf. Lozouet & Maestrati, 1987; Marquet *et al.*, 2002) or of *Drepanocheilus* Meek, 1864 (type species *Rostellaria americana* Evans & Shumard, 1857) (cf. Kronenberg, 1991; Morton, 1997).

Simone (2005) examined three aporrhaid species (*Aporrhais pespelecani*, *Aporrhais serresiana* and *Arrhoges occidentalis*) in a phylogenetic study of stromboidean gastropods based on morphological characters and found that the aporrhaid species and *Aporrhais* are paraphyletic: *A. serresiana* is sister group of a clade including the other two aporrhaid species plus all the xenophorid and strombid species studied; inside this clade, *A. occidentalis* and *A. pespelecani* constitute a monophyletic group which, in turn, is the sister group of a clade including all the other species. He therefore tentatively assigned *A. serresiana* to the Jurassic genus *Cuphosolenus* Piette, 1876 (type species: *Pterocera tetracera* D'Orbigny, 1825). The putative paraphyly of the aporrhaid species is completely new and requires further verification. The anatomical differences (Simone, 2005) between the two groups of aporrhaid species strongly support the existence of at least two lineages, but the inclusion of one of them in a genus recorded only from the Jurassic is not realistic, since aporrhaid species underwent significant mass extinctions in the late Cretaceous (Roy, 1994). Moreover, study of other living species (especially *A. pesgallinae* Barnard, 1963) is fundamental for a better understanding of their phylogeny and systematics. We therefore use the conventional approach, including all living species in the genus *Aporrhais* pending comprehensive revision of generic systematics.

Some recent authors used *Aporrhais* as feminine, others as masculine and others indifferently as a feminine or masculine noun. According to Peck (1970: 45), the noun "*haporrhais*", as plural nominative *απορραιδες*, is found only in two Greek codices (Vaticanus graecus 262 and Vaticanus graecus 1339) of Aristotle's *Historia animalibus* (cf. 530a 19) and is a misspelling of *αμωρροιδες* meaning "which bleed", a name used to denote muricid gastropods with a pallial gland producing purple. As far as we know, the first author to use *Aporrhais* in the early modern zoological literature was Rondelet (1555) who applied it to *Lambis lambis* (Linnaeus, 1758) (cf. 79-81). This noun was later reported by Aldrovandi (1606) again for a *Lambis* species, maybe *L. truncata* (Humphreys, 1786) (cf. 341-344), by Lister (1685-92) in a plate illustrating a strombid and an aporrhaid gastropod (cf. 4: Pl. 866), Petiver (1702-1706) for *A. pespelecani* (according to Da Costa, 1778) and Klein (1753) for strombid gastropods (cf. 79-80). Despite its

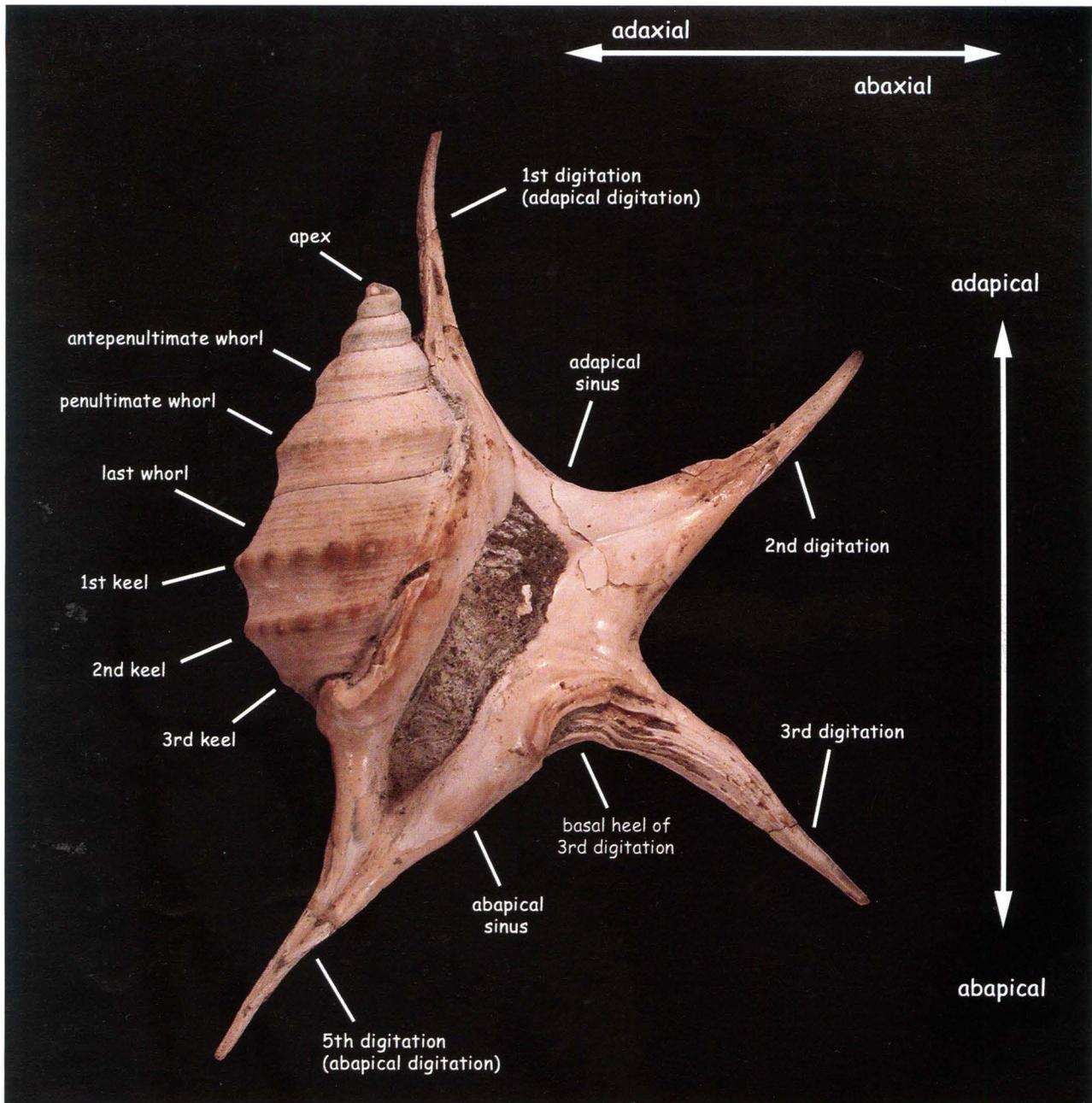


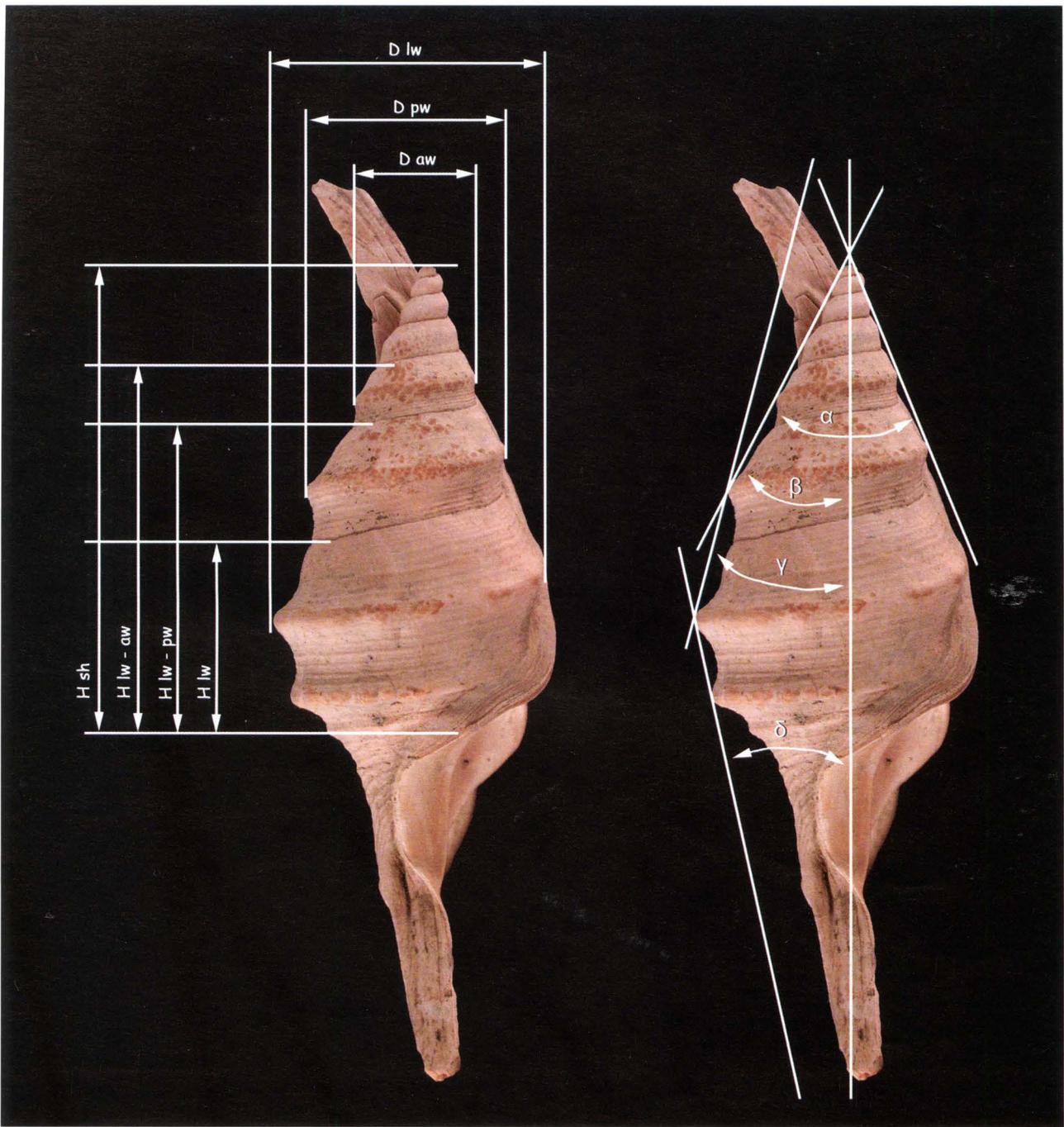
Fig. 1 Shell terminology on a shell of *Aporrhais uttingeriana* (Risso, 1826) from Podere Terrarossa (FPC). Note that fourth digitation is only present in *A. serresiana* (Michaud, 1828).

early use in the masculine (Petiver, 1702-1706; Da Costa, 1778), its grammatical gender is feminine because the suffix *-id-* indicates feminine nouns in ancient Greek (Buck & Petersen, 1984). Alternative etymologies – *Aporrhais* from the Greek “*aporrho*”, to flow away (Woodward, 1851-56), the Greek “*apò*”, from, and the Latin “*radius*”, ray (Settepassi, 1971) and the Greek “*apo*”, asunder, and “*raiw*”, I break (Fretter & Graham, 1981) – are clearly unrealistic.

MATERIALS AND METHODS

Morphological nomenclature That used by Fretter & Graham (1981) and Marquet *et al.* (2002) has usually been adopted because these authors published the best descriptions of *Aporrhais* shells (some terms are illustrated in Fig. 1).

Material examined Details on the collection localities are given in the Appendix. Acronyms for the collections in which the material examined

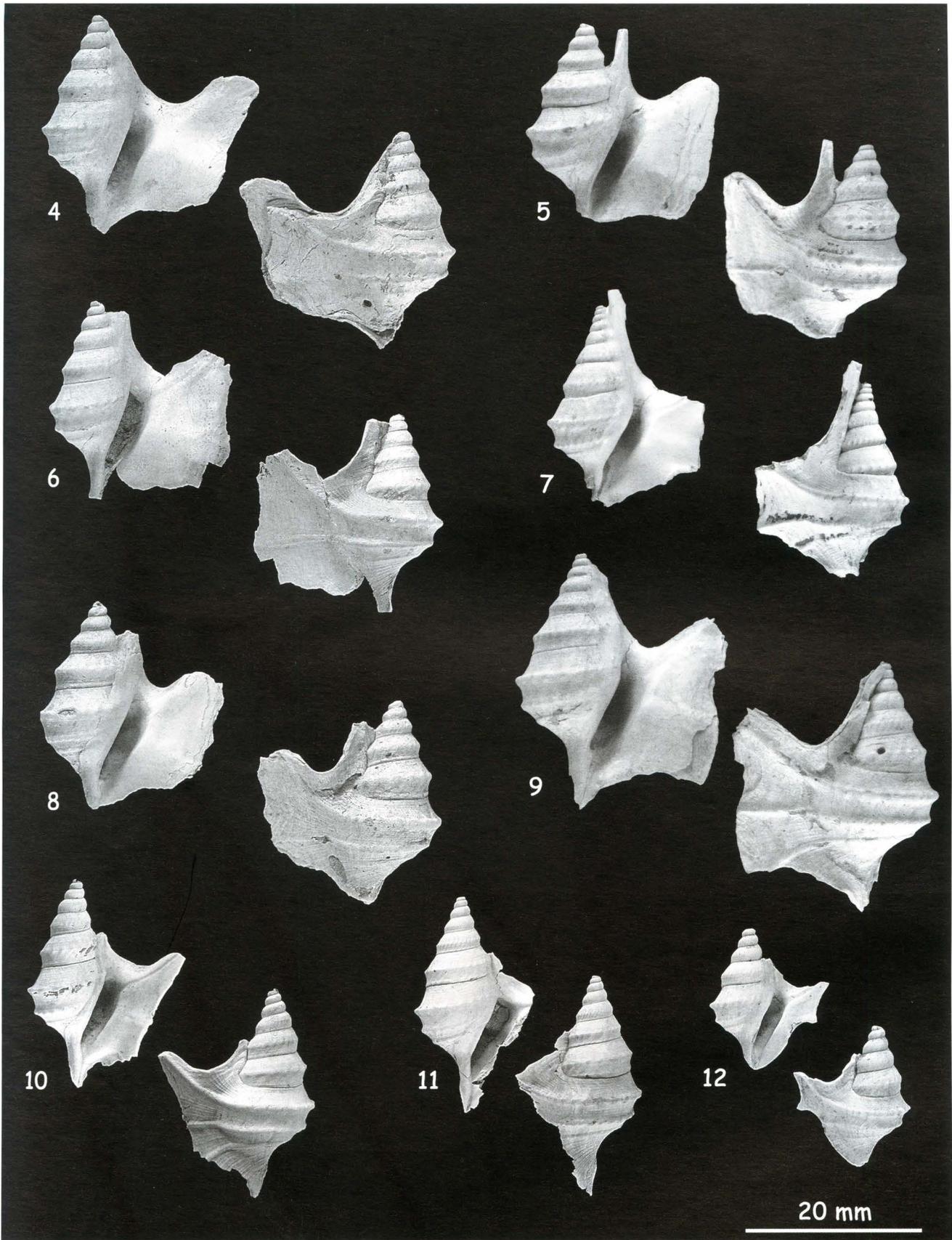


Figs 2-3 Linear (Fig. 2) and angular (Fig. 3) variables considered in the statistical analysis on a shell of *Aporrhais uttingeriana* (Risso, 1826) from Podere Capanna (VSC) (for a description of the variables, see Materials and Methods).

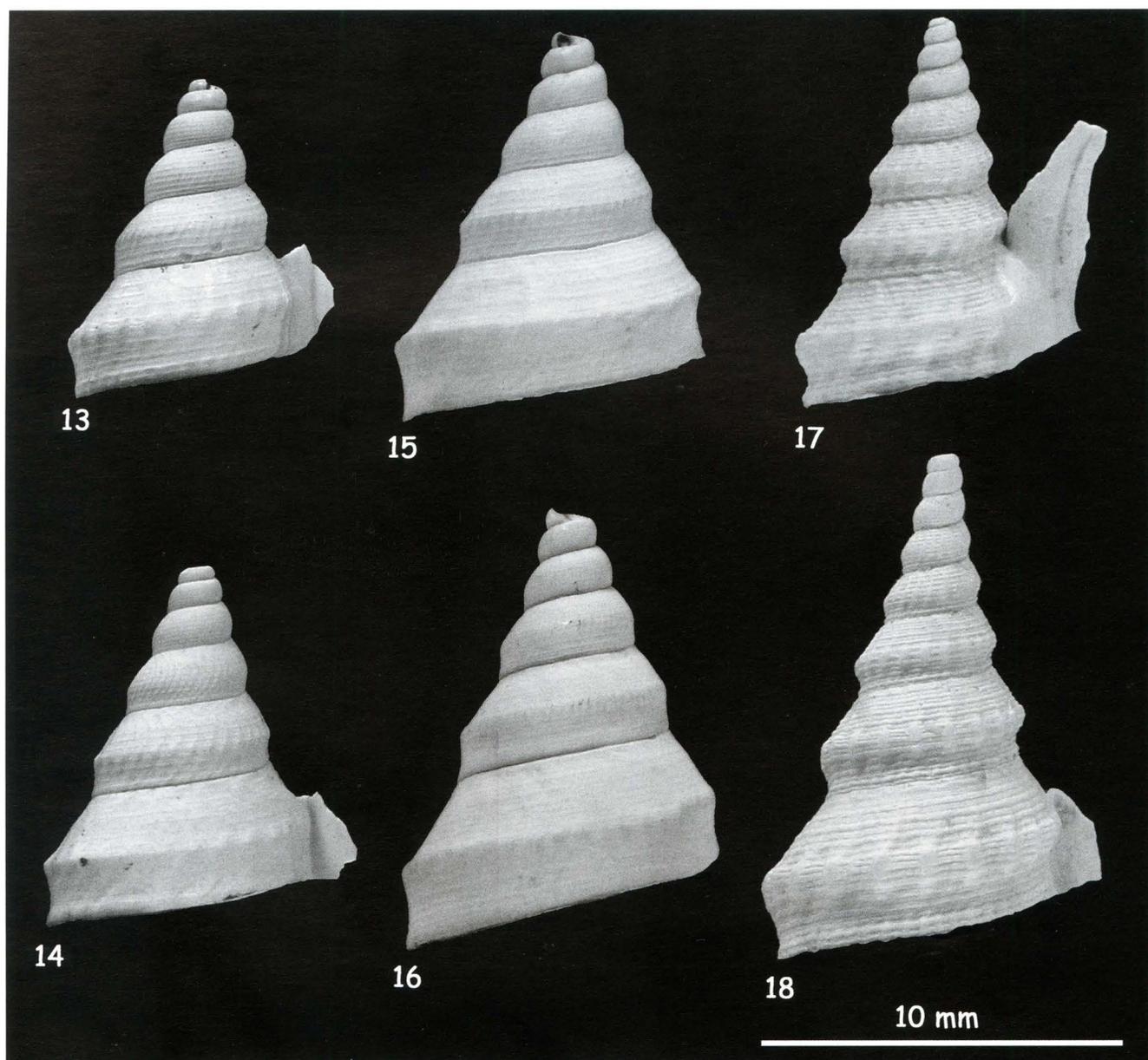
is kept are: FPC, F. Pizzolato collection, Arezzo; GMC, G. Manganelli collection, Siena; VSC, V. Spadini collection, Lucignano.

Measurements Measured on digital images using Adobe Photoshop 7.0.1. To obtain comparable measures, lateral views opposite the peristomal lip were used. The point where the third keel of the last whorl meets the periphery was chosen as the base of the height (the height of shells of

A. pespelecani could be taken from the shell apex to the apex of the abapical digitation, but this is impossible for the other species because their abapical digitation is always broken). Shell diameter was not taken as the distance between the two lines parallel to the axis and tangential to the periphery of the last whorl in apertural view (Cox, 1960: Fig. 80) because the peristomal lip and the 2nd and 3rd digitations are often broken at different points. The spire angle was taken as the angle



Figs 4-12 Shells of *Aporrhais peralata* (Sacco, 1893) from I Poggetti (Fig. 4), I Sodi (Figs 5-6, 8, 10-12) and Podere Caggio (Figs 6, 8) (Figs 4, 6, 8, 12 VSC; Figs 5, 7, 9-11, GMC). Note the long adapical digitation attached or separate from the spire (Figs 5, 7), the wide abaxial lip (Figs 4-6, 8-9) and the short abapical digitation (Figs 9-11).



Figs 13-18 Shell apex of *Aporrhais peralata* (Sacco, 1893) from I Sodi (Figs 13-14, GMC), *Aporrhais uttingeriana* (Risso, 1826) from I Sodi (Figs 15-16, GMC) and *Aporrhais pespelecani* (Linnaeus, 1758) from Poggio Rotondo (Figs 17-18, VSC).

between the lines connecting opposite peripheries of the penultimate and antepenultimate whorls. The variables considered were: shell height (H sh), last - antepenultimate whorl height (H lw-aw), last - penultimate whorl height (H lw-pw), last whorl height (H lw), last whorl diameter (D lw), penultimate whorl diameter (D pw), antepenultimate whorl diameter (D aw), angle between the lines connecting opposite peripheries of penultimate and antepenultimate whorls (α), angle between the axis and the line connecting the peripheries of penultimate and antepenultimate whorls (β), angle between the axis and the line connecting periphery of penultimate whorl

and first keel of last whorl (γ), angle between the axis and the line connecting first and second keels of last whorl (δ) (Figs 2-3).

Statistical analysis Fifteen populations (5 for each species) were studied statistically, measuring ten specimens chosen randomly, to a total of 150 specimens (*A. peralata*: Fontanelle, I Sodi, Montepollini, Podere San Fabio II, turnoff to Castelnuovo Berardenga; *A. pespelecani*: Borro delle Macerie, Casino di Barca, Podere Casanuova, Podere Nuovo, Poggio Rotondo; *A. uttingeriana*: I Sodi, La Querce, Podere Capanna, Podere Cavallara I, Podere Pian del Bulettino). The vari-

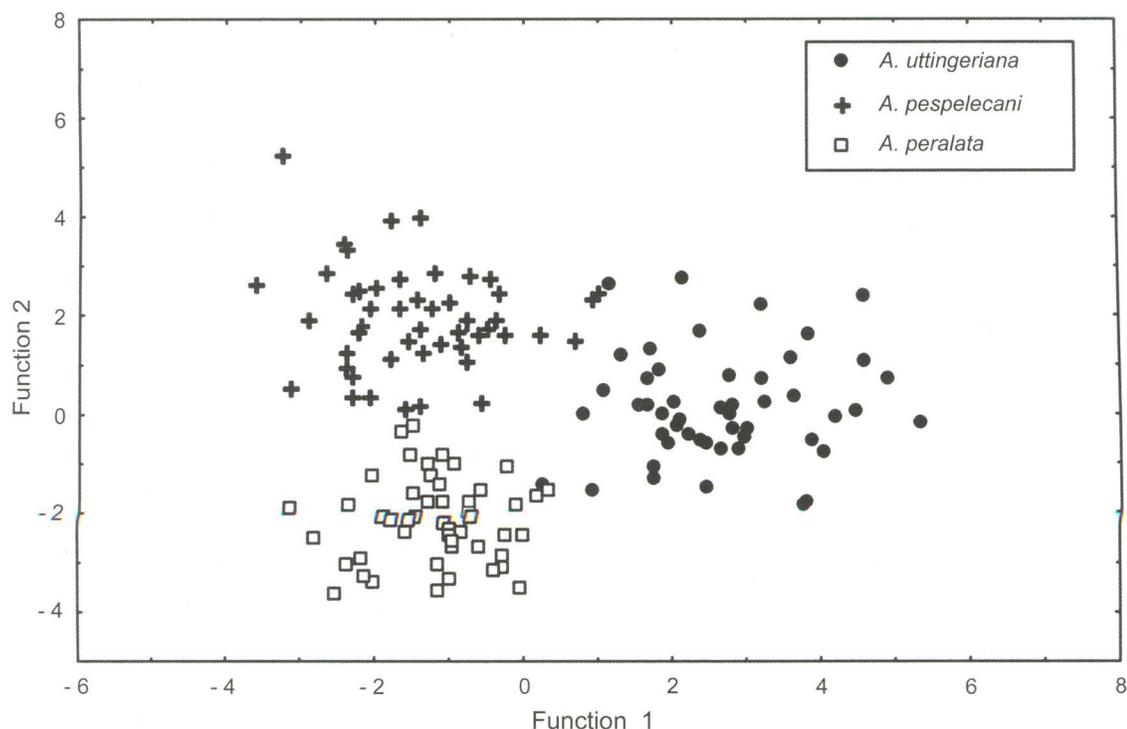


Fig. 19 DFA ordination graph for species discrimination on the basis of the first two discriminant functions (Wilks-Lambda = 0.05726; $F_{(20, 276)} = 43.872$, $p < 0.001$).

ables considered (Figs 2-3) were measured to the nearest 0.01 mm. Discriminant function analysis (DFA) was performed considering all variables. This analysis shows which measurements help to discriminate into groups defined *a priori*. The analysis was run taking the three species to be distinguished as groups. The sequential Chi-square test was used to quantify the extent to which each discriminant function significantly separated the groups. A structure coefficient table was used to establish the contribution of each measurement to the first two discriminant functions. MANOVA was used to compare the significance of differences between the three species. As *a posteriori* pair-wise comparison, MANOVA was also run for each possible pair of species (three tests). Multiple pair-wise comparison tests increase the probability of type I error. The Bonferroni method was therefore used taking $p < 0.001$ as the limit of significance. All variables were used in one-way ANOVA to test the significance (at $p < 0.05$) of differences between the three species. Before running ANOVA, the data was tested ($p < 0.05$) for normality and homogeneity of variance and was log-transformed when it violated ANOVA assumptions. Statistical analyses were carried out with STATISTICA 5 (StatSoft Inc., Tusla, USA).

DESCRIPTION OF SPECIES

Aporrhais peralata (Sacco, 1893)

Figs 4-14

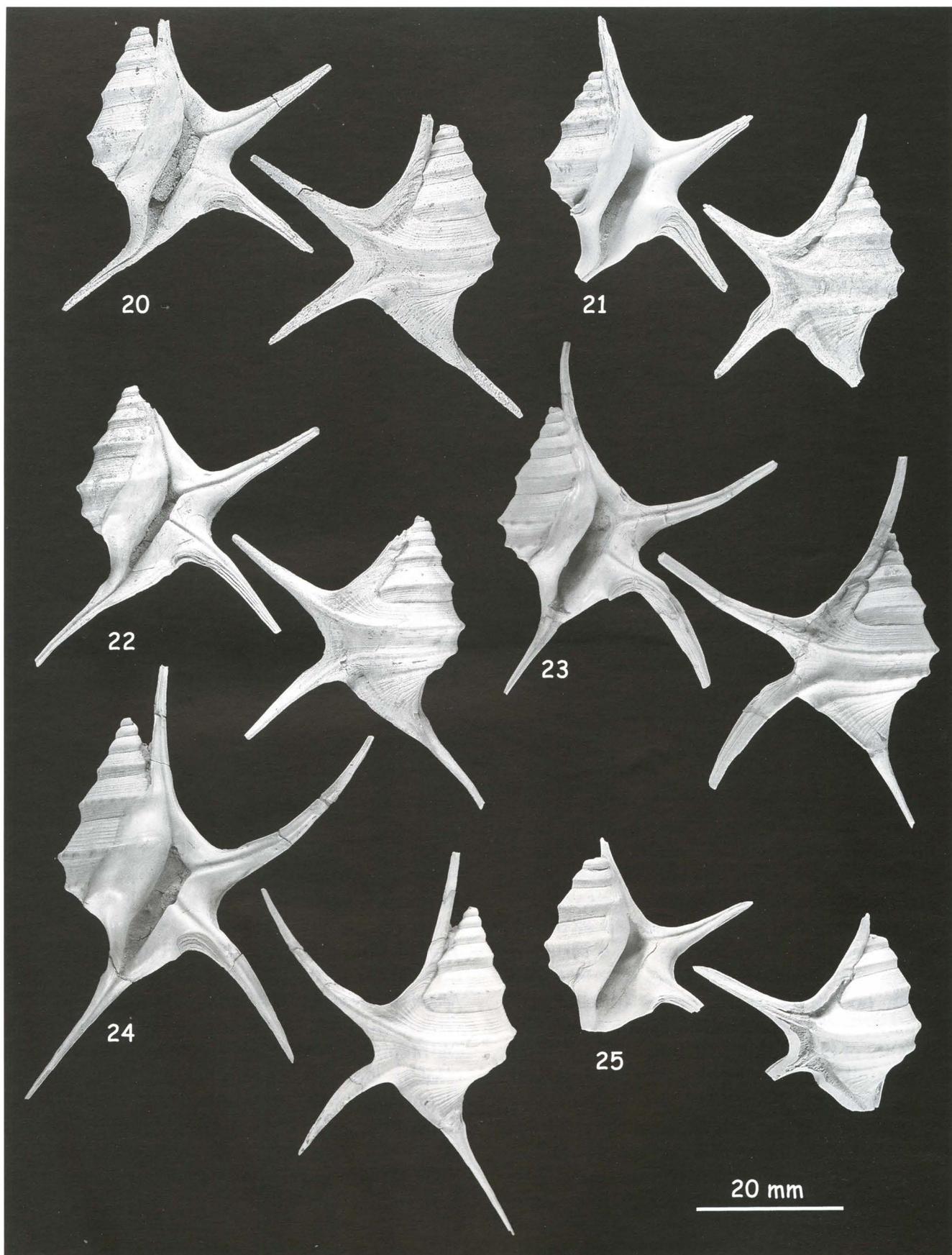
Primary reference C[henopus]. *uttingerianus* var. *peralata* [sic] Sacco, 1893: p. 26, Pl. 2, figs 25^a-25^b.

Type material One syntype is in the Bellardi - Sacco collection at the Museo Regionale di Scienze Naturali of Turin (BS.041.01.013) (Ferrero Mortara *et al.*, 1984).

Type locality "Piacenziano: Bordighera".

Material examined Fontanelle (55 GMC), Gragli (10 GMC), I Sodi (100 GMC, 295 VSC), Montepollini (64 GMC), Orsina Vecchia (11 GMC), Podere Caggio (12 GMC), Podere Capanna (1 VSC), Podere San Fabio II (35 GMC), Poggetti (1 VSC), Poggiodarno (7 GMC), Poggio Vangelo (5 GMC), Senese - Aretina State Road, km 96 (10 GMC), turnoff to Castelnuovo Berardenga (40 GMC).

Diagnosis A species of *Aporrhais* characterized by peristome with large parietal callus, long



Figs 20-25 Shells of *Aporrhais uttingeriana* (Risso, 1826) from Podere Pian del Bullettino (Figs 20-22) and I Sodi (Figs 23-25) (Figs 20-22, VSC; Fig. 23, GMC; Figs 24-25, FPC). Note the very short spire of specimen in Fig. 25.

Table 1 One way-ANOVA for all variables analysed. Significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. $p \geq 0.05$

Variable	F _(2, 147)
α	46.72 ***
β	145.15 ***
γ	6.97 ***
δ	47.31 ***
H sh	120.77 ***
H lw-aw	152.95 ***
H lw-pw	170.00 ***
H lw	192.19 ***
D aw	80.53 ***
D pw	121.32 ***
D lw	121.32 ***

adapical digitation, thick laminar abaxial lip with three short digitations (?) and short abapical digitation.

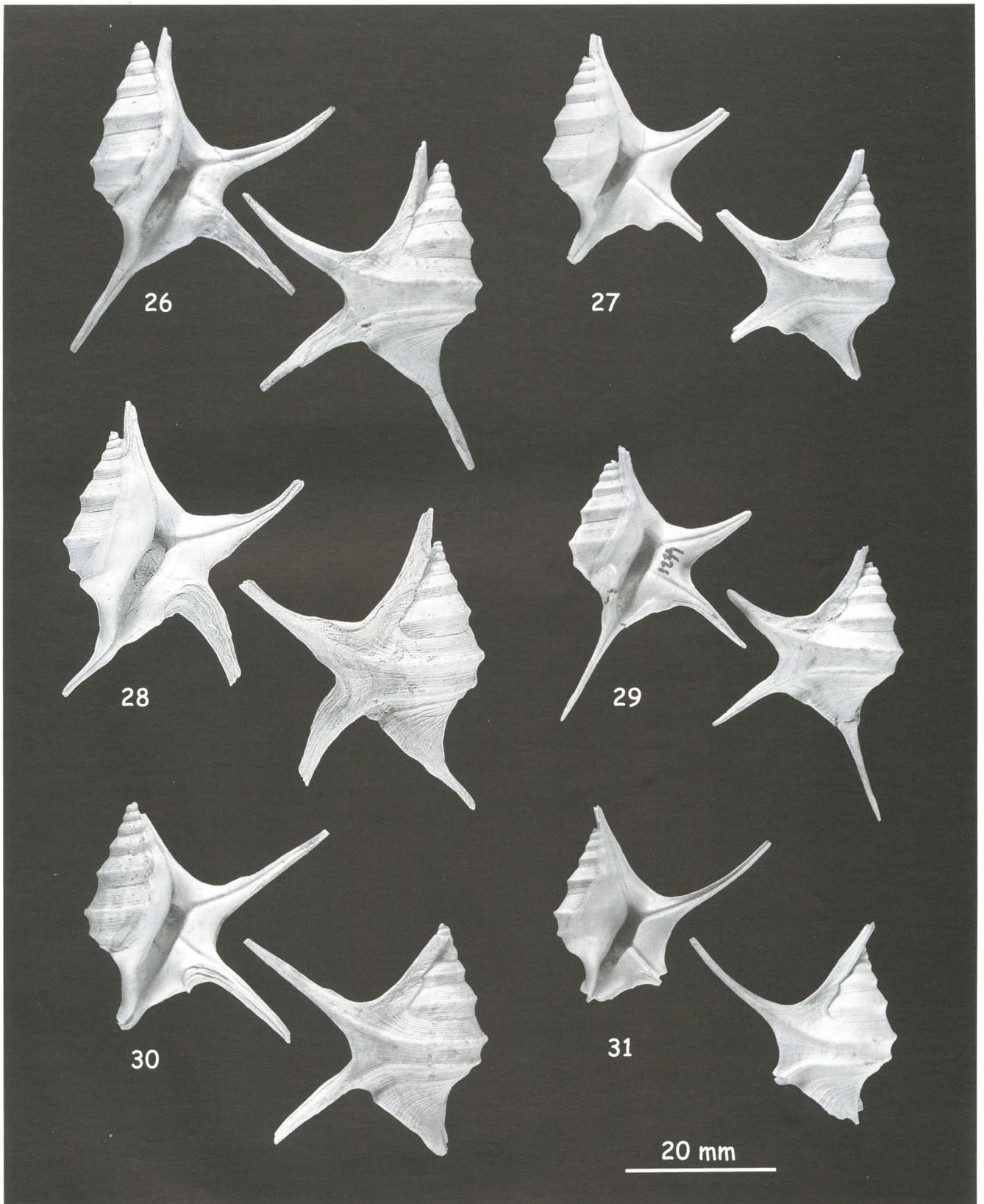
Description Adult shell (Figs 4-14) small-medium in size, robust, turriculate, with large wide thick fan-like peristomal lip and 5-6 regularly growing whorls (protoconch and early teleoconch whorls always worn, so that shell is decollated); spire conical; first teleoconch whorls rounded or slightly angled, last ones keeled, with prominent obtuse nodular keel slightly below mid-whorl; last whorl large, about half total height, with three prominent acute to obtuse keels which diverge on

peristomal lip: mid-whorl keel (first keel) and two abapical accessory keels, first of which (second keel) similar to mid-whorl keel (sometimes only slightly weaker) and other (third keel) smaller; spiral sculpture consisting of thin fine cords parallel until peristomal lip, then widely divergent; axial sculpture (Figs 13-14) variable: in first whorls of well preserved specimens consisting of many fine sinuous collabral riblets, often evident almost from suture to suture, but more prominent on mid-whorl; in last whorls consisting of barely evident collabral growth-lines and indistinct collabral ribs giving rise to faint to prominent tubercles at keels; aperture narrow, elongate, bordered by very thick peristome with large parietal callus, adapical digitation, thick laminar abaxial lip with three short digitations (?) and abapical digitation; parietal callus large, thick, extending over last two whorls and columella; columella short straight; abaxial lip edge obtusely angled, round in old specimens; adapical digitation (first digitation) longer than spire (usually broken; Figs 5-10), dorsally keeled, initially fused to spire then detached and upturned (sometimes completely fused to spire; Fig. 4); second digitation forming continuation of first-last whorl keel, dorsally keeled, wide short and blunt (cf. Fig. 4); third and fourth digitations forming continuation of second and third-last whorl keel, probably very short or only rough-hewn (cf. Figs 4, 5, 8); abapical digitation (fifth digitation) forming continuation of shell neck, short pointed and straight (rarely complete; Figs 10-11); apertural surface of peristome porcelaneous, shallowly grooved in correspondence with digitations and first and second keels though grooves obliterated in old specimens.

Measurements Shell height (H sh): 15.8 ± 1.55 mm (n: 50); last whorl diameter (D lw): 9.90 ± 0.93 mm (n: 50); spire angle (α): $47.42^\circ \pm 3.33$ (n: 50).

Table 2 Pair-wise MANOVA test. Acronyms: PER *A. peralata*, PES *A. pespelecani*, UTT *A. uttingeriana*.

Species pair	Wilks-Lambda	RAO	p level (d.f.: 9, 90)
UTT - PES	0,19	43,73	<0.001
UTT - PER	0,16	51,41	<0.001
PES - PER	0,17	49,00	<0.001



Figs 26-31 Shells of *Aporrhais uttingeriana* (Risso, 1826) from Podere Capanna (Figs 26-27, 29, GMC; Figs 28, 30-31, VSC).

Geographic and stratigraphic distribution At present the species is known only from some localities of the Italian Pliocene (Bordighera: Sacco, 1893; environs of Castrocaro: Ruggieri, 1962, as *A. serreseana* [sic]; Lascari: Moroni & Torre, 1965, as *A. serresiana*; Rio Albonello near Faenza: Tabanelli & Segurini, 1994; Campore di Salsomaggiore: Marquet *et al.*, 2002, as *Aporrhais pespelecani* form *peralata*; Torrente Samoggia near Monte Fortino: Tabanelli, 1998; Crete Senesi: this paper) and basal Pleistocene (Monte Gebolo: Tabanelli, 1981, as *A. serresiana*), but its distribution is probably wider. In the Crete Senesi it is widespread in many outcrops, dating back to the Piacenzian (Middle Pliocene), mainly consisting of clayey sediments of deep facies together with *Korobkovia oblonga* (Philippi, 1844), *Leucosyrinx angelonii* (De Stefani, 1875) and *Stellaria* cf. *plioextensa* (Sacco, 1896).

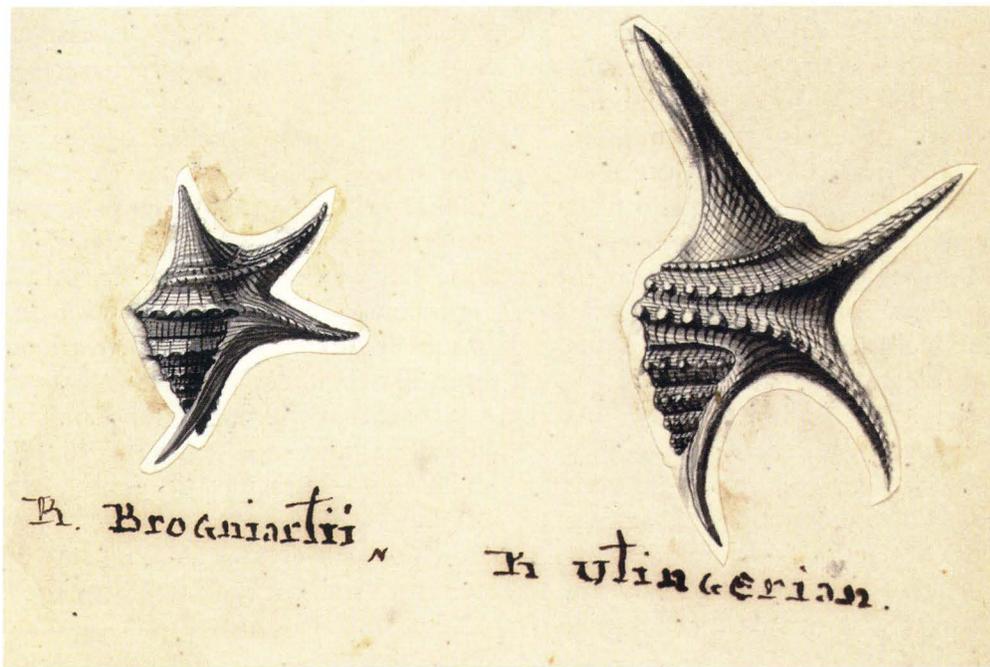
Derivation of name The specific epithet *peralata* is formed by the prefix "per", thoroughly, and the adjective "alata", winged.

Nomenclature Many taxa introduced by F. Sacco as varieties in *I Molluschi dei terreni terziari del Piemonte e della Liguria* are often infrasubspecific and as such not available (ICZN, 1999: Art. 45.6.4). Their infrasubspecific status is supported by the fact that these nominal taxa often coexist temporally and geographically with other varieties and the species (Sacco never distinguished a "typical variety", but only the species). They may only be available if a subsequent author adopted them as the valid name of a species or subspecies before 1983 (ICZN, 1999: Art. 45.6.4.1). If this provision of the Code is applied to the letter, most of Sacco's new nominal taxa are not available, although they have usually been used as valid. This is also the case of *Chenopus uttingerianus* var. *peralata* Sacco, 1893. We therefore follow the usual praxis of considering them available.

An earlier available name for this species might be *Chenopus desciscens* Philippi, 1844, from the Sicilian and Calabrian Pliocene. However the original description and figure are inadequate for establishing its identity and all attempts to trace any type material in Berlin (Germany) and Santiago (Chile) were unsuccessful.

Remarks *Aporrhais peralata* is distinct from all other congeneric Euromediterranean Pliocene to Recent species, such as *A. uttingeriana* (Risso, 1826), *A. serresiana* (Michaud, 1828), *A. pespelecani* (Linnaeus, 1758) and *A. scaldensis* (van Regteren Altena, 1954) by virtue of its peristome and axial sculpture. The peristome, extending into large wide thick laminar abaxial lip with three short digitations, distinguishes *A. peralata* from the other species (peristome with four-five long divergent thorn-like digitations in *A. uttingeriana* and typical *A. serresiana* or with four wide short winged divergent digitations in *A. pespelecani* and *A. scaldensis*) while the axial sculpture distinguishes it from all other species except *A. uttingeriana*; the latter and *A. peralata* share axial sculpture consisting of numerous thin collabral riblets on the first whorls and faint collabral growth-lines and indistinct collabral ribs, which give rise to weak to prominent tubercles at keels on the last whorls (collabral ribs more prominent mid-whorl and which give rise to prominent tubercles at the mid-whorl keel in other species) (for *A. pespelecani*, see Figs 17-18, 34-45 and Settepassi, 1971; Lozouet & Maestrati, 1987; Kronenberg, 1991; Giannuzzi Savelli *et al.*, 1997; for *A. scaldensis*, see Marquet, 1998; for *A. serresiana*, see Settepassi, 1971; Lozouet & Maestrati, 1987; Kronenberg, 1991; Giannuzzi Savelli *et al.*, 1997; Simone, 2005; for *A. uttingeriana*, see Figs 1-3, 15-16, 20-31 and Malatesta, 1974; Cataliotti-Valdina, 1975; Caprotti, 1976; Lozouet & Maestrati, 1987; Brambilla & Lualdi, 1988; Brambilla *et al.*, 1988; Cavallo & Repetto, 1992; Solsona *et al.*, 2001; Marquet *et al.*, 2002; Landau *et al.*, 2004).

Problems remain for specimens of *A. serresiana* having a wider lip and shorter digitations (cf. Kobelt, 1906: Pl. 104, figs 5-10; Bouchet & Warén, 1993: Figs 1661-1663). The latter were formerly assigned to a different species, *A. macandreae* Jeffreys, 1867 (cf. Kobelt, 1906), but are now considered conspecific with *A. serresiana* (Kronenberg, 1991; Bouchet & Warén, 1993) of which they constitute a northern subspecies (Fretter & Graham, 1981). However reanalysis of their taxonomic status with modern approaches (statistical analysis of morphological data; anatomical investigations; molecular studies) would be useful. *A. peralata* is distinct from these specimens by virtue of its more delicate axial sculpture, more obtuse spire and larger



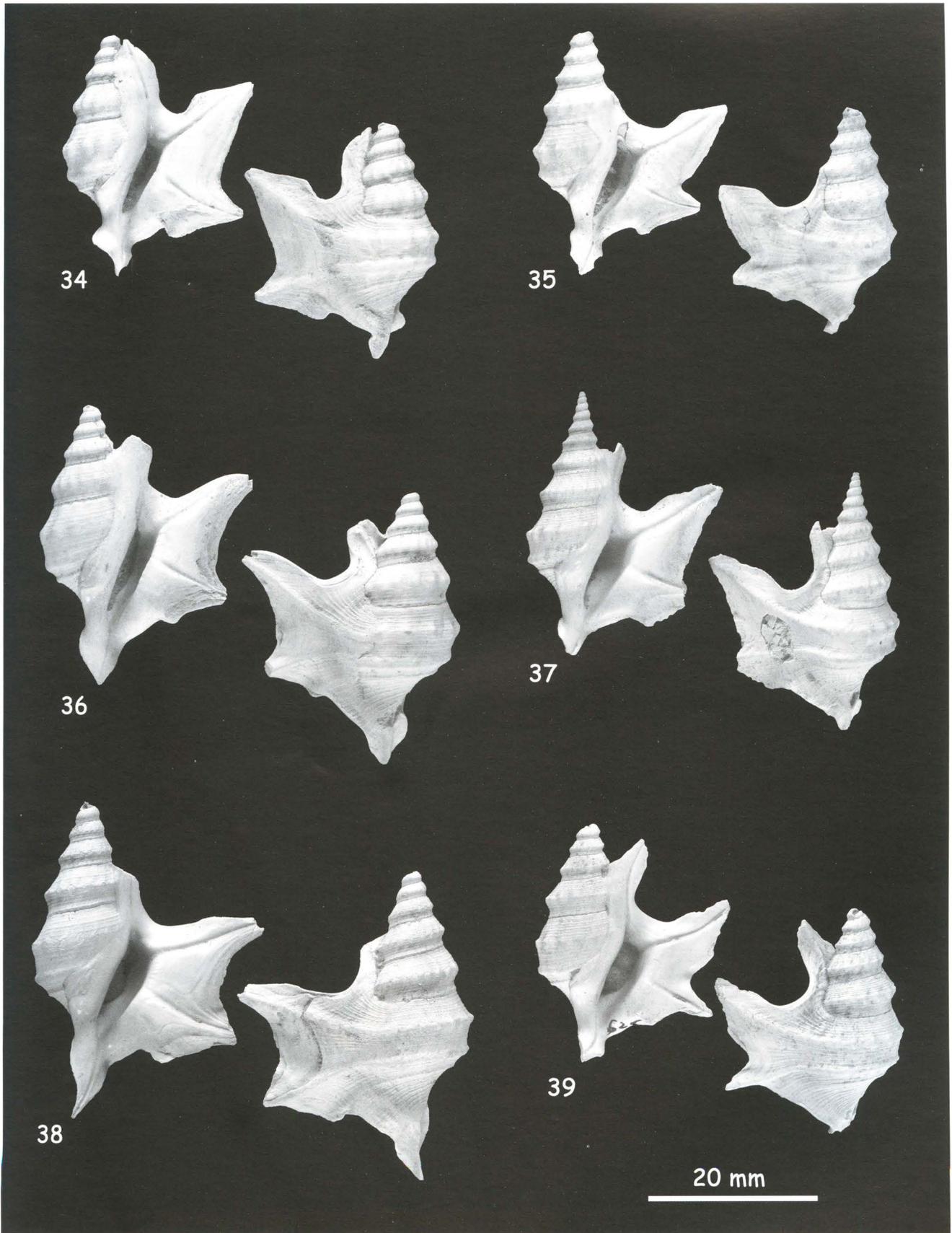
Figs 32-33 P. Gény's drawings of Risso's aporrhoids (Library of Muséum National d'Histoire Naturelle, Paris; courtesy of Virginie Héros).

abaxial lip with shorter digitations.

The distinction of *A. peralata* from coeval specimens of the other two species is confirmed by statistical analysis. Indeed, the first two functions obtained by DFA (Fig. 19) detected significant differences between the three species: function 1 ($\chi^2 = 407.6$, d.f. = 20, $p < 0.001$; Wilks Lambda = 0.06) clearly discriminated *A. pespelecani* and *A. peralata* (negative scores) from *A. uttingeriana* (positive scores) and function 2 ($\chi^2 = 190.9$, d.f. = 9, $p < 0.001$; Wilks Lambda = 0.26) separated *A. pespelecani* (positive scores) and *A. peralata* (negative scores). Notably, the two functions explained more than 99% of the data variance. Canonical and structural coefficients indicated that: along the first function, species with high positive scores (*A. uttingeriana*) had large values of variables H lw and D pw, whereas species with negative scores (*A. peralata* and *A. uttingeriana*) had large values of variables D aw, D lw and H sh; along the second function a species with high positive scores (*A. pespelecani*) had large values of variables H lw-aw and D pw, while a species with negative scores (*A. peralata*) had large values of D aw and β . One-way ANOVA confirmed that the three species differed significantly in all the variables analysed (most significant results in Tab. 1). MANOVA showed significant differences (always $p < 0.001$) for each pair of species, confirming the DFA clustering (Tab. 2).

This species has remained misidentified and overlooked for so long. It was only recently rediscovered but identified as *Aporrhais serresiana* (Ruggieri, 1962, 1971; Moroni & Torre, 1965) or *Aporrhais serresianus pliorara* (Sacco, 1893) by Tabanelli & Segurini (1994: Pl. 1, figs 1-2) or declassified to a form of *Aporrhais pespelecani* by Marquet *et al.* (2002: Figs 38-39). Specimens of *A. peralata* from Brisighella and Castrocaro, assigned by Ruggieri to *A. serresiana*, are kept in the Museo Civico di Scienze Naturali of Faenza and in the private collection of C. Tabanelli (Ravenna); specimens from Lascari were not re-examined as it proved impossible to find them, but it is probable that they belonged to *A. peralata* (before marrying Ruggieri, Moroni was one of his close coworkers).

Describing this taxon, Sacco (1893) claimed that it was an apparently anomalous form with adult characters before complete development. Vinassa de Regny (1897: p. 29, Pl. 3, fig. 10) interpreted a shell of *A. peralata* as a juvenile of *A. uttingeriana*. The parietal callus and adapical and abapical digitations less developed than those of *A. uttingeriana* suggest juvenile specimens, especially if found without lip. However this is not true of the wide thick peristomal lip: it is difficult to explain how it could be re-absorbed and transformed into that of *A. uttingeriana*. Moreover, in the Pliocene Basin of Siena, *A. peralata* is absent



Figs 34-39 Shells of *Aporrhais pespelecani* (Linnaeus, 1758) from Guistrigona (Figs 34, 36-38, VSC; Figs 35, 39, GMC).



Figs 40-45 Shells of *Aporrhais pespelecani* (Linnaeus, 1758) from Poggio Rotondo (Figs 40-43, 45) and Guistrigona (Fig. 44) (all VSC).

from most sites where *A. uttingeriana* is found.

A. peralata has no relationship with species of the *A. pespelecani* group, especially with the coeval *A. pespelecani* which Marquet *et al.* (2002) regarded as a form. The two species are morphologically and ecologically distinct. *A. peralata* is found in the clayey sediments of deep facies, whereas *A. pespelecani* is a sublittoral species (Fretter & Graham, 1981) living on a wide granulometric spectrum from muds to gravels (Fretter & Graham, 1981; Solsona *et al.*, 2001).

Ruggieri and co-workers assigned specimens of this species to *A. serresiana* probably based on their similarities to specimens of *A. serresiana* with wider lip and shorter digitations. *A. serresiana* has a distribution that extends from Iceland and Norway southward to Morocco in the Atlantic, including the Mediterranean (Fretter & Graham, 1981; Bouchet & Warén, 1993). It is rare and infrequently recorded as a fossil (cf. Sacco, 1893; Gignoux, 1913; Greco & Lima, 1974). The oldest report is from the Pliocene of northern Italy (Sacco, 1893) and is probably based on only two specimens, both tentatively assigned to *A. serresiana*. The best preserved of them (cf. Sacco, 1893: Pl. 2, fig. 27; Ferrero Mortara *et al.*, 1984: Pl. 22, fig. 9) has five long digitations and strong axial sculpture typical of this species. This may prove that *A. serresiana* has existed since the Middle-Late Pliocene, within the known stratigraphical range of *A. peralata*, but the absence of more accurate data on the collecting localities precludes an exact palaeoenvironmental and stratigraphical setting for this record.

Ruggieri hypothesized that *A. peralata* [as *A. serresiana*] was derived from small specimens of *A. alata* that lived in the Atlantic in the last part of the Miocene. Specimens of *A. alata* (auct. non Eichwald, 1830) from the Early to Late Miocene of the North Sea Basin (Belgium, Denmark, Germany and The Netherlands) are now assigned to *A. dingdenensis* Marquet, Grigis & Landau, 2002, and are somewhat reminiscent of *A. peralata* by virtue of their peristomal lip and digitations.

The affinity between *A. peralata* and specimens of *A. serresiana* formerly assigned to *A. macandrae* is evident and consequently the taxonomic status of this entity is a problem of subjective sensitivity. Between the two possible alternatives (i.e. a distinct species or a chronosubspecies of *A.*

serresiana) we opted for the former (certain *Aporrhais* species are distinguished by much less; cf. Marquet *et al.*, 2002), though we recognize that others may prefer the latter alternative. Further useful elements could emerge from statistical analysis of a suitable number of populations of *A. serresiana* and *A. peralata*.

Aporrhais uttingeriana (Risso, 1826)

Figs 1-3, 15-16, 20-33

Rostellaria uttingerianus [sic] Risso, 1826: 225-266.

Type material Unknown.

Type locality "Fossile à Magna et à la Rochette du Var".

Material examined Casino di Barca (1 GMC), Fontanelle (3 GMC), Fornaci di sotto (12 GMC), Fosso Rigo (4 GMC), Gragli (6 GMC), Guistrigona (9 GMC), I Sodi (20 GMC, 82 VSC), La Querce (6 GMC, 14 VSC), Monsindoli (6 VSC), Montepollini (17 GMC), Podere Capanna (22 GMC, 98 VSC), Podere Casanuova (2 GMC), Podere Cavallara I (114 VSC), Podere Pian del Bullettino (22 VSC), Podere San Fabio II (1 GMC), Podere Sant'Antonio (3 GMC, 109 VSC), Podere Terrarossa (1 FPC, 1 GMC, 2 VSC), Poggiodarno (2 GMC), Poggio Rotondo (2 VSC), Senese - Aretina State Road, km 96 (1 GMC), turnoff to Castelnuovo Berardenga (1 GMC).

Diagnosis A species of *Aporrhais* characterized by peristome with very large parietal callus and four long divergent thorn-like digitations all keeled on dorsal side and grooved on apertural side.

Description Adult shell (Figs 1-3, 15-16, 20-31) medium to large in size, robust, turruculate, with large thick digitate peristome and 4-6 regularly growing whorls (protoconch and early teleoconch whorls always worn, so that shell is decollated); spire conical; first teleoconch whorls rounded or slightly angled, last ones keeled, with prominent obtuse more or less nodular keel slightly below mid-whorl; last whorl large about half total height, with three prominent acute to

obtuse keels: mid-whorl keel (first keel) and two abapical accessory keels, first of which (second keel) similar to mid-whorl one (sometimes only slightly weaker) and other (third keel) smaller; spiral sculpture consisting of fine cords, parallel until peristomal lip, then widely divergent; axial sculpture (Figs 15-16) variable: in first whorls of well preserved specimens consisting of numerous thin sinuous collabral riblets, more prominent mid-whorl; in last whorls, consisting of barely evident collabral growth-lines and indistinct collabral ribs giving rise to weak-to-prominent tubercles at keels; aperture narrow elongate bordered by very thick peristome with very large thick parietal callus and four long divergent thorn-like digitations all keeled on dorsal side and grooved on apertural side; parietal callus very large thick and extending over last two-three whorls and columella; columella short straight; abaxial lip edge obtusely angled, round in old specimens; adapical digitation (first digitation) much longer than spire, initially fused to it, then often detached and turned upwards; second digitation forming continuation of first-last whorl keel and describing angle of about 80° with first digitation; third digitation forming continuation of second-last whorl keel and describing angle of about 80° with second digitation; in old specimens, third digitation slightly twisted adapically and with large basal heel on abapical side (Figs 1, 20-23, 26, 28, 30); fourth digitation absent; abapical digitation (fifth digitation) forming continuation of shell neck, diverging about $10\text{-}20^\circ$ from shell axis and describing angle of about 90° with third digitation; abapical sinus delimited abaxially by basal heel of third digitation; apertural surface of peristome porcelaneous.

Dimensions Shell height (H sh): 22.5 ± 2.90 mm (n: 150); last whorl diameter (D lw): 14.4 ± 1.94 mm (n: 150); spire angle (α): $49.66^\circ \pm 3.91$ (n: 150).

Geographic and stratigraphic distribution According to Solsona *et al.* (2001), *A. uttingeriana* is known from the Middle Miocene of the Atlantic (Aquitania, France), eastern Mediterranean (Po, Italy; Karaman, Turkey) and Paratethys (Korytnica, Poland; Vienna, Austria).

Derivation of name Unknown. Risso may have conceived the specific epithet after a German geologist, Uttinger (deceased in 1829; name

and date of birth unknown) who was active in the early 19th century and wrote a number of papers on geological and mineralogical subjects (cf. Poggendorff, 1863).

Nomenclature Risso (1826) described two aporrhaid species from the environs of Nice: *Rostellaria uttingerianus* (pp. 225-226; "fossile à Magna et à la Rochette du Var") and *Rostellaria brongniartianus* (p. 226, Fig. 94; "fossile à la Trinité"). These two nominal taxa have always been regarded as synonyms or varieties of the same species (Bronn, 1831; Sacco, 1893; Vinassa De Regny, 1897; Arnaud, 1977) and their reciprocal precedence was determined by Bronn (1831: 30) who listed *R. brongniartianus* in the synonymy of *R. uttingerianus*. Type material of these taxa has probably been lost (Arnaud, 1977). Risso's diagnosis does not support certain elements for definitive identification (cf. also Sacco, 1893: 24, 25-26), but the figure of *R. brongniartianus* was clearly *Aporrhais uttingeriana*. Risso's molluscs were also drawn by P. Gény and his illustrations, kept in the library of the Muséum National d'Histoire Naturelle in Paris, were recently published by Arnaud (1977). Risso's figure of *R. brongniartianus* does not match Gény's drawing of this species but that of *R. uttingerianus* (though the adapical digitation is much longer, the abapical digitation is more robust and the last whorl has three keels instead of two). Unfortunately we were unable to determine whether the legend of Risso's or of Gény's figure was erroneous (in any case both shells illustrated by Gény match those of *A. uttingeriana* cf. Figs 32-33).

Remarks Using an allegedly "more modern" approach, Vialli (1963: 781-782) claimed that the four aporrhoids listed by Sacco (1893, 1894) (i.e. *A. meridionalis*, *A. uttingerianus*, *A. serresianus* and *A. pespelecani*) for the Euro-Mediterranean Neogene represented a single species having some shell parts relatively invariable (whorls, columella) and others varying widely in relation to depth, type of sediment and other factors apparently not yet considered. Although some authors (e.g. Caprotti, 1970) accepted this point of view, others (e.g. Pelosio, 1967; Ruggieri, 1971) disregarded it. In fact, apart from *A. meridionalis* sensu Sacco (1893, 1894) whose status is controversial, distinguishing the other species poses no

problems.

A. uttingeriana was very common in the Pliocene, but the only accurate description is that of Vinassa de Regny (1897) because most subsequent authors seem to have thought it superfluous to detail features which characterize and distinguish this species (e.g. Cerulli Irelli, 1911; Pelosio, 1967; Malatesta, 1974). Recently, however, Landau *et al.* (2004) gave another fine description based on specimens from the Pliocene of Estepona. According to Vinassa de Regny (1897), this species has a shell with 7-9 whorls and an apical angle of about 45°. Most specimens examined by us have shells with protoconch and first teleoconch whorls eroded (as first noted by Landau *et al.*, 2004), so that the shell is severely decollated, the number of whorls is fewer than reported by Vinassa de Regny (1897) and the apical angle (measured as illustrated in Fig. 3) is larger (about 50°). It is strange that nobody ever noted that the Pliocene shells of this species are decollated.

The relationships of *A. uttingeriana* are still uncertain and this has repercussions on the stratigraphic and geographical distribution. According to Marquet *et al.* (2002) and Landau *et al.* (2004) this species is known from the Middle Miocene of Paratethys (Korytnica, Poland) to the Lower Pleistocene of the central Mediterranean (Latium, Lombardy and Sicily), while according to Solsona *et al.* (2001) it is known from the Middle Miocene of Paratethys (Korytnica, Poland; Vienna, Austria), Atlantic (Aquitania, France) and eastern Mediterranean (Po, Italy; Karaman, Turkey) to Recent western Atlantic. Apart from its close relationships with Middle Miocene *A. dactylifera* (Boettger, 1896) – Marquet *et al.* (2002) kept this taxon distinct because it “differs [from *A. uttingeriana*] by the upper digit, which is free from the spire and consequently forms a smaller angle with the second digitation” (cf. Marquet *et al.*, 2002: p. 158, Figs 14-16), but this character is also occasionally present in *A. uttingeriana* (Figs 1, 20, 24, 26 and Cerulli Irelli, 1911: Pl. 43, fig. 27) – much of the controversy concerns its relationships to the Recent western Atlantic *A. pesgallinae* Barnard, 1963, which is regarded as a species distinct from *A. uttingeriana* by von Cosel (1977), Lozouet & Maestrati (1987), Abbott & Dance (1990), Ardevini & Cossignani (2004) and Landau *et al.* (2004) and as conspecific by Mienis

(1976), Kronenberg (1991), Giannuzzi Savelli *et al.* (1997), Solsona *et al.* (2001) and Marquet *et al.* (2002). *A. pesgallinae* differs from *A. uttingeriana* by virtue of its more delicate structure, an adapical digitation diverging proximally from the spire (in *A. uttingeriana* the adapical digitation only rarely diverges from the spire and when it does, it diverges distally) and a shorter, thinner abapical digitation usually less divergent from the axis (for *A. pesgallinae*, see Settepassi, 1971, as *A. pseudoserresianus procerus*; Lozouet & Maestrati, 1987; Kronenberg, 1991; Giannuzzi Savelli *et al.*, 1997, as *A. uttingerianus*). *A. pesgallinae* recalls the Paratethyan Oligo-Miocene *A. digitatus* (Telegdi-Roth, 1914) (cf. Marquet *et al.*, 2002: p. 157, Figs 20-22), apparently the most ancient member of the *A. uttingeriana* group.

The last Mediterranean reports of *A. uttingeriana* date back to the Pleistocene (Solsona *et al.*, 2001; Landau *et al.*, 2004) and are from Latium (Cerulli Irelli, 1911), Lombardy (Brambilla *et al.*, 1988), Romagna (Ruggieri, 1971) and Sicily (Glibert, 1963). However, at least three of these reports are based on materials in historical collections which may have been found in different stratigraphic contexts (e.g. Cerulli Irelli, 1911, cf. Bonadonna, 1968) or mislabelled (e.g. Glibert, 1963, cf. Ruggieri, 1971). The presence of the species in the Early Pleistocene therefore only seems to be supported by Ruggieri (1971).

Aporrhais pespelecani (Linnaeus, 1758)

Figs 17-18, 34-45

[*Strombus*] *Pes pelecani* Linnaeus, 1758: 742.

Type material Unknown, lost? No specimens of this species are kept in the Linnean collection at the Linnean Society of London (Dance, 1967) and no information is available on others quoted by Linnaeus (1758) from the literature (Buonanni, 1684; Lister, 1685-92; D'Argenville, 1742; Gualtieri, 1742).

Type locality “Habitat in O[ceano]. Europaeo, Norvegico, Mediterraneo, Americano”.

Material examined Borro delle Macerie (3 GMC, 41 VSC), Casino di Barca (28 GMC), Fornaci di

sotto (2 GMC), Guistrigona (28 GMC, 19 VSC), Podere Capanna (1 VSC), Podere Casanuova (38 GMC), Fosso Rigo (18 GMC), Poggio Rotondo (5 GMC, 30 VSC).

Diagnosis A species of *Aporrhais* characterized by peristome with large parietal callus and four large divergent winged digitations, all keeled on dorsal side and grooved on apertural side; adaxial lip edge roughly angled, often with ribbon sometimes partly divided into minute denticles.

Description Adult shell (Figs 17-18, 34-45) small-medium in size, robust, turriculate, with large thick digitate peristome and 5-6 regularly growing whorls (protoconch and early teleoconch whorls almost always worn so that shell is decollated); spire conical; first teleoconch whorls rounded or angled, last ones keeled, with prominent obtuse more or less nodular keel below mid-whorl; last whorl large, about half total height, with three prominent obtuse keels: mid-whorl keel (first keel) and two abapical accessory keels, first of which (second keel) weaker but with more nodules than mid-whorl one and other (third keel) smaller; spiral sculpture (Figs 17-18) consisting of evident fine cords, parallel till peristomal lip, then widely divergent; axial sculpture consisting of numerous collabral ribs more prominent mid-whorl, giving rise to prominent tubercles at mid-whorl keel; in first whorls collabral ribs extending almost from suture to suture, but in last whorls evident only in mid-whorl; aperture narrow, elongate, bordered by very thick peristome with large parietal callus and four large divergent winged digitations all keeled on dorsal side and grooved on apertural side; adaxial lip edge roughly angled, often with a ribbon sometimes partly divided into minute denticles; columella short straight; parietal callus large thick, extending over last two whorls and columella; adapical digitation (first digitation) usually shorter than spire, initially fused to it, then detached and upturned; second digitation usually longer than all others, forming continuation of first-last whorl keel and describing angle of about 70-80° with first digitation; third digitation forming continuation of second-last whorl keel and describing angle of about 60-70° with second digitation; fourth digitation absent or consisting of a small notch forming continuation of third-last whorl keel; fifth digitation forming

continuation of shell neck, diverging and turning downwards; apertural surface of peristome porcelaneous.

Dimensions Shell height (H sh): 19.0 ± 2.11 mm (n: 50); last whorl diameter (D lw): 10.7 ± 1.47 mm (n: 50); spire angle (α): $43.1^\circ \pm 3.26$ (n: 50).

Geographic and stratigraphic distribution According to Marquet *et al.* (2002) and Landau *et al.* (2004), *A. pespelecani* is known since the Middle Miocene of the Atlantic Europe (Aquitania and Loire, France), western Mediterranean (Alt Penedès, Spain), eastern Mediterranean (Po, Italy; Karaman, Turkey) and Paratethys (Korytnica, Poland; Vienna, Austria; Hungary and Bulgaria). Now the species occurs in the eastern Atlantic from Iceland and Norway to Mauritania, the Mediterranean and the Black Sea (Fretter & Graham, 1981; Kronenberg, 1991).

Derivation of name The specific epithet *pespelecani* – “pelican’s foot” – denotes the fact that the large winged digitations of the peristomal lip are reminiscent of the palmate foot of aquatic birds.

Remarks Fretter & Graham (1981) noted that the shells of recent specimens have 8-10 whorls depending on how many have been lost from the apex. Landau *et al.* (2004) reported that specimens of *A. pespelecani* from the Pliocene of Estepona (Spain) have protoconch whorls worn and are smaller in size than others, such as contemporary specimens from the Atlantic deposits of Huelva. Solsona *et al.* (2001) found wide variability in size and a significant correlation between adult size and sediment type (muddy substrates: smaller size; sandy substrates: larger size). Many specimens examined by us had usually 5-6 whorls, because the protoconch and the early teleoconch whorls were eroded and the shell decollated (though to a lesser extent than *A. uttingeriana*) and they were also smaller in size than Recent specimens.

The *A. pespelecani* group includes aporrhais with slender spire, adapical digitation usually shorter than spire, and short, winged, usually downturned abapical digitation. It includes: *A. tridactylus* (Sandberger, 1861) from the Rupelian and Chattian of Mainz Basin, *A. meridionalis* (Basterot, 1825) and *A. burdigalensis* (D’Orbigny, 1852) from the Early – Middle Miocene of

Aquitania, *A. pespelecani* from the Middle Miocene of Paratethys, the Mediterranean and Atlantic France and Pliocene to Recent of the Mediterranean, Atlantic and the North Sea, and *A. scaldensis* van Regteren Altena, 1954, from the Middle and Late Pliocene of North Sea (Marquet *et al.*, 2002; Landau *et al.*, 2004).

A. meridionalis has been reported from the North Italian Tortonian (Sacco, 1893, 1894; Marquet *et al.*, 2002) but may be based on misidentifications: these specimens have a pointed abapical digitation (cf. Ferrero Mortara *et al.*, 1984: Pl. 22, figs 7-8) unlike species of the *A. pespelecani* group. Indeed Sacco (1893, 1894) regarded his *A. meridionalis* as an ancestor of *A. uttingeriana*.

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ADDENDUM

When the paper was in press, we noted that Seguenza (1876) reported specimens of *Aporrhais macandreae* from the bathial Pliocene of Sicily (near Messina; Barcelona) and Calabria (Santa Cristina). These reports probably refer to *A. peralata* although all attempts to trace voucher specimens were unfruitful. Seguenza also stated that *A. macandreae* was reported from Panormus by Jeffreys, that it could correspond to *Chenopus desciscens* of Philippi and that it may not be distinct from the Mediterranean *Chenopus serresianus*. With regard to the report by Panormus, we think that Seguenza misunderstood the discussion of *C. desciscens* by Jeffreys (1867: 254).

JEFFREYS JG 1867 *British conchology, or an account of the Mollusca which now inhabit the British Isles and the surrounding seas. Vol. IV. Marine shells, in continuation of the Gastropoda as far as the Bulla family.* John Van Voorst, London.

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APPENDIX 1

Collecting sites from Siena and Radicofani Pliocene basins (southern Tuscany).

Topographical and stratigraphical details on localities of palaeontological concern for Pliocene marine molluscs of Tuscany are given by Chirli (1997), Dell'Angelo & Forli (2000), Bogi *et al.* (2002), Scarponi & Della Bella (2003), Manganelli *et al.* (2004) and Pedriali & Robba (2005). Unfortunately some of these papers contain some incomplete or contradictory information. For each site the nearest toponym, municipality and kilometric UTM references are given with a short description. Locality names and UTM references are according to the *Carta Topografica Regionale* (Scala 1:25.000, Edizione 1^a, anno 1980) of Tuscany. For site descriptions we used the Italian terms *biancane* and *calanchi* because they are used in the geomorphological literature (e.g. Phillips, 1998).

Borro delle Macerie (Castelnuovo Berardenga, 32TPP0801)

A series of small outcrops exposed on right slope of Borro delle Macerie at Terre Rosse; yellow fine or medium sands and silts of Middle Pliocene age. This site is reported as "Serre di Rapolano – Il Campino" by Dell'Angelo & Forli (2000) and "Il Campino, Rapolano Terme" by Pedriali & Robba (2005); however "Il Campino" is not a toponym, but the name that two earlier fossil collectors in this locality (Franco Pallanti and Angiolo Spadini) gave to the site to distinguish it from one located downstream ("Il Campone", i.e. Borghi di sopra).

Casino di Barca (Castelnuovo Berardenga, 32TPN9802)

Outcrops on the slopes of Torrente Malena west of Casino di Barca, exposed by excavation and deep ploughing in 1980s; yellow medium sands and sandstones of Early Pliocene age. This site is reported as "Barca" by Manganelli *et al.* (2004) and Pedriali & Robba (2005).

Fontanelle (Asciano, 32TQN0394)

Badlands (*biancane*) along the road between Arbia and Asciano, west of Fontanelle; grey clays of Middle Pliocene age.

Fornaci di sotto (Castelnuovo Berardenga, 32TPP9703)

Outcrop exposed by levelling for a vineyard north of Fornaci di sotto; grey and yellow silts and clays of Early Pliocene age.

Fosso Rigo (Siena, 32TPP9400)

Outcrop exposed by levelling for a vineyard on the right slope of Fosso Rigo; grey and yellow clays, silts, sands and sandstones of Early Pliocene age.

Gragli (Asciano, 32TQN0497)

Badlands (*calanchi*) along the road between Torre a Castello and Monte Sante Marie, east of Gragli; grey clays of Middle Pliocene age.

Guistrigona (Castelnuovo Berardenga, 32TQN0199)

Outcrop exposed on the left side of the Siena – Bettolle State Road (no. 326) between the underpass on the secondary road connecting Croce del Chiantino to Guistrigona and the bridge on Borro di San Cristofano; grey or yellow sands and sandstones and grey silty or clayey sands of Middle Pliocene age.

I Sodi (Asciano, 32TQN0198, 0298)

Quarry of the brick factory "Laterizi Arbia" near Stazione di Castelnuovo Berardenga; grey clays of Middle Pliocene age. This site is reported as "Castelnuovo Berardenga Scalo" by Bogi *et al.* (2002; in Table on page 39 as "Castelnuovo Berardenga").

La Querce (Castelnuovo Berardenga, 32TQP0300)

Outcrop exposed by deep ploughing and erosion east of La Querce; yellow or grey sandstones and sands and grey silty sands and clays of Middle Pliocene age.

Monsindoli (Siena, 32TPN8894)

Ex-quarry of the brick factory "Fornaci Cialfi"; grey clays of Early Pliocene age.

Montepollini (Asciano, 32TQN1188)

Badlands (*biancane*) south of Montepollini; grey clays of Middle Pliocene age.

Mucigliani (Asciano, 32TQN0196)

Bed of the country road between Stazione di Castelnuovo Berardenga and Mucigliani, northwest of Mucigliani; grey clays of Middle Pliocene age.

Orsina Vecchia (Asciano, 32TQN1188)
Badlands (*biancane*) south of Orsina Vecchia; grey clays of Middle Pliocene age.

Podere Caggio (Asciano, 32TQN0399)
Badlands (*calanchi*), along the road between Croce di Carnesecca and Torre a Castello on the right, 0.5 km east of Podere Caggio; grey clays of Middle Pliocene age.

Podere Capanna (Rapolano Terme, 32TQN0999)
Outcrop exposed by excavation on the left slope of the Siena – Bettolle State Road (no. 326) at Podere Capanna; grey clays of Middle Pliocene age. This site is reported as “Armaiolo” by Bogi *et al.* (2002) and Pedriali & Robba (2005).

Podere Casanuova (Castelnuovo Berardenga, 32TPP0300)
Ex-quarry west of Podere Casanuova. Yellow or grey sands and silty sands and clays of Middle Pliocene age.

Podere Cavallara I (Castelnuovo Berardenga, 32TPP9900)
Outcrop exposed by levelling southwest of Podere Cavallara I; grey silts and clays of presumably Middle Pliocene age. The site reported as “Podere Cavallara” by Pedriali & Robba (2006) is probably different.

Podere Pian del Bullettino (Rapolano, 32TQP0800)
Outcrop exposed by excavation for a small artificial lake southwest of Podere Pian del Bullettino (now submerged and covered by vegetation); grey silts and clays of Middle Pliocene age.

Podere San Fabio II (Castelnuovo Berardenga, 32TQN0599)
Outcrop exposed on left side of the Siena – Bettolle State Road (no. 326) at Podere San Fabio II; grey clays of Middle Pliocene age.

Podere Sant’Antonio (Castelnuovo Berardenga, 32TPP9801)
Outcrop exposed down the right side of the road between Ligure and Pieve di Pacina, 1 km before Podere Sant’Antonio (now covered by vegetation); grey silts and clays presumably of Middle Pliocene age.

Podere Terrarossa (Castelnuovo Berardenga, 32TPP0801)
Outcrop exposed along path descending from the Senese – Aretina State Road (no. 73) into Borro Bicornia – Borro delle Macerie (now covered by vegetation); fine sands, silts and clays of Middle Pliocene age.

Poggetti (Asciano, 32TQN1092)
Ex-quarry of the brick factory “Fornaci di Rapolano”; grey clays of Middle Pliocene age. This site is reported as “Fornaci di Rapolano” by Manganelli *et al.* (2004).

Poggiodarno (Asciano, 32TPN9996)
Badlands (*biancane*) along the road between Monte Sante Marie and Asciano, northwest of Poggiodarno; grey clays of Middle Pliocene age.

Poggio Rotondo (Sarteano, 32TQN3064)
Outcrop exposed by excavation at Poggio Rotondo, on the right slope of the road between Sarteano and Pietraporciana (now covered by vegetation); sands and silts of Middle Pliocene age. This site is reported as “Castiglioncello sul Trinoro” by Dell’Angelo & Forli (2000) and Bogi *et al.* (2002).

Poggio Vangelo (Asciano, 32TPN9996)
Bed of the country road between Casacce and Fiorentina di sopra; grey clays of Middle Pliocene age.

Senese – Aretina State Road, km 96 (Asciano, 32TQN0299)
Outcrop exposed on left side of the Senese – Aretina State Road (no. 73), at km 96; grey clays of Middle Pliocene age.

Turnoff to Castelnuovo Berardenga (Castelnuovo Berardenga, 32TQN0399)
Outcrop exposed on left side of the Siena – Bettolle State Road (no. 326), at turnoff to Castelnuovo Berardenga; grey clays of Middle Pliocene age.