PHYLOGENETICS OF BRITISH SADDLE OYSTERS (BIVALVIA: ANOMIIDAE) — A REVIEW OF THE SHELL MORPHOLOGY, INTERNAL ANATOMY AND GENETICS OF *PODODESMUS* IN BRITISH WATERS

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Abstract *The number of Saddle Oyster species (Anomiidae) in British waters has long been a contentious subject and the genus* Pododesmus *the main cause of this confusion. To clarify the issue a study was carried out on several samples of* Pododesmus *species from around the coast of the United Kingdom. Integrative taxonomy using anatomy, shell morphology and molecular methods revealed 2 species of* Pododesmus. *Conclusive results in all three areas of study provide evidence of two distinct species of* Pododesmus: Pododesmus patelliformis *(Linnaeus, 1761) and* Pododesmus squama *(Gmelin, 1791).*

Key words *Saddle Oyster,* Pododesmus patelliformis, Pododesmus squama, *COI, Anomiidae, radial striations*

INTRODUCTION

The Anomiidae (Saddle Oysters, jingle shells or mermaid's toenails) evolved in the Cretaceous period and are now found worldwide in tropical, temperate and sub-Arctic seas. Members of the family Anomiidae have thin valves, the lower (right) of which commonly has a byssal foramen or hole through which the byssus extends to attach the bivalve to hard substrates. Due to this character state anomiids are used in oyster farms in several countries to provide a stable attachment surface for juvenile oysters.

Problems with identification of saddle oysters are commonly due to their mode of life as their shape depends on the contour of the hard substrate that they attach to. Distortion of valves is common and can make individuals from the same species look superficially different. Despite such ecophenotypic variation, both generic and specific definitions persistently use shell characters (Huber 2010).

Within the British fauna three genera of Anomiidae are recognised: *Anomia*, *Pododesmus* and *Heteranomia*. Separation of the genera has been dependent on muscle scars on the inside of the upper valve (Tebble 1966; Winckworth 1922): *Anomia ephippium* has three muscle scars on the inside of the upper (left) valve, the other two genera (*Heteranomia* and *Pododesmus*) have only 2 muscle scars. *Heteranomia* has smooth muscle scars and *Pododesmus* has furrowed muscle scars. While Smith & Heppell (1991) adopted *Pododesmus* Philippi, 1837 at the generic level they also used *Monia* Gray, 1850 as a subgenus. Huber (2010) gives full generic recognition to both and introduces the subgenus *Tenuimonia* with *Anomia squama* (Gmelin, 1791) as the type species. These designations are based on small differences in shell form and given the extent of ecophenotypic variation are discounted; consequently the earliest generic name, *Pododesmus* Philippi, 1837, is herewith adopted.

Few valid species exist for these genera and although many species have been described the majority have been synonymised. *Heteranomia* is cosmopolitan, monospecific and is represented by only *Heteranomia squamula* (Linnaeus 1758). In the British fauna one species of *Anomia* is recognised; *Anomia ephippium* Linnaeus 1758. *Pododesmus* is confused and variously represented in the British fauna by *Pododesmus patelliformis* (Linnaeus 1761), *Pododesmus patelliformis* var *striata* Lovén, 1846 and *Pododesmus squama* (Gmelin 1791). Forbes & Hanley (1853) and Winkworth (1922) recognised *P. patelliformis* and *P. squama* as distinct species, however later checklists (Smith & Heppell, 1991) class *P. squama* as a variety of *P. patelliformis*. Huber (2010) recognises both species under the genus *Monia* and this is currently accepted in CLEMAM (2016) and WoRMS (2016).

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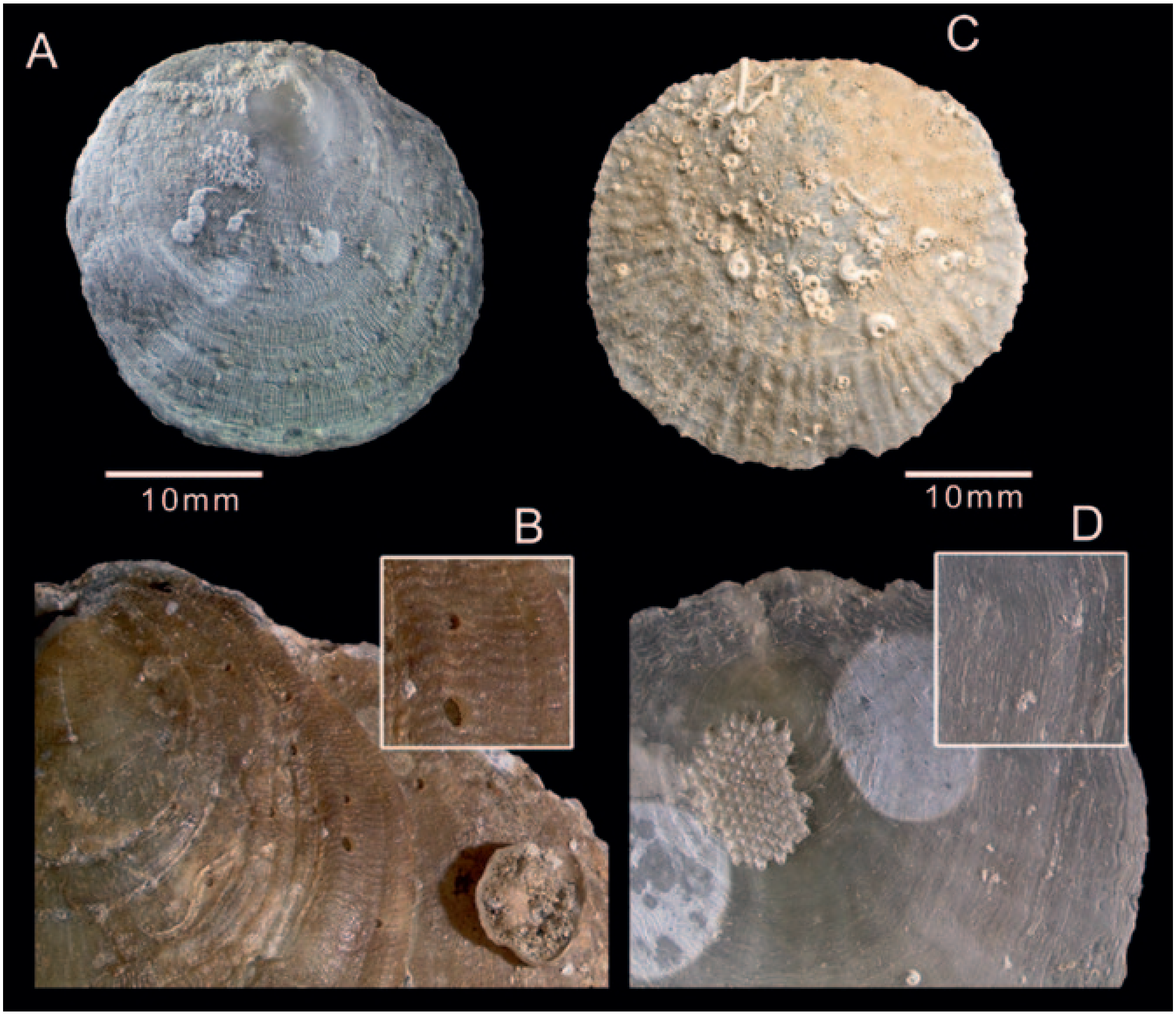

Figure 1 Upper valve sculptural forms of *Pododesmus*: A–B, radial striations in *P. squama*. C–D, prominent or weak radial riblets and without radial striations in *P. patelliformis*.

The two morphotypes of *Pododesmus* were traditionally separated by the position of the muscle scars: *P. patelliformis* has two separate scars and *P. squama* has two joined scars. *Pododesmus squama* was described as possessing radial striations on the upper valve compared to *P. patelliformis*, which has radial riblets but no radial striations (Fig. 1) and the former usually found in 20-200m whereas the latter is found intertidally to 20m. However, while preparing images for the 'Marine Bivalve Shells of the British Isles (Oliver *et al*. 2016) the usage of muscle scars to separate species became questionable.

A further complication has arisen with the discovery of *Pododesmus rudis* specimens attached to marine litter washed ashore on British beaches (Holmes *et al*., 2015). The ability to be able to accurately identify species of *Pododesmus* is necessary to substantiate such records of alien species.

Consequently the aim of this study was to clarify how many species of *Pododesmus* are present in British waters, to test if radial striations and muscle scars are reliable characters to separate species and if not to determine the most consistent way to separate the species. The species boundary between the two morphs was studied using the COI gene. The results were used to test the physical characters to discover which characters, if any, could be used to visually separate the two species in the field and in museum collections.

DNA Study

Tissue was preserved in 100% ethanol and shells dried and kept separate for further examination. *Pododesmus* specimens were collected from east and west of Scotland and 10 specimens chosen for the study: 5 with radial striations and 5 with radial riblets but without radial striations. These 10 specimens, along with 1 specimen each of *Anomia ephippium* and *Heteranomia squamula* were then sequenced for the COI gene. (See Table 1 for locality information accession numbers and Genbank numbers and Fig. 2 for map).

DNA extraction and sequencing methods

Ethanol fixed mantle tissue was blotted and then soaked in 1xTE Buffer for two hours to remove any remaining ethanol then DNA extracted using Qiagen's DNeasy Blood & Tissue Kit. A 920bp fragment of the COI gene was amplified using COIF-5'-3' (ATYGGNGGNTTYGGNAAYTG) and COIR-5'-3' (ATNGCRAANACNGCNCCYAT) (Palazzi *et al.* 2010). 25µl reactions contained 5mm $MgCl_2$, 200µM of each dNTP, one tenth volume of 10x Bioline Buffer, 0.25µM of each Primer, 2.5µl template DNA, 1 unit Bioline Taq. Tubes were added to the thermal cycler when plate temperature was at 95°C and then a touch-down PCR as follows: 95°C for 2 mins, 59°for 45s (-0.5°C ramped at 0.3°/s), 72°C for 2 min, Repeated 19 times, 94°C for 30s, 94°C FOR 30s.

Bands were excised and cleaned using Sigma's GenElute Gel extraction Kit and sequenced using Big Dye version 3.1 on an ABI Prism 3130xl Genetic Analyzer running Data Collection v 3.0.

The COI sequences were edited in ApE v2.0.47. The only COI *Pododesmus/Monia* sequence on GenBank is *Monia umbonata, (*China (AB076951.1), which was added to the analysis. Many higher-level analyses to classify the bivalvia as a whole or as subclasses have been ongoing for over a decade, but most agree that the Anomioidea group with the Pectinoidea and Limoidea (Steiner & Hammer, 2000; Matsumoto, 2003; Plazzi & Passamonti, 2010, Plazzi *et al*. 2011) and that the Pectinoidea are a sister taxon to the Anomioidea. Based on these findings two outgroup species from the Pectinoidea were added to the dataset from Genbank: *Parvamussium crypticum* (AB084106.1) and *Chlamys farreri* (GU119999.1).

Sequences were aligned using Clustal W in MEGA v7.0.20 (Kumar *et al.* 2016) using default

Figure 2 Map of sample locations. Circles: *Pododesmus* no radial striations; Squares: *Pododesmus* with radial striations; Diamond: *Anomia ephippium*; Star: *Heteranomia squamula*.

parameters. Uncorrected pairwise distances were calculated using MEGA v7.0.20. Evolutionary history was inferred using Maximum parsimony in MEGA v7.0.20 with Subtree-Pruning-Regrafting (SPR) and search level set at 0 (10 replicates), and Bootstrapping at 2000 replications. Maximum likelihood analyses were carried out in MEGA v7.0.20 using Hasegawa-Kishino-Yano model with Rates Among Sites set at Gamma distributed with Invariant Sites (G+I). Bootstrap value was set at 2000 replications and The Nearest Neighbour Interchange Heuristic Model used. Neighbour Joining was also run in MEGA v7.0.20 using Pairwise deletions and Maximum composite Likelihood Method.

DNA Results

Maximum Likelihood, Maximum Parsimony and Neighbour Joining all produced trees with similar topologies (Fig. 3) and all show separation of *P. squama* (with radial striations) and *P.*

Table 1 Locality and accession information for specimens used in creating phylogenetic tree

Species	Label	Site data	Coordinates	Accession number
Anomia ephippium	A.e.Tig.1	Loch Sween	55°591N 5°37′W	NMW.Z.2011.005.11
Heteranomia squamula	H.s.McK8	West of Shetland	60°01′N 01°29′W	NMW.Z.2013.020.08
Pododesmus squama	P.p.McK5	20′NNE of Butt of Lewis-46E3, 108m, station: 2MP	58°51′N 06°10′W	NMW.Z.2013.020.25
Pododesmus squama	P.p.McK6	West of Kintyre, 29m, Station: I22	55°33′N 05°45′W	NMW.Z.2013.020.30
Pododesmus squama	P.p.McK7	West of Kintyre, 29m, Station: I09	55°33′N 05°45′W	NMW.Z.2013.020.35
Pododesmus squama	P.p.McK5	Sound of Mull, 50m, station: RM1	56°34′N 05°58′W	NMW.Z.2013.020.44
Pododesmus squama	P.p.McK4	West of Kintyre, 29m, Station: I15	55°33′N 05°45′W	NMW.Z.2013.020.36
Pododesmus patelliformis	P.p.McK9	West of Gigha, 27m, Station: I04	55°37′N 05°46′W	NMW.Z.2013.020.40
Pododesmus patelliformis	P.p.McK10	West of Gigha, 27m, Station: I05	55°37′N 05°46′W	NMW.Z.2013.020.41
Pododesmus patelliformis	P.p.McK11	East of Fife Ness-41E7, 60m	56°17′N 02°09′W	NMW.Z.2013.020.29
Pododesmus patelliformis	P.p.McK12	West of Kintyre, 29m, Station: I21	55°33′N 05°45′W	NMW.Z.2013.020.31
Pododesmus patelliformis	P.p.McKCra	20′NNE of Butt of Lewis-46E3, 108m, Station: 1MP	58°51′N 06°10′W	NMW.Z.2013.020.26
Pododesmus patelliformis	P.p.IRS	Off E coast of Anglesey, Irish Sea	53°23′N 04°0′W	NMW.Z.2011.005.12

patelliformis (no radial striations). Maximum Likelihood results show most nodes have high levels of support (>86%).

Maximum Parsimony produced 8 trees that all show separation of the two species of Pododesmus (tree length of 862, consistency index=0.696 and composite index=0.5488).

P distances within both species samples of *P. squama* and *P. patelliformis* were 0.000–0.002, between the two groups were 0.256–0.258 and between *Monia umbonata* and *P. patelliformis*/*squama* 0.242/0.269. This provides additional support for the two different British *Pododesmus* species groups.

The COI results provide evidence for two distinct species of *Pododesmus* in UK waters: one with radial striations and one without radial striations. However, the striations are not always easy to see so further characters were investigated to further aid in separation of the two species.

Muscle scars

The two species of *Pododesmus* in British waters were traditionally separated by the condition of the muscle scars (Winkworth, 1922; Tebble, 1966): 2 separate scars=*P. patelliformis* and 2 joined scars=*P. squama* (see Fig. 4). However, on examination of this character whilst preparing material for the British Bivalves online guide (Oliver *et al*. 2016), it was concluded that this method was inconsistent. The muscle scar condition was tested by examination of the same ten individuals that were used in the DNA study and hence were already identified as *P. patelliformis* (with radial riblets but without radial striations) and *P. squama* (with radial striations).

Results

The results (see Table 2) demonstrate that *P. squama* always exhibits the joined muscle scar condition but *P. patelliformis* exhibits both the joined and separated muscle scar condition, depending on the individual. Therefore this character alone is not a consistent separator of species. If the scars are separate then the species is definitely *P. patelliformis* but if scars are joined it could be either *P. patelliformis* or *P. squama*.

Anatomy – mantle tentacles

Material Examined P. squama: 2 specimens Magnus, Trawl 3, NMW.Z.1988.144.00010; 2

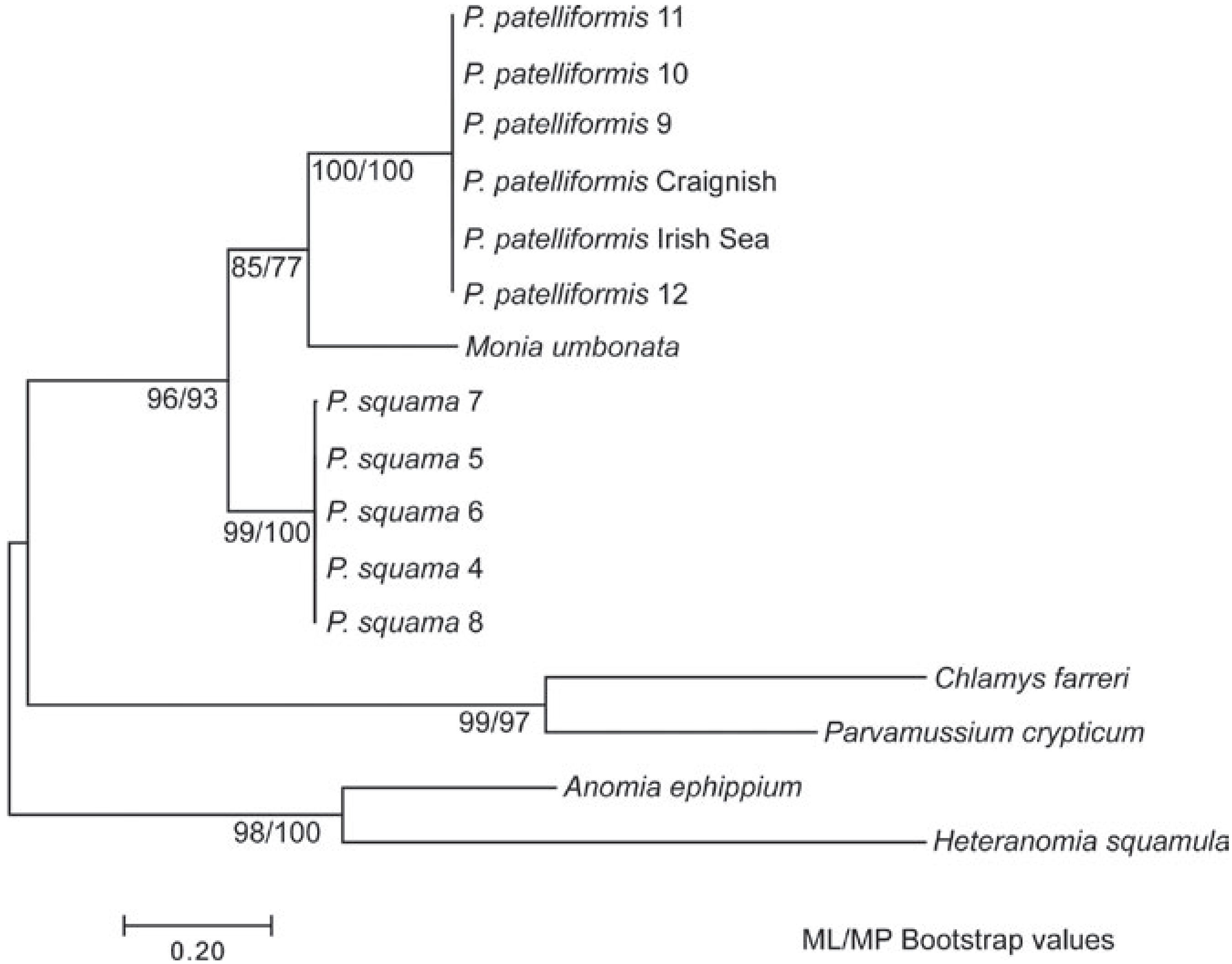

Figure 3 Phylogram to illustrate Maximum Likelihood tree drawn to scale with branch lengths measured in number of substitutions per site. Branch labels show bootstrap values for both ML and MP analyses.

specimens Celtic Sea, Station 73 50°45.1'N 07°05.0'W, 101m, NMW.Z.1982.069. *P. patelliformis:* 3 specimens Loch Creran, 56°31.1'N 05°23.2'W, NMW.Z.1985.092.00002; 7 specimens Tighavullin, Loch Linne Murich, Loch Sween, 56'12.9N, 05'37.6W, 26/9/09, NMW.Z.2011.005.00010; 5 specimens Causeway to Eilean Buidhe, Loch Craignish 56'09.55N, 05'33.95W, NMW.Z.2011.005.00009.

The right (lower) valve was removed from individuals of *Pododesmus patelliformis* and *P. squama* to view and compare the structure of the mantle. Differences were observed in the mantle and tentacles between the two species (Fig. 5).

Tentacles Tentacles appear for the whole circumference of the mantle edge protected by a short frill and on observation the two species of *Pododesmus* differ in tentacle length, width and frequency. The mantle of *P. patelliformis* has more densely packed tentacles (on average 13 per mm in large specimens), which overlap each other. They are short and have rounded tips. *P. squama* has more spaced out (on average four per mm in large specimens), elongated, pointed tentacles. Tentacles in both species can be divided into three size categories based on their comparative sizes in length ratios of 3:2:1.

Mantle In *P. patelliformis* much of the outer edge of the mantle, in particular the ventral margin is opaque for around two long tentacles' length. *P. squama* has a much thinner mantle and the base of the longest tentacles radiate inward through the mantle as a thick line. There is no sign of inward extension of tentacle base in *P. patelliformis*,

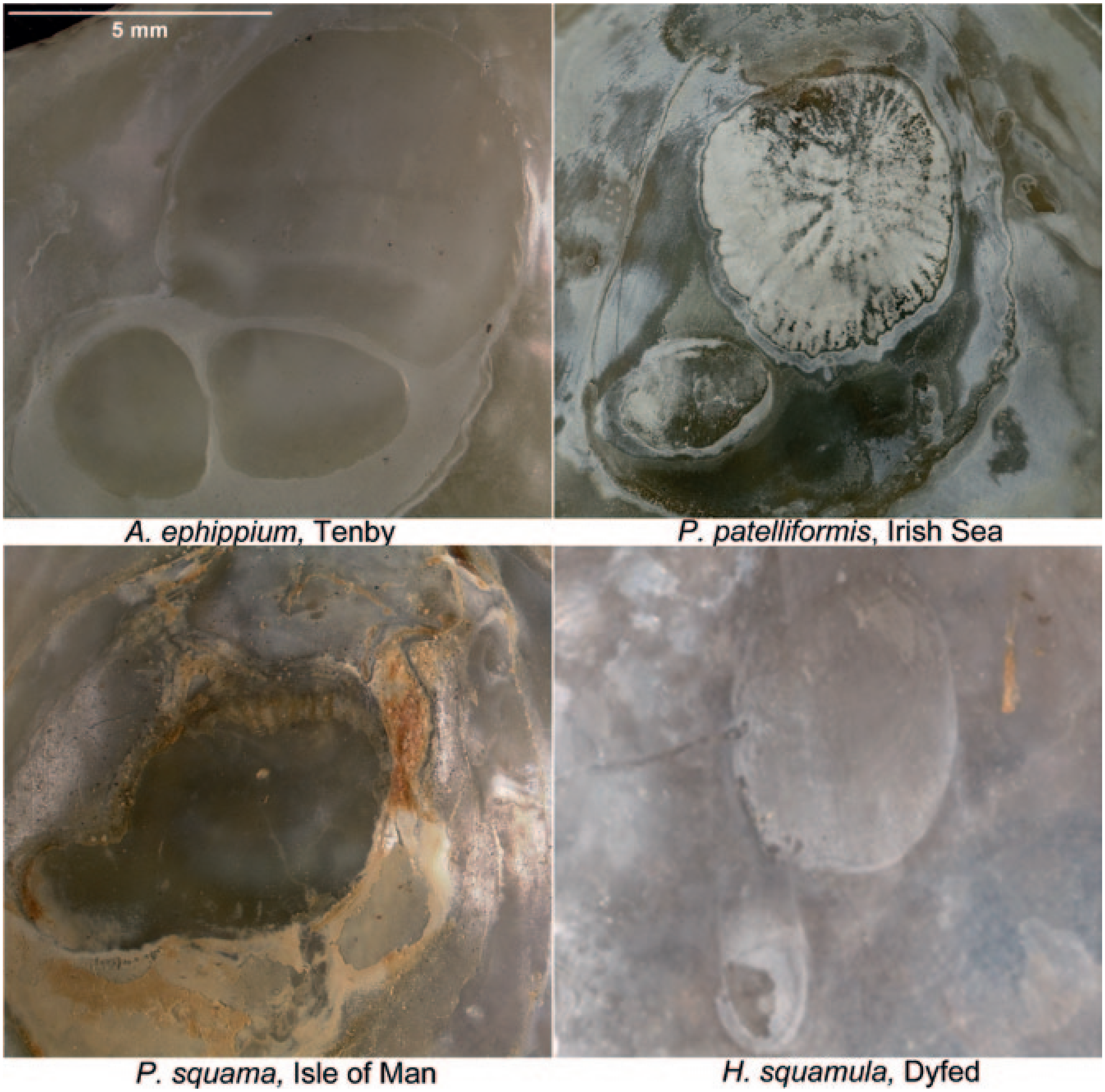

Figure 4 The four species of British Anomiidae showing the number and position of muscle scars.

although the whole section of mantle is opaque and so it would not be clearly visible.

Nomenclature

Nomenclature of this group is difficult to resolve with current literature and a full review of the Anomiidae supported by molecular data is required, which was beyond scope of this paper. Earlier British works such as Winckworth (1922) and Tebble (1966) used *Monia* (Gray, 1850) (type species: *Anomia zelandica* Gray in Dieffenbach, 1843, New Zealand). *Pododesmus* (Philippi, 1837) (type species: *P. decipiens* Philippi, 1837 from Cuba [=*Placunanomia rudis* (=*Pododesmus rudis*) Broderip 1834]) was later introduced into European check-lists, and was in wide usage in European checklists by 1986 (Backeljau,1986; Smith & Heppell,1991; Jensen & Knudsen,1995). Philippi (1837) observed only the larger of the two muscle scars, as illustrated by his figures (t.9, f.1) and description, although when Gray (1850) synonymised *P. decipiens* and

Table 2 Summary of identifying characters of both species of *Pododesmus* in Britain

Species	Radial striations?	Muscle scar	Tentacles	Mantle
P. patelliformis	no	Separated or joined	Squat, rounded, densely packed	Opaque
P. squama	yes	Joined	Slender, pointed, not densely packed	Thin transparent, base of largest tentacles radiate inward

P. rudis his description of *P. rudis* included two rounded, separate scars of nearly equal size. Keen (1969) described *P. (Monia)* as 'Byssal retractor scar large, foramen of moderate to large size' and P. *(Pododesmus)* as 'Foramen small to partially or entirely closed outside'. However, this character can be misleading since the size of foramen is variable within species and changes with growth from juvenile to adult specimens.

Huber (2010) quite rightly dismisses Younge's (1977) conclusions of *Monia* and *Pododesmus* since he did not use the type species of either

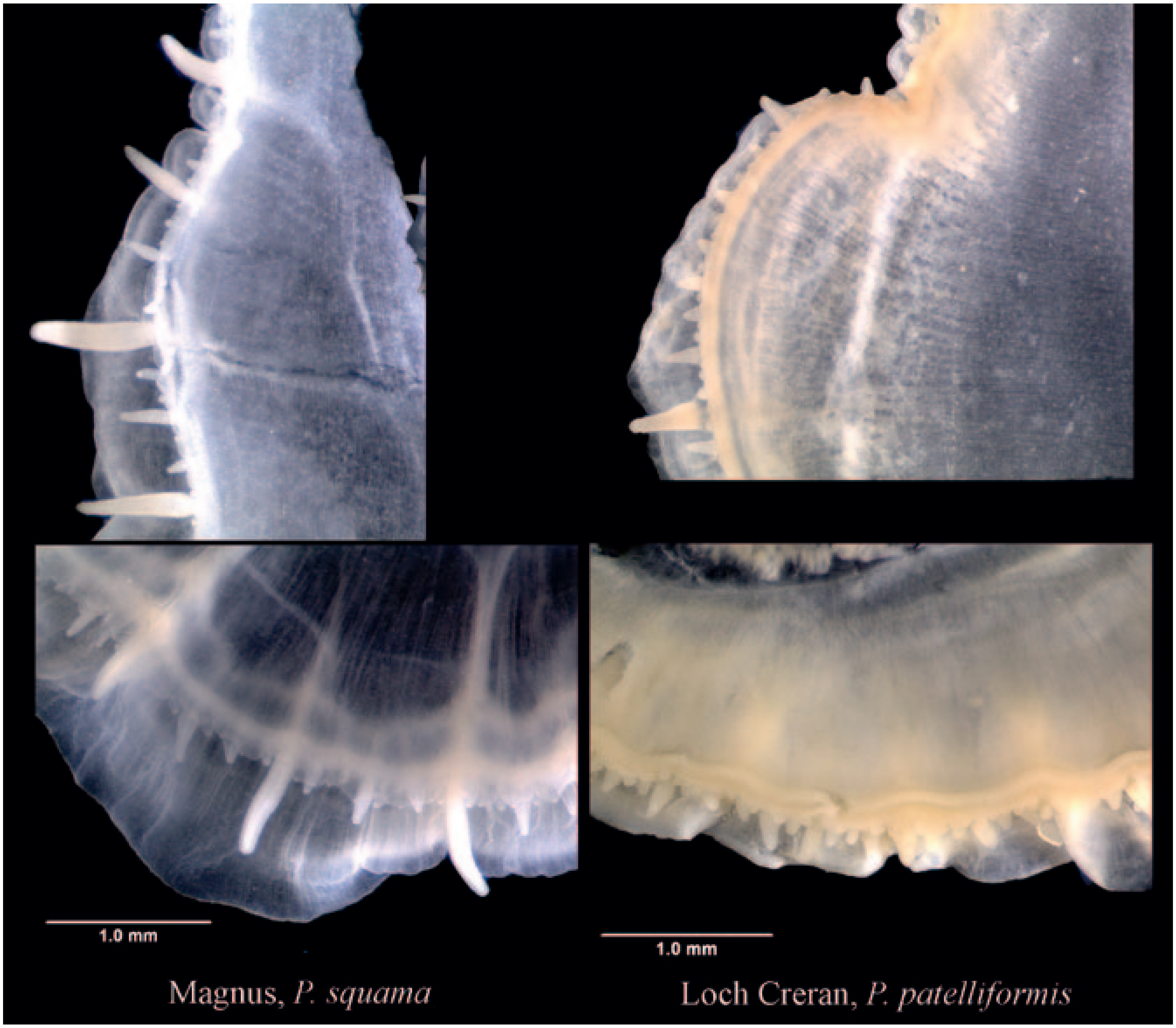

Figure 5 Mantle tentacles of *Pododesmus squama* (left) and *Pododesmus patelliformis* (right).

genus. Huber (2010) states that the northern Pacific *macrochisma* fits well in *Monia* and that the European *patelliformis* with 'two rounded, separate scars' fits here too. He places both British species in *Monia* and also introduces a subgenus *Tenuimonia: Monia (Monia) patelliformis* and *Monia (Tenuimonia) squama*. However, results herein of muscle scar separation show that *patelliformis* exhibits both confluence and non-confluence of muscle scars and thus Huber's reasoning of placing *patelliformis* in *Monia* due to separate muscle scars should be discounted. Clarification of genera requires more than examination of basic shell characters and a full review of the family worldwide is required; until then I choose to continue to use *Pododemus* for both British species.

Regarding the use of squama Gmelin, 1791 or striata Lovén, 1846

Gmelin (1791) defines *Anomia squama* as having longitudinal striata and refers to an image in Chemnitz (1785, viii, p. 87, T. 77 f. 697), described by Chemnitz as *Anomia squama magna* from "Norwegian Seas". This description and locality fit well with our understanding of *squama* so that the later *Anomia striata* Lovén 1846 can be regarded as a junior synonym; it is also preoccupied by *Anomia striata* Brocchi 1814.

Depth and habitat constraints

Two saddle oysters were recently washed ashore (November 2014) on the same piece of litter on Chesil beach and sent to the National Museum of Wales for identification. Examination of the valves, sculpture and mantle tentacles confirmed them as an individual each of *Pododesmus patelliformis* and *P. squama*. Traditionally *P. squama* was recorded as the deeper water species but with this recent discovery clearly the spat of both species have managed to colonise a piece of anthropogenic litter; however, it is unknown from where the litter originated.

P. squama has not been recorded south of Pembrokeshire in Wales in the west and Aberdeen in Scotland in the east but are these records accurate given the difficulty of finding robust characters to separate species? With uncertainty of P. squama qualifying as a separate species recorders may have played safe and recorded it as the much more well known species *P. patelliformis*. This suggests that some historical records could be erroneous, but how much do the species ranges overlap? Southern records should be checked and those specimens of '*P. patelliformis*' re-examined for presence of radial striae and with that it is likely that the range of *P. squama* can be extended much further south in Britain.

Conclusions

Results confirm the presence of two species of *Pododesmus* from the material studied: *Pododesmus patelliformis* and *P. squama* (Fig. 1). *Pododesmus patelliformis* is commonly known from intertidal and shallow waters but can be found at depths of greater than 100m. The external of the upper valve has radial riblets but no striations, the muscle scars can be joined or separated, the mantle is thickened and opaque and the mantle tentacles are dense, short, stubby and rounded. *Pododesmus squama* is recognised at depths of 20m or deeper. The external of the upper valve always has radial striations but no riblets, the muscle scars are always joined, the mantle is thin and mostly transparent and the mantle tentacles are thin and narrowly rounded. Whilst depth of habitat can be used as an indicator of species there is a large crossover of depth range of these species as shown by samples used for the this study and the Chesil beach discovery above.

WoRMS (2016) recognises nine anomiid genera worldwide, one third of which are monospecific, one third are represented by just two species and the final third contains the remaining twenty-two species, although with historically variable generic nomenclature. The lifestyle of cementation onto hard substrates creates problems with distortion of valves making identification of specimens difficult. Research on genera of this group, occasionally in regional isolation, has sometimes focused on singular shell characters when diagnosing genera ie. 'foramen closed' or 'muscle scars separate' further exacerbating the problem. Additional data is required, preferably of the whole family worldwide, before further conclusions can be drawn and the generic position of the British species can be properly resolved.

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