Is the cosmopolitan model still valid for deep-sea podocopid ostracods?

With the discussion of two new species of the genus *Pseudobosquetina* GUERNET & MOULLADE 1994 and *Cytheropteron testudo* (Ostracoda) as case studies

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With 8 Figures

Abstract

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Despite the increasing recognition of a global shortage of taxonomists (the 'taxonomic impediment'; see the Governments Convention on Biological Diversity, Darwin Declaration 1998) and the impact this will have on our ability to scientifically assess loss of biodiversity in the context of contemporary global change, there has been little indication (accepting specific funding initiatives such as 'SINTHESYS' in Europe and 'PEET' in America) as to how young scientists might be encouraged to undertake training in that field, or what educational approach would be appropriate to train taxonomists. There is also clear evidence from the literature that many recognised protocols in terms of the methodology of taxonomy have been eschewed by numerous practitioners, such that problems associated with synonymy and homeomorphy must significantly impact on quantitative assessments of biodiversity in many groups of plants and animals. We use deep-sea podocopid ostracods (Crustacea) to illustrate how less than rigorous taxonomic practice not only leads to confusion with respect to definitions of individual taxa, but also affects on the total number of species and their inferred ecology, distribution and geological record. Descriptions of two new species from the Angola Basin, southern Atlantic Ocean (*Pseudobosquetina semireticulata* n. sp. and *Pseudobosquetina nobilis* n. sp.) illustrate the level of historical enquiry we consider mandatory to clearly establish definitions for each taxon. A focus on such detail, although time consuming, in our view establishes an important, almost personal historical context for the subject, few other areas of science offer such continuity. Concerns for biodiversity give taxonomy its relevance, historical linkages and strands give that subject its life.

Kurzfassung

Trotz des zunehmenden Bewußtseins bezüglich eines weltweiten Mangels an Taxonomen (the ,taxonomic impediment' [der „taxonomische Stolperstein"]; siehe dazu ,The Governments Convention on Biological Diversity, Darwin Declaration 1998') und des damit einhergehenden Einflusses dieser Tatsache auf unsere Fähigkeit, den ,Verlust an Biodiversität' im Zusammenhang mit einer sich mehr und mehr verändernden Welt wissenschaftlich einzuschätzen, wurden bislang nur wenige Wege aufgezeigt (abgesehen von Ini-

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tiativen wie ,SINTHESYS' in Europa und ,PEET' in Amerika), wie angehende, junge Wissenschaftler ermutigt werden könnten, eine Ausbildung auf dem Felde der Taxonomie anzustreben, oder aber auf welche Weise sich die auszubildende Seite selbst verändern müsste, um die Taxonomie wieder interessant zu machen. Ebenso lassen sich deutliche Anzeichen aus der Literatur ableiten, dass selbst grundlegende taxonomische Methoden von Bearbeitern geradezu gemieden werden, mit dem Erfolg, dass eine problembehaftete Synonymie und/oder Homeomorphie zwangsläufig erheblichen Einfluß auf die quantitative Einschätzung hinsichtlich der Biodiversität vieler Pflanzen- und Tiergruppen hat.

In der vorliegenden Fallstudie benutzen wir podocopide Tiefsee-Ostracoden (Crustacea) um aufzuzeigen, wie inkonsequent angewendete taxonomische Praxis lediglich zur Verwirrung bezüglich der Definition individueller Taxa führen, aber auch Einfluß auf die Anzahl von Arten und damit ihre Ökologie sowie geographische und geologische Verbreitung nehmen kann.

Die Beschreibung zweier neuer Arten aus dem Angola Becken des S-Atlantik (*Pseudobosquetina semireticulata* n. sp. und *Pseudobosquetina nobilis* n. sp.) sollen die Notwendigkeit von historischen Untersuchungen aufzeigen, die wir für unerlässlich halten, um ein Taxon zweifelsfrei zu definieren. Die Herausstreichung solcher Details, wenngleich zeitraubend, birgt aus unserer Sicht einen geradezu persönlichen historischen Kontext für die Sache, und nur wenige andere Felder der Wissenschaft bieten eine solche Verbindung. Sorgen um die Biodiversität geben der Taxonomie ihre Bedeutung und historische Verbindungen hauchen dieser Sache Leben ein.

Introduction

The methods by which taxonomists solve problems associated with synonymies are many and varied and, sadly, often lack a level of scientific rigor normally considered appropriate for other aspects of research in that discipline. Investigations of the history of the systematics of a species are an integral part of taxonomic research, the objective of which is to give definitions more precision and utility. We have indicated elsewhere (JELLINEK & SWANSON 2003) that, despite a perception that literature research and examination of catalogued collections is a time consuming 'necessary evil', a sideline to the real research aspects of taxonomy, there is an alternative viewpoint. It is increasingly evident that there is a global shortage of taxonomists [part of the so-called 'taxonomic impediment' identified in the Convention on Biological Diversity (see the 1998 Darwin Declaration for definition)], ironically, at a time when rational, informed discussion of global biodiversity is demanded. The significant aspect of much of the current dialogue is that it focuses on the progressive reduction (up to 66%) in manpower over the last three decades (GASTON & MAY 1992, HOPKINS & FRECKLETON 2002), but offers few solutions as to how that trend might be reversed. If the demand for taxonomic expertise is to be met, then senior researchers in that discipline have an obligation to proselytise the attractions and merits of their chosen profession. There are few, if any other areas of scientific endeavour where the ideas and decisions of previous researchers are routinely acknowledged and so scrutinised. This, we believe, is where synonymy-related research has enormous potential in a educational sense. "It is this historical perspective, the need to make connection with what has gone before, which contributes so much to the resonance of taxonomy. This is the crux and the foundation of the subject; it is also the key by which young initiates will be encouraged to cross the threshold" (JELLINEK & SWANSON 2003: 12).

The case studies herein are presented as illustrations of procedures and complexities, and that at the completion of same, resolution of problems of synonymy are often more satisfactorily achieved by the addition of new taxa rather than a loss associated with the merging of pre-existing species. That observation has a general implication with respect to the methods of taxonomy, more specifically however, our data relates to the marine environment and to a group of organisms which are unique, in the sense that ostracods present a Cenozoic evolutionary history which is unparalleled in any other benthic marine organism or by the fragmented geological histories of terrestrial life. These are the stuff of extinctions and speciations which provide the hard data for the geological past, and it is in the context of those histories that current trends and 'crises' need to be assessed.

As ostracodologists, we are acutely aware of the fact that much of the uncertainty generated by synonymies could have been avoided, had previous workers taken more care with respect to their original descriptions and illustrations, literature searches and examination of type materials or well authenticated specimens. Additionally, as indicated by McKENZIE (1982), and others more recently, those who study ostracods are confronted with the most oligomerised of crustaceans and as a consequence, must always consider homeomorphy as a "persistent joker in the taxonomic pack". Predictably therefore, dealing with the problem of synonymies has to be seen as an integral part of a process by which the systematics of each taxonomic group are given more precision. Significantly in this regard, it has been our experience that in most instances, appropriate solutions to synonymy-related problems in Ostracoda inevitably lead to an increase in species numbers, rather than a reduction (as indicated for most groups by GASTON & MOUND 1993, MAY 1994, SOLOW et al. 1995 and numerous authors more recently).

The fact that only about 15% of the total described species (plant and animal) were recovered from the oceans (MAY 1994) and the bulk of these from sea-floor samples, is seen by some as anomalous in the sense that sea-water covers such a high proportion of the Earth's surface (approx. 75%). It would appear that this confirms an observation which is almost as old as oceanography itself, i.e. in comparison to terrestrial environments, oceans may be considered 'deserts', depleted in nutrients and diversity. Despite the rhetoric with respect to threats to 'global biodiversity', in terms of research effort and manpower, the 'founder effect' is still alive and well whilst the

'marine dragon' of KAUFMAN (1988) continues to sleep. The results of a study by FRANCE & RIGG (1998: 77) are as sobering as they are acute in their observation. "Biodiversity research was found to be narrowly focused with little deviation from an initial course set of being a discipline concerned largely with the implications of forest habitat loss on charismatic terrestrial megafauna; i.e. the 'founder effect' is very much in evidence." It is also evident that the traditional concept of cosmopolitanism in deep-sea benthic assemblages is alive and well amongst biologists and marine paleontologists and having a significant impact on how deep-ocean faunas are assessed in a taxonomic sense. We see what we expect to see. "Hence there are absolutely no barriers to the migration of animals in the deep-sea. Time only is required for any deep-sea animal to roam from any distant part of the earth to another" (MOSLEY 1879: 583f), and "to be acclimatised at great depths the conditions of existence becoming more and more constant, or even in the deeper regions perfectly uniform, species of the most varied derivations, when they had once attained a certain zone, could spread everywhere" (AGASSIZ 1913: 186). There is no question that the total number of ostracod species described from bathyal and abyssal depths over the last few decades has remained essentially static. This, to a large extent, is the result of the perception that representative podocopid taxa especially are considered cosmopolitan and, as a result, anticipated to occur in dredge/core samples collected from ocean basins often separated by some considerable distance (acknowledging also a progressive reduction in the number of ostracod taxonomists over the last three decades). "Compared with planktonic organisms, the ostracodes seemed to have reacted only to major events in the history of the oceans. It is as if the process of evolution in this animal group has been proceeding in slow motion" (BENSON 1983: 411). Later, WHATLEY & AYRESS (1988) concluded that many more Ostracoda were pan-abyssal than was indicated by previous studies and as evidence, listed 65 'cosmopolitan' species occurring in Quaternary sediments of the North Atlantic, Indian and SW Pacific oceans. It is instructive to observe, although not common, that concerns were being expressed about the impact of cosmopolitanism and usually by those attempting to present a modern ostracodal taxonomic scheme in which carapace morphology and anatomical detail were integrated. Thus MADDOCKS (1990: 36) in her exemplary monograph on Macrocyprididae was led to observe that "it is a common misconception that stable physical conditions in the abyss should cause deep-sea species to have very broad or even cosmopolitan geographic ranges. Lacking the extensive collections and soft-anatomy necessary to discriminate deep-sea species, many workers have opted to treat them as global in range and broadly inclusive in morphologic scope – a truly self-fulfilling prophecy."

Abbreviations: C = carapace; MC = male carapace; FC = female carapace; LV = left valve; MLV = male left valve; RV = right valve; FRV = female right valve; seg. I = segment I; segs I-VI = segments I-VI; T1–3 = thoracic legs 1–3.

Both types of *Pseudobosquetina mucronalatum* (BRADY 1880) are kept in the collections of the *Natural History Museum* (NHM), London, under catalogue number BM. All other material is housed in the collections of the *Forschungsinstitut Senckenberg*, Frankfurt, under catalogue numbers SMF Xe.

Pseudobosquetina, a case study

Family Trachyleberididae

Pseudobosquetina GUERNET & MOULLADE 1994

Type species: *Cytheropteron mucronalatum* BRADY 1880.

Remarks: The genus *Pseudobosquetina* is currently monotypic, with *Cytheropteron mucronalatum* BRADY 1880 as the only representative. The genus was introduced by GUERNET & MOULLADE based on descriptions of upper Miocene to Pliocene ostracods from the central Atlantic which they tentatively assigned to BRADY's species. We can only assume that those authors chose to erect a new genus in an attempt to resolve apparent generic confusion surrounding BRADY's species. The fact that they assigned their material only tentatively to that species is discussed below. To date, only GUERNET (1998), who used Neogene material from the E-Atlantic and MAZZINI (2005) who described Recent material from the Tasman Sea have assigned specimens to *Pseudobosquetina*.

Although it is acknowledged that erecting a new genus for deep-sea *mucronalatum*-like specimens presented one possible solution to the generic problem, published definitions of the genus *Pseudobosquetina* are inadequate and associated comparisons with similar or closely-related genera are superficial. Additionally, GUERNET & MOULLADE compared *Pseudobosquetina* with *Pterygocythereis* BLAKE 1933 and *Ruggieria* KEIJ 1957, genera to which *mucronalatum* had never been assigned. One of the two morphological contrasts presented by GUERNET & MOULLADE focuses on the lobate posterior hinge element of *Brachycythere*. Significantly, we make the observation that this is also present in *mucronalatum*, but may have not been observed by GUERNET & MOULLADE due to the lack of RVs (based on our observation that only LVs were figured). We do, however, agree with GUERNET & MOULLADE's conclusion that *Bosquetina* can be further discriminated on the basis of possessing a slightly different shape, more numerous marginal pore canals, a moderately wide marginal zone and double frontal muscle scars. We share the opinion of GUERNET & MOULLADE that *mucronalatum*-like species should best be assigned to a distinct genus, however, in that context we also believe that additional discussion of the differences between *Pseudobosquetina* and other similar genera is required.

BRADY, in his original description, assigned the species *mucronalatum* to *Cytheropteron* SARS 1866 and was followed in that opinion by TRESSLER (1941), HULINGS (1967) and PURI & HULINGS (1976). PURI & HULINGS (1976) in general retained the generic assignments of BRADY since their intention with respect to the *CHALLENGER* material was not to rectify generic problems, but rather to document and illustrate that ma-
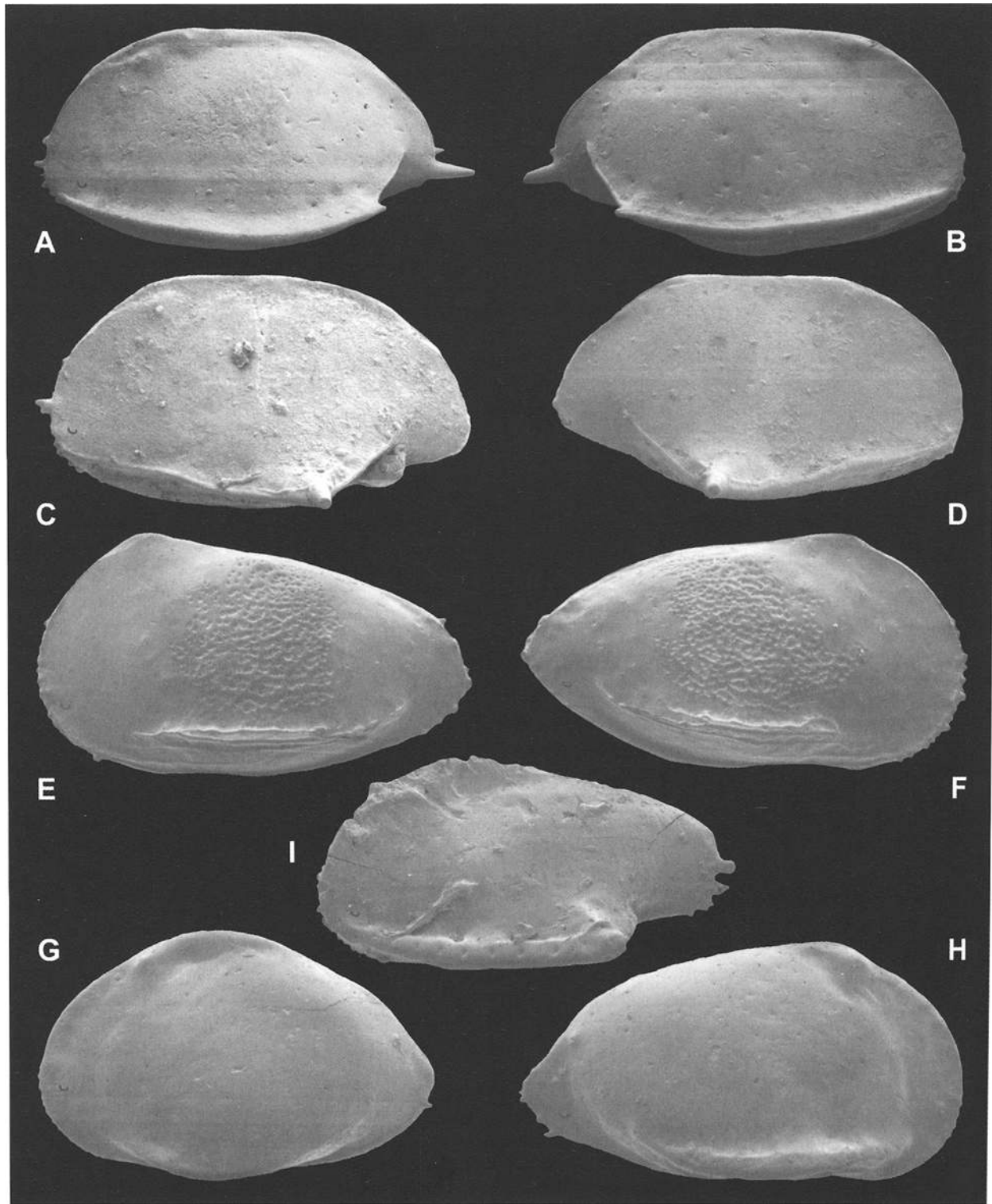
Fig. 1: **A–B:** *Carinovalva marginata* (TERQUEM 1878), Pleistocene (Sicilian), Lakonia, Peloponissos Peninsula, Greece; sample LE12. **A:** LV (0.92/0.53), external view, ×80; ex SMF Xe 12594. **B:** RV (0.92/0.50), external view, ×80; ex SMF Xe 12594. – **C–D:** *Carinovalva keiji* (SISSINGH 1972), Pleistocene (Emilian), Lakonia, Peloponissos Peninsula, Greece; fig. C sample LE6, fig. D sample LE7. **C:** LV (0.85/0.48), external view, ×85; SMF Xe 12591. **D:** RV (0.81/0.45), external view, ×85; SMF Xe 12592. – **E–F:** *Bosquetina pectinata* (BOSQUET 1854), Middle Pliocene, Vaugrenier S-France. **E:** LV (1.22/0.68), external view, ×60; SMF Xe 21710. **F:** RV (1.25/0.68), external view, ×60; SMF Xe 21710. – **G–H:** *Brachycythere sphenoides* (REUSS 1854) sensu ALEXANDER 1933, Upper Cretaceous, Taylor Marl; 5 miles W of Kockwall/Texas, USA. **G:** ?FLV (0.95/0.57), external view, ×70; SMF Xe 21711. **H:** ?MRV (1.07/0.57), external view, ×70; SMF Xe 21711. – **I:** *Pterygocythere* sp., Upper Cretaceous (Maastrichtian), Curfs near Houthem, The Netherlands. LV (1.17/0.62), external view, ×60; SMF Xe 21712.

terial to modern standards. – Significantly, the assignment of *mucronalatum* to *Cytheropteron* may have been appropriate in BRADY's time but could not be defended in 1976 using current podocopid ostracod taxonomic definitions.

PURI (1971), in fact, had already recognised this difficulty and as a result assigned the species to *Bosquetina* KEIJ 1957 but, unfortunately, his reasons for that assignment were not discussed, the species appearing only as a single item in a list of taxa. This assignment was then continued by DUCASSE & PEY-POUQUET (1979), WHATLEY & COLES (1987), DINGLE & LORD (1990), DIDIÉ & BAUCH (2000), MAJORAN & DINGLE (2001) and finally CRONIN & DWYER (2003). However, we note that *Bosquetina*, as described by KEIJ (1957), displays several carapace characteristics, which do not occur on *mucronalatum*:

1. the median hinge element in *Bosquetina* lacks the additional groove which is present in *mucronalatum*;
2. the marginal area of *Bosquetina* is significantly wider than that found on *mucronalatum*;
3. *Bosquetina* displays a large number of closely set marginal pore canals, most of which have median swellings (as illustrated by MÜLLER 1894: fig. 23); in contrast, *mucronalatum* has only a few, all of which are widely spaced;
4. the adductor muscle scars of *Bosquetina* are of slightly different size, shape and arrangement.

For these reasons we believe the genus *Bosquetina* cannot accommodate *mucronalatum*. It is also significant that KEIJ (1957) placed MÜLLER's (1894) extant species *Cythereis dentata* in *Bosquetina* because supplementary anatomical detail, more recently presented by McKENZIE & BONADUCE (1993), indicated that on the basis of the possession of complex P1–3 knee supports, *Bosquetina* was clearly hemicytherid. This despite the fact that *Bosquetina dentata* presents other anatomical detail which seemed to those authors convincingly trachyleberidid. The trachyleberidid affinities (expressed by the possession of simple knee supports) of the new species of *Pseudobosquetina* described herein is unequivocal with respect to the systematic relationship of that genus and *Bosquetina*. Additionally, despite the fact that we have previously indicated some doubt about the taxonomic utility of the frontal lobe of the copulatory apparatus (JELLINEK & SWANSON 2003), comparison of that structure in the present species and *Bosquetina dentata* (MÜLLER 1894: pl. 32 fig. 31) affirms that separation of these two taxa is warranted at the familial level. With respect to shape and size, the frontal lobe of *Pseudobosquetina* conforms to that found in the 'birdshead' group of trachyleberidids (JELLINEK & SWANSON 2003), with closer 'affinities' (implying similarities in geometry which *may* represent an important phylogenetic signal) to *Legitimocythere* COLES & WHATLEY 1989 rather than any other genus in that group.

Brachycythere ALEXANDER 1933 was the next piece added to the *mucronalatum* generic puzzle by BENSON (1974), although again this alteration was indicated in a list of taxa without illustration or discussion. This assignment was repeated by BENSON et al. (1983) and STEINECK et al. (1988). *Brachycythere* was introduced by ALEXANDER for specimens from the Upper Cretaceous of Texas, with *Cythere sphenoides* REUSS 1854 as the type species. *Cythere sphenoides* REUSS was described from Upper Cretaceous sediments of the eastern Alps in Europe. Topotypic material of *Brachycythere sphenoides* sensu ALEX-

ANDER from the Upper Cretaceous Taylor Marl of Texas was available to us and specimens of same are presented herein. We believe there are compelling arguments for not assigning *mucronalatum* to *Brachycythere* which include: 1) overall shape (more ovoid in *mucronalatum* and more sub-rectangular in *Brachycythere sphenoides*), 2) the hinge, which is similar but more strongly developed in *Brachycythere sphenoides* (especially the anterior tooth in the RV), and 3) the central muscle scars of *Brachycythere sphenoides* are significantly different from those found on valves of *mucronalatum*. "According to ALEXANDER (1933) there are only three adductor muscle scars in a vertical row (of which the middle one is subdivided into two separate scars) and an anterior V-shaped frontal scar. Other authors, however, mention four adductor muscle scars and two frontal scars" (VAN MORKHOVEN 1963: 214).

Pterygocythere HILL 1954 was another taxon seen by some authors as an appropriate locale for *mucronalatum*-material, PEYPOUQUET & BENSON (1980), AYRESS (1988), VAN HARTEN (1990) and CRONIN (1996) all assigning such specimens to that genus. *Pterygocythere* was established by HILL to accommodate extreme-winged Upper Cretaceous to Oligocene species of *Brachycythere*. But HILL's statement (1954: 820) that "*Pterygocythere* n. gen., is a winged *Brachycythere* and therefore differs from the type species of *Brachycythere*", certainly does not provide the best criterion to distinguish two genera. However, species of *Pteryogocythere* do all carry extremely large 'wings', in contrast to *mucronalatum*, a species which is inflated rather than winged, and also possesses a ventral ridge.

Additionally, there are other genera to which *mucronalatum* could potentially be assigned and, on that basis, we believe further discussion of these is warranted.

Incongruellina RUGGIERI 1958; although the type species, *Incongruellina semispinescens* RUGGIERI 1958 from the Neogene of Italy, displays a very similar shape and hinge, that species has eye tubercles, very wide marginal zones and deep vestibula all features which are absent in *mucronalatum*.

Lixouria ULICZNY 1969 was originally described as a subgenus of *Incongruellina* with *Cythereis unicostulata* KUIPER 1918 as the type species. ULICZNY initially regarded his Pliocene material from Greece as conspecific with *C. unicostulata* from the Oligocene of The Netherlands, which was later disproved by SISSINGH (1973) after examining KUIPER's original material, and subsequently confirmed by ULICZNY. In 1971, ULICZNY proposed the substitute-name *patrasiensis* for what had as a result, become a new species. MALZ & JELLINEK (1984) then demonstrated that *Incongruellina (Lixouria) patrasiensis* ULICZNY 1971 was in fact a junior synonym of *Carinovalva marginata* (TERQUEM 1878) and also that the remaining *Lixouria* species, *L. keiji* SISSINGH 1972 and *L. nipponica* YAJIMA 1978, had to be reassigned to other genera (*L. keiji* to *Carinovalva* and *L. nipponica* to *Yajimaina*). As a result, the subgenus *Lixouria* became a *nomen nudum* and was therefore invalid. *Lixouria*, as described by ULICZNY, not only displays a different shape (elongate rectangular) compared to *mucronalatum* (sub-oval to sub-quadrate), but also has a hemiamphidont hinge which contrasts with the holamphidont type found in *mucronalatum*.

Carinovalva SISSINGH 1973, is unusual in the sense that the type species was introduced almost simultaneously from two different localities: specimens from the Pliocene of Italy were named *Lixouria aquila* by RUGGIERI (1972: 102) whilst

Sissingh (1972: 109) described equivalent specimens from the Pliocene of Greece as *Incongruellina* (*Lixouria*) *keiji*. In 1973, Sissingh introduced the genus *Carinovalva* and designated *I.* (*L.*) *keiji* as the type species and *L. aquila* as a junior synonym. *Carinovalva* to date includes species such as *C. keiji* and *C. marginata* (Terquem 1878) [= *Incongruellina* (*Lixouria*) *unicostulata* (Kuiper 1918) sensu Uliczny 1969 and *I.* (*L.*) *patrasiensis* Uliczny 1971], exhibiting a wide and often conflicting range of carapace characters. *C. marginata*, for example, indicates that species of *Carinovalva* may present a shape and ventral ridge similar to that found on *mucronalatum* (not so for *C. keiji*, which is more trapezoidal and ventrally winged), however, *Carinovalva*-species always carry an eye tubercle and a different hinge.

On the basis of this discussion, we therefore conclude that *Cytheropteron mucronalatum* Brady 1880 and other similar deep-sea species of the *mucronalatum*-type, should best be assigned to *Pseudobosquetina* Guernet & Moullade 1994. *Pseudobosquetina* is clearly a deep water genus and as a result of the new data presented herein, now comprises at least three distinct species; namely *P. mucronalata* (Brady 1880) from the Pacific Ocean and *P. semireticulata* n. sp. and *P. nobilis* n. sp. from the Atlantic Ocean.

Pseudobosquetina mucronalata (Brady 1880)
(Fig. 2)

● 1880   *Cytheropteron mucronalatum* Brady. – 140, pl. 33 figs 8a-d.

non 1941   *Cytheropteron mucronalatum*. – Tressler: 102, tab. 14–15; pl. 19 fig. 25. (= *P. nobilis* n. sp.)

non 1941   *Cytheropteron* sp. (a). – Tressler: 102, tab. 14–15; pl. 19 fig. 10. (= juvenile specimen of *P. semireticulata* n. sp.)

non 1967   *Cytheropteron mucronalatum*. – Hulings: 318, tab. 2; text-fig. 3A-F; pl. 4 figs. 10–11. (= *P. nobilis* n. sp.)

? 1971   *Bosquetina mucronalatum*. – Puri: 168.

1971a   *Bosquetina*? aff. *B.*? *fenestratum* (Brady). – Swain: 487, pl. 36.1 fig. 8a-b, pl. 36.2 fig. 3a-b, pl. 36.3 fig. 8, pl. 36.4 fig. 7.

? 1971b   *Bosquetina*? aff. *B.*? *fenestratum* (Brady). – Swain: 597.

? 1974   *Brachycythere mucronalatum*. – Benson: 1038.

? 1975   *Bosquetina fenestratum* (Brady 1880). – Peypouquet: 889.

* ● 1976   *Cytheropteron mucronalatum*. – Puri & Hulings: 307; pl. 22 figs. 14–18.

? 1976   *Cytheropteron* sp. 4. – Wall & Quilty: 737, tab. 1, pl. 1 figs. 22–23. (= juvenile specimen)

? 1980   *Pterygocythere mucronalatum*. – Peypouquet & Benson: 9, text-fig. 2.

non 1983   *Brachycythere mucronalatum*. – Benson et al.: 438, tab. 2–3; pl. 1 figs. 6–7. (= *P. nobilis* n. sp.)

non 1987   *Bosquetina mucronalatum*. – Whatley & Coles: 44ff, text-figs. 6, 8–10 pl. 5 figs. 1, 2. (= *P. nobilis* n. sp.)

1988   *Brachycythere mucronalatum*. – Steineck et al.: 607, tab. 1; text-fig. 4; pl. 1 fig. 9.

1988   *Pterygocythere mucronalatum*. – Ayress: 201, pl. 4 fig. 23. (= juvenile specimen)

non 1990   *Bosquetina mucronalatum*. – Dingle & Lord: 214ff, tab. 1, 2, 4; text-fig. 2/9. (= *P. nobilis* n. sp.)

? 1990   *Pterygocythere mucronalata*. – van Harten: 325, tab. 2.

? 1990   *Pterygocythere mucronalatum*. – Coles et al.: 299, tab. 2.

? 1993   *Pterygocythere mucronalatum*. – Corrège: 265.

non 1994   *Pseudobosquetina* cf. *mucronalatum*. – Guernet & Moullade: 264, pl. 2 figs. 1–2, 4. (n. sp.?)

non 1996   *Pterygocythere mucronalata*. – Cronin: 43, tab. 1; text-figs 1, 2; pl. 1 fig. 5. (n. sp.?)

? 1997   *Pterygocythere mucronalatum*. – Ayress et al.: 293ff.

non 1998   *Pseudobosquetina mucronalatum*. – Guernet: 525, tab. 1, 3–5; pl. 3 fig. 4. (= juvenile specimen of n. sp.?)

non 2000   *Bosquetina mucronalatum*. – Didié & Bauch: 115, pl. 4 figs. 23–24. (= *P. nobilis* n. sp.)

non 2001   *Bosquetina* sp. – Majoran & Dingle: tab. 2; pl. 1 fig. 11. (= juvenile specimen of n. sp.?)

non 2003   *Bosquetina mucronalatum*. – Cronin & Dwyer: pl. 1 fig. h. (= *P. nobilis* n. sp.)

● 2005   *Pseudobosquetina mucronalata*. – Mazzini: pl. 20 figs. 1–4.

Remarks: *P. mucronalata* is one of Brady's '*CHALLENGER*-species' with a history (as expressed in the synonymy) which despite its convolution and complexity, must be assessed critically. The species was introduced by Brady (1880: 140) based on material from the '*CHALLENGER Expedition*' and assigned to the cytherurid genus *Cytheropteron*. Brady indicated that his material originated from samples recovered at six different localities widely distributed in the Pacific and N-Atlantic Oceans. Significantly, no information was given for localities where the figured specimens were collected, and Brady also failed to designate types.

Puri & Hulings (1976: 307), in an attempt to resolve some of the problems associated with Brady's '*CHALLENGER*-species', designated a lectotype (BM 80.38.157) for *C. mucronolatum* from station 296 (Chile Rise in the SE-Pacific). However, those authors further added to the confusion by describing the lectotype as a LV (1976: 307, 1st paragraph), and then later as a RV (1976: 307, 3rd paragraph); from their plate 22 it is evident that the lectotype is in fact a carapace as was originally figured by Brady. One of the present authors (IM) has examined the *CHALLENGER*-material at the Natural History Museum, London, and confirmed that the hololectotype is a LV from *CHALLENGER* Station 296. Unfortunately, several other specimens (paralectotypes) from the same station in two additional slides have been allocated the same catalogue number as the hololectotype. Furthermore, from the dimensions of Tasman Sea *mucronalata*-material available to us (Mazzini 2005), we conclude that the hololectotype with dimensions of 1.31/0.87 is probably a female LV.

Additionally, Puri & Hulings indicated several features of the 'lectotype' which contrast with Brady's original description.
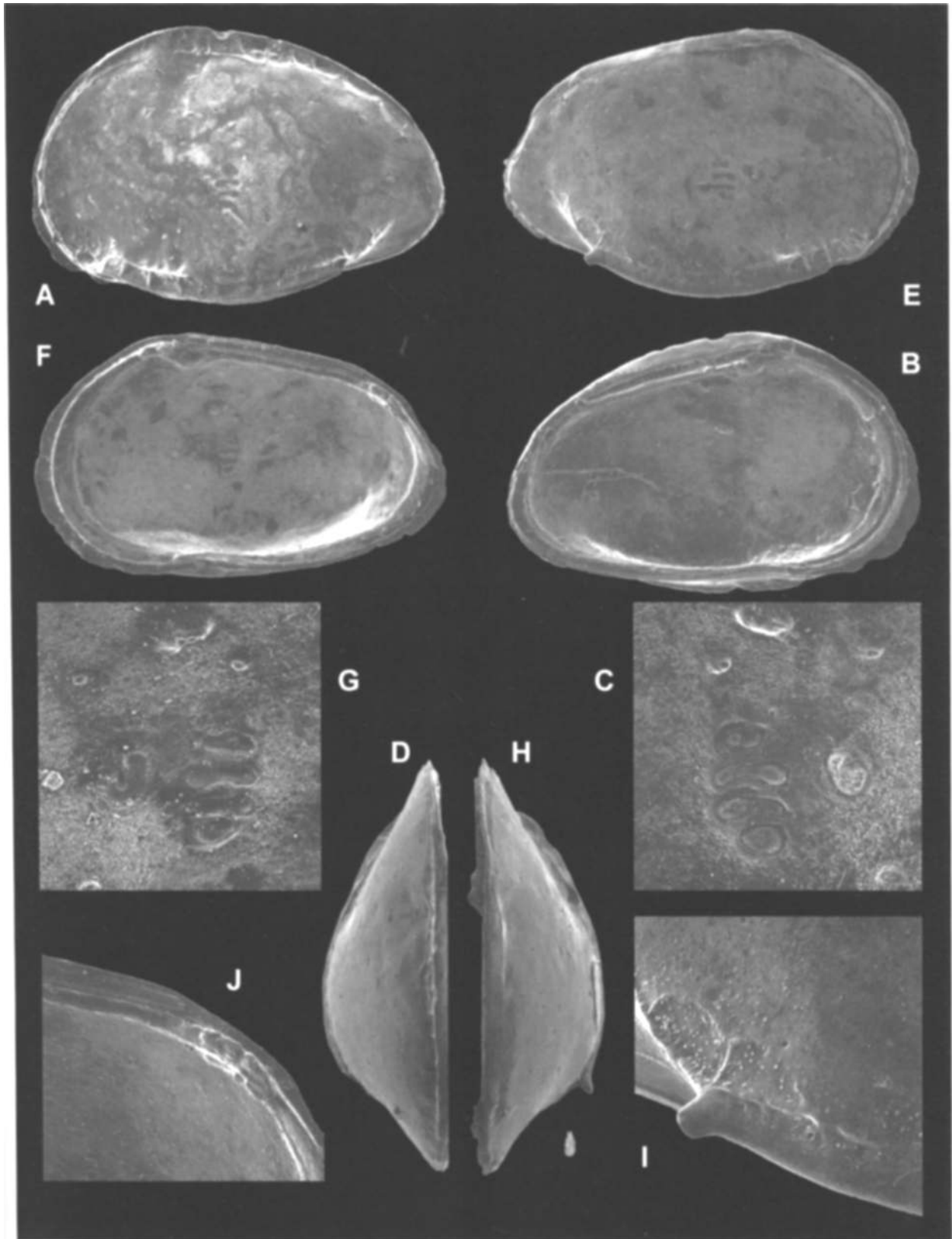
Fig. 2: *Pseudobosquetina mucronalatum* (BRADY 1880), Recent, *CHALLENGER* station 296, near Chile Rise; 1825 fathoms (= 3285m). Courtesy of Dr. J. WHITTAKER, Palaeontological Department, Natural History Museum, London. – **A–D:** LV (1.31/0.87), **hololectotype; A:** external view; **B:** internal view, **C:** central muscle scars, ×300; **D:** dorsal view. BM 80.38.157. – **E–J:** RV (1.32/0.81), paralectotype; **E:** external view; **F:** internal view; **G:** central muscle scars, ×300; **H:** dorsal view; **I:** terminal spine on ventral ala, ×300; **J:** Posterior hinge element, ×300. BM 80.38.157. If not otherwise stated, all magnifications ×55.

1. "Height equal to more than two-thirds of the length" (BRADY); "Height is not equal to more than two-thirds of the length" (PURI & HULINGS). – With dimensions of 1.30/>0.86 (BRADY) and 1.30/0.84 (PURI & HULINGS), both statements are correct, however, our measurements of the hololectotype resulted in dimensions of 1.31/0.87 which are closer to BRADY's observation than to those of PURI's & HULINGS's.

2. "Anterior extremity ... irregularly and roughly dentate, posterior ... bearing a few blunt spines" (BRADY); "Anterior end scarcely dentate, posterior end devoid of spines" (PURI & HULINGS) – From the photographs we have taken of the hololectotype, the posterior spines described and figured by BRADY are not present on the hololectotype which supports the opinion that the designated hololectotype is in fact a different specimen (if not species) from that figured by BRADY.

3. "Dorsal margin very boldly arched, not flattened ..." (BRADY); "Dorsum not broadly arched" (PURI & HULINGS). – Both statements are a question of interpretation. Our observations suggest very little difference in the shape of the LV figured by BRADY and that of the 'LV-hololectotype' figured by PURI & HULINGS.

4. "Within and parallel to the anterior and ventral margins of the valves runs an elevated ridge, which terminates not far from the posterior extremity of the shell in a strong, but not very long spinous projection" (BRADY); "The elevated ridge ... is practically absent anteriorly and does not terminate in a strong short spine on the lectotype" (PURI & HULINGS) – With regard to the 'elevated ridge' we are convinced that BRADY was correct, as can be seen clearly in our micrographs of the hololectotype (text-fig. 2 figs. A-D). BRADY's "not very long spinous projection" on the posterior end of the ridge is obviously broken off the hololectotype but is present on paralectotypes.

From these observations we conclude that *Cytheropteron mucronalatum* BRADY 1880 and the 'lectotype' of *Cytheropteron mucronalatum* as figured by PURI & HULINGS 1976 are in all probability two distinct species.

It is apparent from the synonymy presented above, that before and after PURI & HULINGS (1976), specimens were often reported and assigned to *mucronalatum* (and *Cytheropteron fenestratum* BRADY 1880). These materials were derived from widely distributed sites in the world oceans but few of the determinations withstand critical appraisal:

SWAIN (1971a) reported and figured specimens from the Pleistocene of the SE Pacific as *Bosquetina? aff. B.? fenestratum* (BRADY 1880). This assignment clearly reflects the taxonomic difficulties confronting SWAIN, and through that he signals his unease at adopting the generic assignment of PURI (1971). The specific assignment refers to another BRADY *CHALLENGER*-species, *Cytheropteron fenestratum*, which is now assigned to *Pelecocythere* ATHERSUCH 1979, and is easily distinguished from *Pseudobosquetina mucronalata*. However, from the figures presented by SWAIN, we conclude that his specimens fit the definitions of *mucronalata*.

WALL & QUILTY (1976), in a very short report on DSDP Leg 34 (north of the Easter Islands), figured a broken juvenile specimen from the middle Miocene which they called *Cytheropteron* sp. 4. We believe that that specimen is a true *Pseudobos-*

quetina, and despite uncertainties relating to the 'extreme' age of that material consider because it was recovered from a site in close proximity to the type locality, warrants being tentatively assigned to *mucronalatum*.

A third and problematic reference is the unpublished thesis of AYRESS (1988). He reported *Bosquetina mucronalatum* from six Pleistocene core samples, three of which were taken in the Indian Ocean and three from the SW Pacific. Although in the text that author indicated he had rare adult specimens available, he chose a juvenile valve for his plate illustrations. Unfortunately, he also failed to indicate from which of the six possible locations that specimen came from, however, our comparisons with the hololectotype indicate assignment of that specimen to *mucronolatum* is warranted.

In the same year (1988), STEINECK et al. reported the species from lower Oligocene to Quaternary sediments of the eastern equatorial Pacific (DSDP Leg 85), with an upper Miocene LV being figured.

The last reference for *mucronalata* is that of MAZZINI (2005), based on Recent sediments from the Tasman Rise, Southern Ocean.

All other *mucronalatum*-references can be related to either of our new species, or, in a number of cases not discussed further, simply dismissed as records of no value because only the name is mentioned in the text and no figures were given. Such references have been indicated in the synonymies by a question mark. As a result of the revisions and reassignments indicated by our research, we conclude that *Pseudobosquetina mucronalata* is an extant, deep-water Pacific species which first appeared in that ocean in the Miocene.

We also acknowledge the existence of specimens in six other references which could not be assigned to any species of *Pseudobosquetina*: GUERNET & MOULLADE (1994) and CRONIN (1996) figured adult specimens which differ in shape when compared to existing species. GUERNET (1998) and MAJORAN & DINGLE (2001) figured juvenile specimens which could not be assigned to any existing species because the juveniles of the known taxa are all so similar. Another juvenile (RV) from the middle Eocene of Barbados was figured as *Brachycythere maerkyi* VAN DEN BOLD 1957 by STEINECK et al. (1984). We believe this specimen is not related to the VAN DEN BOLD species from Trinidad but is a juvenile *Pseudobosquetina*. Finally, DUCASSE & PEYPOUQUET (1979) figured a juvenile specimen from early Pliocene sediments of the Rockall Plateau in the N-Atlantic as *Bosquetina fenestratum*. However, this specimen is clearly a *Pseudobosquetina* and not *fenestratum*.

These six citations are linked by the fact that they all refer to material recovered from Tertiary sediments of the Atlantic, which suggest the possibility of a fourth, older species which may represent the ancestral stock of all other *Pseudobosquetina* species.

Pseudobosquetina semireticulata n. sp.
(Figs. 3–5)

1941 *Cytheropteron* sp. (a). – TRESSLER: 102, tab. 14–15; pl. 19 fig. 10. (= juvenile specimen)

Derivation of name: From semi (Lat.) = half and reticulatus (Lat.) = reticulate; referring to the ornamentation which covers only half of the valves.
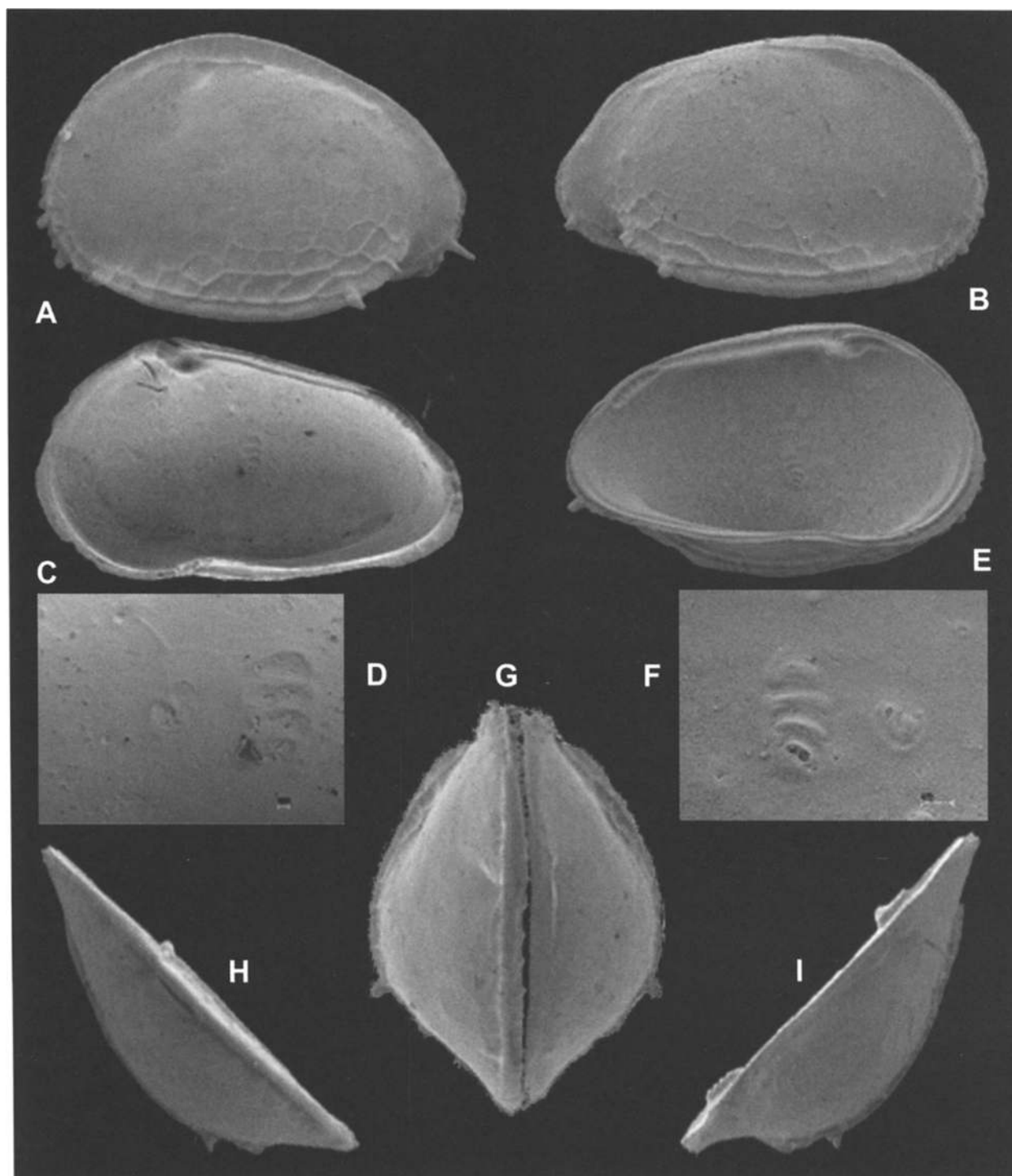
Fig. 3: *Pseudobosquetina semireticulata* n. sp. – **A:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–345KG6 (box corer), 16°17.024'S, 005°27.021'E; 5433m. FLV (1.30/0.85), **holotype**, external view; SMF Xe 21713. – **B:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–326ES (epibenthic sledge), 19°57.516'S, 002°56.997'E; 5495m. FRV (1.32/0.80), paratype, external view; SMF Xe 21714. – **C–F:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–344ES (epibenthic sledge), 17°07.454'S, 004°42.276'E; 5497m. MC, paratype (specimen AB025); **C:** RV (1.27/0.72), internal view; **D:** central muscle scars, × 300; **E:** LV (1.25/0.75), internal view; **F:** central muscle scars, × 300; SMF Xe 21715. – **G:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–345KG7 (box corer), 16°17.010'S, 005°27.002'E; 5432m. ?MC (1.22/0.87.0.80), paratype, dorsal view; SMF Xe 21716. – **H–I:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–341KG8 (box corer), 17°08.062'S, 004°41.948'E; 5464m. **H:** ?MLV (1.28/0.80), paratype, dorsal view; SMF Xe 21717. **I:** ?MRV (1.27/0.73), paratype, dorsal view; SMF Xe 21717. If not otherwise stated, all magnifications × 55.
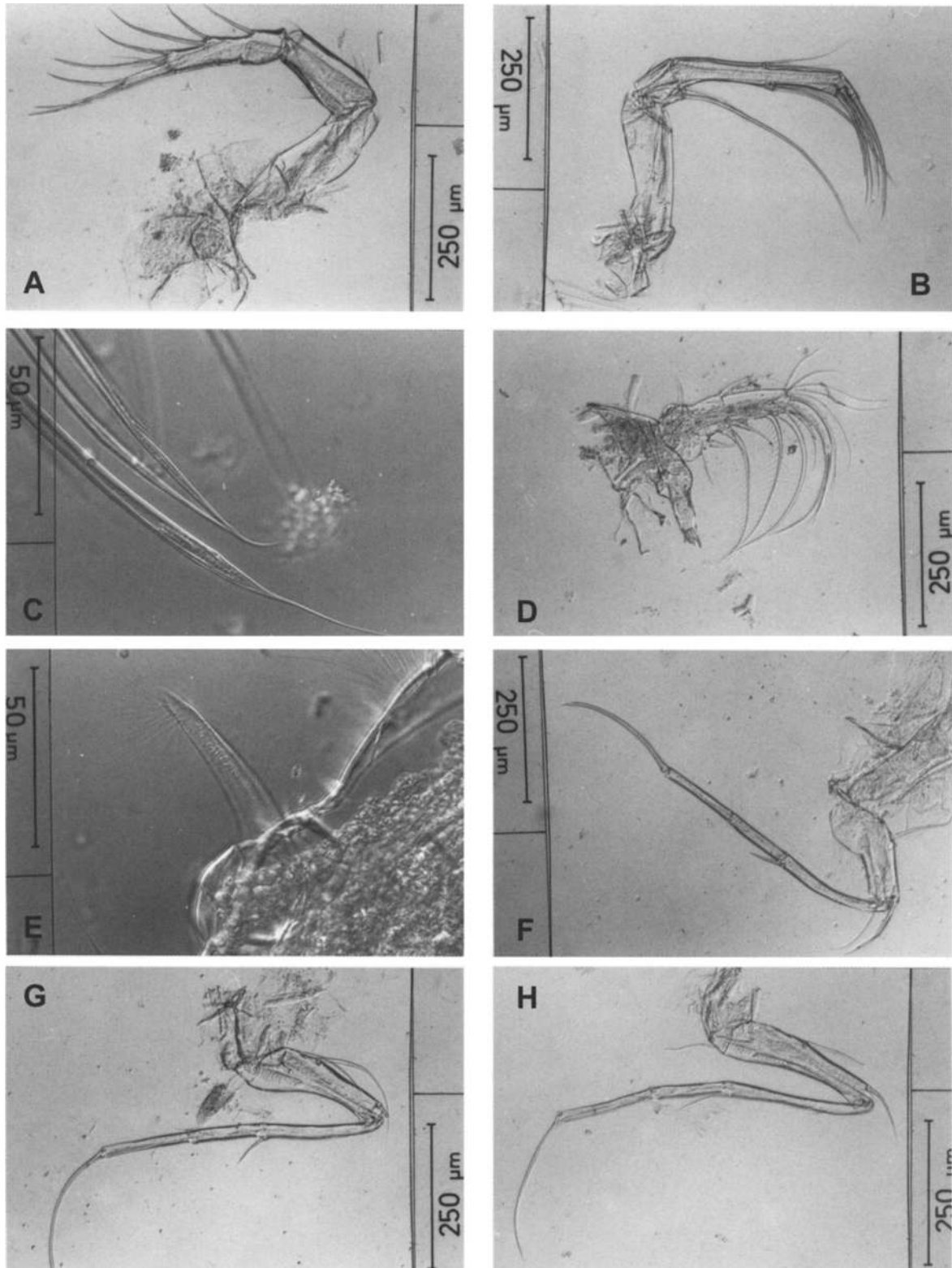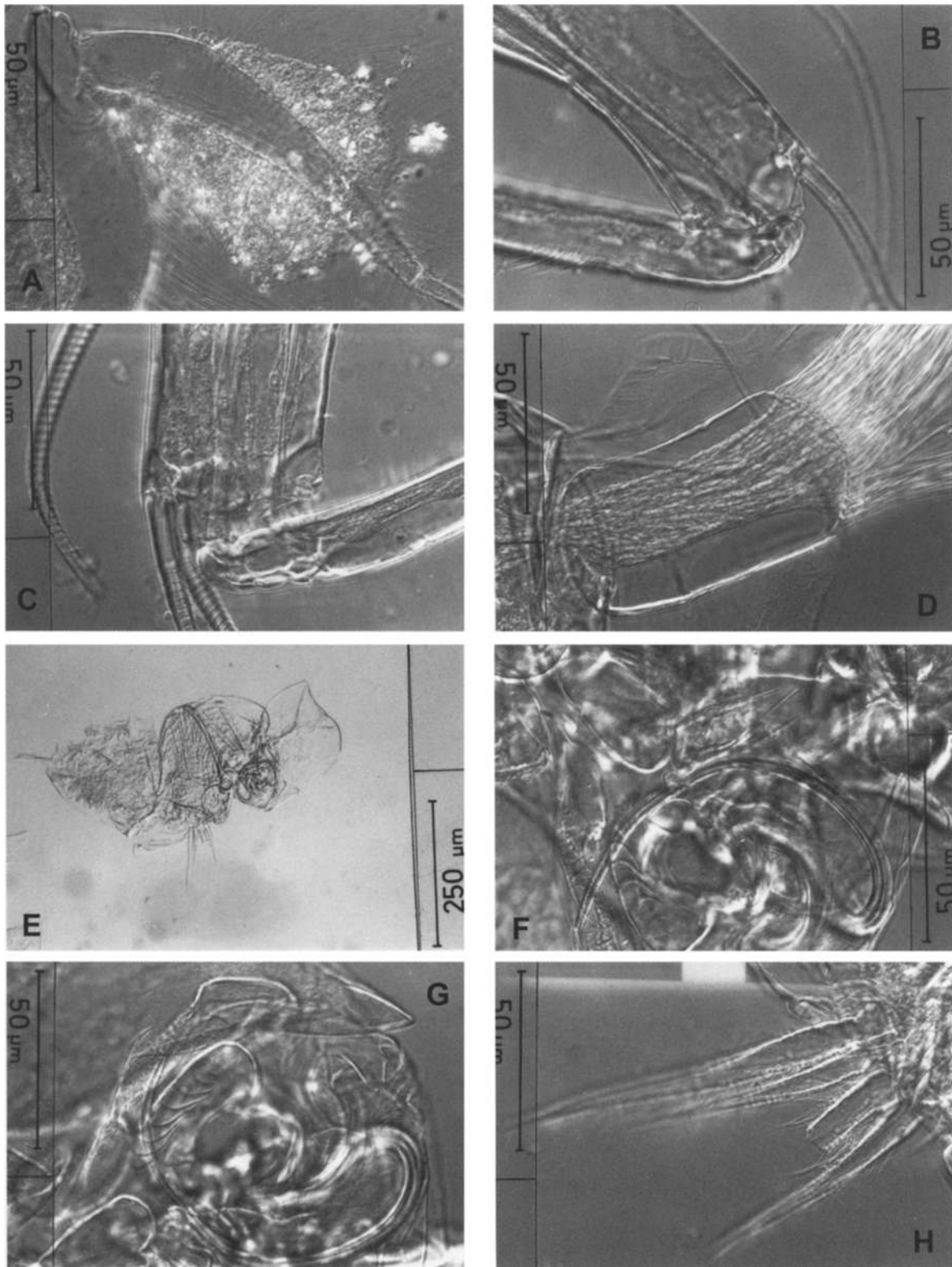
Fig. 4: *Pseudobosquetina semireticulata* n. sp., Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–344ES (epibenthic sledge), 17°07.454'S, 004°42.276'E; 5460m. – **A–H:** Female, specimen AB-026, paratype; **A:** antennule; **B:** antenna; **C:** lance-like terminations of antennal claws; **D:** mandible palp and coxa; **E:** dorso-distal blade of epipod, note row of setules; **F:** 1st thoracic leg; **G:** 2nd thoracic leg; **H:** 3rd thoracic leg; SMF Xe 21718. For magnifications see scale bar on each Fig.

Fig. 5: *Pseudobosquetina semireticulata* n. sp., Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–344ES (epibenthic sledge), 17°07.454'S, 004°42.276'E; 5460m. – **A–H:** Male, specimen AB-025, paratype; **A:** 'carrot' seta on 2nd thoracic leg; note refractile material trapped on setules; **B:** simple knee joint on 3rd thoracic leg; note medial fulcrum contracting heavily chitinised proximal end of second joint; **C:** chitinous buttressing in protopod of 2nd thoracic leg; **D:** brush organ; **E:** hemipene; **F:** distal end of copulatory process; note abrupt termination; **G:** beak of frontal lobe (top of picture) with copulatory process exiting into 'channel' between lobe and peniferum; **H:** 'furcal' setae (2 pairs); SMF Xe 21715. For magnifications see scale bar on each Fig.

Holotype: FLV, fig. 3A. – SMF Xe 21713.

Paratypes: More than 600 juvenile and adult specimens from different samples. – SMF Xe 21714–21745.

Type locality: RV *METEOR* cruise M48/1; box-corer sample Me48–345KG6 from the Angola Basin, water depth 5433 m; 16° 17.024' S, 005° 27.021' E.

Dimensions(in mm): Holotype FLV 1.30/0.85; Paratypes: LVs 1.20–1.31/0.77–0.90, RVs 1.20–1.27/0.71–0.80; C 1.25/0.85/0.77

Distribution: The new species has been found in almost all of the box-core samples collected during RV *METEOR* cruise M48/1 to the Angola Basin, SW-Atlantic, the sampling depths of which were always greater than 5000 m. Recovered only rarely in epibenthic sledge samples. It has also been found in the N-Atlantic (TRESSLER 1941).

Diagnosis: A large *Pseudobosquetina* species characterised by a fine reticulation on the posterior half of the valves.

Description: Valves large and ovoid in lateral view, with only faint irregularities dorsally which are better developed in RV. Greatest length in both valves at about mid-height; greatest height in LV almost at mid-length, in RV in the anterior third. Greatest width at mid-length. Anterior broadly and evenly rounded. Thin and moderately elevated antero-marginal ridge present, with 3–5 tiny knob-like protrusions on the lower half. Moderately wide flange developed (wider in instars). Between flange and antero-marginal ridge 5–6 thick but stout spines are developed (easily broken). Posterior narrowly and obliquely rounded, also with a narrow flange; with single, long spine at the postero-ventral angle. Dorsal outline strongly arched in FLV, less so in MLV. Cardinal angles in LVs not developed whereas RVs with conspicuous cardinal angles. LVs only with a dorsal plicated area, widest medially. Parallel to the ventral outline and beginning near the anterior is a ventral ridge or wing-like extension. The ventral side of this wing is flat with three thin ridges, giving the ventral outline a slightly convex impression, the distal edge is relatively sharp. The wing terminates in the posterior third with a short stout spine, posterior to which is a thick frill. In instars, the wing is much shorter both anteriorly and posteriorly, the frill is absent, however, a terminal spine is developed. The wing-like structures and the posterior half of the valves are covered with a thin, polygonal and mesh-like reticulation, typical for that species. Sexual dimorphism apparent, males being less highly arched. In dorsal view, valves evenly inflated laterally, widest at mid-length. Dorsal plicate area of LVs slightly swollen in dorsal view. Both ends stout and rounded.

In internal view, fused marginal areas moderately wide with 15–20 simple, straight marginal pore canals anteriorly and approx. 10 posteriorly. Ventral margin slightly concave in the oral region. Hinge hemiamphidont; RV with a large stepped frontal tooth which is slightly lobate dorsally and with a posteriorly adjacent deep round grove. Median hinge element smooth, posterior tooth large and elongate with 6 crenulations. Elements of LV complementary. Central muscle scars consisting of vertical row of four elongate scars and a U- to V-shaped frontal scar.

Soft anatomy females (all dimensions in μm): Antennule 6-segmented with long, slender protopodite which has a weakly

chitinised 'dorsal' surface with a chitinised 'notch' approx. one third from distal end. Segments II-VI moderately chitinised. Dimensions: I 245:73; II 163:71; III 82:61; IV 61:47; V 71:33; VI 92:15; terminal claw 168. Antenna long and slender (protopodite especially) 5-segmented; segs III and IV fused, postero-distal seta of seg. II extremely long, exopodite not observed; aesthetasc small (49 long) weakly spatulate distally. Dimensions: I 235:51; II 82:55; III 143:36; IV 112:41; V 40; terminal claw 214. Mandible coxa small (306:54) relative to palp (basis 367:82), carrot sets of basis with relatively narrow base (8), dental platform weakly chitinised dorsally. Respiratory plate of maxilla asymmetrically bean-shaped, with 14 strahlen many of which are constricted sub-medially (70 from base) and 2 aberrant (1 antero-dorsal, 1 weak, short very transparent antero-ventral). Note aberrant antero-dorsal strahl originates forward of the main strahl cluster and that the basal platform of same is partially sutured where it connects with the respiratory plate. Thoracic legs long and slender, weakly (especially postero-dorsal half of protopod) to moderately chitinised; knee-joint simple with submedial, horizontally oriented V-shaped fulcrum, protopodites especially lengthen posteriorly. Carrot seta of T1 and T2 large (166:30) and with significant accumulation of fine refractile detrital matter in the numerous, long filamentous setules. Dimensions: T1 I 196:88; II 214; III 114; IV 135; terminal claw 219. T2 I 260:85; II 234; III 117; IV 185; terminal claw 265. T3 I 298:73; II 283; III 131; IV 189; terminal claw 262. Genital lobes oval-quadrate with thick, curved central 'bridge' and thin sinuous external margin. 'Furcal' setae exceptionally long (205) originating behind each genital lobe (there may be others which are shorter), with a few filamentous setules.

Soft anatomy male (all dimensions in μm): Antennule with long (80) slender aesthetasc, weakly spatulate distally; seg.V with small (35) setule antero-distally. Dimensions: I 240:70; II 155:70; III 65:52; IV 55:42; V 75:33; VI 95:16; terminal claw 175. Exopdite of antenna 3-jointed (62:49:70) with significant narrowing between joints II and III; 'antero-proximal' seta of seg. II extremely long (400). Dimensions: I 200:50; II 60:52; III 150:32; IV 110:28; V 40:20; terminal claw 230. 'Antero-distal' carrot seta of basis of mandible palp with unusual ovoid-triangular lobation at base (seta 50 long, lobation 13). Basis oval and much wider than remaining segments (basis 92, distal seg. 53). 'Dorso-distal' seta of seg. II of palp complex (115 long), basal seta 13 long, plain; second seta 36, gently tapered with dense covering of fine, long (57) setules, terminating with a pronounced constriction (remainder of setal shaft plumose and evenly tapered). Basal seg. of maxilla palp large (64:41), endites 67:20:43;18:61:11. Thoracic legs moderately chitinised. Dimensions: T1 I 204:92; II 204; III 111; IV 127; terminal claw 212; carrot seta broad based, long (147, base 19) and densely pappose. T2 I 275:51; II 226; III 122; IV 153; terminal claw 255; carrot seta narrower than for T1 but equal in length. T3 I 316:51; II 285; III 127; IV 173; terminal claw 270; seta of protopodite small (82) evenly tapered and finely annulated. Hemipene moderately large but frontal lobe proportionately large in comparison to peniferum. Ventral half of peniferum inclined at 45° to broadly arched dorsal marin, 'birdshead' frontal lobe with a large triangular dorsal crest and small 'beak' located slightly under the peniferum. Vertical chitinous strut moderately strong, coincident with dorsal margin of proximal half of peniferum. Ventrally,

peniferum with rectangular chitinous box-work which connects with ventral strut at a 'ball and cusp' structure. Labyrinth very heavily chitinised (detail difficult to resolve optically). Copulatory process and sperm duct (?) consisting of a thin, but well-chitinised semi-circular tube which terminates close to the proximo-distal surface of the 'beak' in a channel formed between the 'beak' and the anterior of the peniferum. 'Furcal' setae (1 large, 1 small) originate at a quadrate basal platform, pappose and annulated.

Remarks: In size, overall shape and appearance all *P.*-species are very similar. However, minor differences in the dorsal outline can be observed on the extant material we have examined. With respect to the dorsal outline, the FLV of *P. semireticulata* n. sp. is slightly more angular dorsally than *P. mucronalata* and *P. nobilis* n. sp. The outline of the ventral ridge in dorsal view is similar to that of *P. mucronalata* but is less pronounced than that found on *P. nobilis*. Furthermore, *P. semireticulata* can easily be distinguished from the other species by its mesh-like, polygonal reticulation which is absent in *P. mucronalata* and *P. nobilis*. Instars of *P. semireticulata* can be distinguished from instars of *P. nobilis* because they possess a shorter ventral ridge. TRESSLER (1941: pl. 19 fig. 10) figured a juvenile valve from the Recent of the central N-Atlantic between Newfoundland and Ireland as *Cytheropteron* sp. (a). That specimen conforms in all aspects to our juvenile material of *P. semireticulata* n. sp. Anatomically *P. semireticulata* n.sp. is distinguished from *P. nobilis* n.sp. by having a larger protopod on the antennule (*P. nobilis* = 270 µm, *P. semireticulata* = 310 µm); the proportion of segs. I, II & IV of the antenna (larger in *P. nobilis*); the length of the postero-distal seta of seg. II is shorter; the dental platform of the mandible coax in females (at least) is larger; the respiratory plate is slightly smaller, elongate bean-shaped (in *P. nobilis* it is symmetrically bean-shaped) with 1 large broad-based 'antero'-distal and 1 extremely thin, transparent, short ventro-proximal aberrant strahl and 14 strahlen (*P. nobilis* presents 2 aberrant and 12 'normal' strahlen); and protopods of T1 & T2 are narrower. It is also noted that the termination of the copulatory process is spatulate while that on *P. nobilis* is abrupt and straight.

Pseudobosquetina nobilis n. sp.
(Figs. 6–8)

1941 *Cytheropteron mucronalatum.* – TRESSLER: 102, tab. 14–15; pl. 19 fig. 25.
1967 *Cytheropteron mucronalatum.* – HULINGS: 318, tab. 2; text-fig. 3A-F; pl. 4 figs. 10–11.
? 1975 *Pterygocythere* ?. – BENSON: 27, text-fig. 9(4).
1983 *Brachycythere mucronalatum.* – BENSON et al.: 438, tab. 2–3; pl. 1 figs. 6–7.
1987 *Bosquetina mucronalatum.* – WHATLEY & COLES: 44ff, text-figs 6, 8–10 pl. 5 figs. 1, 2.
1990 *Bosquetina mucronalatum.* – DINGLE & LORD: 214ff, tab. 1, 2, 4; text-fig. 2/9.
? 1999 *Bosquetina mucronalatum.* – CRONIN et al.: 234, tab. 1.
2000 *Bosquetina mucronalatum.* – DIDIÉ & BAUCH: 115, pl. 4 figs. 23–24.
2003 *Bosquetina mucronalatum.* – CRONIN & DWYER: pl. 1 fig. h

Derivation of name: From nobilis (Lat., adj.) = noble; referring to the elegant architecture of the valves.

Holotype: FC, opened for dissection, fig. 6A. – SMF Xe 21746.

Paratypes: 36 adult and 2 juvenile valves. – SMF Xe 21747–21761.

Type locality: RV *METEOR* cruise M48/1; epibenthic sledge sample Me48–344ES from the Angola Basin, water depth 5460 m; 17° 07.454' S, 004° 42.276' E.

Dimensions: Holotype: MC, LV 1.30/0.83, RV 1.27/0.75; Paratypes: LVs 1.22–1.27/0.78–0.92, RVs 1.17–1.25/0.68–0.85.

Distribution: *Pseudobosquetina nobilis* n. sp. had been found in the Angola Basin material in two epibenthic sledge samples (#344-EBS10 and #318-EBS01) and 8 box corer samples (#324-KG9, #341-KG1, 8 and 9 and #345-KG2, 4, 6 and 9. Together with the references which have been assigned to the new species, *P. nobilis* occurs in the N-Atlantic and the SE-Atlantic.

Diagnosis: *Pseudobosquetina nobilis* n. sp. is characterised by its very high plicate dorsal area of the LVs and the wide, sharp-edged ventral wing.

Description: Valves large and ovoid in lateral view with pronounced dorsal cardinal angles which are more developed in RVs. Greatest length in both valves at about mid-height; greatest height in anterior half. Greatest width at mid-length. Anterior end broadly but obliquely rounded. Thin and moderately elevated antero-marginal ridge present, with 3–5 tiny knob-like protrusions in the lower half. Moderately wide flange developed. 5–6 thick but stout spines are developed between flange and antero-marginal ridge. Posterior end narrow and obliquely rounded; narrow flange present. Three tiny spines are present at the postero-ventral angle, which decrease in size ventrally. Dorsal outline highly arched in FLV, less so in MLV. Cardinal angles in LVs weakly developed, very pronounced in RVs. LVs only with a very wide dorsal plicated area. A well developed ventral wing starts at the anterior end and extends to the posterior third. It is terminated by a short, stout protrusion and followed by an adjacent frill. The ventral area of that wing is flat, smooth and with a single faint ridge. The edge of the wing is sharp. In instars, the wing already presents the length appropriate for adults. A terminal spine is developed as well but the frill is not yet developed. The wing-like structure is covered with 1–2 thin lines and a 'plication'. The edge of the wing is extremely sharp. Laterally valves smooth. Sexual dimorphism weakly developed with females being slightly higher than males. In dorsal view, valves evenly inflated laterally, widest at mid-length. Dorsal plicate area of LVs swollen in dorsal view. Both ends stout and rounded. Edge of ventral wing conspicuous.

Internally, fused marginal areas moderately wide with 10–15 simple and straight marginal pore canals anteriorly and approx. 10 posteriorly. Ventral margin slightly concave in the oral region. Hinge hemiamphidont; RV with a large stepped frontal tooth being slightly lobate dorsally and with a posteriorly adjacent deep round grove. Median hinge element smooth, posterior tooth large and elongate with 6 lobes. Elements of LV complementary. Central muscle scars consisting of vertical row of four elongate scars and a U- to V-shaped frontal scar.
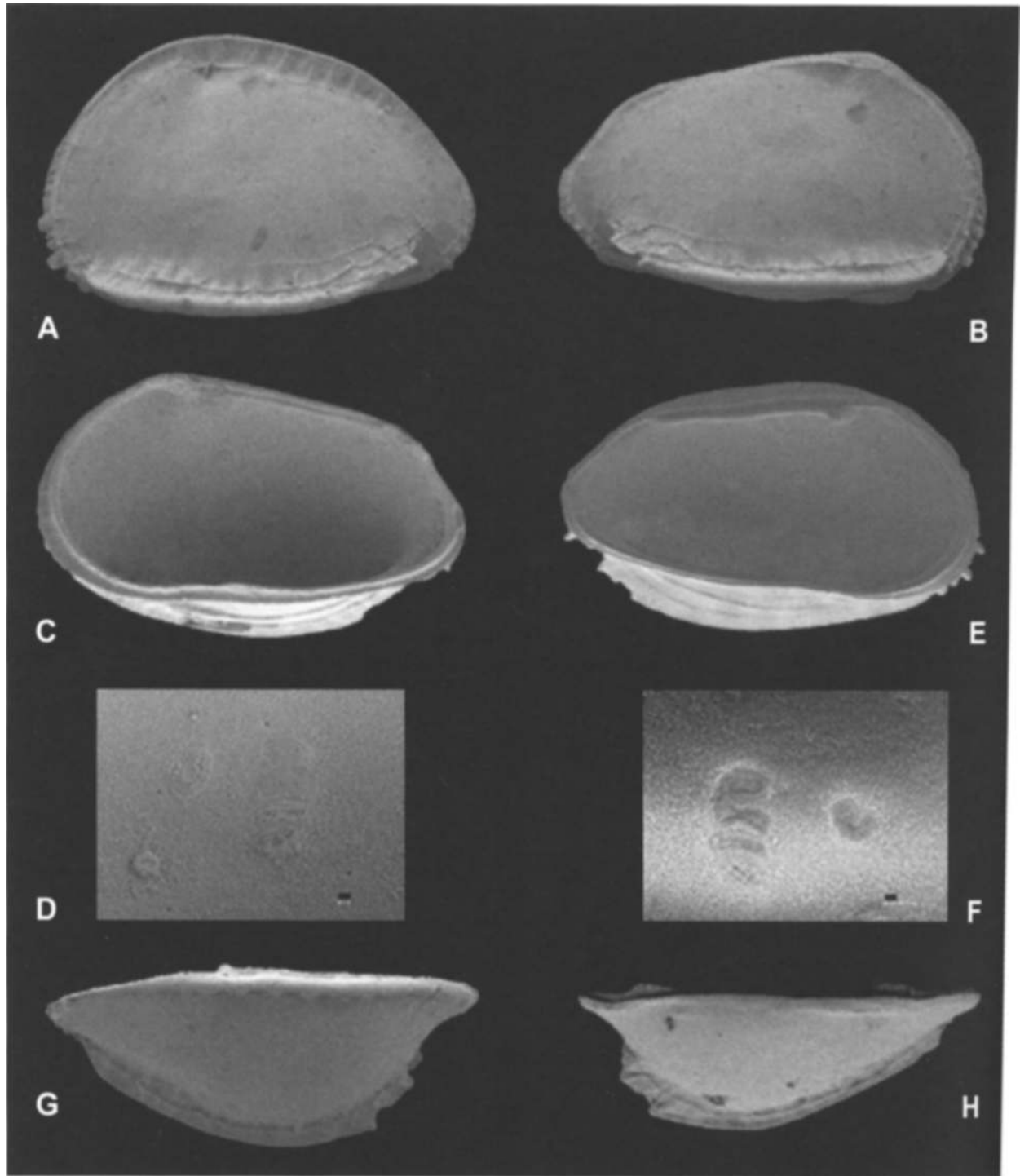
Fig. 6: *Pseudobosquetina nobilis* n. sp. – **A–B:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–344ES (epibenthic sledge), 17°07.454'S, 004°42.276'E; 5497m. FC, specimen AB-024, **holotype**; **A:** LV (1.30/0.83), external view; **B:** RV (1.27/0.75), external view; SMF Xe 21746. – **C–D:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–341KG1 (box corer), 17°07.974'S, 004°42.011'E; 5466m. ?MRV (1.27/0.75), paratype; **C:** internal view; **D:** central muscle scars, ×300; SMF Xe 21747. – **E–G:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–318ES (epibenthic sledge), 22°20.249'S, 003°18.439'E; 5180m. **E:** ?MLV (1.30/0.80), paratype; internal view; **F:** central muscle scars, ×300; SMF Xe 21748. – **G:** ?FLV (1.28/0.85), paratype, dorsal view. – Broken after photographing. – **H:** Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–345KG4 (box corer), 16°16.984'S, 005°27.127'E; 5434m. ?MRV (1.22/0.75), paratype, dorsal view; SMF Xe 21749. If not otherwise stated, all magnifications ×55.
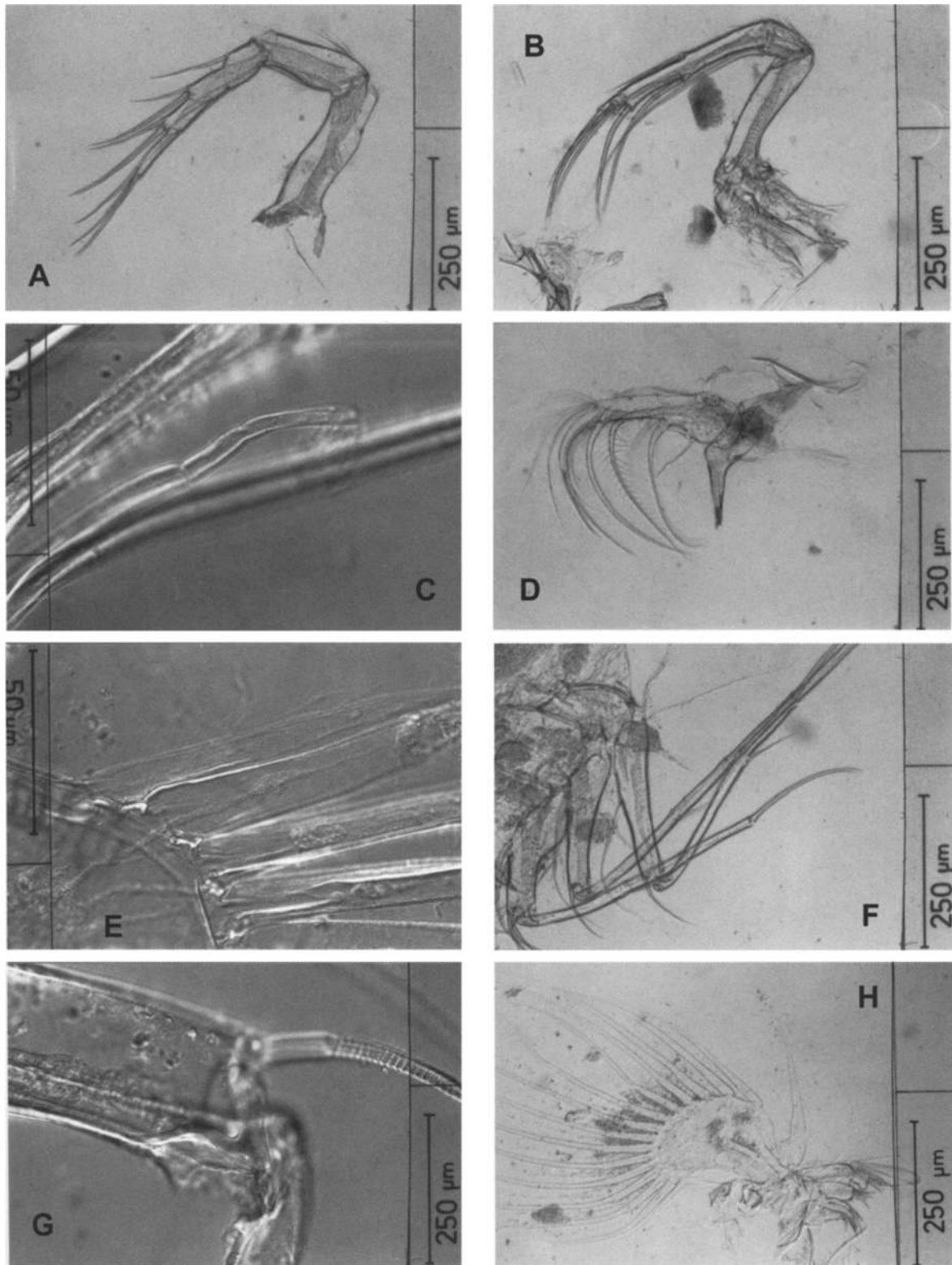
Fig. 7: *Pseudobosquetina nobilis* n. sp., Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–344ES (epibenthic sledge), 17°07.454'S, 004°42.276'E; 5497m. – A–G: Female, specimen AB-027, paratype; **A:** antennule; **B:** antenna; **C:** distal portion of exopodite of antenna; note proximal segment and possible seg. II to the right; **D:** mandible palp and coxa; **E:** respiratory plate of maxilla, base of strahlen and aberrant strahl (top); **F:** thoracic legs; **G:** knee joint of thoracic leg T3; SMF Xe 21750. – **H:** Female, specimen AB-024, **holotype**; maxilla and respiratory plate; SMF Xe 21746. For magnifications see scale bar on each Fig.
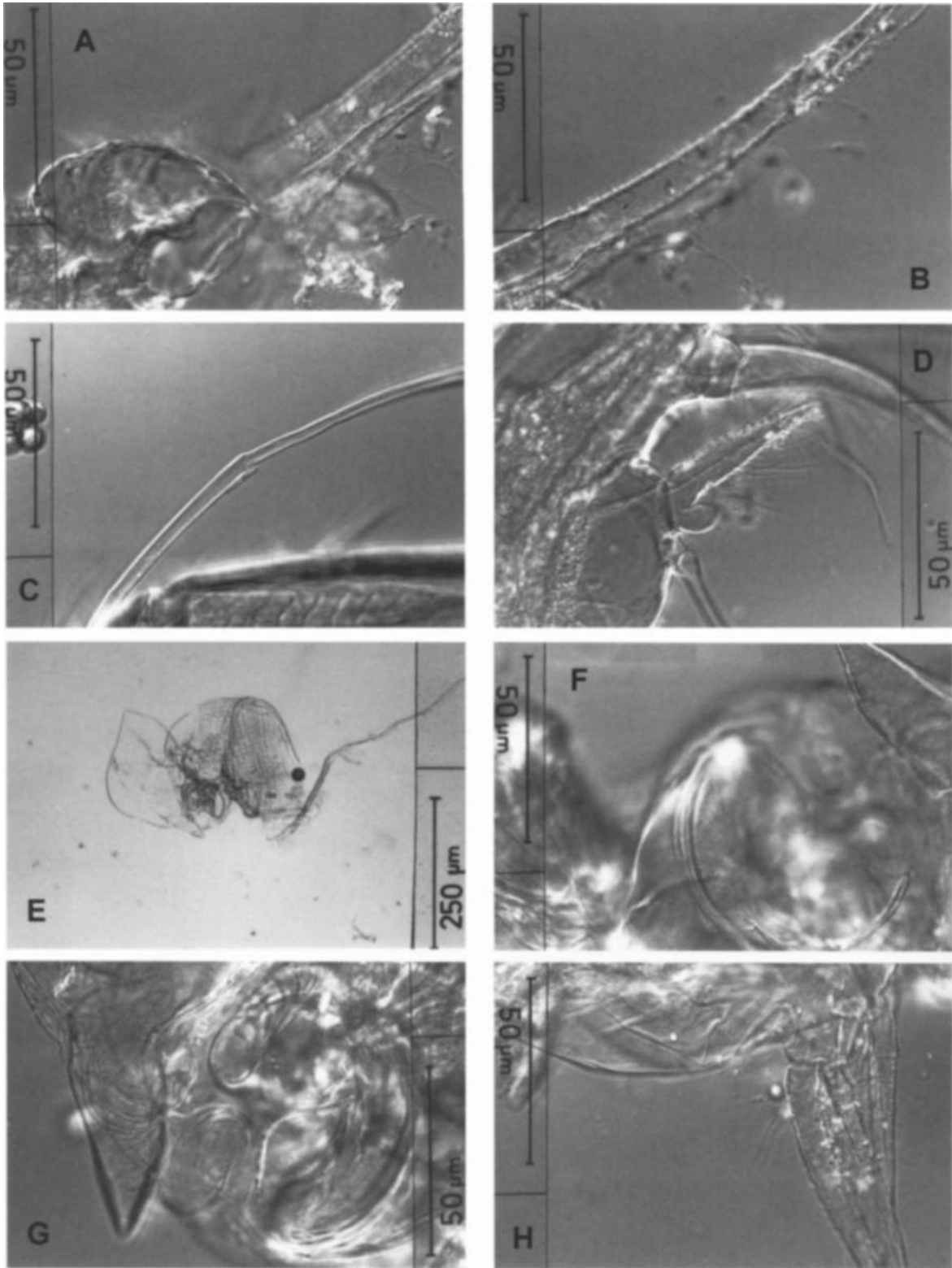
Fig. 8: *Pseudobosquetina nobilis* n. sp., Recent, Angola Basin, SE Atlantic Ocean; FS *METEOR* cruise 48/1, sample Me48–344ES (epibenthic sledge), 17°07.454'S, 004°42.276'E; 5497m. – **A–B:** Female, specimen AB-027, paratype; **A:** genital lobe and base of 'furcal' seatae, **B:** sparse setules on distal portion of 'furcal' seta; SMF Xe 21750. – **C–H:** Male, specimen AB-028, paratype; **C:** segmented (2?) distal portion of exopodite of antenna; **D:** 'carrot' seta on basis of madible palp; **E:** hemipene; **F:** distal end of copulatory process; **G:** beak of frontal lobe of hemipene, note channel between the beak and the peniferum; **H:** bases of 'furcal' setae (2 pairs); SMF Xe 21751. For magnifications see scale bar on each Fig.

Soft anatomy (all dimensions in μm): Antennule 6-segmented; seg. I weakly chitinised and with basal chitinous strut from the head to the anterior wall, remainder moderately chitinised. DIC imagery of seg. VI indicates wall of that segment at least may be 'pustulate'. Terminal aesthetasc of seg. VI 100 long with extremely narrow terminal blade. Dimensions female: I 275:94; II 187:83; III 68:62; IV 68:57; V 83:36; VI 88:19; terminal claw 177. Male: I 261:82; II 163:77; III 65:53; IV 65:44; V 76:38; VI 98:22. Antenna 5-segmented, 3–4 fused and moderately chitinised, 'postero'-distal seta of seg. II extremely long (438), evenly tapered with an obliquely angled row of fine, long (50) setules. Terminal claws long (220), lance-like terminating in a extremely fine 'setule'. Exopodites of moderate length, dimorphic (female = 236; male = 173), 3-jointed (II = 20, III = 33). Aesthetasc 57 long with narrow terminal 'blade'. Mandible coxa bow-shaped (315:79), palp proportionately large, basal segment broad and round (106:67). Epipod with a well-defined, blade-like 'dorso-distal' setal element (with setules) and 4? transparent (weakly defined) fingers. Respiratory plate of maxilla bean-shaped (262:157) with 13 extemely long (509) strahlen and one aberrant strahl in isolation at the dorso-anterior extremity of the plate. Brush organs of male quadrate (84:42), longest seta 158. Thoracic legs with well developed protopod, remaining segments long and slender; knee apparatus simple consisting of two (1 ventral, 1 dorsal), chitinised curved fulcra on the protopod. Carrot setae of P1 and P2 large (P2 = 110:15), with dense array of fine, long (up to 25 μm) setules (note in many cases these setules are enveloped in a coating of fine 'debris' which sometimes gives an impression of being 'colloidal'). Protopod of T3 with a single, simple seta. Dimensions male: T1 I 162:101 base; II 205:24; III 113:24; IV 130:20; terminal claw 248. T2 I 248:76; II 229:23; III 113:23; IV 133:23; terminal claw 243; T3 I 329:76; II 340:18; III 124:20; IV 174:16; terminal claw 297. Peniferum of hemipene asymmetric; posterior half forms obtuse triangle, anterior ovoid. Central chitinous vertical strut thin but with pronounced basal ring. Frontal lobe large, 'birdshead' shaped with obvious postero-ventral 'beak'. Copulatory process well chitinised near base, entire structure broadly arched forming half loop (151 long), the finer distal end of which terminates abruptly near or within the frontal lobe, close to the 'beak'. 'Furcal' setae consisting of a cluster of 2 (1 long, 1 medium), long (up to 115) setae with a dense covering of setules.

Remarks: As already stated for *P. semireticulata*, all three *P.*-species display similar dimensions, general shape and outline. *P. nobilis* differs from the other two species in its very wide dorsal plicate area and a very well developed ventral wing, best seen in dorsal view. The juveniles of *P. nobilis* differ substantially from other juveniles in that the ventral wing extends to the carapace extremities whereas in other juveniles the length of the ventral wing is reduced.

Several references are found in the literature, the specimens figured in which we refer to our new species.

TRESSLER (1941) figured an adult RV from the N-Atlantic (3420 m) which displays the same well-developed ventral wing as our own material. Although it is very large for a RV (1.39/0.85), as for our specimens, it is also smooth.

Similar comments apply to the two valves figured by HULINGS (1967) from the western N-Atlantic (3369 m). Although the LV displays the same very wide plicate dorsal area, there is also an indication from the soft parts that the 1967 material should be assigned to this species. However, based on HULINGS' drawings and descriptive text some contrasts are evident. For example in his descriptive text it is stated (p. 318) that the "copulatory organ bears an inverted U-shaped distal segment" and that "two stiff bristled setae project from the dorsal inner margin". Clearly, the present species differs in the shape of the peniferum and frontal lobe, however, we believe this arises from inadequate attention to detail on the part of HULINGS with respect to both his text and illustrations.

BENSON (1975) in his paper on the morphologic stability of Ostracoda, presented a drawing of a LV which he simply called *Pterygocythere?*. Although BENSON gave no indication as to the origin of that specimen, we believe that it is conspecific with our new species. Also from the western N-Atlantic (2800–3000 m) are two specimens figured by BENSON et al. in 1983. Both figured valves are identical in all aspects to our material. Two valves figured by WHATLEY & COLES (1987) are from DSDP Leg 94 (3884 m) from the eastern N-Atlantic. The LV is from Pleistocene sediments whereas the RV is from upper Miocene sediments. DINGLE & LORD (1990) referred to the material of WHATLEY & COLES (1987) and re-figured their LV. CRONIN et al. (1999) briefly mentioned *Bosquetina mucronalatum* from Holocene sediments in the central N-Atlantic; we assign that material only tentatively to *P. nobilis*. DIDIÉ & BAUCH (2000) figured a juvenile and an adult LV from the Holocene of the Rockall Plateau in the eastern N-Atlantic and finally CRONIN & DWYER (2003) figured a LV from the 'Atlantic'.

Cytheropteron testudo (SARS 1869), a case study

The discussion of *Pseudobosquetina* represents only one of a number of case studies in ostracodology which illustrate (acknowledging that the problems are not the domain of that discipline alone) how a cosmopolitan perspective not only impacts on assessed levels of diversity, but also acts to constrain phylogenetic, biogeographic and paleoecologic interpretations for constituent taxa. To further illustrate this point, we make reference to another 'cosmopolitan' ostracod species. *Cytheropteron testudo* (SARS 1869) was originally described from and taken "at the considerable depth of 120 fathoms" [219 m] (SARS

1869: 29) near the Lofoten Islands off northern Norway. Subsequent collections from other fjords were seen as confirmation that the taxon is a deep-sea species. More recently, *C. testudo* has received special attention because: a) its identification was apparently straightforward, b) the fact that it was restricted to cold-water environments offered utility to those involved in palaeoecological/climatic studies, and c) it was considered an index species for Pleistocene sediments in the Mediterranean (RUGGIERI 1972) and subsequently as the key marker for the Neogene-Quaternary boundary in the stratotype Vrica Sec-

tion in Italy (PELOSIO et al. 1980, COLALONGO et al. 1982). In 1984, however, BONADUCE & SPROVIERI published results of a study of a Plio-Pleistocene sequence from Sicily in which those authors estimated the first appearance of *C. testudo* occurred at 2.35 my BP and that this reflected the impact of a sharp, bottom-water cooling first recorded in 2.5 my old sediments by THUNNEL & WILLIAMS 1984); in other words, the first appearance of *C. testudo* pre-dated the Plio-Pleistocene boundary by approx. 700,000 years. Later, JENKINS (1987) quoted the opinion of WHATLEY (made in a personal comment) who indicated that the specimen figured by COLALONGO et al. (1980) was not *C. testudo*, but a new, deep-sea, pan-abyssal species closely related to *C. wellmani* HORNIBROOK 1952. JENKINS (1987) concluded therefore that the first appearance of '*C. testudo*' (*sensu* COLALONGO et al. 1980 and 1982) was diachronous in Italy and that some other datum should be nominated (he suggested using nannofossils, either the extinction of *Discoaster brouweri* or the initial appearance of *Gephyrocapsa oceanica*). Finally in 1996, AIELLO et al. presented evidence indicating that in the Mount San Nicola Section (Sicily), *C. testudo* first appeared in mid-Pliocene sediments with a range which terminated in the Lower Pleistocene. However, those authors did note some differences (and it should be highlighted that they did have topotypic material from the Skagerrak for comparison) between the Norwegian specimens and those from Italy, suggesting that such contrasts may reflect the existence of geographical 'races' within *C. testudo*. Significantly, access to the topotypic material then lead those researchers to observe that Atlantic specimens described by WHATLEY & COLES (1987) as *C. testudo* were smaller and lacked longitudinal ribs on the baso-distal portion of the alar process, with the conclusion that the 1987 assignment was doubtful. Yet contrasts in lateral outline, the extent of the anterior depression and caudal process warranted only '*testudo*-race' status for the Italian material. In our view, this leaves questions relating to the use of '*C. testudo*' as a key stratigraphic/palaeoclimatic marker in the Mediterranean unresolved, especially since AIELLO et al. (1996: 172) suggested that the morphic variations they observed may have been a response to "different environmental conditions". It is not the purpose of this paper to further discuss the continued debate relating to how the Plio-Pleistocene boundary might be defined, but rather to illustrate how much of the debate could have been avoided had the traditions of good taxonomic practice been applied.

In the New Zealand region, *C. wellmani* is known to occur in Tertiary sediments and has also been recovered living in shelf sediments off both North and South Islands. HORNIBROOK indicated Recent valves were from sediments dredged from a depth range of 20–150 m and SWANSON & AYRESS (1999) recovered live specimens of this species from 122 m

and 133 m in the east Tasman Sea, one 'rare' occurrence at 700 m (Station 26, 350 fathoms) is, we believe, probably part of a reworked assemblage. In Pliocene and older sediments, specimens identified as *C. wellmani* display marked similarities with *C. testudo* but are easily discriminated from the extant *C. wellmani* morphotype on the basis of the anterior margin and alar process (SWANSON & AYRESS 1999). Significantly, WHATLEY & DOWNING (1983) discriminated a new species *Cytheropteron parawellmani* from *C. wellmani*, but noted close affinities between those two taxa and *C. testudo*, which they also recorded in the Middle Miocene sediments sampled for that report. Those authors then noted that their study further extended the known spatial and temporal distribution of *C. testudo*. In fact, from their own data readers could also conclude that during Miocene times, that species inhabited tropical-subtropical, shelf-outer shelf environments. This obvious paradox was not discussed in subsequent publications by the Aberystwyth micropaleontological group; their records of occurrences of *C. testudo* in DSDP and ODP cores simply seemed to confirm the cosmopolitan, deep-water nature of its distribution. Despite the potential utility offered by *C. testudo* (as an example), it is evident that most workers cannot discriminate between this and other closely-related species (e.g. *C. perlaria* HAO 1988 in the Northern Hemisphere and *C. wellmani* HORNIBROOK 1952 in the Southern Hemisphere). In an attempt to resolve this problem SWANSON & AYRESS (1999) undertook a complete review of *C. testudo* and its close relatives. This study focused on specimens from modern and Tertiary sediments collected primarily in the SW Pacific (supplemented with archived material from other ocean basins) and included a significant number of specimens with soft-parts intact. From that study, the following conclusions were reached: a) definitions of *C. testudo* were imprecise such that this taxon and *C. perlaria* were regularly confused in the literature, b) at least three other described species of *Cytheropteron* (*C. litwini* BLASYK 1987, *C. stictum* VAN DEN BOLD 1973 and *C. "tabuki"* ZHOU 1995) were considered part of an increasingly large complex of species clustered into an informal '*Cytheropteron testudo* Group', and c) four new species from the SW Pacific were then added to that informal amalgamation. Significantly, definitions of 3 of those 4 new species were based in large part on variations in the soft anatomy.

The results of these studies require most ostracodologists working on deep-ocean samples to make a philosophical shift from a methodology in which recovery of a few 'cosmopolitan' species (for example *C. testudo* or *C. perlaria*) is expected, to one which recognises those taxa as a persistant accompaniment to 'regional' diversification which is the norm for deep-ocean, podocopid ostracod assemblages.

Conclusions

With respect to the deep ocean, complex microorganisms which precipitate a calcareous test or shell offer enormous opportunity to study 'natural' extinction rates through time, since the preserved remains of their exoskeletons are often recovered in cored sequences of bathyal and abyssal carbonate sediments. The most obvious conclusion which can be reached on the ba-

sis of our observations is that 'cosmopolitanism' and an often less than rigorous practice in terms of taxonomy has lead to a significant underestimate of ostracod diversity through time and time ranges for individual taxa which are excessive. Perhaps the most important conclusion that can be reached as a result, is that calculated extinction rates for deep-water ostra-

cods through the Cenozoic will be very low except in those horizons where extinction events have been identified in other organisms (e.g. benthic foraminiferids), and where special emphasis is placed on the search for equivalent events in the ostracod assemblage. This will clearly influence how the current biodiversity crisis is assessed. When species losses in the extant ostracod assemblage are described, those data will be documented in relation to a documented, long period of relative stability. In that context, there can be no question therefore that the importance of the 'modern' extinction event will be exaggerated, such an aberration is, however, almost certainly not restricted to ostracodology. Consider also the potential impact that contrasting indices of cosmopolitanism (which according to RAPOPORT 1994 are 4× higher for marine species) could have on prioritisation of research funding allocations and resource management policies (McKINNEY 1998). Often quoted indices appear to confirm a concept that deep marine species especially are buffered, in some way isolated from rapid environmental change. In our view, however, the fact that such a small portion of the marine invertebrate assemblage has been described and much of that which has been written is in need of review makes much of the data contributing to estimates of cosmopolitanism equivocal.

Our call for a rigorous, scientifically disciplined approach to ostracod taxonomy is timely. There is increasing international awareness of a shortage of trained taxonomists and that this applies especially to urgently needed, base-line data gathering in the marine environment. No other benthic marine organism has as much potential as the podocopid ostracod to contribute to our understanding of diversification and extinction in that environment. This claim is based on the fact that as a group they have 'successfully' occupied all ocean basins (from the margins to the abyss) but, more importantly, because their fossil record is not replicated by any other marine metazoan. It is also timely to repeat a recurrent observation, that increasingly in Earth Science the principle of uniformitarianism is under scrutiny (see WHATLEY 1996 for example). We further make the observation that genetic sequencing is of the present and, despite the promise of biological clocks, must be considered as one of a number of tools available to taxonomists to conceptualise and define species and their historical context. The geological history of those species (usually based on fossil remains) is the past which provides an appropriate context in which to look forward and make predictions about the fates of plants and animals.

Acknowledgements

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