

Keynote lecture

SPECIES-LEVEL TAXONOMY OF MALESIAN MARINE MOLLUSCS AND THE BIODIVERSITY CRISIS

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"If taxonomists were a species, they would be classified as endangered" (Norse 1993)

ABSTRACT

All global biodiversity initiatives agree on the urgent need for each region to inventory its fauna. The Malesian region (Andaman Sea east to the Weber Trough and north to the Philippines and Gulf of Thailand) possesses the richest marine molluscan fauna in the world. However, no comprehensive faunal surveys have ever been undertaken, and there is also very little information on endemism. For those in a position to do such surveys, a few aspects of inventarisation are introduced from the viewpoint of the museum taxonomist, namely some basic principles of sampling and the use of identification resources.

INTRODUCTION

I have chosen to look at taxonomy mainly from one viewpoint - that of the Biodiversity Crisis. This is selected not merely because it is topical, but because for marine molluscs it can be shown that the Malesian region is a biogeographical hotspot. The term Malesia is here used for the Malaysian and Philippines regions and most of Indonesia, more or less in the sense of Whitmore (1987), but from west to east approximately from the Andaman Sea to the Weber Trench, and north to the Gulf of Thailand. I have rather arbitrarily included Maluku, even though its terrestrial fauna at least is usually classed as Melanesian, because many early records from "Indonesia" probably (but not definitely) originated from Ambon or the "Moluccas".

NATURE OF THE BIODIVERSITY CRISIS

This can be very loosely summed up as:

1. Known (and estimated) diversity is vast, particularly in the Indo-West Pacific.
2. Taxonomic data are inadequate.
3. Number of practising taxonomists is small, and diminishing.
4. Habitat degradation is escalating.

The commonest measure of biodiversity

(Williams 1993) is species-richness. Estimates of bivalve diversity for most regions have been published, although for the Malesian region these are only available for the Philippines. For that area two widely differing figures have been given, namely Flessa & Jablonski's (1995) total of only 512 species, and that of 1037 cited by Stehli *et al.* (1967); the latter authors, however, reject their own total as a "towering anomaly". In my opinion this figure is actually a conservative one, as my estimate for the bivalve fauna of the rest of Malesia ("Malayo-Indonesia") is 830 species, yet this region is more poorly studied than the Philippines. (Among my main sources were the reports of Lynge (1909), Prashad (1932), Tantanasiwong (1978) and Morris & Purchon (1989), and the papers of Lamy (1907-1939), Bertin (1878-1881) and other revisers; these were collated and revised to reduce synonyms). Taking into account considerable commonality of species on one hand, but the incomplete state of our knowledge on the other, these figures together probably indicate a total bivalve fauna in excess of 1,300 species.

It must be admitted that the Philippine figure is actually exceeded, in theory, by

Japan: a rough count of the bivalves living at 100 m or less, cited by Habe (1977), gives a very approximate figure of about 1,060. However, in contrast to the Malesian region, Japan has a relatively continuous history of malacological research into its fauna, which is moreover a complex of tropical, subtropical and boreal elements.

For comparative purposes, some supplementary original estimates of bivalve species numbers have been compiled for a diagonal transect across the Indian Ocean (Fig. 1). However, when extrapolating figures based on bivalve faunas to the Mollusca as a whole, one must bear in mind that Kohn (1971) estimated bivalve: gastropod proportions on tropical continental islands (such as those of Malesia) to be higher than on oceanic islands (about 30: 70, against 17: 83). There is merit in the suggestion of Vermeij (1990) that high bivalve diversity in the Indo-Malayan arc and low diversity in Pacific oceanic islands (ebbing on Easter Island to only 6 species) can be related to higher organic enrichment of the environment. However, this would not explain why bivalve diversity in the waters of Mozambique - which receive detrital output from major river systems such as the Limpopo, Zambezi, Save, etc., and presumably also from Madagascar - is no greater than that of the oceanic Mascarene Islands (Mauritius, Reunion and Rodriguez).

Another measure of biodiversity is endemism; unfortunately faunal uniqueness cannot be gauged in the absence of adequate studies of the relevant faunas, of which marine molluscs have received little attention. One area that stands out is the Andaman Islands - the barrier formed by the Bay of Bengal and its position on the edge of Malesia has led to several species and subspecies evolving as peripheral isolates. Examples include *Amalda booleyi* (Melville & Sykes, 1896), *Oliva andamanensis* Bridgman, 1909, *Conus nobilis renatae* Cailliez, 1993, *C. andamanensis* Smith, 1878, *Littoraria delicatula* (G. & H. Nevill,

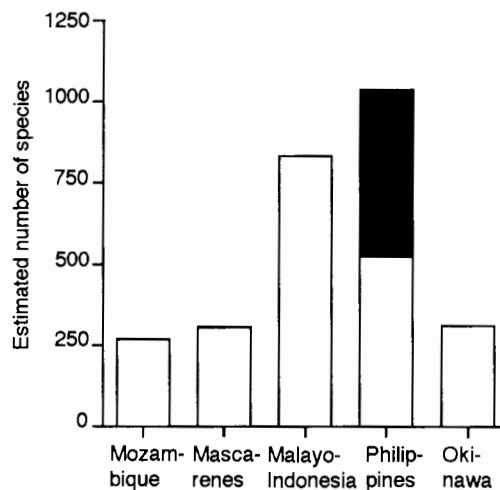


Figure 1. Bivalve-species diversity in selected areas of the Indo-West Pacific, at depths below approximately 100 m. Source of figures as follows: Mozambique: Natal Museum collection; Mascarenes: Viader (1937, but taxonomy revised) and Natal Museum collection; Malayo-Indonesia: see text; Philippines: Flessa & Jablonski (1995) and Stehli *et al.* (1967); Okinawa: Flessa & Jablonski (1995).

1885), and *Gyrineum gyrinum wilmerianum* (Preston, 1908). Another area inviting investigation is the south coast of Java and Sumatra, whose molluscan fauna, in contrast to the South China Sea coast, has much in common with the Indian and Western Indian Ocean regions. Species such as *Babylonia spirata* (Linnaeus, 1758), *Conus abbas* Hwass in Bruguiere, 1792, and *Haustellum dolichourus* Ponder & Vokes, 1988, spring to mind; in other such areas, situated at the extreme limits of the Indian Ocean, peripheral isolation has led to the evolution of a swarm of endemic species, and the Indian Ocean coast of Indonesia appears to present a similar scenario.

THE NEED FOR INVENTORYING

All biodiversity initiatives agree that the first essential step is for each region to inventory its fauna. For marine molluscs, no-

where is this more imperative than in the Malesian region.

Important expeditions have been recently carried out in the region by Dutch, French and Australian institutes. However, practically all that is published on the fauna of Malesia is expedition-based. This is not an ideal situation, as the research-workers involved can rarely draw on field experience; furthermore, there will never be enough taxonomists available, even in the foremost museums of the world, to deal timeously with all groups of molluscs, even less all regions. The prime need is for more taxonomists to be trained in those countries where the fauna is threatened, as they are in the best position to adequately sample and to understand their fauna through routine familiarity with the local environment.

The following brief introduction fall within the realm of what is usually termed "museum taxonomy". Museum taxonomy is basically alpha taxonomy, but with as much input from fieldwork and life observations into taxonomic decisions as possible. I shall not be considering systematics, or cladistics, molecular biology, biometry, or any of the other important tools needed for fuller taxonomic studies.

QUALITATIVE SAMPLING

The basic units in taxonomy are populations, not individuals, and taxonomic decisions will be influenced by the adequacy of the available samples: the larger the sample, the easier it becomes to draw sound inferences about species limits. An ideal sample has the same mean and variance as the whole population (Unfortunately, in the case of rare species, an "ideal" sample may be perilously close in size to the entire population!). One should certainly strive to make even a small sample as representative as possible, by incorporating not only all observed variation patterns, but an adequate set of juvenile and immature individuals. Juveniles are important in taxonomy, as the apical whorls, which often contain significant characters, are usu-

ally eroded or lost in the adult (even a fresh-looking protoconch or prodissoconch may resemble the surface of the moon under SEM).

Do not expect a single example to be necessarily typical. It may be adapted to unusual conditions outside its normal range, it may even show growth deformities or it may be immature.

It is extremely important to maintain a parallel collection preserved in 70-80 % ethyl alcohol. Many tropical species are known only from empty shells, including the type species of some important genera and subgenera (e.g., *Ancilla*, *Cancilla*, *Pusia*, and *Latirus*), which as a consequence cannot be defined. Conversely, many species cannot be placed in their correct genus without anatomical or at least radular characters. For example, the *Inquisitor-Ptychobela-Funa-Cheungbeia-Aguilaria* series of turrid genera share the same shell characters, and can only be distinguished by their foregut anatomy and radulae (Taylor & Wells 1992). However, specimens required for their shell should be preserved dry, the body being first removed for separate preservation where needed; despite the common belief to the contrary, ethyl alcohol solutions (like so-called buffered formalin) seldom remain neutral indefinitely and shell surfaces will deteriorate in time.

Field (and tank) observations may contribute useful data to supplement morphological characters. Body colour, for example, may assist in distinguishing otherwise similar species, nudibranchs being the most obvious example. A collection of colour transparencies of live molluscs is a useful (sometimes essential) supplement to a specimen collection.

Field observations may reveal variation patterns to be ecophenotypic, which will seldom be obvious in museum samples. For example, Bernard Tursch and his colleagues have proved that shell colour in *Oliva oliva* (Linnaeus, 1758) depends on substrate colour; thus samples translocated from black

sand to coral sand will change future shell coloration in response, the shell of each preserving an exact record of the translocation.

Observations on microhabitat and diet may provide an insight into niche-partitioning, which may serve to distinguish closely related species in sympatry. Even associated organisms may provide supporting characters: for example, the shell in certain *Chicoreus* species (such as *C. aculeatus* (Lamarck, 1822) and *C. fosterorum* Houart, 1989) may have a coating of red or orange sponge in life. The shell in some *Nassarius* species may bear a species-characteristic colony of hydractinian coelenterates, which lives nowhere else.

Reproductive data is not only essential to understanding the distribution (*i.e.*, developmental mode) of a taxon, but structure of egg capsules or spawn masses may provide valuable taxonomic characters. Tank observations are often the most reliable. A classic case is Frank Perron's 1979 hatching and rearing of the Hawaiian *Conus* then often known as "*Conus elisae* Kiener, 1845": most grew into typical *Conus pennaceus* Born, 1778, providing indisputable proof that "*elisae*" is not a valid taxon.

IDENTIFICATION RESOURCES

The primary resources in identification are:

- Literature: Original texts
- Subsequent interpretations
- Primary types
- Secondary types
- Identified collections

Literature

Although modern illustrations and interpretations of a proportion of the Indo-Pacific fauna are available, these are not always error-free and wherever possible identifications should be checked against original sources. Probably at least 75 % of known Indo-Pacific marine molluscs were described prior to 1900, and the relevant literature extends back to the pre-Linnean texts of the

early 18th century (*e.g.*, Rumphius's (Rumpf's) 1705 work on the molluscs of Ambon).

It is now impossible for any fledgling institute without unlimited finances to accumulate all of the journals, books and monographic series needed for exhaustive taxonomic research. It has been estimated (Bieler & Kabat 1991) that by the year 2000 a total of 210,000 journals and other publications on molluscs will have been published. The most difficult works to acquire are the great monographic series - notably Sowerby's *Thesaurus Conchyliorum* (1842-87), Reeve's *Conchologia Iconica* (1843-78), Kiener's *Species general* (1834-79) and Kuester's *Systematisches Conchylien-Cabinet* (1837-1921) - in which most Indo-Pacific species were first described or figured. Because of their attractive hand-coloured plates, these works are in great demand among book-collectors, which has inflated their prices as much as it has reduced their availability.

At present the only affordable compromise is to buy microfiche copies - a Dutch firm, IDC, sells positive microfiche editions of most of the classic malacological works and older journals. It is also probable that many of these will eventually be available also on CD-ROM.

Primary types

When working with pre-20th century species, one soon discovers that most original descriptions are too brief to be useful and figures lack detail or accuracy. Often a species will be unrecognisable until the type material has been studied. This does not of course imply that a holotype or its equivalent contains all the essential attributes of the species. However, somewhere within the range of variation of a species there has to be a morphotype that matches the holotype of that species.

Much of one's research will delve into pre-20th century literature, and one soon discovers that in some families there are a

very high proportion of synonyms - different names proposed for the same species. Often these were the result of the common failure to recognise variation patterns, or lack of familiarity with previous literature, or the inability to recognise the inadequately-described species of others. The rule of priority was not rigorously followed by earlier workers - Lamarck for example thought nothing of proposing a new name to replace one that he disliked. Also, names proposed by some authors (*e.g.*, Roeding and Perry) were not initially considered valid, and other writers who were once widely used (Martini, Chemnitz, Martyn, Meuschen, Schroeter, etc.) are now rejected as non-binomial.

The principles involved in recognising specimens in old collections as types are a complex subject that will not be discussed in detail here. The greatest complications result from the fact that the type concept is really very recent in origin, and early workers such as Linnaeus, Lamarck and Reeve saw no conflict in substituting a better specimen for the original, or in adding additional examples to the type set. Early figures too, often omitted natural blemishes that would aid in recognition of the actual specimen. With modern photographic techniques such problems should be greatly reduced.

Occasionally, a defective holotype will render a name unusable as it lacks a character that is crucial to the recognition of the species, for example, protoconch or microsculpture. In such cases one must seek cryptic characters (perhaps morphometric) that will enable the holotype to be placed taxonomically. As a last resort it must be rejected as a *nomen dubium* and an alternative (later) name sought.

Secondary types

Most taxonomists must sooner or later make "pilgrimages" to museums in London, Paris, Berlin and other centres, in order to compare material with the actual types. A specimen that matches may be labelled

"homeotype" and may prove extremely useful for subsequent identification purposes. Homeotypes are purely a practical tool, being highly subjective, and obviously no replacement for genuine types.

Topotypes are simply specimens from the same locality as the holotype. Their use in identification is limited (particularly as early type localities were often erroneous). However, they become important when a neotype needs to be designated, or when geographic variation is under investigation. Indonesia is the type locality for many of the earliest described Indo-Pacific species, mainly because of the key position occupied in the literature by Rumphius's work on Ambon. But a note of caution! In 18th century texts, "East Indies" often meant no more than the iniquitous "Eastern Seas" so beloved of some mid-19th century writers. Thus Chemnitz makes it clear that his "ostindischen Meeren" sometimes meant Tranquebar in India (where a Danish colony during the 18th century served as a source of shells for European collectors).

Identified collections

South-east Asian malacologists are disadvantaged by the scarcity of extensive, well-curated public collections, and an urgent attempt should be made to strengthen the main collections at present in existence. In other words, within each country, other institutes as well as amateur collectors should be encouraged to deposit samples in national collections. Voucher specimens are in fact crucial to all reports and faunal surveys, and are equally important in ecological and other non-taxonomic research, in order to ensure that one's work has permanence. In other words, samples of each species should be lodged in a public collection (preferably in several), to enable posterity to confirm (or at least standardise) identifications. Of course one must be assured of professional collection management, so that not only will specimens be well looked after and rigorously curated, but will be made accessible

to other workers. Paratypes of any new species should be treated as a special international category of voucher specimen: ideally, they should not be concentrated in one institute but rather distributed to important museums around the world (perhaps in exchange for other paratypes). This will not only permit wider understanding of these taxa, but protect against potential loss of all types through any natural (or unnatural) disasters (such as befell the Bocage, Goddefroy and Stuttgart Museums).

SUMMING UP

Collections of tropical Indo-Pacific molluscs have tended to be expeditional in origin: *i.e.*, collected *en masse* over a short period with minimal time for field observations. Very seldom has the reviser of an Indo-Pacific group had personal in-depth field experience of living populations of their group. In Malesia, with its vast biodiversity the need for local expertise is perhaps greater than

anywhere else in the world.

Although the difficulty of securing taxonomic training, the lack of reference tools and the dearth of research facilities are major obstacles in building up local expertise, the practical possibilities of field studies will to some extent balance this. "There ... is a growing body of evidence that suggests that the fundamental taxa recognised in folk systematics correspond fairly closely with scientifically known species" (Berlin 1973). Of course no-one would suggest that "folk systematics" in its strictest sense would differentiate species of Triphoridae or Turridae! But first-hand familiarity with one's region and the molluscs that live there, irrespective of how up-to-date one's nomenclature might be, would go a long way to counter any handicaps of having less than complete access to resources. In some respects this will give you an advantage over those with the finest facilities, but only expeditionary samples to study.

REFERENCES

- Berlin, B. 1973. Folk systematics in relation to biological classification and nomenclature. - *Annual Review of Ecology and Systematics* **4**: 259-272.
- Bertin, V. 1878. Revision des tellinides du Museum d'Histoire Naturelle. - *Nouvelle Archives du Museum d'Histoire Naturelle, Paris* [2]**1**: 201-361, pls. 8-9.
- Bertin, V. 1880. Revision des garides du Museum d'Histoire Naturelle. - *Nouvelles archives du Museum d'Histoire Naturelle, Paris* [2]**3**: 57-129, pls. 4-5.
- Bertin, V. 1881. Revision des donacides du Museum d'Histoire Naturelle. - *Nouvelles archives du Museum d'Histoire Naturelle, Paris* [2]**4**: 57-121, pls. 3-4.
- Bieler, R. & A.R. Kabat. 1991. Malacological journals and newsletters, 1773-1990. - *Nautilus* **105**(2): 39-61.
- Flessa, K.W. & D. Jablonski. 1995. Biogeography of recent marine bivalve molluscs and its implications for paleobiogeography and the geography of extinction: a progress report. - *Historical Biology* **10**: 25-47.
- Habe, T. 1977. Systematics of Mollusca in Japan. Bivalvia and Scaphopoda. - Hokuryukan, Tokyo. xiii + 372 pp [In Japanese].
- Kohn, A.J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. - *Limnology and Oceanography* **16**(2): 332-348.
- Lamy, E. 1907-1941 [Series]. Revision des vivants du Museum naturelle de Paris. - *Journal de Conchyliologie* vols. **55-84**.
- Lynge, H. 1909. The Danish Expedition to Siam, 1899-1900. IV. Marine Lamellibranchiata. - *Kongelige Danske Videnskabernes Selskabs Skrifter*. [7]**5**: 99-299.

- Morris, S. & R.D. Purchon. 1981. The marine shelled Mollusca of West Malaysia and Singapore. Part 3, Bivalvia. - *Journal of Molluscan Studies* **47**: 322-327.
- Norse, E.A. (ed.) 1993. *Global marine biological diversity*. - Island Press, Washington. 383 pp.
- Perron, F.E. 1979. Larval rearing as an aid in molluscan taxonomy. *Hawaiian Shell News* **27**(4): 1, 12.
- Prashad, B. 1932. The Lamellibranchia of the Siboga Expedition. Systematic part. II. Pelecypoda (exclusive of Pectinidae). - *Siboga Expedition* **118** (Monograph 53c): 1-354, pls. 1-9.
- Rumphius, G. E. 1705. *D'Amboinsche Rariteitkamer, behelzende eene Beschryvinge van allerhande zoo weeke als harde Schaalvisschen, te weeten raare Krabben, Kreeften, en diergelyke Zeedieren, als mede allerhande Hoorntjes en Schulpen, die men in d'Amboinische Zee vindt ...* - Amsterdam: Francois Halma. pp xxix + 340, index 43 pp, pls 1-60.
- Stehli, F.G., A.L. McAlester & C.E. Helsley. 1967. Taxonomic diversity of Recent Bivalves and some implications for geology. - *Geological Society of America Bulletin* **78**: 455-466.
- Tantanasiriwong, R. 1978. An illustrated checklist of marine shelled gastropods from Phuket Island, adjacent mainland and offshore islands. - *Phuket Marine Biological Centre Research Bulletin* **21**: 1-22.
- Taylor, J. & F.E. Wells. 1992. A revision of the crassispirine gastropods from Hong Kong (Gastropoda: Turridae). Pages 101-116 in Morton, B. (ed.) *The Malacofauna of Hong Kong and southern China* **3**. Hong Kong University Press, Hong Kong.
- Vermeij, G.J. 1990. Tropical Pacific pelecypods and productivity: a hypothesis. - *Bulletin of Marine Science* **47**(1): 62-67.
- Viader, R. 1937. Revised catalogue of the testaceous Mollusca of Mauritius and its dependencies. - *Bulletin of the Mauritius Institute* **1**(2): 1-111.
- Whitmore, T.C. 1987 (ed.). *Biogeographical evolution of the Malay Archipelago*. - Clarendon Press, Oxford. 147 pp.
- Williams, P.H. 1993. Choosing conservation areas: using taxonomy to measure more of diversity. Pages 194-227 in T.-Y. Moon (ed.) *International Symposium on Biodiversity and Conservation*. Korean Entomological Institute, Seoul.