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Critical Estimate of the Number of Recent Mollusca

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INTRODUCTION

The Mollusca constitute one of the largest and most speciose phyla in the Animal Kingdom. Assessments of the total number of species sharply conflict, and to indicate the wide range of totals, Sabrosky (1953) cited several estimates, which ranged from 40,000 (Hunter and Hunter, 1949) to 150,000 (Shrock and Twenhofel, 1953). Recently, Mayr (1969) and Nicol (1969) independently arrived at an estimate near 107,000. Documenting various totals and their sources, Schilder (1949) showed that authorities have continually increased the sum from the 674 species treated by Linnaeus in 1758 to the 127,000 indicated by Jaeckel in 1958. Table I presents a breakdown of totals given by several authorities.

These widely divergent estimates imply that several authors have come to diverse opinions largely because of differences in sources and outlook. The sophistry evident in the work of some authorities contrasts sharply with the more empirical approaches of Sykes (1901) or Wenz (in Schilder, 1947) for the prosobranchs.

Consultation of the primary malacological literature justifies a reassessment of the total number of species of mollusks.

THE HISTORICAL PROSPECT

The species concept in zoology was clarified with the advent of the synthetic theory of evolution. The great descriptive period in the 19th century has begun to give way to revisionary

works based on the conceptual framework of Neo-Darwinism. The modern approach to alpha taxonomy, namely familial and generic monographs, which in the case of widely dispersed organisms transcend the bonds of geographic provinciality, tends to focus attention on the real, rather than the illusory.

In malacology, systematics has often suffered from an overburdened nomenclature which historically was generated by schools of conchologists who attempted to name all variations in the morphology of the shell. For example, Bourguignat, basing his descriptions on the outline of the valve, led a group of French workers, including Locard and Servain, to name hundreds of 'species' of the common fresh-water mussels in Europe. The ultimate *reductio ad absurdum* was propounded by Coutagne (1895) who provided a latinized descriptive nomenclature which, according to Schnitter (1922), would allow for 43,740 names for the unios of France!

Several estimates of the total number of living mollusks are untenable in that they, too, bear the marks of an overenthusiastic acceptance of an exaggerated nomenclature. The task ahead is to refine these estimates and to strive for greater accuracy.

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In a work of this nature, there is ample room for error for which I take all responsibility.

Methods

There are several methods of estimating the total number of living species of mollusks. The most obvious is a taxon by taxon tally, preferably at the familial level. Although many families are not well known, I have summarized totals in this manner for bivalves (Table V) and for fresh-water pulmonate gastropods (Table IV). For other groups tallies are from the literature at levels other than the family, from calculations involving synonymy ratios and from various other data including counting the species in the collections (USNM = United States National Museum; MCZ = Museum of Comparative Zoology) (Table XII).

Another method is to assess the totals by geographic areas. Review of large or significant portions of the world faunas also points to a figure considerably lower than recent estimates (Tables II and III).

Finally, because there are many catalogues of available names in the literature, a mere counting of nomina provides a source of information. However, there is the question of how to deal with lists of names. I have devised the concept of the synonymy ratio, which is here defined as the proportion of nominate taxa to the number of real taxa (species). In paper after paper, particularly recent and sophisticated revisions which utilize synthetic evolutionary theory and cover wide zoogeographical areas, there are far fewer species than available nomina. Abbott (1968) documented the reductionary tendency: since the middle of the last century the several revisions of the neogastropod family Cassidae have consistently reduced the total number of recognized species.

Geographic Analysis of Total Fauna

By observing estimates of total faunas one can also gain some

insight into the numerical diversity of the Mollusca (Tables II and III). Few of the numbers listed for the land mollusks (Table II) can be considered accurate, but they can be appraised in the light of the individual author's tendency toward over-naming. The rich tropical faunas of South America, Africa and the Indo-Malayan-Philippine areas each comprise two or more thousand molluscan species, but, in view of some of the data discussed under the synonymy ratios of land mollusks, a downward revision is probable. The comparatively high number of nomina for Palearctic or European snails is due to overnaming.

The Nearctic figure derived from Pilsbry (1948) may well be reduced (*vide* Vagvolgyi's revision of *Triodopsis* discussed on p. 92).

The insular faunas, particularly Jamaica, Cuba, and Hawaii, have exceptionally high numbers, which in fact are based on *named* forms. The studies of Solem (1961) on the pomatiasids indicate that many of these are synonyms.

Incomplete as these data are, they indicate that the terrestrial molluscan fauna, both prosobranch and pulmonate, numbers fewer than 15,000 species.

Table III allows an analysis of marine benthic mollusks of the world. In 1892 Dall and Harris discussed marine faunas of shelled benthic mollusks and tallied totals from several faunal reports. The estimates of numerical diversity were: boreal, 250 species; cool temperate, 400; warm temperate, 500; tropical, not less than 600. Recent studies cast doubt on the accuracy of Dall's estimates. For example, Maes (1967) intensively studied the littoral marine mollusks of the Cocos-Keeling Islands in the tropical Indian Ocean and recognized just over 500 species. Also the reef-associated malacofauna of the Seychelles has been tallied at about 350 (Taylor, 1968). Notwithstanding these studies, all the estimates in Table III are significantly higher than any that might be inferred from Dall and Harris. Since many species have planktonic larval forms, over 80 per cent of the molluscan fauna is widely distributed throughout the Indo-Pacific. Several of the figures can be used to arrive at an estimate of the total marine fauna of that area, and it can be seen that the figure would be well below 10,000. However, using a figure of 10,000 and combining it with 8000

Atlantic, 500 Antarctic and let me estimate 4000 eastern Pacific, 1200 abyssal, and about 500 pelagic, one arrives at a total less than 25,000. These figures can be an estimate of the diversity in the marine realm.

Fresh-Water Mollusks

The fresh-water element could not be mentioned in the section on total faunas because too little data for geographic provinces are available. However, some interesting information does exist: Canada, 81 species (Clarke, *in press*); the Soviet Union, 470 (Heptner, 1956); and Australia, about 150 (McMichael and Iredale, 1959; McMichael, 1967). These faunas might be considered relatively impoverished when one considers the diversity in the Great Basin of North America or the giant river systems of India, Southeast Asia and China. There may be fewer species in some of these areas than has previously been assumed. For example, both Rosewater (1960) and Sinclair (1969) have indicated high synonymy ratios for North American pleurocerid prosobranchs.

Also the species-flocks of the ancient lakes must be considered. The grand fauna of Lake Tanganyika has been admirably reviewed by Leloup (1953), who recognized about 70 species from the hundreds of described forms and reduced to 55 the number of gastropods which had once been given as 133 by Cunnington (1920). Likewise the pleurocerid *Semisulcospira* in Japan, once numbering some 30 nominate forms, has been reduced to 10 species (Davis, 1969). Similar reductions might be expected in more modern studies on such ancient lakes as Baikal (Kozhov, 1936; 1963), Ohrid (Stankovic, 1960) and the Malili Lakes (Kruimel, 1918).

It appears there are fewer than 2000 species of fresh-water clams (Table V), including unionaceans, corbiculaceans, and the odd estuarine forms. This estimate is in substantive agreement with that of Nicol (1969), whose estimate of 12,000 species of fresh-water gastropods appears much too high. Table IV subsumes some information on several families of fresh-water gastropods. The aquatic pulmonates are reasonably well known though immense problems relate to their taxonomy; however, there are fewer than 1000 species of fresh-water pulmonates although there are that many nomina for the lymnaeids alone.

In comparison with the pulmonates, the fresh-water prosobranchs are poorly known, although several of the families (e.g. Syrnolopsidae, Stenothyridae and Iravadiidae) are numerically insignificant. So few data are available that I have not tabulated them, but it is known that there are fewer than 100 viviparids (Prashad, 1928), 75 ampullariids (Alderson, 1925; Prashad, 1925; Pilsbry, 1927; Scott, 1957; Yen, 1943) and 15 valvatids, Clarke (*in press*). Taylor (1966) gave lists of species for some hydrobiid subfamilies and from his paper I estimate about 1000 species for the Hydrobiidae. We are left to consider the truncatellid, buliminid, micromelaniid, and thiarid stocks. Scattered literature (Davis, 1969; Leloup, 1953; Riech, 1937; Rosewater, 1960; Sinclair, 1969), indicates that there are certainly fewer than 9000 species in these groups—a figure which is necessitated by the estimate of Nicol (1969). The total number of fresh-water prosobranchs is probably nearer the 2000 mark as indicated by Wenz (*in* Schilder, 1947).

Synonymy Ratios

I have used synonymy ratios to make estimates in groups for which the total number of available nomina are known from compiled lists. Although some molluscan groups have very high synonymy ratios, most taxa appear to have ratios of 4/1 or 5/1 and for this reason, if the total number of nomina are known for a family or genus, I have used a ratio to give a rough approximation of the total number of species. However, since different workers have different degrees of subjectivity in their research and use collections of varying quality, I have used the SR only as a crude approximation of the number of species in any one group.

Fresh-Water Mollusks

The synonymy ratios tend to be highest among fresh-water groups, and the suggested numbers of fresh-water bivalve and gastropod species in taxa which have not been critically monographed are highly questionable. For the prosobranch ampullariid *Pomacea flagellata,* a polytypic complex of four subspecies in Central America, Pain (1964) noted some 40 nomina and thus established a singularly high SR; however, he (1961) considered seven species of African ampullariids, two of which

are polytypic. Here there were 21 named forms, giving a SR of 3/1. Clench (1962) pointed out that the well-known east American *Viviparus georgianus* had been named 13 times over.

The taxonomy of the small rissoacean and cerithiacean fresh-water prosobranchs is poorly known so it is difficult to provide a reliable estimate of the number of species. Indeed there may be many undescribed species (Thompson, 1968). However numerous their species may seem, Berry (1943) noted only 60 ammicolids in the North American fauna, and Taylor (1966), although giving no specific numerical data, presented the most thorough account of several subfamilies of hydrobiids, from which it may be deduced that there are probably fewer than 1000 species. Synonymy ratios vary, but they are usually high: thus in the European micromelaniid *Emmericia,* Radoman (1967) recognized four Adriatic species where over 60 nomina had been applied. From Ant's data (1962), there is a SR of 10/1 in the Balkan hydrobiid, *Horatia.*

The larger fresh-water prosobranchs, variously derived from the Cerithiacea, present special problems because of their great variability. Goodrich (1936) recognized a SR of 3/1 for *Goniobasis* in the Coosa River, and Riech (1937) showed that the 15 melaniid species of Papua and Melanesia had 114 available nomina, giving a ratio of nearly 8/1. One of the highest figures can be tallied from Rosewater (1960) who placed about 100 nomina in the synonymy of *Pleurocera canaliculata* of the Ohio River. In the Tennessee River, long known for its rich pleurocerid fauna, Sinclair (1969) recognized only six species.

The taxonomy of fresh-water bivalves suffered immeasurably by the school of Bourguignat in Europe and by the singularly eager pen of Isaac Lea in North America. Schnitter (1922) discussed the naming of varieties by the nineteenth century workers, including Bourguignat, Locard, and Servain in France and Rossmässler, Clessin, and Westerlund in Germany. He showed that *Unio requienii* had been named about 35 times and that the common swan mussel, *Anodonta cygnea,* had over 250 available nomina. Astounding as the latter may seem, it is less than partially complete since Haas (1969) listed 552 names in the synonymy of *A. cygnaea,* an all-time record for superfluity in molluscan taxonomy. However, a similar tendency is evident in other areas of the world: Johnson (1970)

noted 100 nomina for the North American *Elliptio complanata;* for the African mutelids, Pain and Woodward (1962; 1964) established SRs of 40/1 for *Aspatharia* (*Spathopsis*) *rubens* and about 20/1 for the genus *Pleiodon;* and, Dell (1953) reduced some 15 nomina to two species of *Hyridella* in New Zealand (see also McMichael and Hiscock, 1958).

In fresh-water bivalves, other than the unionaceans, the same pattern obtains, but possibly not so strikingly. Thus, the SR for the 34 North American species of fingernail clams or sphaeriids is nearly 4/1 (Herrington, 1962). Parodiz and Hennings (1963) noted that most of the 30 named South American corbiculids are synonyms of three widely distributed species.

The fresh-water pulmonate gastropods are better known taxonomically than the fresh-water prosobranchs, and evidence is accumulating that indicates that these hermaphroditic mollusks are less speciose than had been assumed. The classic study is Hubendick's paper (1951) on the Lymnaeidae, which by its very nature and scope (it was the first worldwide monograph of a fresh-water molluscan family by an author of the school of synthetic evolutionary theory) had to be somewhat superficial. However, Hubendick reduced some 1110 nomina to 40 species and brought the wrath of the splitters down on him; he also ushered in a new era of realism to a science marred by its provinciality. With a 27/1 ratio in the lymnaeids, the planorbids cannot be far behind: Harry (1962) indicated that there is a SR of about 11/1 in Neotropical planorbids. Basch (1963) found a 11/1 ratio in one of the North American limpets, *Ferrissa,* and Clarke (*in press*) reduced 26 nomina to four species of *Physa* in the Canadian Basin. Recently, Hubendick (1970) has indicated that the Palearctic limpet, *Ancylus fluviatilis,* has over a hundred synonyms.

Prosobranchs

Widely diverse lineages make up the sum of marine gastropods: their specializations are, with the exception of the Cephalopoda, unequaled, and their numbers contrast or compete with the land gastropods. In diotocardians or archaeogastropods, the phasianellids are under review by Robertson (*pers. comm.*) who reports that, in one extreme case, a species has a SR of 21/1. There are 40 to 50 species in the family and some 450

nomina, giving a SR of 10/1. Robertson (1957) also discovered a 7/1 ratio in the turbinid *Halopsephus.*

Probably because of their small size, the mesogastropod rissoaceans show an immense numerical diversity. The superfamily itself may embrace over twenty families. Although few thorough systematic analyses are available, one that is shows the same reductionary trend: Abbott (1958) reviewed the cosmopolitan assimineids, a group of small prosobranch snails that have adapted to estuarine and semi-terrestrial habitats but retained a pelagic larval stage which is responsible for their wide distribution; 50–60 species are recognized and about 250 names are available so that the SR is about 5/1.

The littorinacean mesogastropods are no exception to the problem of over-naming: names for the land groups of the pomatiasids and chondropomids are reducible; Solem (1961) estimated that of 600 known New World forms [about 350 of which are Cuban annulariids (Torre and Bartsch, 1942)], at least 25 per cent are not species. This digression on terrestrial littorinaceans is meant to preface and compare with the family Littorinidae to which Rosewater (*pers. comm.*) has directed much attention. He reports that there are 1200 named forms and recognizes 100 species, giving a SR of 12/1 which lends credence to the thesis that there are fewer species of mollusks than has usually been assumed. Likewise in the calyptraeacean *Crepidula,* Adam and Leloup (1936) recognized only a single highly variable west African species with at least 10 available nomina.

Fortunately the higher mesogastropods have been studied taxonomically in far greater detail than most groups of mollusks. One can note that about 165 cypraeids are recognized as species and well over 1000 specific names are available (Schilder and Schilder, 1938; Kay, 1957; 1960). Similarly, Abbott has shown a ratio of nearly 6/1 in *Strombus* (1960) and *Cassis* (1968), including both fossil and living species. The strombid *Terebellum terebellum* with a high SR of 12/1 (Jung and Abbott, 1967) is comparable to the bursid *Ranella olearium* with 15/1 (Dell and Dance, 1963). Of the 35 nominal *Distorsia,* only five living species are recognized (Emerson and Puffer, 1953). A lower ratio of 111/39 obtains in a preliminary study of the Tonnidae (Turner, *pers. comm.*).

Among the neogastropods, there is some evidence of overnaming. Tomlin (1917) considered that there were about 250 living species of marginellids with some 950 nomina. For the four species of *Vasum* in the western Atlantic, Abbott (1950) listed 16 available nomina although in the Indo-Pacific, this SR is somewhat reduced (Abbott, 1959). Bullock (unpubl. MS) lists over 20 available names for the highly variable *Oliva reticularis* in the western Atlantic.

Pulmonates and Opisthobranchs

Among marine basommatophorans, several ellobiids have been carefully studied: Hubendick (1956) reviewed the ten species of *Plectotrema* and found 34 available names while Meyer (1955) listed 12 nomina in the synonymy of *Ovatella myosotis*. The SR ratio in the patelliform *Siphonaria* is low, about 2/1 for the 70 known species (Hubendick, 1946) while in the trimusculid *Gadinia,* it is over 5/1, being 37/7.

Among the cephalaspid opisthobranchs, Lemche (1948) recognized some 53 species and about 250 names for Arctic tectibranchs, giving a SR of about 5/1. Also some of the species are world-wide in distribution and the many named forms from different seas have been reduced to a single species: Burn (1959) recognized one cosmopolitan species of the notaspidean *Umbraculum*. Of all opisthobranch groups, perhaps none is better known than the anaspidean aplysiids. *Dolabella scapula* lives throughout the Indo-Pacific to the west coast of America and has a SR of 16/1 (Engel, 1942), all the named forms of MacFarland (1918) notwithstanding. And Eales (1960) in her monograph of the sea hares of the world, recognized 35 Recent species of *Aplysia* with a SR of over 5/1 for this the largest genus of the family.

The so-called systellomatophoran onchidiids, frequently referred to the opisthobranchs, are marine slugs with a lower SR. Although Stantschinsky (1907) admitted but 40 species, Hoffman (1928–9) recognized between 60–70, giving 2/1 as an approximate SR.

Shelled Terrestrial Gastropods

The land gastropods are one of the largest, if not *the* largest, groups of mollusks. Although diverse lineages have adapted

to terrestrial habitats, the so-called pulmonate or euthyneurous snails are most speciose. Prosobranch land snails, though numerous in the tropics, are rarely encountered in temperate or boreal environments. Since the advent of studies by Rensch (1926), several groups of pulmonates have been approached in terms of polytypy. The *Rassenkreis* concept can be traced into the 19th century, but the biological nature of the speciation process has only been clarified in recent decades. Since land gastropods tend to form isolated populations more easily than many marine animals whose immature forms may be widely dispersed by currents, they are more liable to be polytypic. However, I do not want to overstress the polytypic concept in approaching a problem as simple as an overloaded nomenclature, for it is the synonymy ratio which is under discussion, and the 250 or so nomina accorded the polymorphic European helicid snail, *Cepaea nemoralis* (Taylor, 1914) are simple cases of naming every color form and banded condition.

One group which confounds the taxonomist is the mesurethrous pulmonate family Clausiliidae. Of unusually wide and disjunct distribution (Boettger, 1925; Likharev, 1962), the Clausiliids are diverse and rich in numbers of species although in some geographic realms fewer forms occur (Loosjes, 1953). Estimates of 100 species of the nenine *Temessa* in Peru are not uncommon (Loosjes and Loosjes-Bemmel, 1966) but the studies of Nordsieck (1963) and Pfeiffer (1956) question such figures. Nordsieck investigated *Delima* in the southern Alps and recognized three species, two of which are strongly polytypic, particularly *D. itala* with eight subspecies; a burdened nomenclature was reduced by nearly 30/1. Likewise, Pfeiffer eliminated the many nominal forms of *Albinaria* in the Dodecanese to several subspecies of *A. teres*. Similar studies have been applied to the more primitive orthurethrous chondrinids (Nordsieck, 1962) and orculids (Zimmerman, 1932) but unfortunately complete synonymies were not given. And though no specific revisionary studies exist, Clench (1957) indicated that the nearly 600 named Cerionidae are applicable to fewer than 100 species of this halophilic West Indian family. Again, the mesurethrous family Strophoceilidae, the large achatiniform snails from South America, has a SR of about 5/1 (Bequaert, 1948).

Among the higher sigmurethrous pulmonates, the colorful arboreal groups have high SRs: Laidlaw and Solem (1961) recognized 74 species for 309 named *Amphidromus,* and Clench (1946) tallied 140 nomina for the five species of *Liguus,* giving a ratio of 28/1. In the bulimuloid odontostomine *Cyclodontina* of Brasil, Solem (1956) reduced some 13 varieties to a single species, and in the Neotropical helicacean camaenids, *Labyrinthus* and *Isomeria,* he (1966a) found a ratio of nearly 2/1, perhaps because nearly 50 per cent of the taxa are known from fewer than 10 specimens.

Among the earliest studied of *Rassenkreise* is the work of Boettger (1913) who recognized some 11 subspecies of *Iberus gualterianus* in Spain, and although Nicolas (1957) disagreed with Boettger's result and considered 42 nominal forms of *gualterianus,* it seems to me to be two, or possibly three polytypic species. Also in the Helicidae, *Levantina spiriplana* in the Near East has been recognized as a single polytypic species with six subspecies with a SR of 35/1 (Pfeiffer, 1949). It appears that ratios may be higher for advanced land pulmonates than for other mollusks: Steenberg (1949) recognized six polytypic species of 60 named *Eremina* in the Middle East, and in the European *Chilostoma* (*Cingulifera*) *cingulata,* Pfeiffer (1951) implied that some 70 nominal species might be reducible to seven subspecies, though some populations are doubtful races. Even Bartsch (1938) considered fewer than 40 species of the camaenid *Conchlostyla* on Mindoro, Philippine Islands.

Modern systematic revisions will certainly reduce the sum total of terrestrial pulmonates even in carefully reviewed faunas. Pilsbry (1948) listed 714 species of North American land mollusks, among them 24 species of the polygyrid *Triodopsis* (12 monotypic and 12 polytypic with 41 subspecies). Vagvolgyi (1968), employing statistical analyses with extensive field studies, reduced *Triodopsis* to 22 species, nine of which are polytypic with 21 subspecies. Some 20 nomina, excluding previous synonyms, are thus excised from an overburdened nomenclature.

Finally, some mention should be made of the prosobranchs: Neal (1934) indicated that 150 available nomina were applicable to the 10 species of Hawaiian helicinids. About 30 Malayan

species of the minute cyclophorid *Opisthostoma* have been recognized by van Benthem Jutting (1952a) but Berry (1962; 1963) has cast doubt on the conchological taxobases in these forms: growth proceeds daily by adding single axial ribs; in dry conditions these lines are closer together, in adverse environmental conditions the number and spacing of ribs is markedly altered. It is very possible that many "species" of the cyclophorids *Farcimen* and *Aperostoma* (Torre, Bartsch, and Morrison, 1942), of the streptaxids *Discartemon* and *Huttonella* (van Benthem Jutting, 1954; 1961) or of the vertiginids *Boysidea* and *Gyliotrachela* (van Benthem Jutting, 1950) might represent only ecophenotypes.

Land Slugs

Terrestrial slugs have evolved in widely divergent groups of pulmonates. The veronicellids or vaginulids have vague affinities and are placed in a separate order, the Systellommatophora. Hoffman (1925b) recognized 44 species in the family where 304 nomina were available, so that the SR is about 7/1; *Veronicella liberiana* has been named 12 times over (Forcart, 1953). Among the 20 or so species of parmarionine slugs of the Ariophantacea, Hoffmann (1940) noted that *Parmarion pupillaris* had a SR of at least 15/1. And the varietal nomina for the Palaearctic limacids are legion (Hesse, 1926). The voracious, carnivorous testacellids all have high synonymy ratios: *T. maugei,* 18/1; *scutulum,* 14/1: *haliotidea,* 13/1; *bisulcata,* 7/1 (Hoffmann, 1925a).

Oceanic Gastropods

Several diverse groups of gastropods occur in the pelagic or neustonic fauna; they are generally widely distributed and were renamed by the taxonomists who worked up the material of the great expeditions and voyages of the 19th and early 20th centuries (Tesch, 1913; 1948; 1950).

Tesch (1949) listed 107 nomina for the 22 recognized species of prosobranch heteropods, with certain genera prevailing in high ratios: *Pterotrachea,* 9/1; *Carinaria,* 16/1; and *Firoloida,* 13/1. In contrast, the opisthobranchiate thecosomatous pteropods have slightly lower ratios: *Limacina,* 5/1; *Hyalocylis,* 8/1; and *Styliola,* 5/1 (van der Spoel, 1967). The ptenoglossate,

neustonic, *Janthina janthina* has a SR of 34/1, while the average for the remaining species in the genus is 5/1 (Laursen, 1953).

Marine Bivalves

Several monographs, on both restricted and cosmopolitan bases, document the problem of over-naming marine bivalves which, fortunately, does not reach the extravagance found in fresh-water genera. Among the Anisomyaria, particularly the sedentary forms that are highly variable, the synonymy ratios tend to be higher: Ranson (1961) recognized some species of *Pinctada* with ratios of 40/1, while Hynd (1955) established an average of 5/1, among the six species of Australia. As early as 1911, Smith studied the four species of *Vulsella* which have over 50 available nomina.

As might be expected, the common edible mussel, *Mytilus edulis,* has been named at least 25 times (Soot-Ryen, 1955). Less well known species with ratios of 10/1, include the Indo-Pacific arcoid *Cucullaea* (Nicol, 1950b) and the euryhaline aloidid or corbulid *Erodona mactroides* from Argentina (Carcelles, 1941).

In thorough revisions, the ratios are lower. Among phenotypically plastic groups which bore into the substrate, Solem (1954) gave a SR of about 7/1 for the Trapeziidae, and Turner (1966; *pers. comm.*) 4/1 for the Teredinidae and 4/1 for the Petricolidae, with the highly variable *Martesia striata* having a SR of 36/1. Counting both living and fossil species, Rosewater showed a SR of 4/1 for the pinnids (1961) and 3/1 for the giant clam, *Tridacna* (1965).

Polyplacophora

The chitons are a poorly known group taxonomically. In one revision, Leloup (1942) partly monographed the mopaliids, showed that many species are without synonyms, established a SR of 10/1 for the subantarctic *Plaxiphora aurata* and indicated that the average SR for the family was nearly 4/1.

Cephalopoda

Adam and Rees (1966) wrote an extensive, taxonomic monograph on the cuttlefish family Sepiidae. Several of the named

forms are based on single specimens or series from a single locality and will probably prove to be synonyms of each other or better known species. Nevertheless, 235 names are available for the 60 or so species giving a ratio of 4/1.

Among the benthic octopods, Pickford (1945) listed over a dozen nomina for *Octopus vulgaris* along the American coast alone. Thore (1949) showed a SR of 6/1 for the bathypelagic octopods *Eledonella pygmaea* and *Vitreledonella richardi.* Additionally, he noted a 7/1 ratio for the coastal argonautoid *Alloposus mollis.* Many early ommastrephid, cranchiid and chiroteuthid nomina were based upon larval specimens. Revision of these groups, based upon complete ontogenetic series may result in a reduction in the number of recognized species.

The Number of Living Bivalves

Table V lists the number of species of living bivalves by family. Since most taxa have not adequately been revised many estimates were required, and explanatory notes have been appended to indicate how these estimates were derived. The grand total of living bivalves is considerably lower than previous authors have estimated, and though there are certainly several objections to, and inaccuracies in, Table V, the evidence points to a figure of lower than 7500 living species.

The Number of Living Gastropods

Schilder (1947) explained that Wenz had told him that the terms "eine Art, wenige, einige, mehrere, zahlreiche, [and] sehr zahlreiche Arten" which were used in the Handbuch der Paläozoologie, implied 1, 3, 6, 12, 24, and 48 species, respectively. Schilder employed this method for the prosobranchs and arrived at a figure of 12,808 species which he subsequently (Schilder, 1949) enlarged to 57,600! Table VI summarizes Wenz's estimates, and that these numbers are not significantly incorrect is indicated in Tables VII, VIII, IX, and X where the most accurate estimates on specific groups are tallied. The results contrast favorably with Wenz's estimates, 71 Strombacea compared with 100 (Table VII); 250 Tonnacea with 260 (Table VIII), 874 Volutacea with 1500 (Table IX), and 1216 Conacea with 2050 (Table X).

Tables IX and X, which differ more from Wenz's estimate

than do Tables VII and VIII, have more sources of error because the families of the Volutacea and Conacea are not as well known as those in the Strombacea and Tonnacea. In reference to Table X, it should be noted that neither the Conidae nor the Turridae have been completely monographed. The total specific taxa, both Recent and fossil, amounted to 2500 in 1937 (Tomlin), and Kohn (1963) extended this figure to 2700 of which 1100 nomina applied to fossil cones. If the remaining 1600 nomina were treated with a SR of 4/1, some 400 species would be estimated. Kohn himself (1963) suggested that there might be between 200 and 600 living species of *Conus*.

The turrids are probably the most speciose of the neogastropods. The approximately 110 species in each of the Turrinae and Turriculinae in the Indo-Pacific are comparatively well known (Powell, 1964; 1967; 1969). Powell (1966) treated many turrid species in their respective genera with about 4500 species-level taxa indexed. If one applied a SR of 4/1, one might expect some 1100 species, but I have estimated 1500.

Wenz's figures are usually lower than those in Tables VII, VIII, IX and X but they are by no means in as great as a fourfold error which was indicated by Schilder (1949). I have attempted to account for the underestimations of Wenz in Table XIII.

I have applied the Wenz method to the pulmonate gastropods as treated by Zilch (1959–60). The total estimate of pulmonates (Table XI) is remarkably close to that of Winckworth (1950). Although it may be contested that this figure is an underestimate it must be remarked that Pilsbry (1901–1926) in the pulmonate sections of the Manual of Conchology, which did not cover several families, treated about 11,000 species. Comparison with the primary literature establishes a remarkable concordance in estimates for the fresh-water pulmonates (Table IV). I have compared the results of the Wenz method with some figures published in the primary literature (Table XII) and again the totals show a relatively close agreement. Since the definitions of pulmonate families differ from one author to another, the numbers taken from the Manual of Conchology are not strictly comparable; however, I will use a final figure of 15,000 for the Stylommatophora (Table XIII).

SUMMARY

The totals for the bivalves, prosobranchs, basommatophorans and stylommatophorans (Tables IV, V, VI, and XI) are combined with documented information on the remaining groups to produce the preliminary estimates in Table XIII. To assuage critics of my possibly conservative treatment of taxa with which I have had little acquaintance and to account for species yet to be described, I have made final estimates which increase the totals for nearly all groups. These final figures (Table XIII) still contrast sharply with those of several earlier authorities (Table I). It is important to note that there are significantly fewer species than usually estimated, a trend almost consistently substantiated in modern systematic revisions, and that the marshalled evidence indicates that there are fewer than 50,000 living species of mollusks.

TABLE I

Estimates of the total number of living species of mollusks according to various authors.

	Sykes, 1901	R. Hesse, 1930	Jaeckel, 1958	Hennig, 1963	Mayr, 1969	Nicol, 1969
GASTROPODA	40,000	88,000	105,600	88,000	80,000	90,000
BIVALVIA	8,500	15,000	20,000	25,000	25,000	15,000
AMPHINEURA	600		1,150	1,140	1,150	2,000
SCAPHOPODA	220		350	300	350	
CEPHALOPODA	450	570	730	600	750	
	49,770	103,570	127,830	115,040	107,250	107,000

TABLE II

Estimates of total faunas of land mollusks of selected geographic areas of the world. (c = circa)

Area	*Number of species*	*Sources*
North America	714	Pilsbry, 1948
South America	c 2000	Composite (Stuardo, *pers. comm.*; Parodiz, 1957; Morretes, 1949)
Australia	644	Iredale, 1937a & b; 1938
Asia–India	c 2000	Blandford and Godwin-Austen, 1908; Preston, 1915; Gude, 1914; 1921
Africa	c 2000	Kobelt, 1910a
Southern Africa	640	Bruggen, 1969
Congo	400	Pilsbry, 1919
Europe	1500	Waldén, 1963
Central Europe	224	Zilch and Jaeckel, 1962
France	379	Germain, 1930–31
Russia	600	Heptner, 1956
Switzerland	169	van Benthem Jutting, 1952b
Japan	669	Kuroda, 1953
Philippine Islands	c 3000 c 1100	Faustino, 1928 Möllendorf, 1897
Jamaica	564	Vendryes, 1899
New Zealand	254	van Benthem Jutting, 1952b
Hawaii	1308	Caum, 1928

TABLE III

Estimates of marine faunas. (c = circa)

Area	*Number of species*	*Sources*
Western Atlantic	c 6000	Clench, 1959
Caribbean-Eastern Pacific	6525	Valentine, 1967
Eastern Pacific	c 3500	Valentine, 1966; Dall, 1909; Stuardo, *pers. comm.*
West African	c 500	Nicklès, 1950
Eastern Atlantic	c 1500	Thorson, 1965; Nordsieck, 1968
Japanese	c 4000	Kuroda and Habe, 1952
Australian	c 2000	Iredale and McMichael, 1962
New Zealand	c 2200	Powell, 1957
Oceania	c 1100	Dautzenberg and Bouge, 1933
Antarctic	c 500	Dell, 1964; Carcelles, 1953
Philippine Islands	c 5000	Faustino, 1928
Abyssal	1150	Clarke, 1962

TABLE IV

Estimates of the number of living species of fresh-water pulmonate gastropods. Column I, after Wenz; II, from various sources (see text).

Family	*Number of species*		*Sources*
	I	II*	
Chilinidae	24	30	Pilsbry, 1911; Smith, 1881a
Latiidae	3	1	Powell, 1957
Physidae	44	200	Clench, *pers. comm.;* Clarke, *in press;* Crandall, 1901; Walker, 1918
Lymnaeidae	160	40	Hubendick, 1951
Bulinidae	265	100	Hubendick, 1948
Planorbidae		200	Baker, 1946; Harry, 1962; Hubendick, 1955; 1961
Acroloxidae	7	7	Clarke, *in press*
Ferrissiidae (Ancylastridae, Ancylidae & Lancidae)	77	70	Basch, 1959; 1963; Hubendick, 1960; 1964; 1967; Wurtz, 1951; Walker, 1912
Total	580	648	

* The sources indicate papers or files from which I have extracted totals, though in some cases no figures were provided by the author.

TABLE V

Estimates of the number of living species in the class Bivalvia.
(Totals are frequently rounded off; for notes, see Appendix.)

Family	*Number of species*	*Sources*
Solenomyidae	25	(Dall, 1908; Quenstedt, 1962; Vokes, 1955)
Nucinellidae	12	(Allen and Sanders, 1969; Vokes, 1956)
Nuculidae	150	(note 1)
Nuculanidae	250	"
Malletiidae	100	"
Poromyidae	100	(note 2)
Verticordiidae	50	(note 3)
Cuspidariidae	100	(note 2)
Cucullaeidae	1	(Nicol, 1950b)
Arcidae	150	(note 4)
Glycymeridae	50	(note 5)
Limopsidae	25	(Lamy, 1912b)
Philobryidae	15	(note 6)
Mytilidae	250	(note 7)
Vulsellidae +Pteriidae +Isognomonidae +Malleidae	70	(note 8)
Pinnidae	20	(Rosewater, 1961)
Pectinidae +Amussiidae	360	(note 9)
Spondylidae	50	(Fulton, 1915; Lamy, 1938)
Plicatulidae	10	(Lamy, 1939)
Limidae	125	(note 10)
Dimyidae	11	(Berry, 1936; Moore, 1970)
Ostreidae	50	(Ranson, 1967)
Anomiidae +Placunidae	25	(Küster, 1868a & b; Koch, 1868; Winckworth, 1922)
Trigoniidae	3	(Rogers, 1910; Fleming, 1964)
Mutelidae	120	(note 11)
Etheriidae	4	(Pain and Woodward, 1961; Yonge, 1962)

(Table V cont.)

Margaritiferidae	10	(Walker, 1910)
Unionidae	1000	(note 11)
Chamidae	50	(Lamy, 1928; Bayer, 1943; Nicol, 1952; 1953)
Lucinidae	200	(note 12)
Cyrenoididae	10	(note 12)
Fimbriidae	2	(Nicol, 1950a)
Thyasiridae	60	(note 12)
Ungulinidae (=Diplodontidae)	50	(note 12)
Erycinacea (Erycinidae, Chlamydoconchidae, Gaimardiidae, Galeommatidae, Kelliidae, and Montacutidae)	200	(note 13)
Cyamiacea (Cyamiidae, Perrierinidae, Neoleptonidae and Sportellidae)	100	(note 13)
Carditidae	50	(Dall, 1903a)
Condylocardiidae	10	(Lamy, 1922; Dell, 1964)
Crassatellidae	30	(Lamy, 1917b; Harry, 1966)
Astartidae	30	(Smith, 1881b; Dall, 1902b; Lamy, 1919)
Cardiidae	200	(note 14)
Adacnidae	15	(Lamy, 1946)
Tridacnidae	6	(Rosewater, 1965)
Mactridae (+Anatinellidae)	150	(note 15)
Cardiliidae	5	(Beets, 1943)
Mesodesmatidae (+Amphidesmatidae)	40	(Ihering, 1927; Lamy, 1914; Dawson, 1959)
Solenidae (+Novaculinidae +Cultellidae)	100	(note 16)
Tellinidae	350	(note 17)
Donacidae	50	(note 18)
Gariidae (=Psammobiidae +Asaphidae +Sanguinolariidae +Solecuritidae)	100	(note 19)

Table V (cont.)

Semelidae	60	(note 20)
Scrobiculariidae	2	(note 20)
Arcticidae	1	(Boss, 1969a)
Trapeziidae	10	(Solem, 1954)
Dreissensiidae	40	(Andrusov, 1964; Hertlein and Hanna, 1949; Fischer, 1858; Brusina, 1905)
Glossida	10	(note 21)
Kelliellidae (Vesicomyidae)	30	(Boss, 1970)
Corbiculidae (+Cyrenidae)	100	(Prashad, 1924; 1928b; 1929; 1930; Parodiz and Hennings, 1963)
Pisidiidae (+Sphaeriidae)	100	Herrington, 1962; Clarke, *in press*)
Veneridae	500	(note 22)
Petricolidae (+Cooperellidae)	30	(Lamy, 1923b; Turner, *pers. comm.*)
Glauconomidae	10	(note 23)
Myidae	20	(Lamy, 1927; MacNeil, 1965)
Corbulidae (+Erodontiidae +Spheniopsidae)	75	(note 24)
Gastrochaenidae	15	(Boss, notes)
Hiatellidae (=Saxicavidae)	25	(Lamy, 1924; 1925; Dell, 1964; Nesis, 1965)
Pholadidae	92	(Turner, *pers. comm.*)
Teredinidae	66	(Turner, 1966)
Pholadomyidae	10	(Soot-Ryen, 1966)
Pandoridae	25	(Boss, 1965; Boss and Merrill, 1965; Lamy, 1934a)
Chamostreidae (=Cleidothaeridae)	2	(Lamy, 1936a)
Laternulidae (=Anatinidae)	15	(Lamy, 1934b)
Lyonsiidae	20	(Dall, 1916; Lamy, 1929a)
Myochamidae	15	(Lamy, 1935a)
Periplomatidae	28	(Rosewater, 1968)
Thraciidae	30	(Lamy, 1931; Allen, 1961)
Clavagellidae	10	(note 25)
Total	6285	

TABLE VI

Estimates of the number of living species of prosobranchs.
(after Wenz [*in*] Schilder, 1947)

Pleurotomariacea	380
Patellacea	181
Trochacea	929
Neritacea	582
Cocculinacea	41
Cyclophoracea	1562
Valvatacea	23
Littorinacea	605
Rissoacea	1331
Cerithiacea	1297
Scalacea	272
Pyramidellacea	721
Hipponicacea	86
Calyptraeacea	111
Atlantacea	56
Naticacea	178
Strombacea	71
Cypraeacea	387
Tonnacea	250
Buccinacea	1153
Volutacea	874
Muricacea	502
Conacea	1216
Total	12,808

TABLE VII

Total Strombacea (*sensu* Wenz) derived from the literature and estimates from collections.

Xenophoridae	12	Morton, 1958
Struthiolariidae	5	estimate
Aporrhaidae	5	estimate
Strombidae	75	Abbott, 1960; 1961
	97	

TABLE VIII

Total Tonnacea (*sensu* Wenz) derived from the literature and estimates from collections.

Oocorythidae	12	Clarke, 1962
Cassididae	55	Abbott, 1968
Cymatiidae	130	Bayer, 1933; Lewis, *pers. comm.*
Bursidae	24	Bayer, 1932
Tonnidae	39	Turner, *pers. comm.;* Bayer, 1937
Ficidae	10	Bayer, 1939
	270	

TABLE IX

Total Volutacea (*sensu* Wenz) derived from the literature and estimates from collections.

Olividae	160	Burch and Burch, 1960; 1967; Olsson, 1956
Mitridae	350	estimate
Vasidae	20	Abbott, 1959
Harpidae	12	estimate
Volutidae	209	Weaver, 1964
Cancellariidae	150	estimate
Marginellidae	250	Tomlin, 1917
	1151	

TABLE X

Total Conacea (*sensu* Wenz) derived from the literature and estimates from collections.

Turridae	1500	(Charig, 1963; Powell, 1964; 1966; 1967; 1969)
Conidae	400	(Tomlin, 1937; Kohn, 1963)
Terebridae	150	(Miller, *pers. comm.*)
	2050	

TABLE XI

Estimates of the numbers of living species of pulmonates (Zilch, 1959–60), tallied after the method of Wenz (*in* Schilder, 1947). Several slug-like families are omitted.

Family	*Number of species*
BASOMMATOPHORA	
Ellobiidae	255
Otinidae	1
Amphibolidae	6
Stenacmidae	1
Trimusculidae	12
Siphonariidae	65
Chilinidae	24
Latiidae	3
Physidae	44
Lymnaeidae	160
Planorbidae	265
Neoplanorbidae	2
Rhodacmeidae	6
Ferrissiidae	63
Ancylidae	6
Acroloxidae	7
Total (Basommatophora)	920

TABLE XI (continued)

Family	*Number of species*
STYLOMMATOPHORA	
Tornatellinidae	143
Achatinellidae	84
Partulidae	78
Amastridae	198
Cochlicopidae	21
Pyramidulidae	6
Vertiginidae	180
Orculidae	19
Chondrinidae	192
Pupillidae	144
Valloniidae	82
Pleurodiscidae	3
Enidae	615
Succineidae	122
Athoracophoridae	
Endodontidae	502
Otoconchidae	1
Arionidae	
Philomycidae	6
Thyrophorellidae	1
Vitrinidae	90
Zonitidae	284
Parmacellidae	14
Milacidae	13
Limacidae	70
Trigonochlamydidae	17
Trochomorphidae	106
Euconulidae	293
Helicarionidae	261
Ariophantidae	380
Urocyclidae	167
Ferussaciidae	138
Subulinidae	524
Achatinidae	177
Megaspiridae	8
Clausiliidae	822
Oleacinidae	278
Testacellidae	13
Acavidae	130
Bulimulidae	559
Odontostomidae	77
Orthalicidae	67
Amphibulimidae	35
Cerionidae	63

Table XI (cont.)

Urocoptidae	390
Systrophiidae	62
Haplotrematidae	24
Rhytididae	119
Chlamydephoridae	6
Streptaxidae	547
Polygyridae	207
Sagdidae	71
Corillidae	60
Camaenidae	791
Bradybaenidae	511
Helminthoglyptidae	226
Helicidae	722
Total (Stylommatophora)	10,719
Grand Total (Pulmonata)	11,639

TABLE XII

Estimates of the number of living species of selected Stylommatophoran families. Column I after Wenz; II, from various sources (see text).

Achatinellidae (+ Tornatellinidae)	227	200	(Cooke and Kondo, 1960)
Orculidae	19	21	(Pilsbry, 1922; 1924; 1926; Forcart, 1950)
Achatinidae (+ Subulinidae)	700	750	(Pilsbry, 1904b–d; 1905a–b; 1906a–c; 1907; 1908)
Megaspiridae	8	7	(Pilsbry, 1904a)
Oleacinidae	278	334	(Kobelt, 1910b)
Testacellidae	13	4	(Hoffmann, 1925a)
Cerionidae	63	80	(Pilsbry, 1901; 1902a)
Urocoptidae	390	395	(Pilsbry, 1902b–c; 1903a–d; 1904a)
Haplotrematidae	24	20	(Baker, 1930)
Rhytididae	119	127	(Kobelt, 1910b)
Chlamydephoridae	6	6	(Wagner, 1952)
Streptaxidae	547	800+	(Bruggen, 1967)

TABLE XIII

The number of species of living mollusks, derived from various sources with a final estimate.

Taxon	*Preliminary estimate*	*Source*	*Final estimate*
Aplacophora	200	(Thiele, 1925–1926; Salvini-Plawen, 1967a; b)	250
Polyplacophora	500	(Yakovleva, 1952; Smith, 1966)	600
Scaphopoda	300	(Pilsbry and Sharpe, 1897–1898; Henderson, 1920; Habe and Kosuge, 1964; Boissevain, 1906).	350
Cephalopoda	516	(Akimushkin, 1963; Voss, 1956; 1963; Clarke, 1966)	600
Monoplacophora	6	(Menzies, 1968; Filatova and Zenkevitch, 1969)	10
Bivalvia	6285	Table V	7500
Basommatophora	920	Table XI	1000
Stylommatophora	10719	Table XI	15000
Prosobranchia	12808	Table VI	20000
Nudibranchia	750	(Russell, *pers. comm.*)	750
Other Opisthobranchia	750	(Estimate)	750
	33754		46810

APPENDIX

Notes to Table V

1. The status of the families of the Protobranchia is uncertain; several observations cast doubt on relationships indicated by present familial and generic definitions (Sanders, *pers. comm.*). However, there are several available sources from which I have derived the figures used. Verrill and Bush (1897) considered at least 60 species, but less than 100, in the east coast fauna of the United States; Allen (1954) dealt with the five British *Nuculas* and four nuculanids; while Ockelmann (1954) revised the four northern species of the nuculanid *Yoldia,* which had received at least 11 names; Schenck (1936) recognized about seven Recent species of *Acila,* and Prashad (1933) noted 13 Indian species of nuculids; Dell (1955) compiled the 90 generic units of nuculanids and malletiids and listed 14 species from New Zealand and 33 from Australia; Clarke (1962) catalogued the deep sea species (in a largely deep sea group) as follows: 28 nuculids, 62 nuculanids and 45 malletiids; the extensive collection of the USNM houses about 120 species of nuculids, 250 nuculanids and 75 malletiids. From the above data, it seems possible that there might be 500 species of protobranchs.

2. Since there are no accurate figures for the septibranch families Poromyidae and Cuspidariidae, I have given estimates which might be a trifle inflated; Clarke (1962) listed 15 poromyids and 48 cuspidariids in the deep sea; there are more than 30 poromyids and 100 cuspidariids in the collections of the USNM.

3. The Verticordiidae include some 18 'genera' according to Soot-Ryen (1966), who listed about 25 species of *Policordia, Laevicordia, Lyonsiella,* and *Thracidora.* Many of the species are extremely rare, but widely distributed. I have studied both *Verticordia* (*Trigonulina*) and *Euciroa* and am convinced that there are only a few species of cosmopolitan distribution. My estimate of 50 species is probably not too conservative.

4. About 130 species were recognized by Lamy (1907), but many were discussed parenthetically. Geographically there are: 36 Western Atlantic (Dall, 1903b; Sheldon, 1916); about 30 Panamic (Maury, 1922; Rost, 1955; Olsson, 1961); 11 West African (Nicklès, 1950); 15 South African (Barnard, 1964); 43 Japanese (Habe, 1951); 36 Thai (Lynge, 1909). There are probably about 150 species.

5. Thomas (*pers. comm.*) estimates that there are about 50 living species of this family. Lamy (1912a) discussed some 55 species and listed about 180 available names. Nicol (Catalog of the family Glycymeridae, presently in MCZ) includes about 800 fossil and Recent nominal species.

6. Dell (1964) listed 35 applicable names and considered 10 species in this group, which is largely restricted to the southern hemisphere. Of the six philobryids studied by Nicol (1966) there are at least 14 available names.

7. One of the largest of bivalve families, the Mytilidae has not been adequately monographed. Several studies, however, furnish evidence concerning the relative number of species in the family. Lamy (1936b–d; 1937a–d) published the most extensive review of the taxonomy of the Mytilidae; he treated about 175 species and listed some 900 names used in the various genera. A careful, but unpublished world-wide revision of the genus *Brachidontes* by Kenk (1966) reveals a total species number of this genus similar to that of Lamy; Kenk recognized 28 species of *Brachidontes.* Soot-Ryen (1955) discussed the mytilids of the Eastern Pacific of which he reported 57 species, and several of those are widely distributed in other areas. Skarlato (1960) recognized 26 in the northwestern Pacific. Again several species were of very wide distribution. Some revisions suggest that Lamy may have been fairly accurate (*i.e. Lithophaga,* Turner and Boss, 1962); however, I estimate that there are about 250 living species of the Mytilidae.

8. Here are included several groups which are often separated into four families: Vulsellidae, Isognomonidae, Pteriidae, and Malleidae. Without suitable familial monographs, I have

had to collect diverse information. Broadly the Vulsellidae include *Crenatula, Pedalion, Perna* or *Isognomon,* the monotypic *Foramelina, Vulsella* and *Malleus.* There appear to be less than 10 living species of *Malleus* (Boss and Moore, 1967; Yonge, 1968), four species of *Vulsella* (Smith, 1911), about 15 *Isognomon* (Boss, notes) and less than five *Crenatula* (Lamy, 1929b; 1935b). The Pteriidae consist of the genera *Pteria, Electroma* and *Pinctada;* the latter embraces 13 species with synonymy ratios as high as 40/1 (Ranson, 1961); Hayes, *pers. comm.* informs me that there are about 8 American pteriids. My estimate of the total number of species in this group is 70.

9. Teppner (1914–22) listed some 1500 nomina for the Tertiary pectinids. The deeper water, thin-shelled species have been grouped into the family Amusiidae, with three genera mentioned by Franc (1960): *Amussium, Propeamussium,* and *Adamussium. Propeamussium* has been reviewed on a worldwide basis by Oyama (1944) who recognized approximately 30 species. *Adamussium* was described by Thiele and evidently comprises about 11 species (Dell, 1964). Geographical reviews of pectinids included Grau's (1959) study of Eastern Pacific species which number 54; Waller (*pers. comm.*) estimates the Western Atlantic total to reach about 60 species, and Dautzenberg and Bavay (1912) recorded around 45 species collected by the SIBOGA, including nine species of *Amussium.* Bavay was a collector who specialized in the pectinids and his catalog of the living species in the collection of the French National Museum numbers some 162 species (Bavay, 1936). Hertlein (*pers. comm.*) who has contributed several papers on this family, estimates that there are about 360 living species.

10. Stuardo (1968) differentiated 38 species-groups, variously recognizable as superspecies and polytypic species; there appear to be over 100 species and there are 350 nomina. Thiele (1918–1920) treated some 87 species.

11. Simpson (1900) considered about 1100 species and 3600 nomina of freshwater mussels, which included what we now consider to be at least four families. Call (1898, *in litt.,* to Jukes Brown) offered a realistic appraisal of North American union-

ids, 250 species; Simpson listed some 533 species. Johnson reported (1970) only 75 species of Unios in the Atlantic Slope and Apalachicolan Region and certain of them are vastly overnamed. Based on Simpson (1900), I estimate 1000 species of Unionidae and 120 Mutelidae. For the Unionacea, Haas (1969) listed about 5600 nomina in these families; if a moderate SR of 5/1 is employed we can expect less than 1200 species.

12. Dall (1901) listed 120 North American lucinoids, i.e., 63 lucinids, 20 ungulinids, 2 cyrenoididae (=Cyrenellidae), and 35 thyasirids. For the world, Bretsky (*pers. comm.*) estimates between 200–250 lucinids. The USNM collection contains about 60 species of thyasirids and 50 diplodontids (=ungulinids). I am using these as rough estimates.

13. The Erycinacea and Cyamiacea comprise many small and poorly known families. The figures given are estimates derived from several sources: less than 300 nomina were given by Paetel (1888–1890); less than 200 nominal species in the USNM. Specific papers include: Keen (1938) listed 43 named species of *Lasaea;* Harry (1969b) recognized nine species of *Aligena: Chlamydoconcha* appears to be monotypic; Dell (1964) studied four species of *Kidderia,* and other species of Gaimardiidae limit this southern hemisphere family to fewer than 20 species. In the Cyamiidae, Dell (*op. cit.*) considered some 12 species in this predominantly Antarctic family (3 *Cyamiomactra,* 5 *Pesudokellya*) and several *Cyamium.* Of the Perrierinidae, he distinguished three species of *Cyamiacardium,* and Lamy (1917b) considered six. Laseron (1956a) identified 29 leptonids from New South Wales. Thus an estimate of 300 species for these small clams seems to be ample.

14. Dall (1900b) considered the 40 American species of this family; Keen (1937) remarked that there were some 2200 named species of cardiids, including fossils. Application of a synonymy ratio of 5/1 would give about 400 species. If less than half this number are living species, I can consider that there are approximately 200 living species of cardiids. For example, McLean (1939) studied the 21 species in the western Atlantic and listed about 70 nomina. Graham-Ponton (1869)

listed about 150 species in this family, including the Pontian genera presently referred to the Adacnidae. The cardiid collection of the USNM, excellently arranged, includes about 130 species and indicates that my estimate may be high.

15. Dall (1894; 1895) established the modern classification of the families Mactridae and Mesodesmatidae; he recognized between 35 and 40 species in the New World; Strong (1925) confirmed his remarks on west American *Mactra.* Smith (1914) indicated the diversity of the Indo-Pacific elements in the Mactridae and recognized 40 Australian species. Lamy (1917a) reviewed the family and treated over 100 species (actually about 120, including some groups, e.g., *Cardilia,* presently referred to separate families). Chamberlin (1954) claimed that there are approximately 1500 nomina applicable to living and fossil forms, and on this basis I estimate about 150 species, including the anatinellids. The USNM has about 135 species.

16. Dall (1899) distinguished about 20 species in the fauna of North America and the Antilles; the European species of *Ensis* have been discussed by van Urk (1966) who considered six or seven species. The family has not been suitably monographed. There are nearly 300 nomina in the Solenidae, but there appear to be less than 100 species, including the Novaculinidae and Cultellidae.

17. The Tellinidae contains about 350 living species. The monograph of Römer (1870–73) listed only 170 species and some 400 nomina. Dall (1900a) recognized about 110 American species. Of the larger subfamily, the Tellininae, Boss (1966; 1969b; and *in prep.*) listed 52 in the Western Atlantic fauna, 18 in South Africa, 30 in the Eastern Atlantic and Mediterranean. As usual many of the Indo-Pacific species are widely distributed. Dall, Bartsch and Rehder (1938) listed 10 from Hawaii; Skarlato (1965) recognized 55 in coastal China; Habe (1952) noted 75 in Japan; Lynge (1908) listed 47 in Thailand. I estimate that there are about 100–125 species in the Indo-Pacific. The west coast of America has about 60 species (Olsson, 1961).

18. Though this family has not been completely reviewed since the monographs of Römer (1869–70) and Bertin (1881), I have collected information on 180 named forms. Including the several species of West African *Egeria,* there are less than 50 species; Morrison (*pers. comm.*) has distinguished 10 Western Atlantic forms; Lucas (1967) recognized five in European waters.

19. As with the Solenidae, there is no available monograph or systematic treatment of gariids which herein includes asphaphids, sanguinolariids and solecurtids. Bertin (1880) listed about 160 species and Dall (1898) considered the 25 Recent species of North America. Estimated from the literature, there are over 200 available nomina, but certainly fewer than 100 species.

20. Here are included the two species of *Scrobicularia* often cited as a separate family, the Scrobiculariidae. Lamy (1913) recognized about 60 species. In the Western Atlantic, Boss (*in press*) discerned only six living species of *Semele* and less than six other semelids (3 *Abra* and 2 *Cumingia*). The family is richest in the tropical Eastern Pacific where Olsson (1961) has reported about 25 species.

21. The nominate genus is monotypic (Nicol, 1951) while the other genus, *Meiocardia,* has several representatives in the Indo-Pacific and in the Caribbean. I estimate that there are less than 10 species.

22. The Veneridae is the largest family of marine bivalves, with fewer than 500 species. Geographically, there are 137 North American (Dall, 1902a); about 70 Panamic species (Olsson, 1961); 70 Western Atlantic (Palmer, 1927–1929); 125 Japanese (Habe, 1951); 25 West African species (Nicklès, 1955); 32 South African (Barnard, 1964); 54 Thai (Lynge, 1909) and 90 Chinese (QiQian, 1964). Many of the above species overlap in their distribution so that 500 species may be too liberal an estimate, and as Lamy (1923a) has indicated the SR may be high, about 90 nomina for 14 or so species of *Venerupis.*

23. Although there is no modern review of the species available, the extent of this veneroid family was reduced with the removal of the mactroid genus, *Tanysiphon* so that there are probably less than 10 species; nine named forms are in the USNM.

24. Tryon (1869) listed 72 nomina and Vokes (1945) has 21 genera. Geographically, there are: about a dozen Western Atlantic (Dall, 1903b); 16 Panamic (Olsson, 1961); 10 Japanese (Habe, 1951); half a dozen West and South African species (Nicklès, 1950; Barnard, 1964).

25. Smith (1962) reviewed the fossil and living species of clavagellaceans; however only a list of names with references and localities is provided and the study may not be considered monographic. Of some 25 names applicable to living species, I estimate that there are less than 10 species.

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