Variation in the Spire Index of Some Coiled Gastropod Shells, and Its Evolutionary Significance

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The spire index (height/maximum diameter of shell) is a fairly adequate measure of the shape of the coiled shell of most terrestrial and freshwater gastropod shells but less so in complex marine shells with thorns, flanges and spouts. In this study, only adult free-crawling forms with several whorls, able to retract completely into the shell, are considered. In the Stylommatophora of the Western European terrestrial fauna the distribution of the spire index is markedly bimodal, the modes, with values of about 3 and about 0.5, corresponding respectively to shells with a high to very high spire (and small spire angle) and those varying from more or less globular or trochoid to very flattened and disk-like (spire angle from 60° to 180°). The same two modes are found in the taxonomically different terrestrial stylommatophorans of the U.S.A., and in the faunas of Puerto Rico (Caribbean) and New Caledonia (southwest Pacific). Basommatophorans also show two, rather different, modes. North American marine archaeogastropods are mainly equidimensional but with a few disk-like forms and a very few high-spired ones, marine mesogastropods are mainly high-spired but with disk-like forms, neogastropods high-spired, and relevant euthyneurans sharply bimodal, like the stylommatophorans. Fossil archaeogastropods of the Palaeozoic were much more various at first than modern forms. There is some indication that they became restricted in variety as caenogastropods became abundant, but also that the proportion of marine disk-like shells has decreased markedly since the Palaeozoic.

Modes of h/d are characteristic of large taxonomic groups but not taxonomically restricted since given values may appear as specific, generic or subfamilial variants from a mode, and appear sporadically in unrelated forms. There is also no broad association between modal value and broad ecological characters. Since nearly all values do occur in some group or other, no mechanical requirement can be invoked to explain such variation. In the land Stylommatophora enough is known of the broad ecology to suggest that in extreme habitats species with very different size or shell-shape may occur together, and that generalized feeders with similar shells may show separation, ecological or geographical (but in that case, also ecological).

Since different shapes of shell will have different mechanical characteristics when considered as burdens to be carried, it is suggested tentatively that they may be related to the positions in which different species normally walk and hence to their preferred feeding places. This would explain an apparent tendency for different taxonomic groups to occupy the same part of the scatter of h/d in different regions of the world, for many groups in the same region to occupy different portions of the scatter, and perhaps the apparent exclusion by caenogastropods of archaeogastropods from part of the scatter since the Palaeozoic.

It is argued that the distributions discovered are explicable only by natural selection.

1. Introduction

The spire index is the ratio of h to d in figure 1. Usually it is easier to measure on a photograph of a shell than on the actual shell, on which the maximum diameter, not necessarily perpendicular to the columellar axis, is more often measured; the difference, however, in gastropods is often slight. Although variation certainly occurs in shell shape within a species of gastropod, it is often very slight compared with variation in absolute size; the proportions of the shell (except in a few genera such as *Cerion*) are useful in identifying the species. Shell collectors and many taxonomists in the past have seized on any individual or population variants they could find, in shape as well as sculpture or colour, and have named them. Nevertheless, such shape variants usually cluster together in any one species, although monstrous scalariform and other distorted shells are always liable to occur as individual variants. Figure 2 gives the distribution for h and d of individual specimens of six stylommatophoran species, widely different taxonomically, for which there are plenty of data in Pilsbry (1939–48), often expressly including

extremes of variation in shape. Even where there is considerable variation in size, shape remains within fairly narrow limits. It is therefore possible to represent a species by a single value, and if means of h and d for adult shells are used, this value indicates both the spire index and less precisely the adult size.
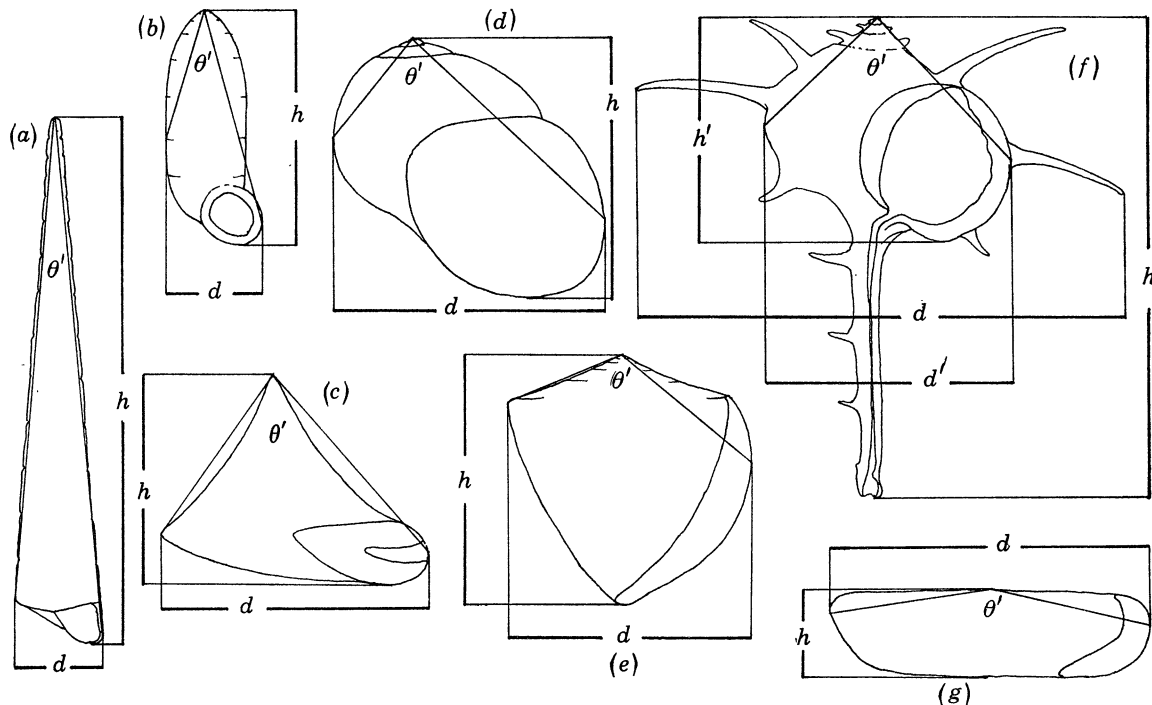

Figure 1. Mode of measurement of h and d, and of θ', on various shapes of simple shells and on a complex one with spout and spines, for which h' and d' are the adjusted values. Shapes, (a) terebroid, (b) pupoid, (c) trochoid and coeloconic, (d) helicoid, (e) angarioid, (f) muricoid, (g) planorboid. In all cases, the columellar axis is vertical, and the adapertural silhouette is measured. In (g), θ' is rather less than 180°, as shown. If the upper surface of the shell were flat or concave, it would be taken in this paper as 180°. Hyperstrophic shells are treated as orthostrophic, i.e. θ' is never greater than 180°, and sinistrality is ignored.

Among the European and North American non-marine snails, there is considerable variation of spire index; some shells, such as those of the Clausiliidae, or *Euglandina* (Spiraxidae), are high, pointed, and narrow (spire index 2–4); others, e.g. some *Polygyra* and *Planorbis* are flat disks (spire index about 0.25), while in such forms as *Helix aspersa* height and breadth are sub-equal (spire index just under 1). Generally the greatest diameter is near or at the mouth and a simple spire index does summarize most of the variation in shape from species to species (although the Clausiliids and a few others are elongate pear-shaped or cigar-shaped). Among marine shells, however, there is far greater variation. In some terebrids the shell is nearly a perfect cone, with the greatest diameter at the mouth, while in *Conus* it tapers downwards, the mouth being greatly elongated. Although periostracal hairs may form a thick felt on a few species of land snail (e.g. *Isognomostoma*) sculpturing and ornamentation generally is poorly developed in terrestrial and most freshwater species. In marine ones, however, long spines or huge flange-like ridges may add greatly to the maximum diameter of the shell. In many neo-gastropods the mouth is prolonged into a spout for the siphon, and in extreme cases this can double the height of the shell (e.g. in *Columbarium*). The height and diameter of a shell with large

spines or thorns and a long spout are not, strictly speaking, morphologically equivalent to those of an uncomplicated shell.

Since, therefore, the spire-index is a crude measure of shape in gastropods (as compared with the various parameters defined by Raup in a series of papers, 1961–7), and since, as is shown below, shells of very different spire index occur in almost all the major groups of gastropods and often within the same habitat, it is not surprising that this index has been used very little, except as a means of specific identification. It is surprising to find, as will be shown in this paper, that within a fauna variation in the index is non-random, often with more than one modal value, and that the modes may be the same in taxonomically unrelated faunas. Moreover, within a suborder, family, subfamily or even genus, species may be found which are clearly in different modes.

The intention in this paper is to study variation of spire index in those adult free-crawling gastropods, with regularly coiled shells with more than one coil (polygyre), that can retract themselves completely into their shells (holocleid). Limpets, therefore (in which the shells are effectively not coiled), slugs, swimming and deep-burrowing forms, and irregularly coiled forms such as the Vermetids are excluded, since they may need a special study, and it is necessary to work on a reasonably homogeneous set of phenomena in order to make valid comparisons. For the same reason only clearly terrestrial, freshwater, or marine forms have been studied.

2. MATERIALS AND METHODS

(a) Faunas

There is no lack of excellent figures of the shells of many gastropods, but it is not always easy to find a monograph that gives a view of a whole fauna. For the present investigation, west European terrestrial and freshwater species were taken from Germain's volumes in the *Faune de France* (1930–1), supplemented by Geyer (1927) and Ehrmann's volume (n.d.) in the *Tierwelt Mitteleuropas*. Together they summarize the fauna for the British Isles, the whole of France and all Germany across to Austria; the addition of the Iberian and Italian faunas would bring in more species but change the results given below very little if at all. Almost all Scandinavian species are included. (Corsica is included in Germain's volumes.) For the land-snails of North America, Pilsbry's monumental monograph (1939–48) is the standard authority. For the study of single tropical faunas, van der Schalie's monograph on the non-marine molluscs of Puerto Rico (1948), and Franc's (1956) on the New Caledonia archipelago, happened to be available. There is no single work on the North American freshwater forms, and Baker's conspectus (1928) over the Wisconsin freshwater fauna has been used.

For marine snails, Abbott's *American seashells* (1974) gives a multitude of excellent representations. Parenzan's figures (1974) and Nordsieck's volume (1968) on the European prosobranchs show no marked divergence of European from North American shell shapes, and Kensley's useful work on South African shells (1973) again produces no surprises. So large a sample of the marine forms as is given in Abbott's book, including all zones from the Arctic to the tropical, both the Atlantic and the Pacific coast faunas, and species from all depths, is probably representative (for the purposes of this investigation) of any present marine fauna.

For fossil forms, the appropriate volume in the *Treatise on invertebrate paleontology* (Knight *et al*. 1960) gives all Palaeozoic genera and subgenera, but with only a single species figured as representative of each fossil subgenus. Many recent subgenera are not figured. The archaeo-

gastropods are followed through to the present day, but only a few other forms are given. To supplement these data, Hudleston's monograph (1887–96) on the gastropods of the Inferior Oolite of Britain has been used to provide a view of all species of Jurassic prosobranch gastropods at one era in Britain, the classification in it being brought up to date with the aid of the *Treatise*, and Cox & Arkell's modernization (1948–50) of an earlier monograph on the mollusca of the Great Oolite. Hudleston's work was the first noticed, and taken at random, among a number of palaeontographical memoirs that dealt with Jurassic gastropods. Since only shell characters are available for fossil forms there are difficulties in their classification which are discussed below (§ 7 (*b*)).

(*b*) *Measurements*

Some authors, e.g. Germain, give for each form ranges of height and diameter, with occasional dimensions of gigantic individuals in brackets; the latter have been ignored and the means of the ranges have been used as representative values. Pilsbry occasionally mentions ranges or extremes, but most often gives measurements of individual shells; in each case one intermediate-sized specimen has been selected. Abbott gives the value of a single dimension in inches or millimetres as an indication of size. All his black and white illustrations have therefore been measured and scaled to the value actually given, converted to millimetres. For some species no value is given, and for a few the illustration does not give an adapertural view of the shell. These have of necessity been omitted, but a good sample of the fauna is obtained.

For the numerous mesogastropods and neogastropods with spouts, spines, thorns, flanges, and other outgrowths, the shell has been measured both with them and without, the curve of the aperture with the spout notionally removed being completed by eye. The resulting measurements are of course very approximate but good enough for present purposes. Measurements with the outgrowths notionally removed are morphologically more directly comparable with those made on simple unadorned shells, and often in fossil material the outgrowths are broken or lost so that only measurements on the body of the shell can be taken. The spire angle has been simply measured with a protractor on the appropriate illustration, to an accuracy of about $\pm 5°$. Cox, in the *Treatise* (**I**, p. 127) distinguishes several sorts of spire angles. Here the angle marked in figure 1 as θ' has been used, which is usually the same as Cox's 'mean spire angle', but departs from it considerably when the maximum diameter is high on the shell, as in *Conus*.

(*c*) *Classification*

(i) *Species*

For a survey of variation in spire index, it is not necessary to determine exactly what is or is not a species. All the forms given specific rank in the authorities quoted are regarded as species and used; all subspecies, forms, varieties etc. are ignored except for special purposes when their utilization is made explicit. Where, as in Pilsbry, subspecies are recognized, the nominate is taken to represent the species since it is as likely to be representative as any other. Various former species in the British and European fauna are now regarded as species-complexes with two or more sibling species (e.g. *Columella edentula* and *aspera*, Paul 1975). The recognition of these would not appreciably influence the distributions shown. Equally, Germain, while sinking a very large number of species, probably still admitted too many, especially of those created by Bourguignat; removal of these would have an imperceptible effect. In many groups of marine gastropods, both living and fossil, we still do not know what are species and what are varieties – witness Heller's well-justified division of the extremely common rough winkle into
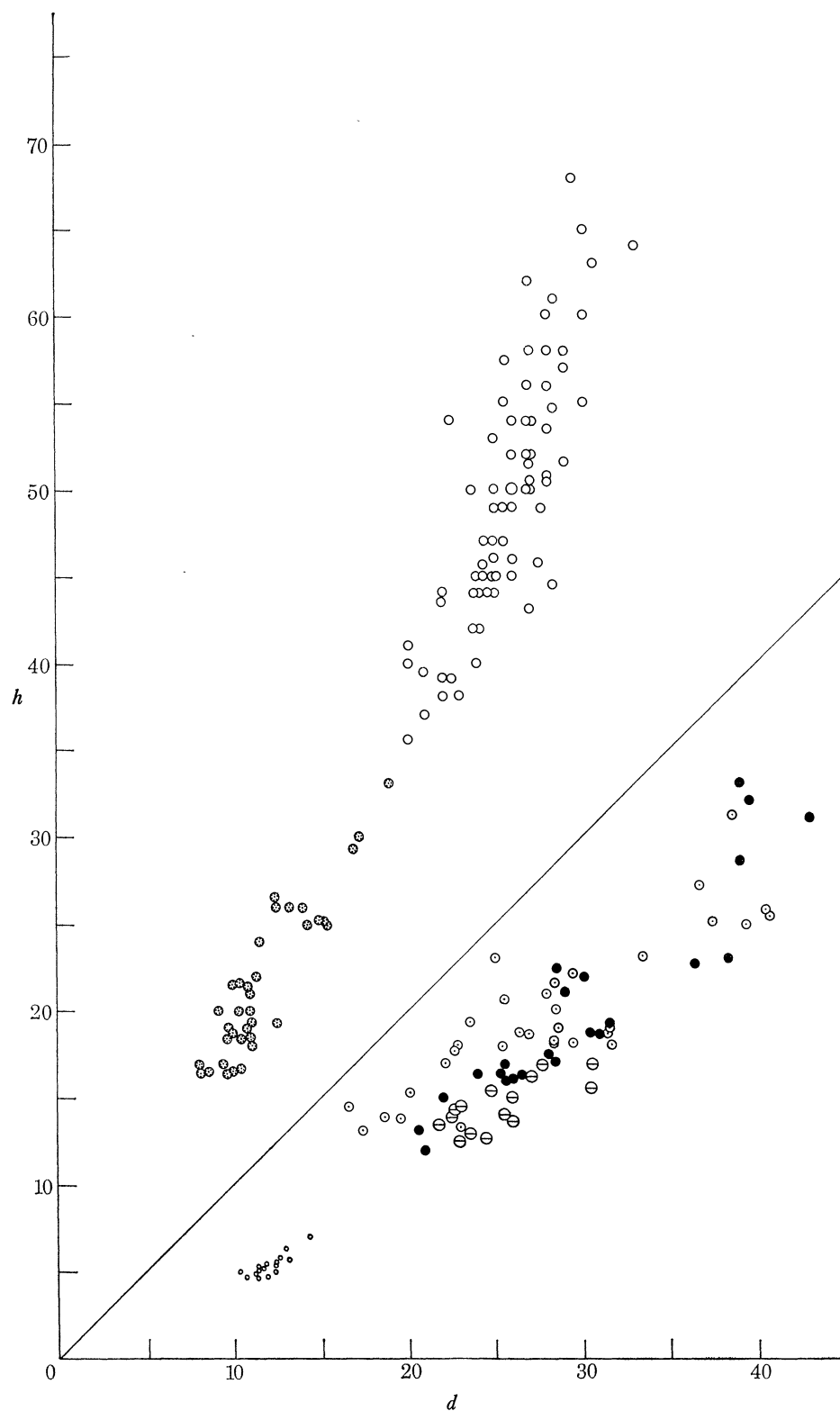
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FIGURE 2. Range of variation of individual shells within a species, data from Pilsbry (1939–48). Open circles, *Liguus fasciatus* (Orthalicidae); stippled circles, *Bulimulus dealbatus* (Bulimulidae); very small circles, *Ashmunella proxima* (Polygyridae Triodopsinae); black circles, *Triodopsis albolabris* (Polygyridae Triodopsinae); circles with central dot, *Helminthoglypta arrosa* and circles with horizontal bar *Monadenia mormonum*, these last two both Helminthoglyptidae Helminthoglyptinae. Even with extremes of variation in shape of shell, the scatters tend to lie along radii of the diagram (that for *Liguus* may be too steep for a radius). In this and all subsequent scatter diagrams except figures 5 and 8, the axes are marked at intervals of 5 mm from the origin (bottom left hand corner; 0, 0) and the line for $h = d$ is drawn.

four distinct biospecies (Heller 1975). For the present paper, all that is required is an adequate sampling of the normal variation in shell shape and size.

(ii) *Higher taxa*

For the same reason, the exact rank of natural groups generally recognized is not of importance; the subfamily Helicellinae of the Helicidae may well be of family rank. But Robertson's demonstration (1973) that *Cyclostremella* is an opisthobranch, not an archaeogastropod involves a major change in composition of groups, not merely in their relative rank and cannot be ignored. For consistency's sake I have followed the classification of the gastropods by Taylor & Sohl (1962), the notes to which indicate other recently moved or uncertain groups. Where necesssary, these are mentioned or discussed below. This classification largely agrees with that of fossil forms in the *Treatise*, merely separating a few forms at family level; the subordinal distinctions used in the *Treatise* have been added to Taylor & Sohl's classification. All the forms mentioned in the present paper are given in their taxonomic position according to Taylor and Sohl, in appendix A. In the present paper, prosobranch is used as equivalent to the Streptoneura minus those forms now definitely regarded as euthyneuran; pulmonate is as usual the Stylommatophora and Basommatophora, included by Taylor & Sohl as separate orders of the Euthyneura.
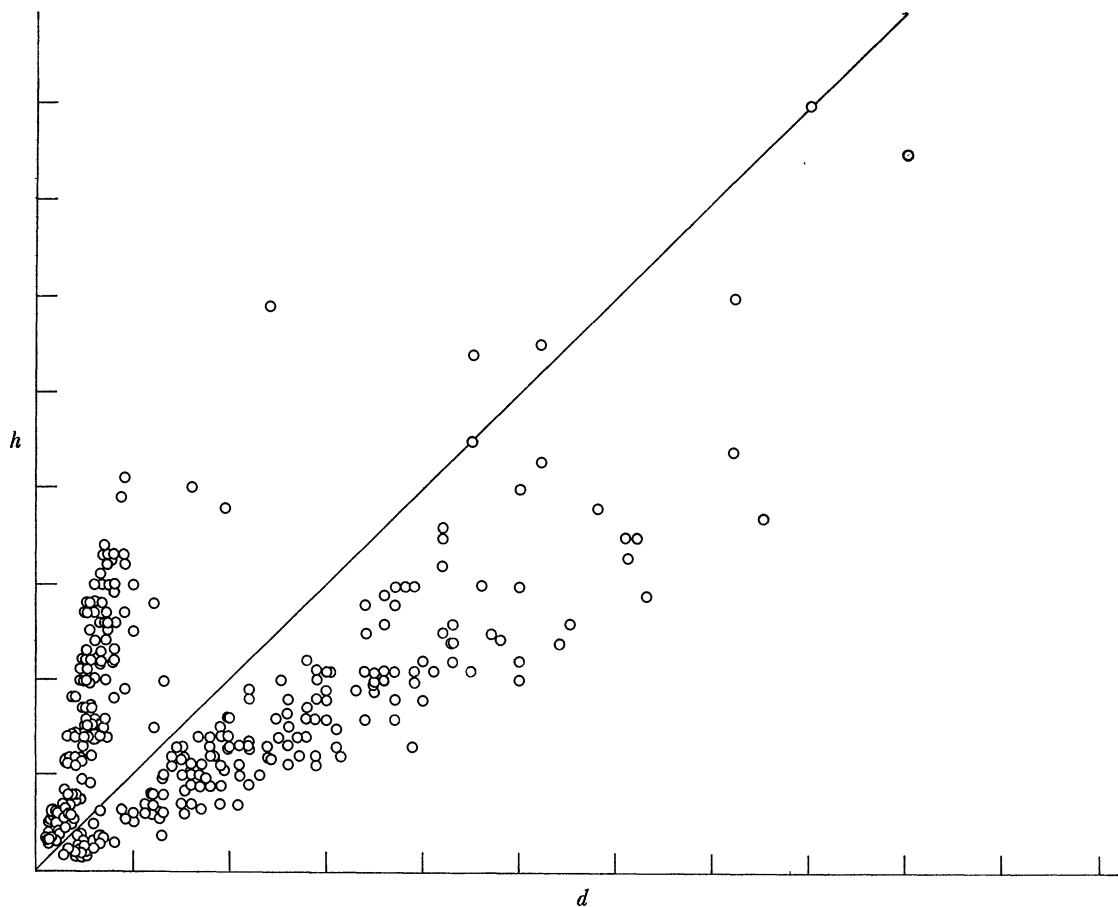

FIGURE 3. All species of free-crawling terrestrial stylommatophorans retractable into their shells, for France (and Corsica), the British Isles, and Germany. Paludicole, habitually burrowing, and sluglike forms excluded.
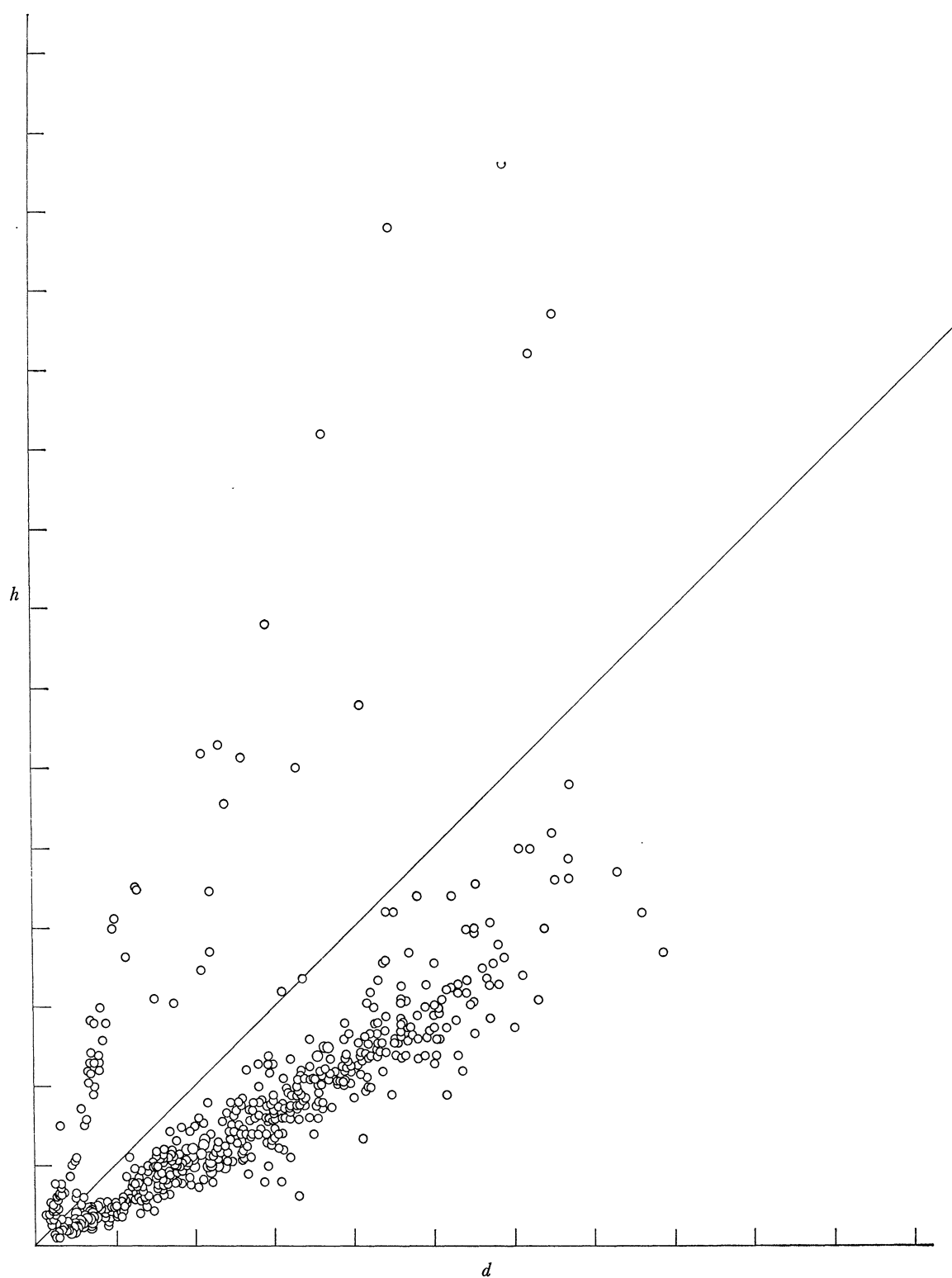
FIGURE 4. Land stylommatophora of the U.S.A., from Pilsbry; directly comparable with figure 3.

3. Western European and North American terrestrial faunas
(a) Stylommatophora

(i) *Distribution of h and d*

If we plot actual height against maximum diameter of shell for the Western European species of Stylommatophora listed by Germain, etc., as terrestrial, i.e. excluding those definitely paludicole or supralittoral, we obtain figure 3. The vast majority of points falls into one of two elongate

Table 1. Terrestrial stylommatophoran families of North America and Western Europe

(Excluding paludicoles, slugs, and perpetual burrowers.)

	U.S.A.	W. Europe
suborder ORTHURETHRA		
superfamily CIONELLACEA		
Cionellidae (= Cochlicopidae)	+	+
PUPILLACEA		
Pyramidulidae		+
Vertiginidae	+	+
Orculidae		+
Chondrinidae		+
Pupillidae	+	+
Valloniidae	+	+
Enidae		+
suborder MESURETHRA		
CLAUSILIACEA		
Ceriidae (= Cerionidae)	+	
Clausiliidae		+
suborder SIGMURETHRA		
infraorder HOLOPODOPES		
ACHATINACEA		
Subulinidae		+
Spiraxidae	+	
RHYTIDACEA		
Haplotrematidae	+	
BULIMULACEA		
Bulimulidae	+	
Orthalicidae	+	
Urocoptidae	+	
infraorder AULACOPODA		
ENDODONTACEA		
Endondotidae	+	+
ZONITACEA		
Vitrinidae	+	+
Zonitidae	+	+
ARIOPHANTACEA		
Euconulidae	+	+
infraorder HOLOPODA		
POLYGYRACEA		
Thysanophoridae	+	
Ammonitellidae	+	
Polygyridae	+	
OLEACINACEA		
Sagdidae	+	
HELICACEA		
Oreohelicidae	+	
Bradybaenidae		+
Helminthoglyptidae	+	
Helicidae	?	+

clusters, which converge towards the origin. One is of markedly high-spired shells with a spire index of about 3. A few approach the line at 45° which bisects the available space and is a useful guide-line for comparing clusters; on this line $h = d$. The second cluster runs below the bisector, although crossing it twice; the spire index is almost always below 1, and at the lower edge of the cluster it is about 0.4, or 0.3 nearer the origin. In the high-spired forms there is some indication of two modes of variation, a well-represented group with spire index of 3 or more, and a thin scatter about 2, better shown in the next diagram.
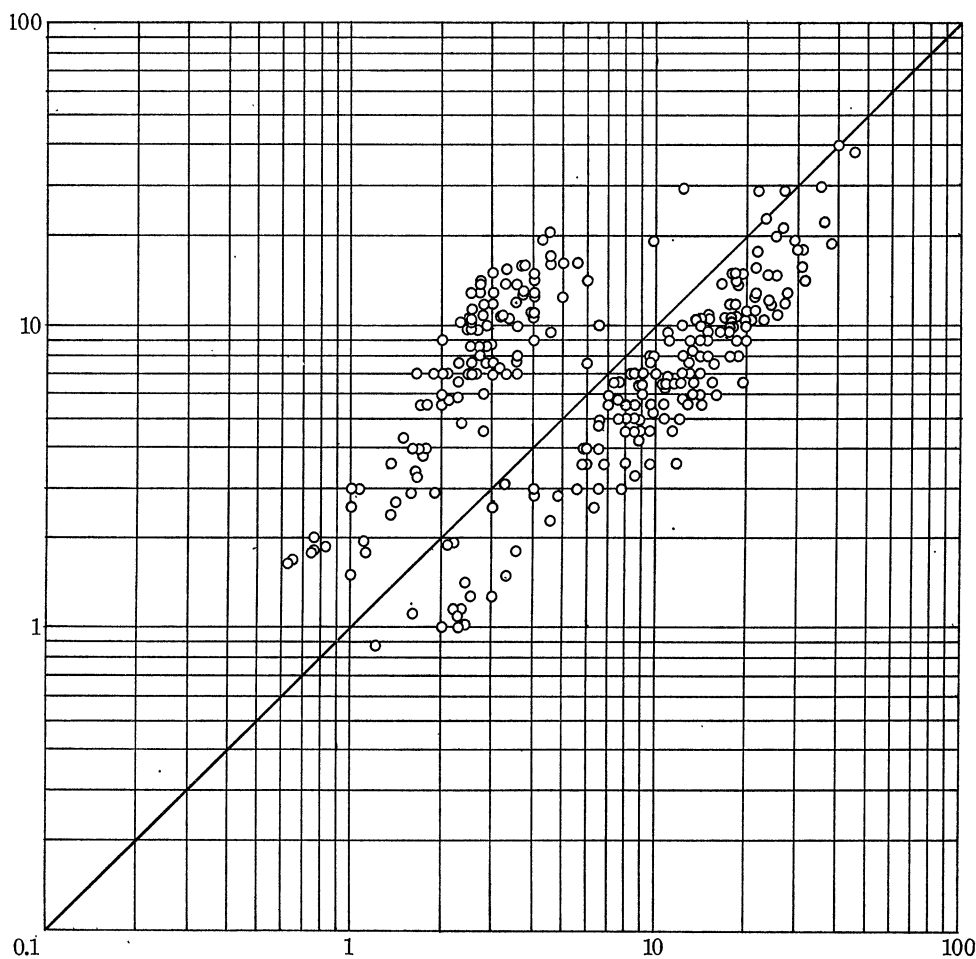

FIGURE 5. Logarithmic plot of the data in figure 3 (three cycles; 1, 10 and 100 mm).

A corresponding exercise with Pilsbry's monograph excluding also introduced European species gives figure 4, which, apart from having a number of much larger high-spired shells, and far fewer small ones, is extraordinarily similar to figure 3. The taxonomic composition of the North American terrestrial stylommatophorans (excluding slugs and near-slugs) and its relation to that of western Europe is given approximately in table 1. Even at the family level there are 12 in North America but not in Europe, 8 in Europe and not in North America, and only 8 shared (or 12, 7 and 9 respectively if *Cepaea hortensis* is the single native helicid of North America). At the subfamily level the difference is rather greater, with, for example, some sub-families of Pupillidae in North America but not in Europe. The Helicidae, with 9 subfamilies in Europe, are known only by *Cepaea hortensis* and a few introduced species in North America;

and the Clausiliidae, also a highly successful family in Europe, are unknown there. About a dozen species, all boreal, are common to Europe and North America, far too few to affect the similarity of the distributions. Taxonomically, therefore, there is no good reason to expect the remarkable similarity of figures 3 and 4. A logarithmic plot for the data in figure 3 is given in figure 5, and confirms the existence of the two main clusters even for those tiny shells near the origin which, because their symbols are necessarily of rather large dimensions for clarity, appear to run together in figure 3. The same result is found for the small shells in figure 4.

FIGURE 6. Western European data taxonomically symbolized. I. Note that the symbols in this and the next two diagrams are chosen for clarity in each diagram, not for taxonomic consistency. ①, Helicidae Tacheo-campylinae; ○, Helicidae Helicinae; ●, Helicidae Helicigoninae; ⊙, Helicidae Helicellinae; ⑤, Subulinidae Obeliscinae; ⊕, Enidae Eninae; ×, Enidae Chondrulinae; +, Zonitidae Zonitinae; +, Clausiliidae; •, Pupillidae Pupillinae.

In figures 3 and 4 it is especially noticeable in the cluster below the bisector, that the variance of h and of d increases with increasing size. A plot of h/d (shape) against $h+d$ (size) does produce a nearly horizontal scatter with constancy of variance for the cluster of low-spired shells. For the high-spired ones, however, since h varies greatly and d rather little, a scatter at about $45°$ inclination is produced. Since h/d bears a rough relation to the spire angle, and shells with the same spire angle will lie along the same radius drawn from the origin (as the symbols in figure 2 tend to do) one may expect that the variance of spire angle is roughly constant within each cluster, and independent of the actual size of the shell. A plot of actual spire angle against whichever of h and d has the larger absolute value does produce the expected relative

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constancy of variance. It follows that for any shell size-group in the faunas, the same distribution of h/d or spire angle can be expected.

(ii) *Taxonomic groups and variation of h and d*

The unexpected agreement between two faunas differing considerably in taxonomic content prompts an investigation into taxonomic deployment within each.

Within several western European families there is considerable stability of h/d and spire angle as compared with the total variation seen in figure 3. Figures 6, 7 and 8 give an analysis of the western European data. In figure 6, all the Clausiliids are very high-spired, and this is true for the family anywhere. All the Eninae are high-spired, but fatter than Clausiliids of corresponding height. In the lower cluster, all Zonitids are very low-spired, as are all Valloniines (figure 8,
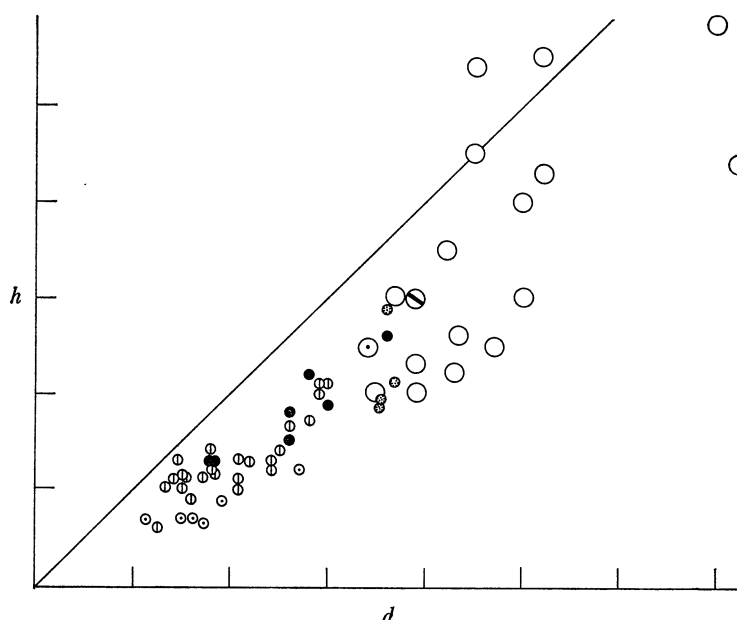
FIGURE 7. Western European data taxonomically symbolized. II. The Murellinae, like the Tacheocampylinae in figure 6 are often merged in the Helicinae. *Leucochroa* (Helicellinae) was given family rank by Germain and older authors. ⊘, *Eulota*; ⊙, *Leucochroa*; ○, smaller Helicinae; ⊕, Fruticicolinae; ⊗, Helicodontinae; ●, Thebinae; ⊛, Murellinae.

small shells), and so on. Within the subfamilies of the Helicidae, again, there is considerable consistency in the Fruticicolines, Thebines, and Helicodontines (figure 7). However, subfamilies and closely allied families, e.g. the Acanthinulinae and Valloniinae within the Valloniidae (figure 8), and the Pupillidae and Valloniidae (figure 8) may be very different in h/d. Two subfamilies of Helicidae are of especial interest. The Helicellinae (figure 6) range from nearly flat shells to nearly globular ones; a single genus, *Cochlicella*, oversteps the bisector. Of its three species, *C. ventricosa* is near the bisector, *C. conoidea* well above it, and *C. acuta* is clearly in the upper cluster with the Enidae. The Helicigoninae (figure 6) run consistently along near the lower edge of the lower cluster, with two exceptions. *Arianta arbustorum* has a nearly globular shell, grouping in the diagram with *Cepaea nemoralis* and *C. hortensis* (Helicinae), and well separated from the main helicigonine scatter; once to my knowledge the resemblance in shell to *Cepaea* was enough to mislead some geneticists into thinking it a hitherto undescribed morph

of *C. nemoralis*. Even more remarkable is the Austrian and Swiss helicigonine *Cylindrus obtusus*, which is clearly in the upper cluster between the enines and Clausiliids, and nearly on the line of the chondrulines. Since the days of Pilsbry and Hesse, the classification of the European and North American gastropods has been based on the anatomy of the animal, the shell being used in the definition of groups only where the comparative anatomy allowed. There is no reason to disagree with the taxonomic positions of *Cochlicella*, *Arianta* and *Cylindrus*. Here we have the strongest indication that the spire index can vary greatly between closely related forms, although remaining very constant within species.
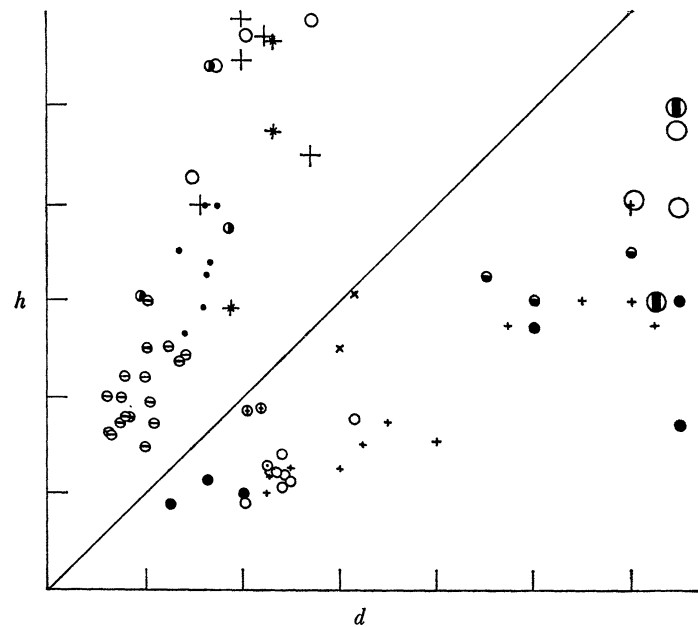
FIGURE 8. Western European data taxonomically symbolized. III. Smaller shells. *Axes marked at 1 mm intervals.* O, Small Helicellinae; ◐, small Fruticicolinae; o, Chondrulinae; o, Valloniidae; ◓, Vitrinidae; ◑, Cionellidae; ●, Endodontidae; ⊙, Pyramidulidae; ⊖, Vertiginidae; ⊕, *Acanthinula*; ●, Pupillidae; +, Ferussaciidae; ✳, Orculidae; +, Zonitinae; ×, Euconulidae; †, Gastrodontinae.
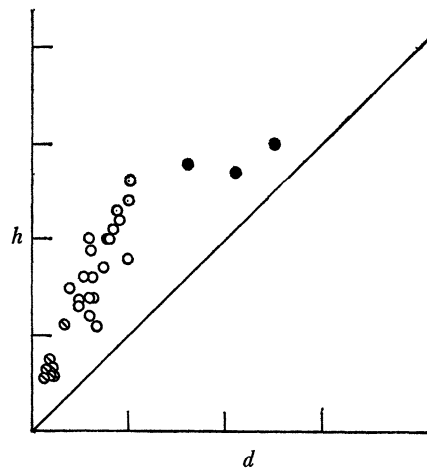
FIGURE 9. Western European terrestrial operculates (only mesogastropods). ●, Pomatiasidae; O, Cochlostomatidae; ⊘, Aciculidae.

In the North American fauna (apart from the Acanthinulinae and Valloniinae, which are shared with western Europe and the Palaearctic generally) there is no good example of this sort of variation; however, one lies only just outside. The Urocoptidae of tropical America have representatives of three subfamilies in North America; all the species, as is almost invariable for the family, have very high-spired shells. A single genus, *Hendersoniella*, which does not come into North America, has a discoidal shell, thus providing an example exactly the inverse of the European helicigonines. Other examples of similar variation occur elsewhere in the world.
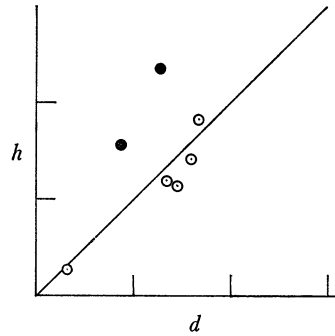
FIGURE 10. North American terrestrial operculates (mesogastropods and archaeogastropods).
●, Pomatiasidae; ⊙, Helicinidae.

(b) Other groups

Archaeogastropoda are represented by a few species of Helicinidae in the North American fauna (figure 10). Unlike any group seen so far, they are distributed along the bisector, and it will be seen later (p. 395) that this is the usual distribution for present-day marine archaeogastropods. They tend, therefore, to fill the gap between the two clusters in figure 4. Of the terrestrial *Mesogastropoda*, the Pomatiasidae are represented by a very few species in both the North American and the west European faunas (figures 9, 10). They approach the bisector from above, again tending to lie in the gap between the two clusters. The (western European) Aciculidae and these mesogastropods show a very similar distribution to that of present-day marine ones (p. 395 below).

4. SOME ISLAND FAUNAS

In order to sample other terrestrial faunas, the first two monographs that came to hand were used, van der Schalie's on Puerto Rico (1948), and Franc's on the New Caledonian archipelago (1956); the results are shown in figures 11 and 12. (Several Bulimulids, too large for the diagrams, are omitted from figure 12.) In Puerto Rico the archaeogastropods (Helicinidae) again tend to run along the bisector but always just below it, and one is almost planorboid. The mesogastropods (Cyclophoridae and Pomatiasidae) take up a position fairly typical for this group, and the stylommatophorans again show the two separate clusters. In New Caledonia the same is true except that the mesogastropods now run close to the bisector and even cross it. Only those species are shown that definitely occur in New Caledonia itself (and only those for which shell dimensions are provided or can be extracted from the illustrations), to make the comparison with Puerto Rico valid. In fact, it is likely that many of those from the other islands of the group occur on the main island as well; addition of these to the diagram would merely thicken the clusters shown, except in one respect. Four species of *Gassiesia* (Poteriidae) would

extend the mesogastropods up among the largest stylommatophorans shown in the lower cluster (height and diameter 12, 20; 18, 29; 7, 11; and 19, 25).

The Puerto Rican terrestrial fauna consists of:

Archaeogastropoda	Helicinidae
Mesogastropoda	Cyclophoridae, Chondropomidae
Stylommatophora	Pupillidae, Vertiginidae, Helicarionidae, Zonitidae, Systrophiidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Haplotrematidae, Streptaxidae, Polygyridae, Sagdidae, Helminthoglyptidae (Cepoliinae), Bulimulidae, Urocoptidae, and Clausiliidae

The New Caledonian fauna contains:

Archaeogastropoda	Helicinidae
Mesogastropoda	Poteriidae, Cochlostomatidae, Assimineidae
Stylommatophora	Achatinellidae, Vertiginidae, Pupillidae, Enidae, Subulinidae, Endodontidae, Helicarionidae, Zonitidae, Bulimulidae, Camaenidae, Rhytididae
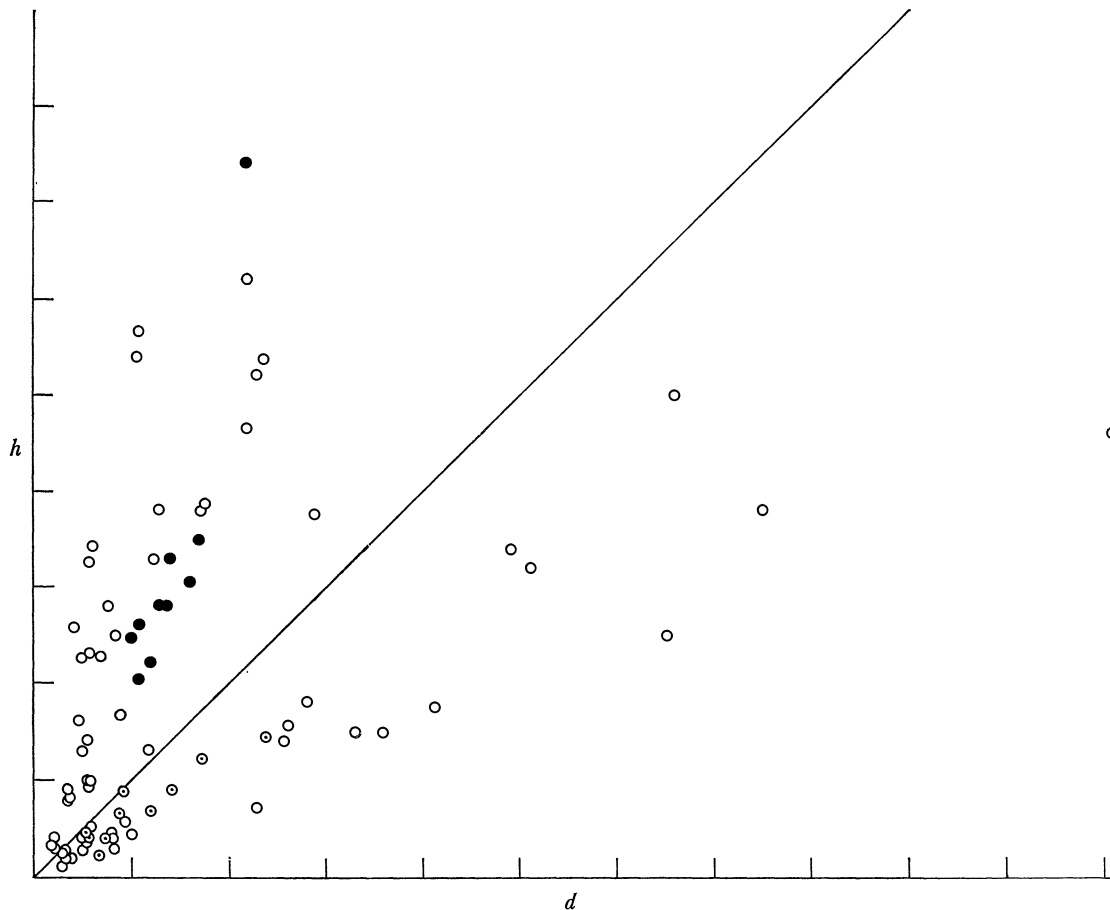
FIGURE 11. Terrestrial gastropods of Puerto Rico; data from van der Schalie.
○, Stylommatophora; ●, Mesogastropoda; ⊙, Archaeogastropoda.

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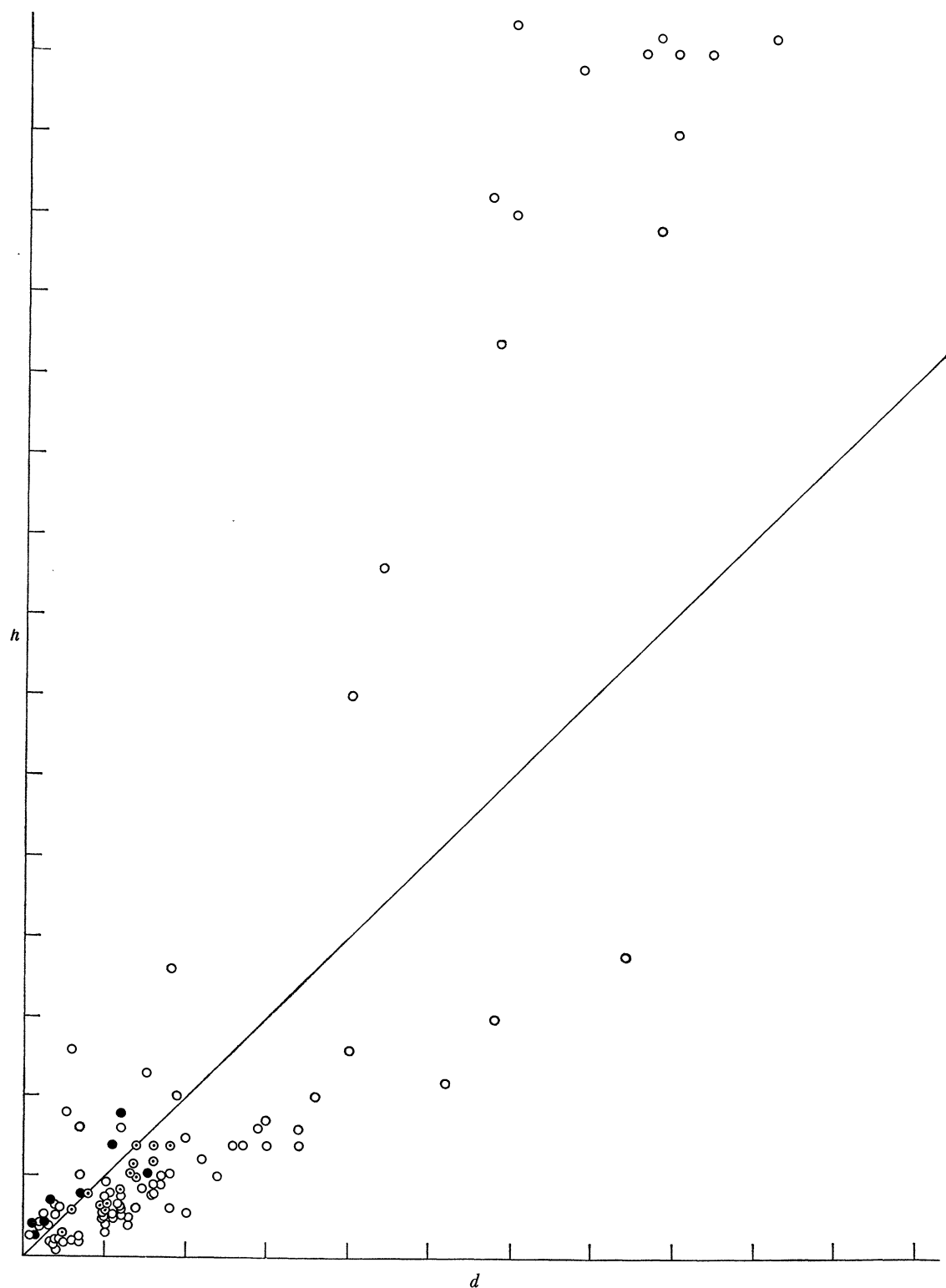
FIGURE 12. Terrestrial gastropods of New Caledonia; data from Franc. Symbols as in figure 11. Data probably very incomplete. Several nearly terrestrial species of various families (including Neritidae) omitted, also a number of high-spired Bulimulids too large to be shown, and continuing the upper cluster upwards.

In the New Caledonian fauna there are numerous Helicinids, Bulimulids and Endodontids. The Puerto Rican fauna has a scatter of forms through numerous families, none well represented; the best are helicinids, chondropomids urocoptids, helminthoglyptids, sagdids and oleacinids. The taxonomic emphasis in the two is therefore very different, yet, making allowance for different degrees of representation of the cluster of high-spired shells, both resemble closely figures 3 and 4.
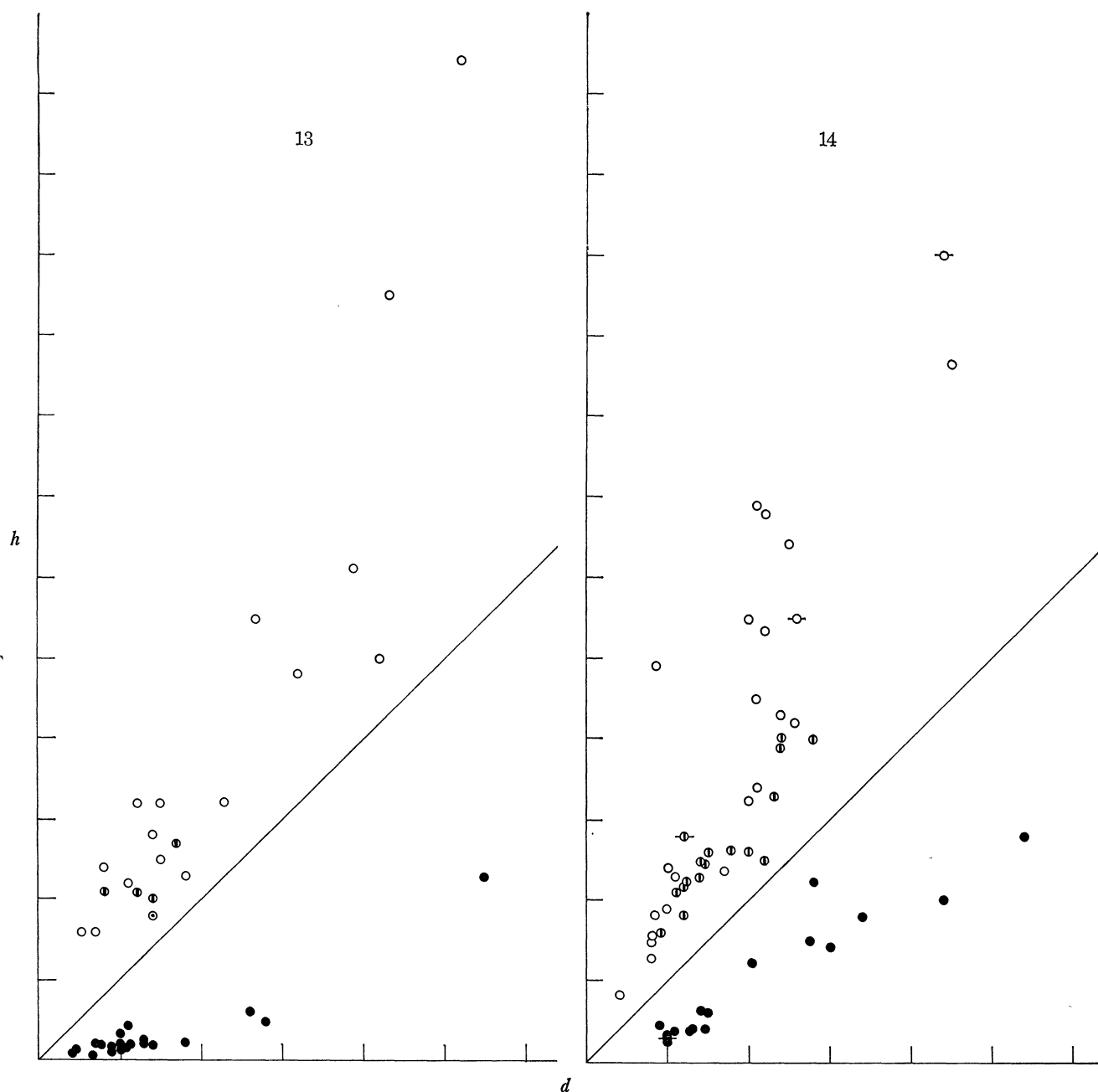
FIGURE 13. Western European basommatophora (excluding limpet-like forms). Symbols as in figure 14.

FIGURE 14. Wisconsin basommatophora; data from Baker. Those marked with a horizontal line are species common to North America and western Europe. O, Lymnaeidae; ⊕, Physidae; ⊙, Planorbidae Bulininae; ●, Planorbidae, other subfamilies.

5. Western European and North American freshwater faunas

(a) Basommatophora

Remarkably, the western European freshwater basommatophorans (figure 13) show a strongly bimodal distribution, as do the terrestrial stylommatophorans (figure 3), but the whole scatter is rotated clockwise through about 30°. The upper cluster is now much closer to the bisector, and the lower one to the x axis – in other words the tall-spired shells (lymnaeids and physids) are fatter and the flattened shells (planorbids) flatter than the corresponding forms on land. As there is no single monograph for the North American freshwater fauna, figure 14 shows the distribution for the basommatophorans in Baker's (1928) survey of freshwater molluscs of Wisconsin. The resemblance to figure 13 is very strong, but the lower distribution is now more like that in the terrestrial forms; the gap between the two distributions is therefore much narrowed, but still obvious.
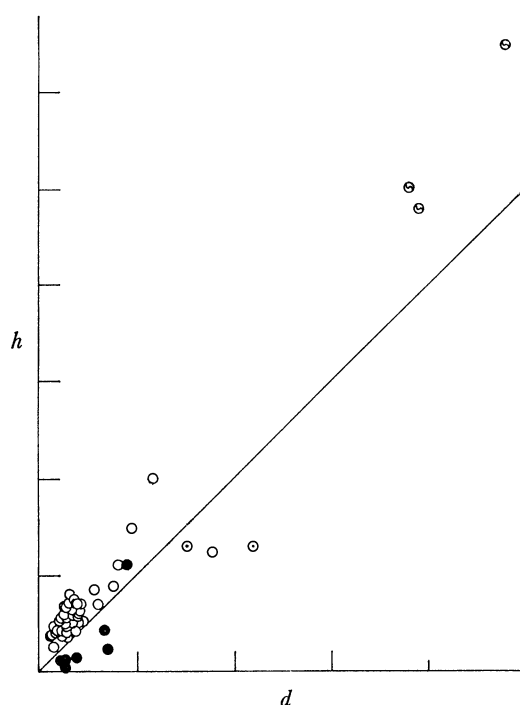

FIGURE 15. Western European freshwater operculates. ⊙, Neritidae; ◓, Viviparidae;
○, Bithyniidae, Hydrobiidae etc.; ●, Valvatidae.

(b) Other groups

Archaeogastropods (Neritidae) are represented in the western European freshwater fauna (figure 15) and are of the neritoid facies with depressed spire and large mouth; if the functional height instead of the columellar dimension of the shell were measured, they would probably be further from the bisector. The mesogastropods take up a distribution characteristic of their order in both faunas (figures 15 and 16) except that in both the Valvatidae fall almost entirely below the bisector, and in the west European fauna, at least, have almost planorboid forms. It is more difficult in these groups to see a gap between the two clusters. Comparing figures 15 and 16 with figures 13 and 14, it seems as though most of the meso- and archaeo-

gastropods do fill a gap between the two basommatophoran clusters in each fauna, with a slight overlap in each. It should be noted that the Wisconsin fauna is, for a North American fauna, poor in Pleuroceridae, but that these would increase the number of spots in the general area in figure 16 indicated by the two representatives already there.
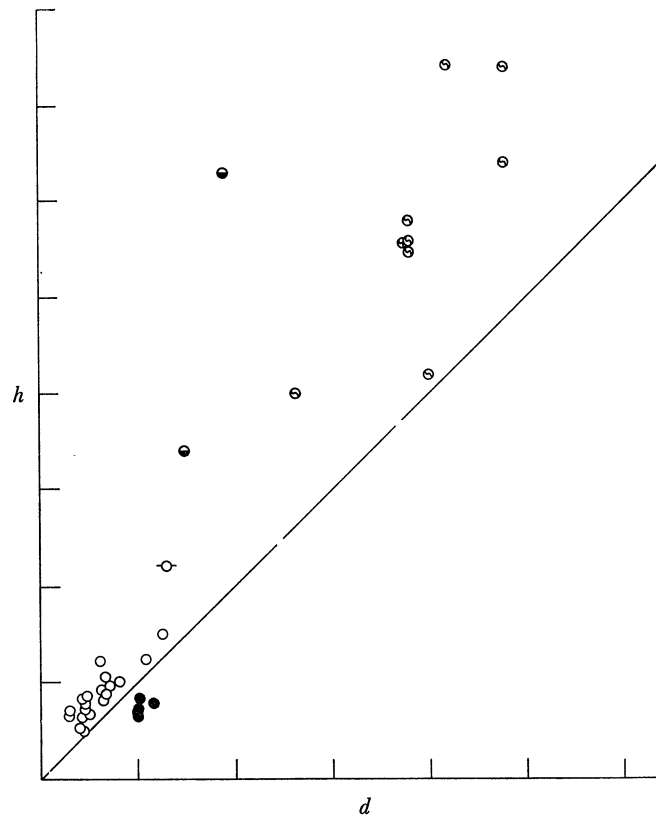

FIGURE 16. Wisconsin freshwater operculates. Symbols as in figure 15, with addition shown.
◓, Pleuroceridae.

6. NORTH AMERICAN MARINE FAUNA

The archaeogastropods for which data can be obtained from Abbott are shown in figure 17. They have a distribution along the bisector in striking contrast to those in figures 3 and 4, but with a scatter of flattened shells corresponding to the lower cluster, and a very few high-spired forms (*Halistylus*), not distinguishable as a separate group in the figure, which belong to the upper group. When we come to the mesogastropods, a certain number have long spines, or a large mouth-flange or spout. In figure 18 are shown only those species with simple shells. The principal group is high-spired, even with a strong hint of the same subdivision as in figures 3 and 4, but with a wider scatter, extending to the midline; again, however, there is a group corresponding roughly to the lower cluster in figures 3 and 4 but connected to the main cluster. Some of these, but not all, may belong elsewhere (p. 402 below). Figure 19 gives the distributions for the complex shells with lateral projections (circles with central dot) or with spouts (plain circles), and for all with these additions removed (circles with a horizontal bar). The distribution of the unaltered values resembles that in figure 18 but is more towards the

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middle line, and removing the excrescences brings it still more towards it, one species actually crossing it. Nevertheless both figure 18 and figure 19 differ sharply from figure 17.

A certain number of neogastropods have so short a spout that it is effectively only a channel cut through the thick lip; these are shown in figure 20 and can be compared directly with figures 17 and 18. In all the scatters derived from Abbott's data there is a strong tendency to horizontal clumping, since shells varying somewhat in size are given simply as 'about one inch', or 'one and a half inches', or 'two inches' high. Nevertheless there are enough with more precise data to give a good idea of the distributions, and that of figure 20 has clearly more affinity with that of figure 18 than of figure 17. Interestingly, it seems to correspond to a plain Enine-Bulimulid type in figures 3 and 4, without the scatter of very high-spired shells
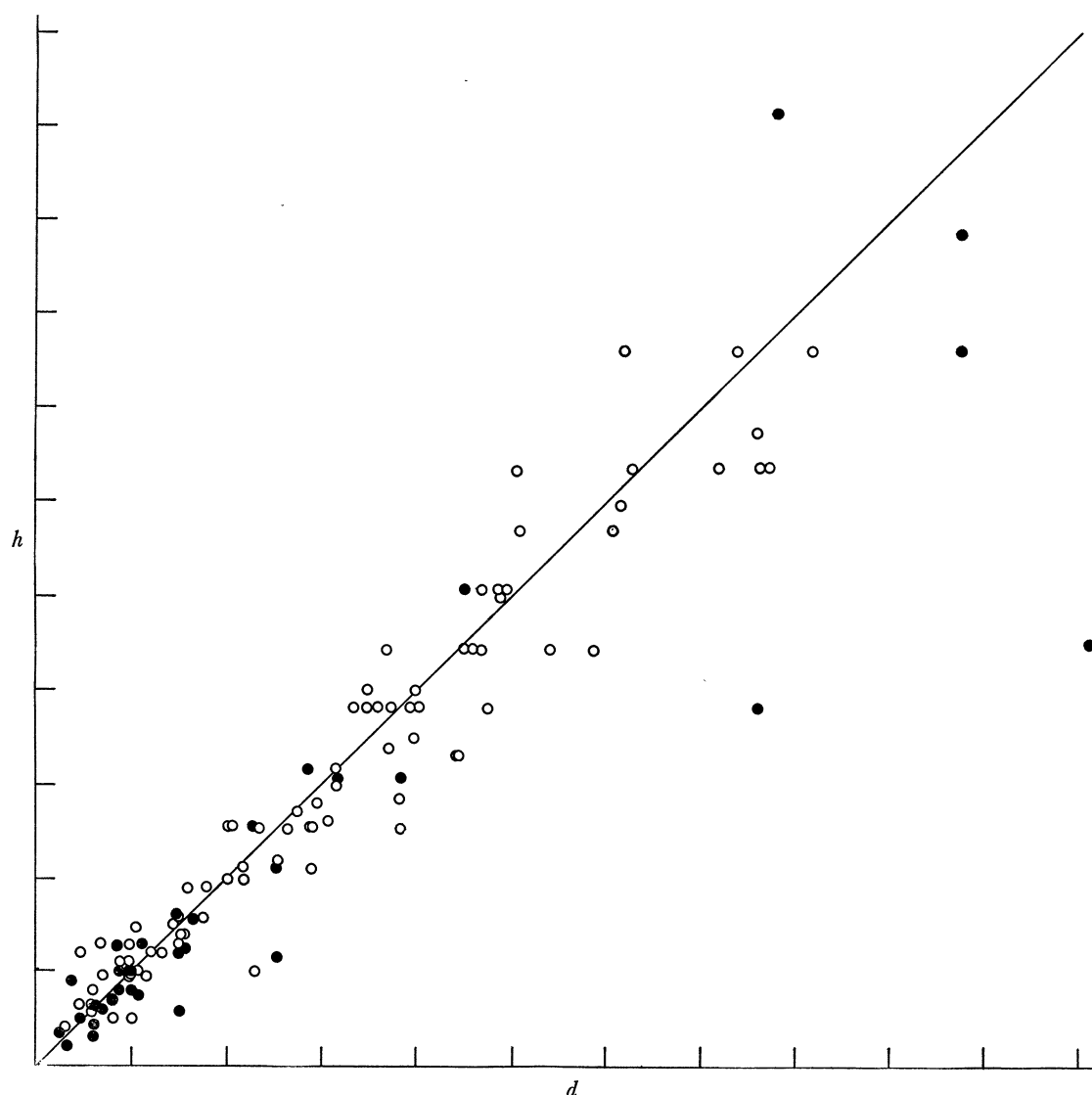

FIGURE 17. North American archaeogastropods; data from Abbott. In figures 17, 18, 20 and 22, black circles are generic representatives for comparison with figures 24–34 (data from the *Treatise*). Only the species giving the extreme right hand black spot (*Astraea*) has spines. On adjustment it would move about 15 mm on the scale of the x-axis to the left.
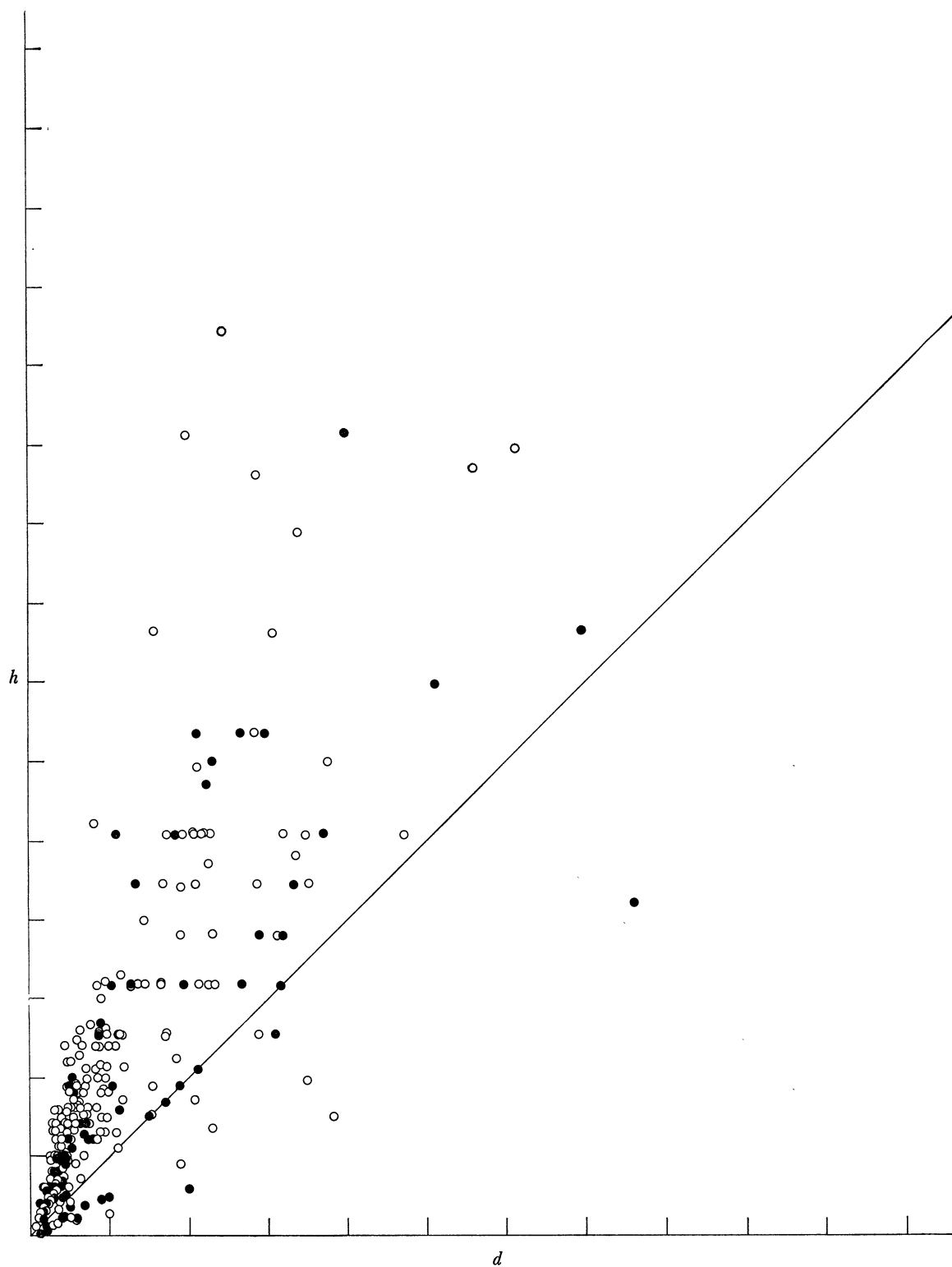
FIGURE 18. North American mesogastropods with simple shells
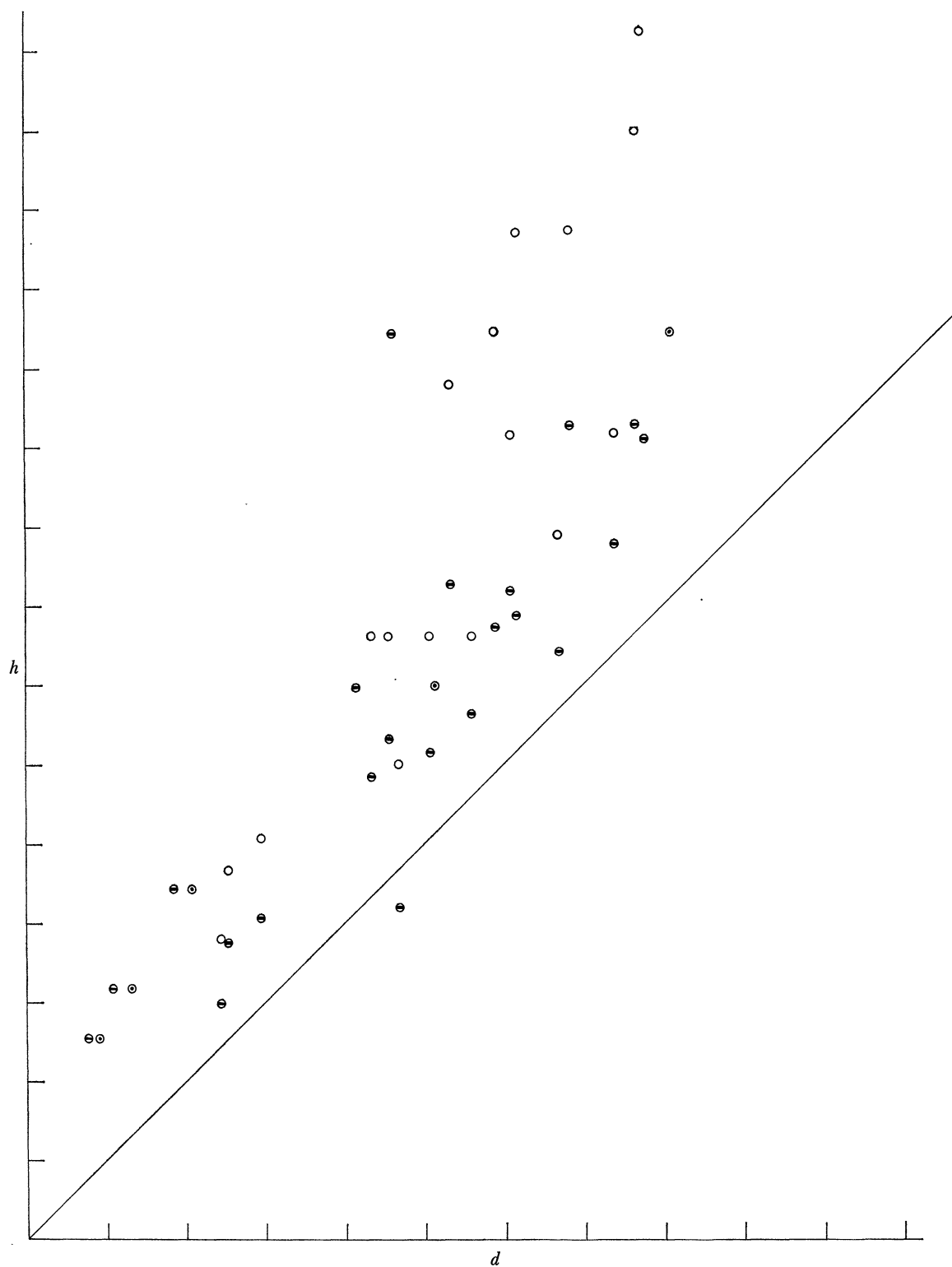(no large spines, flanges or spout).

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FIGURE 19. North American mesogastropods, complex shells. Plain circles, shells with spouts only, unadjusted values. ⊙, Shells with lateral appendages (thorns, spines, flanges etc.). ⊖, All types, adjusted values.

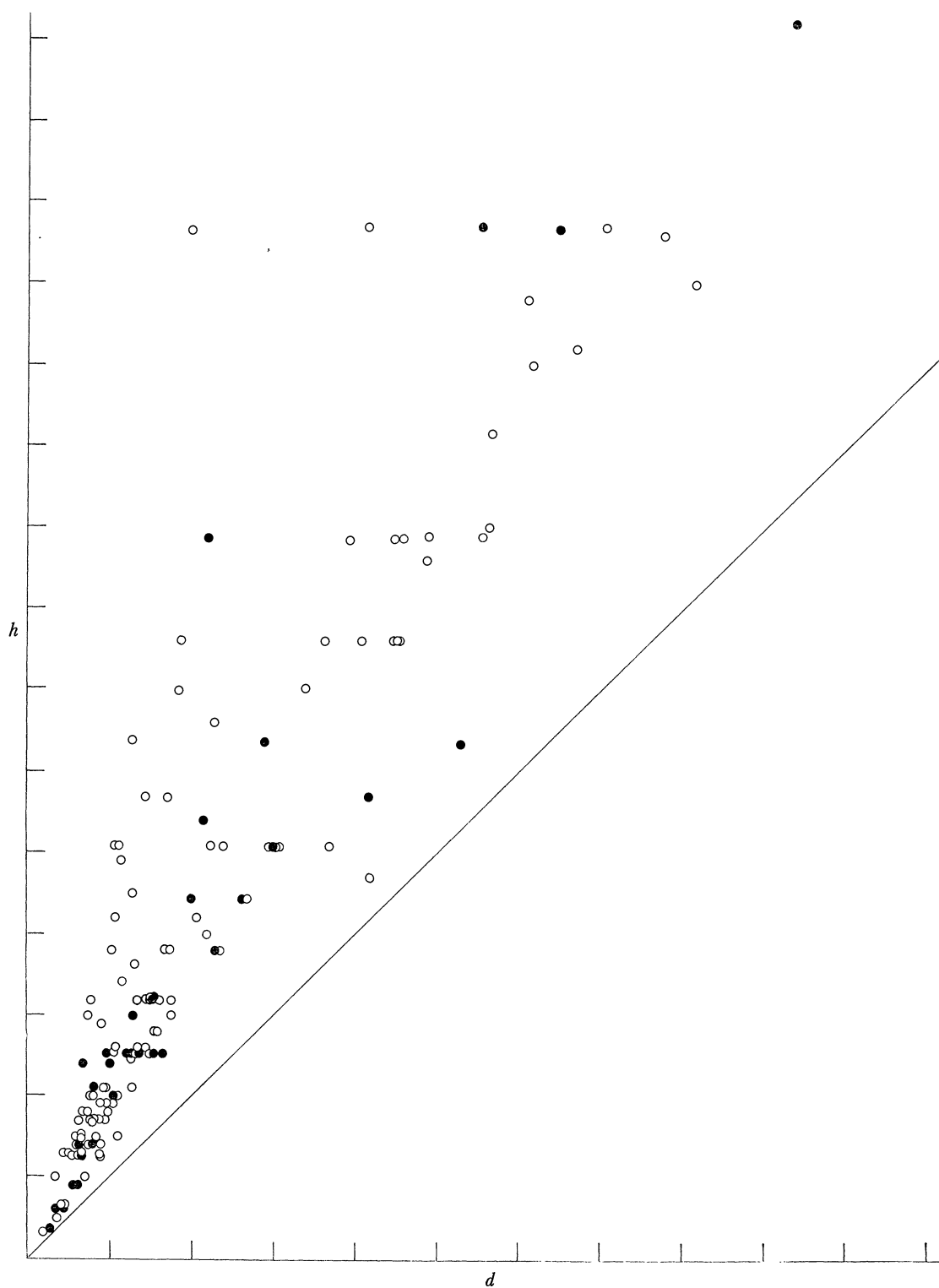FIGURE 20. North American neogastropods, simple shells.
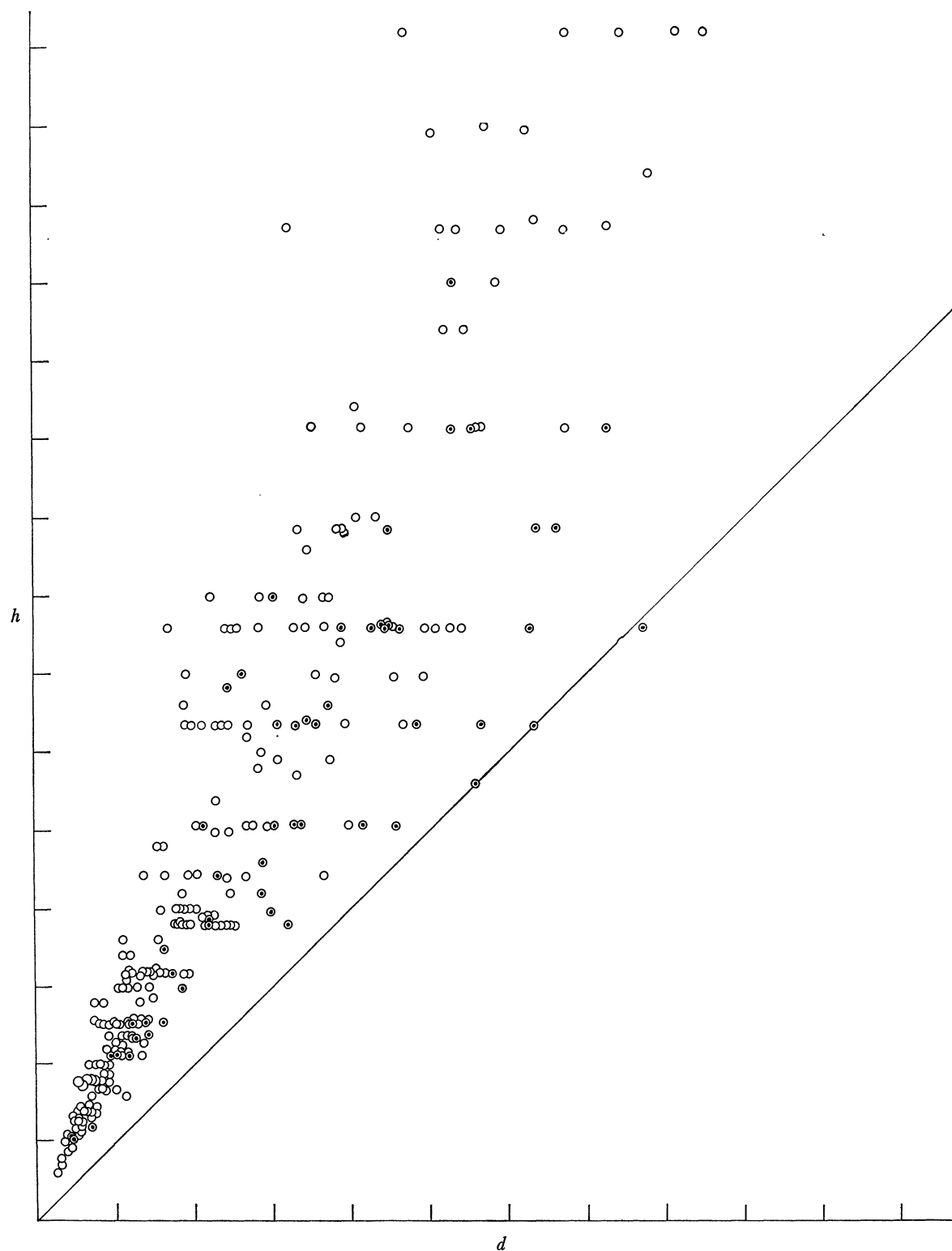
A. J. CAIN

FIGURE 21. North American neogastropods, complex shells, unadjusted values.
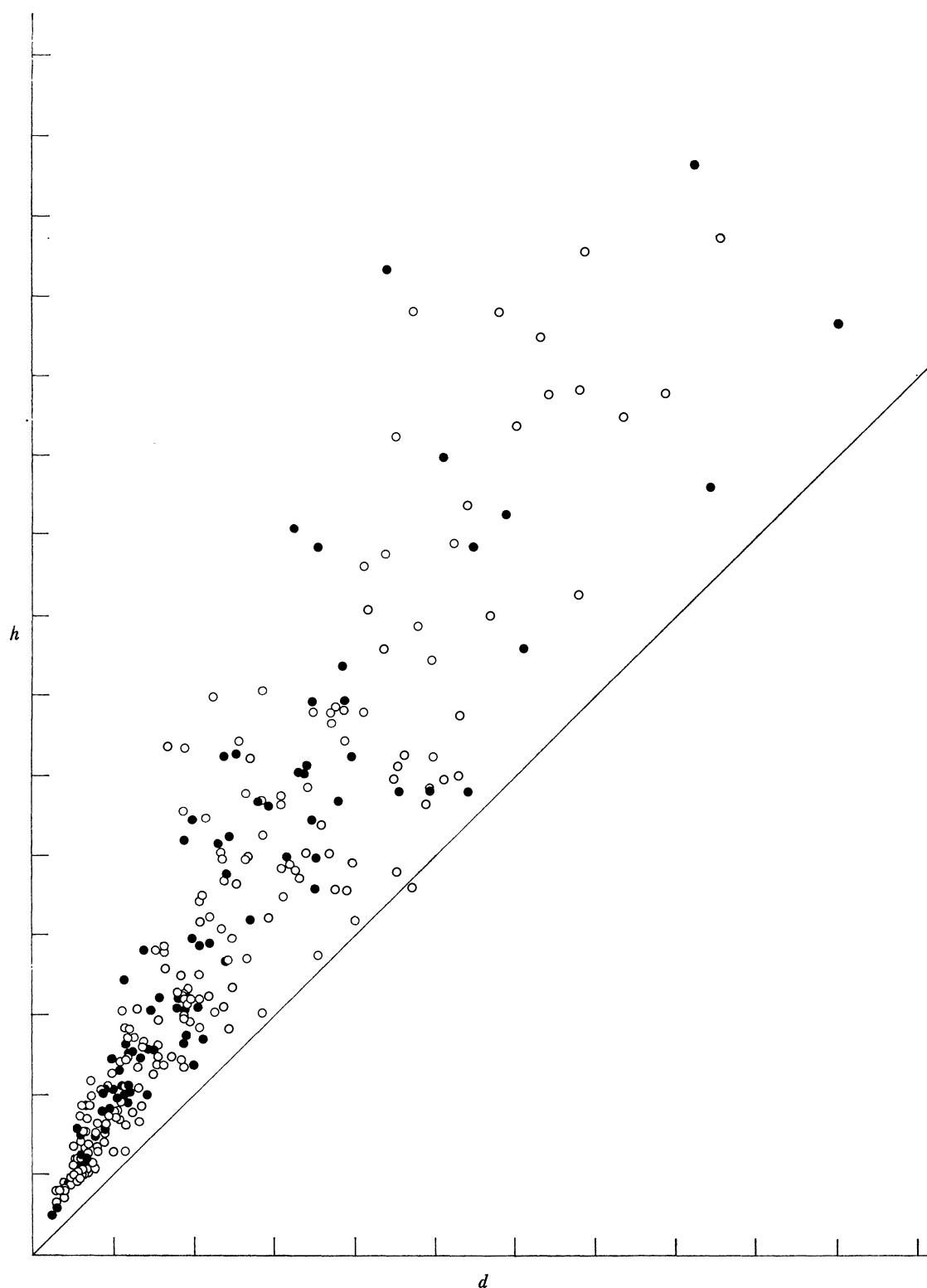All have spouts; ⊙, species with lateral appendages as well.

FIGURE 22. North American neogastropods, complex shells (shown in figure 21), adjusted values.

which reappears in figure 23, and is reminiscent of Clausiliids. Figure 21 gives the complex neogastropods all with spouts and many with lateral spines, thorns or flanges (circles with central dot); figure 22 gives the altered values for the same forms, and these two figures together correspond therefore to figure 19 for the mesogastropods. They bear a close resemblance to each other and to figure 20, and obviously group with the main distribution in figure 18. Considering the exuberance of spines and spouts in some muricids, for example, the similarity o figures 20 and 21 is at first sight remarkable; but when a shell has its effective height lengthened by a siphonal spout, *and* its maximum diameter extended by large thorns, the unadjusted spire-index can be quite close to that of the shell without excrescences.
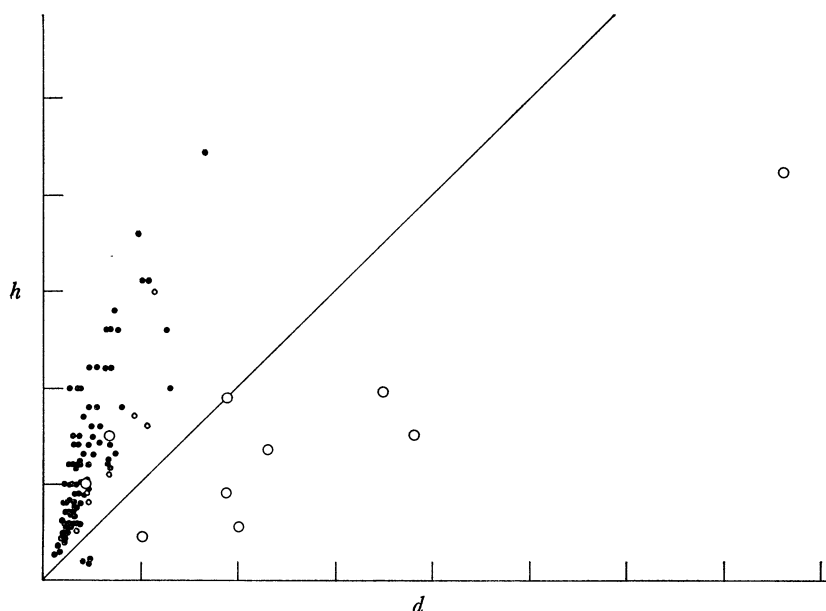

FIGURE 23. North American euthyneurans. o, Actaeonidae, Ringiculidae. ●, above the bisector Pyramidellidae, below the bisector *Cyclostremella* and related forms. O, Probable euthyneurans, already shown among the mesogastropod simple shells (figure 18); above the bisector, *Mathildidae*, below it *Architectonicidae*. Many more pyramidellids should be shown, but will not alter the shape of the cluster.

The diagrams given above comprise the prosobranchs that are free-crawling and fully retractable into their shells. Not many Euthyneura come into this category. Fretter & Graham (1949) gave reasons for regarding the Pyramidellidae as euthyneuran, not mesogastropod, and Robertson (1973) has shown that *Cyclostremella* is a pyramidellid. The Actaeonids are certainly euthyneuran. If the heterostrophic protoconch is a complete guide, then the Architectonicidae and Mathildidae may be euthyneuran. Taylor & Sohl (1962) accept Cossmann's contention that the extinct Nerinaeacea were close to the Pyramidellidae; their notes and references on this topic should be consulted. This would give us, for the present day Euthyneurans coming within the scope of this paper (figure 23) some very planorboid forms (*Cyclostremella*) and others planorboid or with a low spire (Architectonicidae); some with a rather fat shell taller than wide (*Actaeon*); and a number with a high spire index (Pyramidellids, Mathildids). Even without the Mathildids and Architectonicids, we should still have shells close to both extremes of h/d, and others nearer the midline, within the Euthyneura. The removal of the Mathildids and Architectonicids to the Euthyneura would reduce very slightly the number of high-spired shells

in figure 18, and remove all the larger very low-spired shells without affecting the smaller ones. Both with and without these groups of dubious affinity, the distribution in figure 23 is much more reminiscent of the mesogastropods than of either the archaeo- or the neogastropods; but if they are all included, it approaches the Pulmonates.

It appears, then, that high-spired, nearly equidimensional, and planorboid shells occur in all the major groups considered except the neogastropods, which are all, adjusted or not, moderately high spired or approaching the equidimensional. Nevertheless, the archaeogastropods are predominantly equidimensional, the mesogastropods moderately to very high-spired, and the relevant euthyneurans are mainly high-spired.

7. Fossil history of the Archaeogastropoda

(a) Available data

In the *Treatise on invertebrate paleontology* (I) *Mollusca* 1 we have a modern survey of all palaeozoic gastropods, and of those mesozoic and caenozoic forms immediately related to them. (The work on mesozoic and caenozoic mesogastropods and neogastropods has not yet appeared.) In this volume, all genera and subgenera are given with their type species and ranges, and a single species is illustrated for all except some Recent subgenera. If in fact we take the data from Abbott and choose a single representative for each genus, we get recognizably the same distributions as we have shown above, although of course with fewer symbols. In figures 17, 18, 20 and 22, a single generic representative (simply the first species given in Abbott) is shown in solid black, for comparison with later figures. Generally speaking it is true that marked variations in shell shape in fossil material (not just in details of sculpture) have been taken to warrant generic or subgeneric separation.

Figures 24–34 give, with uniform scale and symbols, the *h* and *d* scatters for the geological periods, ending with Palaeogene (Palaeocene, Eocene, Oligocene) and Neogene (Miocene, Pliocene and Pleistocene). For the Palaeozoic (figures 24–29) there is a symbol for every genus or subgenus of prosobranch gastropod. For later times, only the Archaeogastropoda are shown. Where a genus or subgenus ranges through more than one period, a large symbol is used for the period in which the species actually given in the *Treatise* occurs; a small symbol is shown in the same place in the other periods as a reminder of the existence of that group. It is much to be wished that a qualified worker should produce diagrams fully comparable with figures 3 or 4. There are two checks on these distributions, one given by figure 34 (Neogene) in comparison with figure 17 (modern North American archaeogastropods); the two distributions are very similar, especially when contrasted with figures 18–22 (meso- and neogastropods). The second is given by figure 35, in which are shown all the *h* and *d* values for every species and almost every variety of fossil in Hudleston's admirably illustrated account of the gastropods of the British Inferior Oolite (1887–96). The classification (see below for discussion) has been brought up to date with the aid of the *Treatise* and of Cox & Arkell's modernization (1948–50) of Morris & Lycett's monograph on the Great Oolite. Figure 35, therefore, gives a diagram comparable with figures 3, 4 and 17–23, but including also (crosses with a black circle at the centre) the probably euthyneuran nerineids and their allies. A comparison of figure 35 with the corresponding one in the fossil sequence, figure 31, for the Jurassic, does suggest at first that by taking only a single species for each genus and subgenus we are losing a considerable amount of the variation in shell shape; but if this is so, it should apply to all the fossil sequence. We may

make comparisons between the diagrams in it while expecting the actual total variation to be larger than is shown. If therefore, from the limitations of the data in the *Treatise* the diagrams are more similar than they should be, we can take any trends visible with some confidence that they are probably more emphatic than as shown here.

(b) Classification of fossil prosobranchs

Before discussing trends in the fossil forms it is necessary to enter on the vexed question of classification. Again, that followed is Taylor & Sohl's, which agrees closely with that in the *Treatise*. Those groups that are undoubtedly archaeogastropod (Pleurotomariaceans, Trochaceans, Neritaceans and their relatives) are in solid black in figures 24–35. These persist to the present day and their classification is based on the anatomy as well as the shell. The probably untorted and very early Bellerophontines are shown by circles with two horizontal bars. The Macluritina, many of them hyperstrophic, seem to be good archaeogastropods but are marked as circles with a central dot, being somewhat aberrant forms. Archaeogastropods (if they are) of dubious subordinal position (Pseudophoracea, Craspedostomatacea, Palaeotrochacea, and especially the Amberleyacea) are shown by open circles; these may have nacre in the shells like true archaeogastropods, but the aperture is often rather or very different and the state of the gills and pallial cavity is a matter for surmise. The problem is particularly acute with the suborder Murchisoniina, the earlier members of which appear from the shape of the mouth to have been dibranchiate; but the shell is high to very high-spired, often very like the mesogastropod Cerithiacea, not nacreous, and in some members with what seems to be an incipient canal indicating a mesogastropod style of irrigating the pallial cavity. This group seems to show forms evolving from archaeogastropods to mesogastropods, and may be ancestral to the Loxonematacea (Ordovician to Jurassic), Cerithiacea (Devonian to Recent), and perhaps the Subulitacea (Ordovician to Permian) which together make up the mesogastropods shown in the diagrams by plain crosses. The group is therefore indicated separately by stippled circles. No neogastropods appear in any of the diagrams, as they are first known in the Cretaceous. No euthyneurans have been shown, except for the very high-spired Nerineacea (cross with black circle) in figure 35 to complete that diagram. For completeness, the very dubious form *Pelagiella*, which may not be a gastropod, is shown in the Cambrian.

Forms accepted in the *Treatise* (although not necessarily by other authorities) as undoubtedly caenogastropod are shown by crosses. As nothing is known of the animals, and the abundance of high-spired shells in the caenogastropods has been noticed for a long time, it may well be asked whether there is a serious danger of a circular argument – that the earlier caenogastropods were characteristically high-spired simply because high-spired fossils were classed as being caenogastropods on that very character, in the absence of anatomical data. Where, however, the aperture does not have a medial slit or notch as in ancient and modern archaeogastropods, and may even have a definite and asymmetrical sinus suggesting irrigation of a single gill, it is not unreasonable to suggest that the form concerned has at least progressed towards the caenogastropod state, and the absence of true nacre (when it can be demonstrated) would tend to confirm the suggestion. This may well have occurred independently in different lines; the discussions by various authors in the *Treatise* should be consulted. In the following discussion the emphasis will be placed on forms certainly archaeogastropod. If the dubious archaeogastropods are included with them, the trends described are merely strengthened.

(c) Trends in h and d scatters

Forms known from the Cambrian (figure 24) are too few to allow firm conclusions, but all are medium to low spired. (No adequate measurements are available for the Helicionellacea.) All the Bellerophontids are planorbis-like forms although with deep whorls and often widely-flared mouth. Their h/d values can therefore be quite high, approaching 1, but the spire angle in all is 180° – even more in those with rapidly increasing whorls, but 180° is taken as the maximum possible value in this paper. The few others seem to group along the bisector, but with two notable exceptions, suggesting considerable variation in h/d. This suggestion is completely confirmed in the Ordovician (figure 25). A few mesogastropods (Loxonematacea, Subulitacea) appear, and the doubtfully placed Murchisoniacea, all of which are high-spired; but the true archaeogastropods also range high above the bisector as well as below. One, *Loxoplocus* (Ordovician
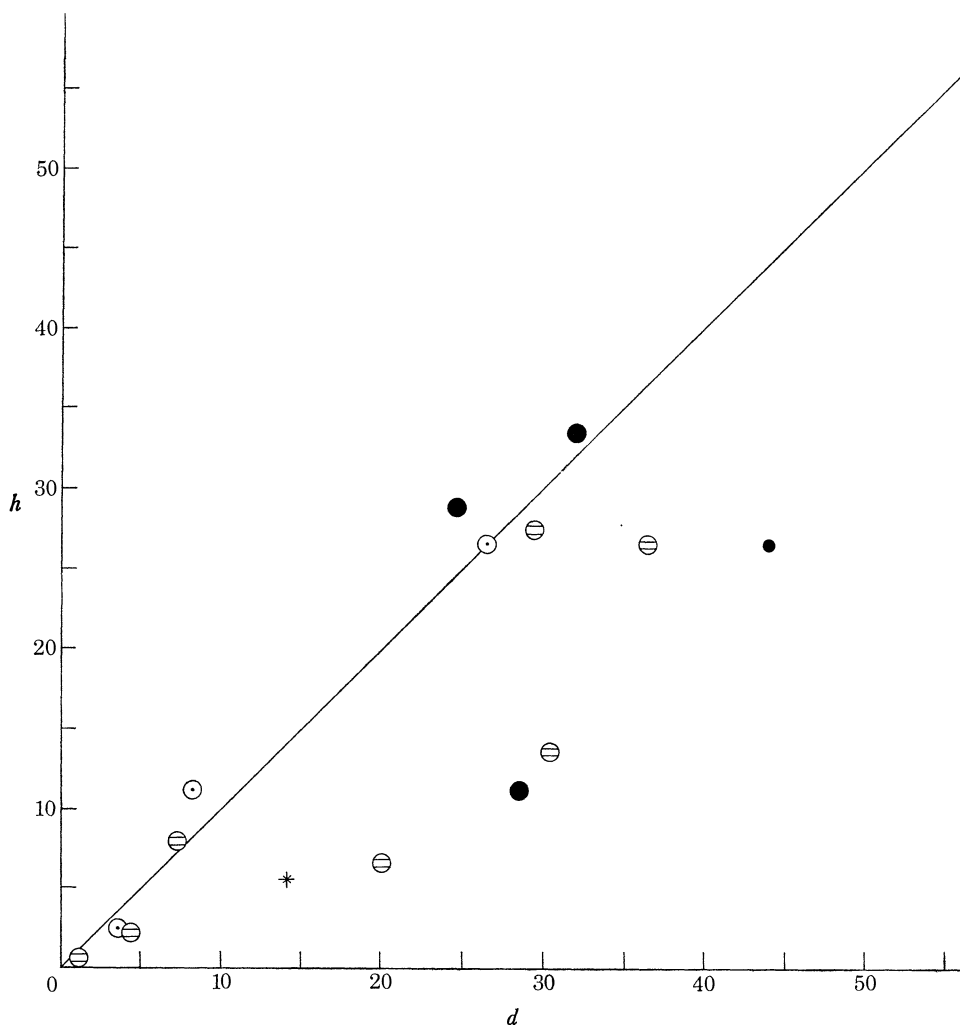

FIGURE 24. Gastropods of the Cambrian of the world; data from the *Treatise of invertebrate paleontology*. The symbols are the same throughout figures 24–34. A large symbol indicates that the species illustrated for a genus or subgenus is from that geological period; a small symbol indicates that a genus or subgenus is found in that period but the species illustrated is from a different period (where it will be found with a large symbol). ⊖, Bellerophontina; ⊙, Macluritina; ●, Pleurotomariacea, etc.; ◉, Murchisoniina; +, Mesogastropoda; ○, doubtful archaeogastropods; ✳, *Pelagiella*.

and Silurian), even has a spire index of 3.2 but is far too large (145 mm; 45 mm) to appear on the diagrams.

The black symbols (true archaeogastropods) in figure 25 have a far wider scatter than in the Cretaceous, Palaeogene, and Neogene (figures 32–34) or at the present day (figure 17). A similar wide scatter appears in the Silurian, Devonian and Carboniferous (figures 26–28) but with fewer above the bisector, and with a tendency for a concentration of symbols below $h = d = 20$ mm. These trends are taken further in the Permian and Triassic (figures 29, 30). A greater scatter appears below the bisector in the Jurassic (figure 31) especially in the larger shells and this is confirmed in figure 35. Thereafter, the scatter is more or less as in modern
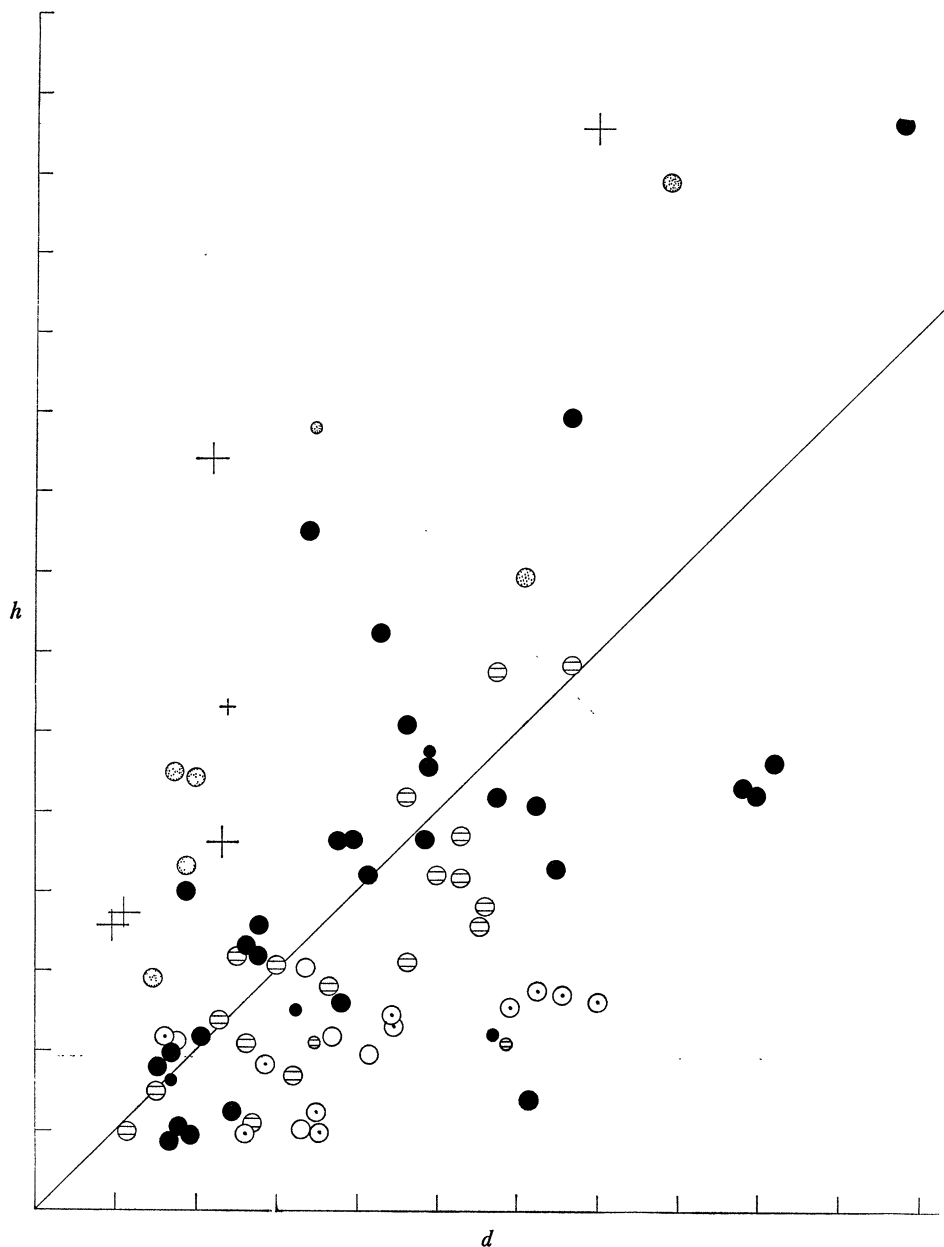

FIGURE 25. Gastropods of the Ordovician.

American forms. In the Eocene occurs the extremely high-spired *Velainella* (figure 33), and in the Miocene *Sinzowia* (figure 34). Of these very high-spired archaeogastropods, *Loxoplocus* is a pleurotomariacean, *Velainella* and *Sinzowia* unrelated Trochaceans.

Generally speaking, the doubtful archaeogastropods except the Murchisoniina run well below the bisector or close to it, but with outstanding exceptions. Thus in the Craspedostomatacea, the Codonocheilidae (Silurian to Jurassic) are mostly fairly high-spired; and *Westerna gigantea* (Devonian, Palaeotrochacea), too large to show on the diagrams, is about 160 mm × 60 mm, *h/d* nearly 3 and spire angle about 25°. In the Macluritina, while most are low-spired, the Onychochilidae are close to the bisector or above it, *Sinistracirsa* (Devonian) well above it. (These forms are hyperstrophic and for complete consistency should be shown
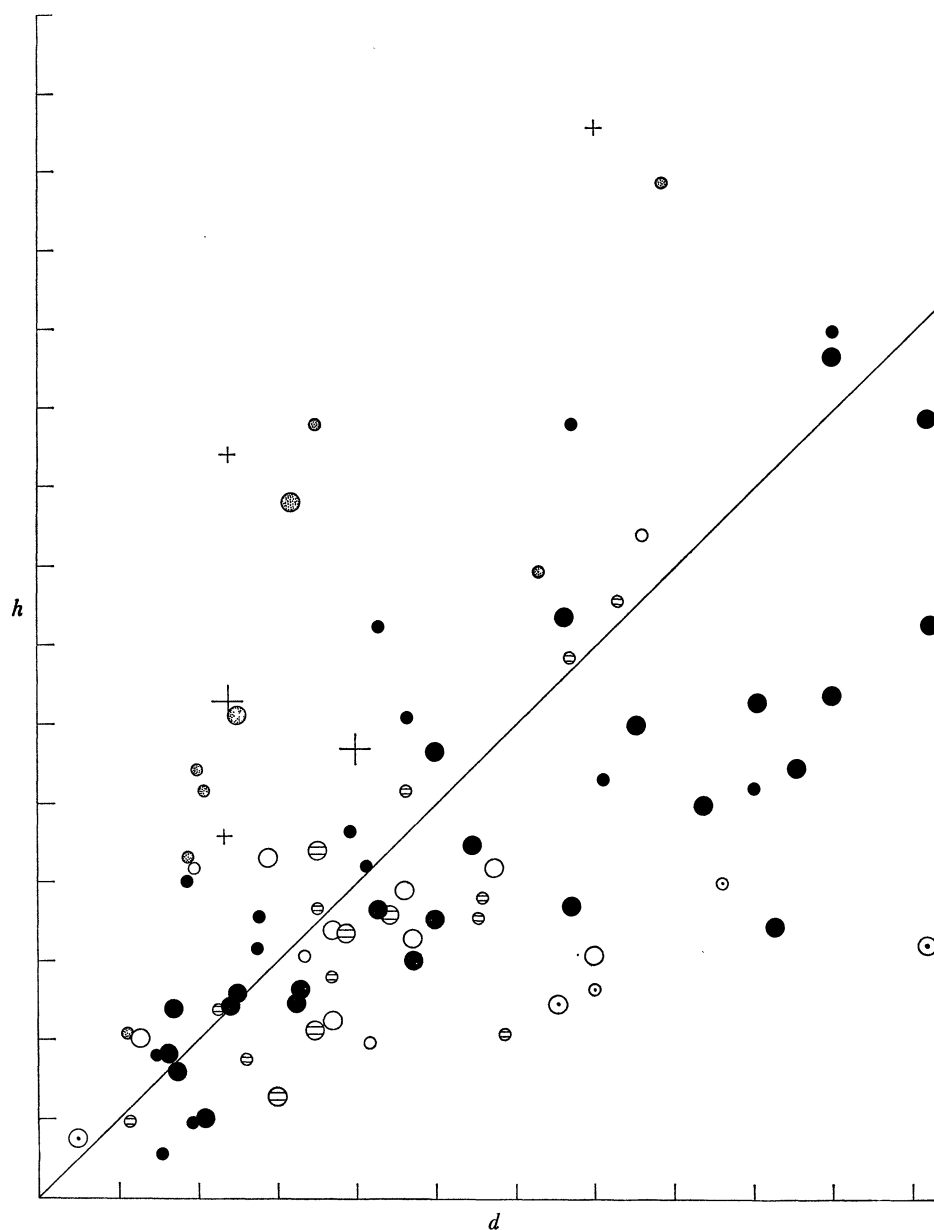

FIGURE 26. Gastropods of the Silurian.

well below the x-axis; in this paper all hyperstrophics are treated as orthostrophics.) The Amberleyacea (Triassic to Oligocene, the principal dubious archaeogastropods in figures 30–32) are usually high-spired. The Murchisoniina are almost all very high-spired, a few only being near the bisector except at their last appearance in the Triassic (figure 30). Several groups, therefore, of true archaeogastropods and dubious ones have produced high-spired forms independently and sporadically.

All the mesogastropods and their close relatives among the dubious archaeogastropods in the Palaeozoic were fairly to very high-spired, although a few approached the bisector. None are certainly known from the Cambrian, and few, mainly Murchisoniines, from the Ordovician,
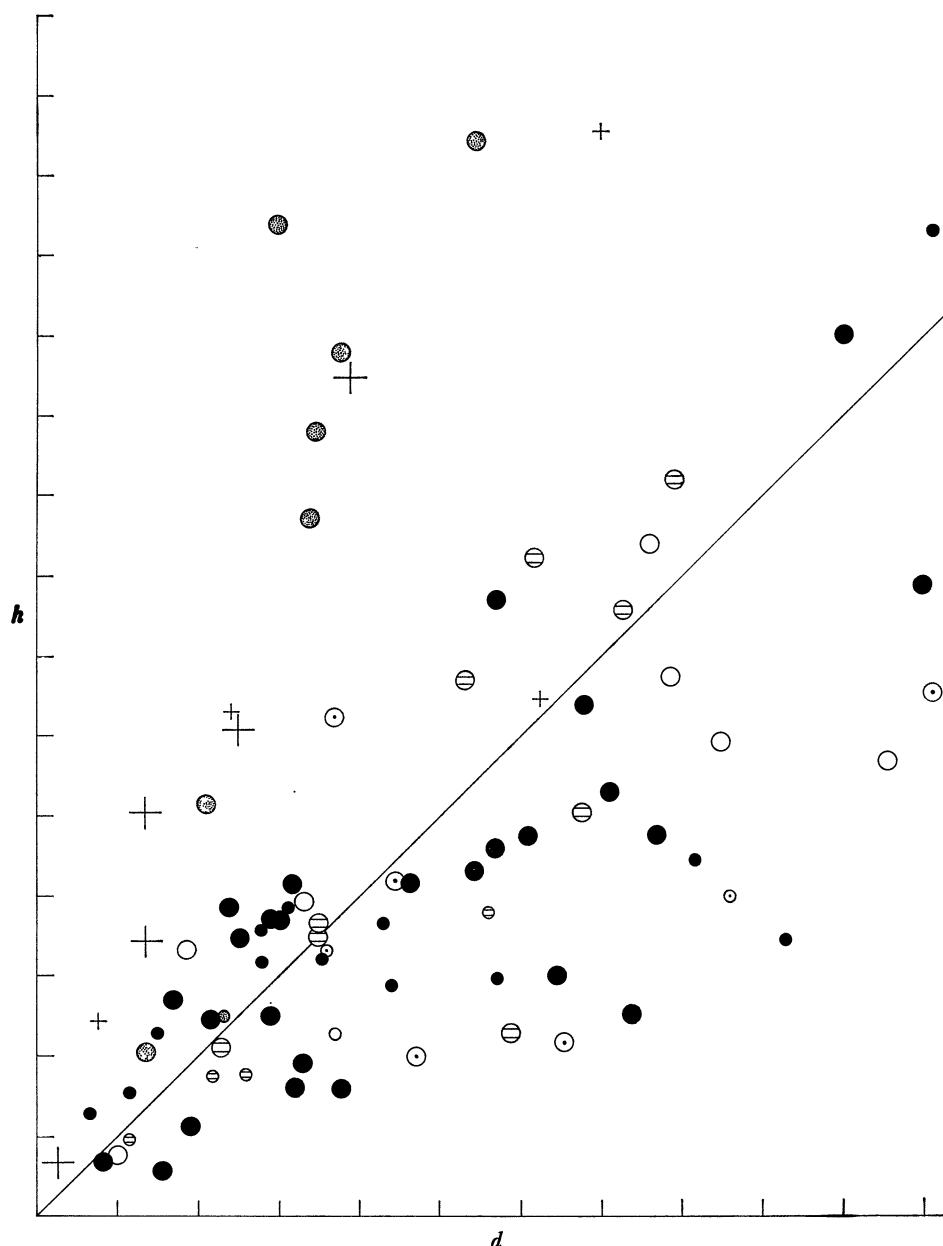

FIGURE 27. Gastropods of the Devonian.

Silurian and Devonian. In the Carboniferous those assigned to the mesogastropods (crosses) become more conspicuous, with one or two approaching the bisector closely. In the Mesozoic and Tertiary they are in fact abundant (but not shown in the diagrams for lack of the comparable data), and figure 35 indicates this clearly for the (Jurassic) Inferior Oolite fauna of Britain. At this period the Nerineacea (Euthyneura) were also well represented (as were Actaeonids). The impression given by this figure is that high-spired and moderately high-spired forms were well represented by Nerineaceans, Cerithiacea and Purpurinids (Littorinacea) in order of decreasing spire index; the doubtful archaeogastropods at this time were almost entirely Amberleyacea, and ran just above the line. Along the line and below it are archaeogastropods
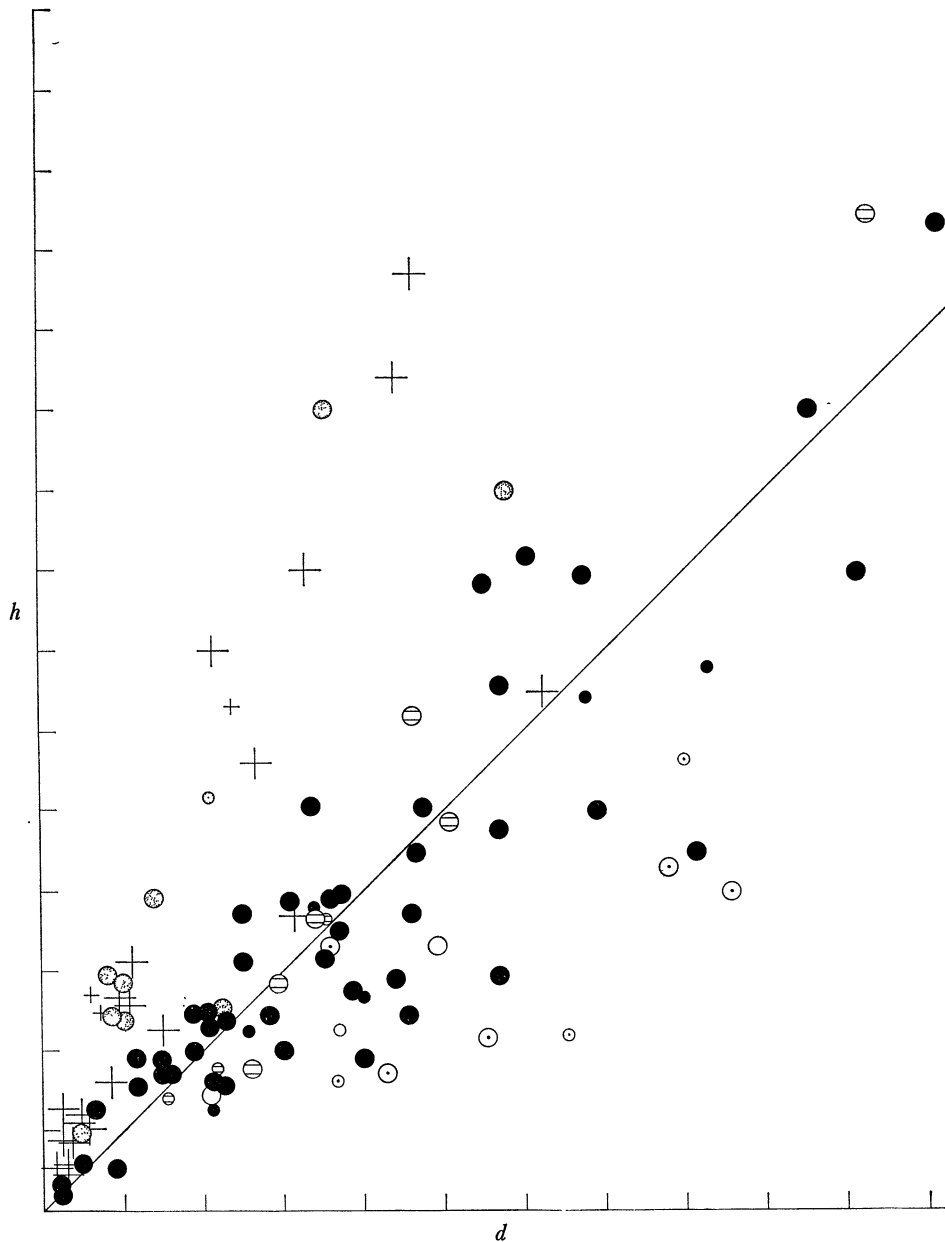

FIGURE 28. Gastropods of the Carboniferous.

except that the last remaining Macluritines, and a crossostomatid (Craspedostomatacea) supply the smaller flattest shells, and a single *Cirrus* (Amberleyacea) one of the larger ones. In short, it would seem as though the archaeogastropods, diverse in the early Palaeozoic were restricted to equidimensional or flatter shells when the Murchisoniines and mesogastropods appeared but produced high-spired forms sporadically. Moreover, there seems to have been a reduction, at least after the Carboniferous (with a possible brief exception in the Jurassic) of the numbers of kinds of very flat shells generally. This reduction, and present restriction, is pointed out by Vermeij (1975).

 If we combine the diagrams for the present North American marine fauna (17–23), we get much the same picture as in figure 35, and nearly that in figure 28, although with different
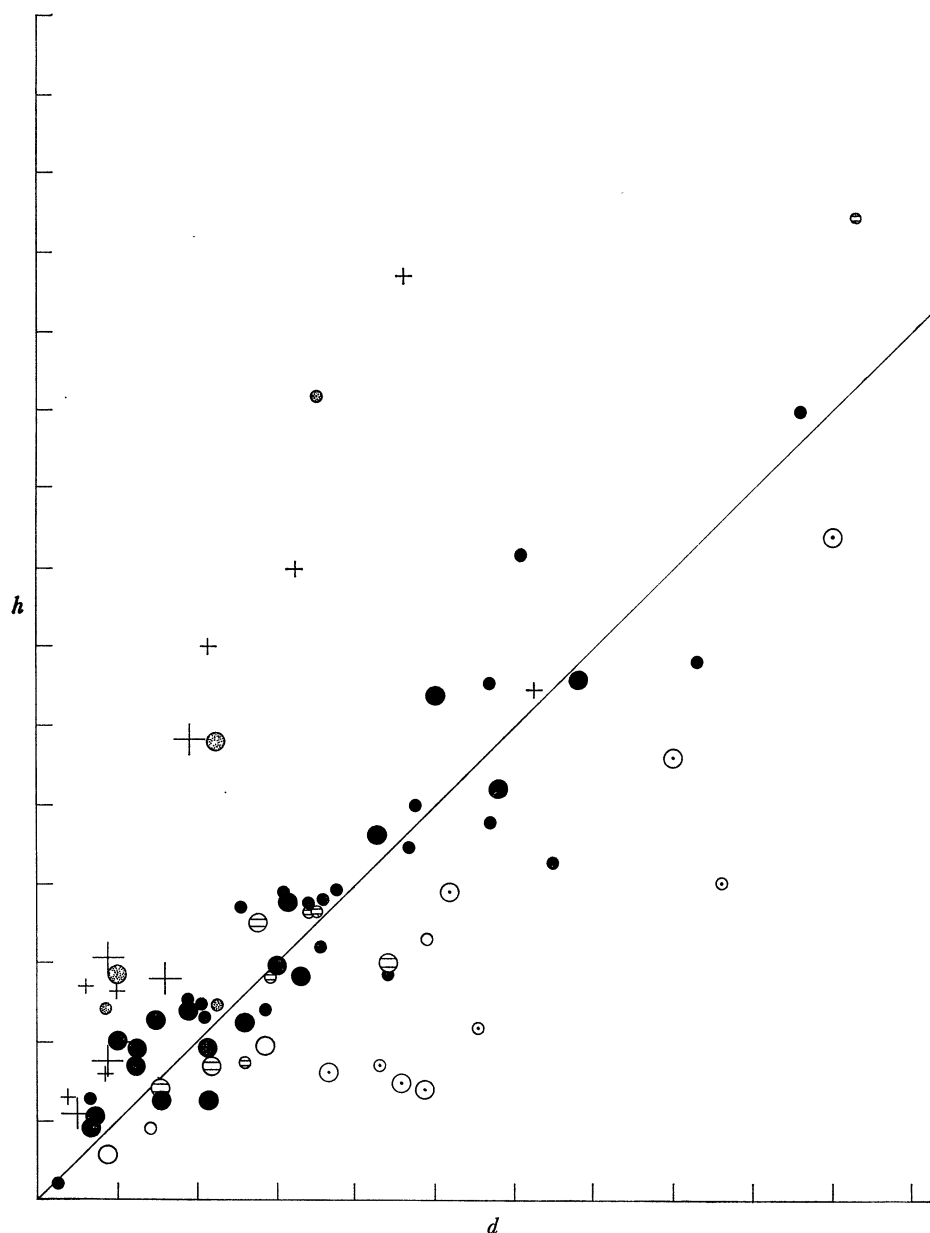

FIGURE 29. Gastropods of the Permian.

taxonomic groups. Mesogastropods (at present with neogastropods as well) occupy the space above the bisector, archaeogastropods are ranged along it, and below it there is a remarkable mixture of different forms, occupying more of the space in the Palaeozoic than at the present day. In the Carboniferous, the flatter shells are true archaeogastropods, Macluritines, and doubtful archaeogastropods, as they are in the Jurassic. At the present day they are a few archaeogastropods and mesogastropods, the possibly euthyneuran Architectonicacea, and the certainly euthyneuran *Cyclostremella*. There seem to have been far greater opportunities for flatter shells in the early Palaeozoic. There were two very different types of these in the Palaeozoic. The Bellerophontines were untorted and, having a pair of symmetrical retractor muscles, probably carried the shell vertically. Present-day gastropods with disk-like shells normally
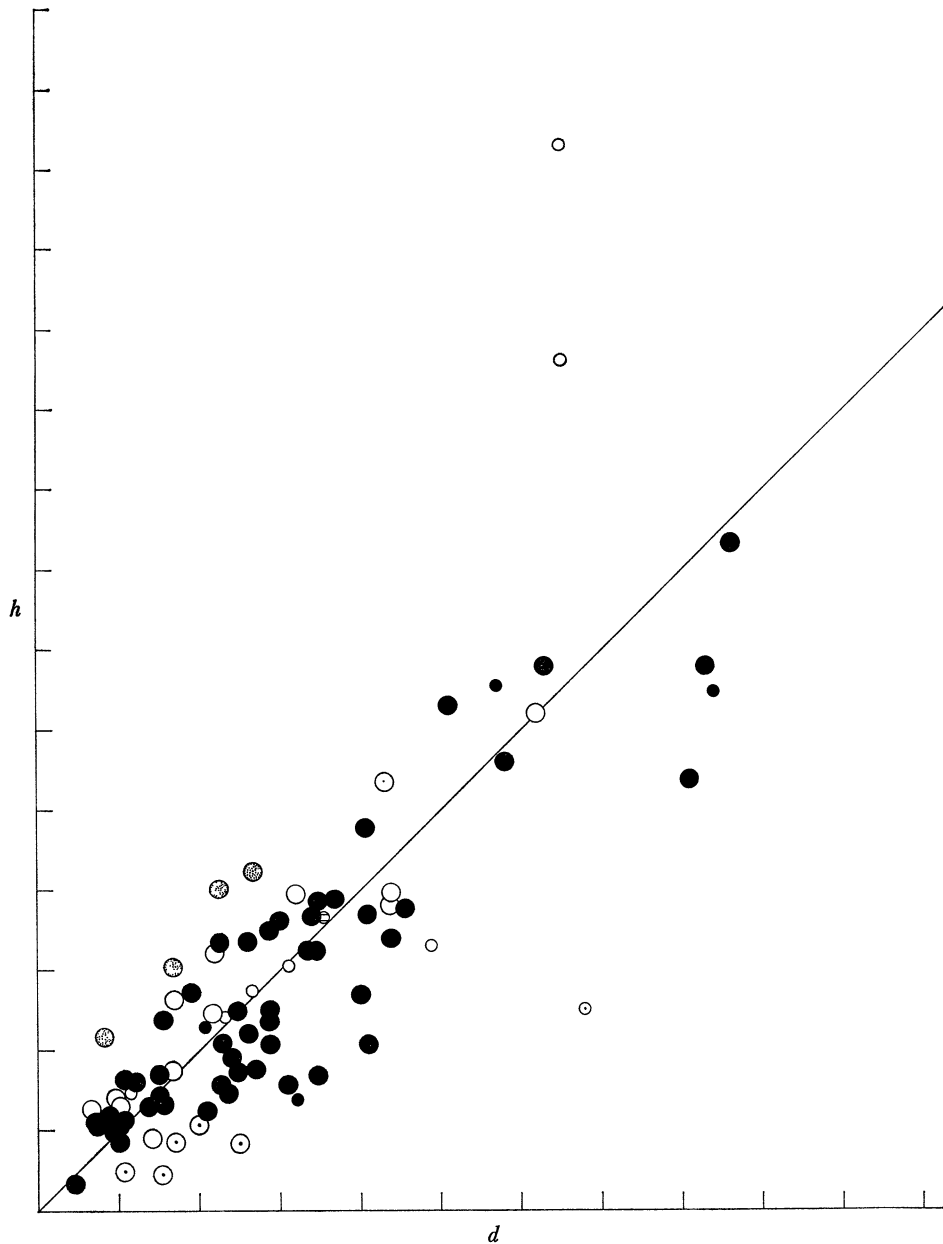

FIGURE 30. Archaeogastropods and related forms of the Triassic.

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carry them horizontally, with the axis of maximum diameter parallel to the horizon, and the emergent animal making a bend through 90° to put its foot on to a horizontal surface; some freshwater forms, however, buoyed up by the water, may occasionally carry them vertically. Figure 36, which gives a frequency distribution of θ' for all the fossil and recent subgenera figures in the *Treatise*, shows that the decrease in flattened shells after the Palaeozoic was due to a decrease in both Bellerophontines and in other archaeogastropods as well, not merely to the decrease and extinction of the Bellerophontines. Besides the Bellerophontacea (Cambrian to Triassic), the Macluritidae (Ordovician and Devonian), Euomphalacea (Ordovician to Cretaceous), many Pleurotomariacea until the Mesozoic, the Oriostomatacea (Silurian and
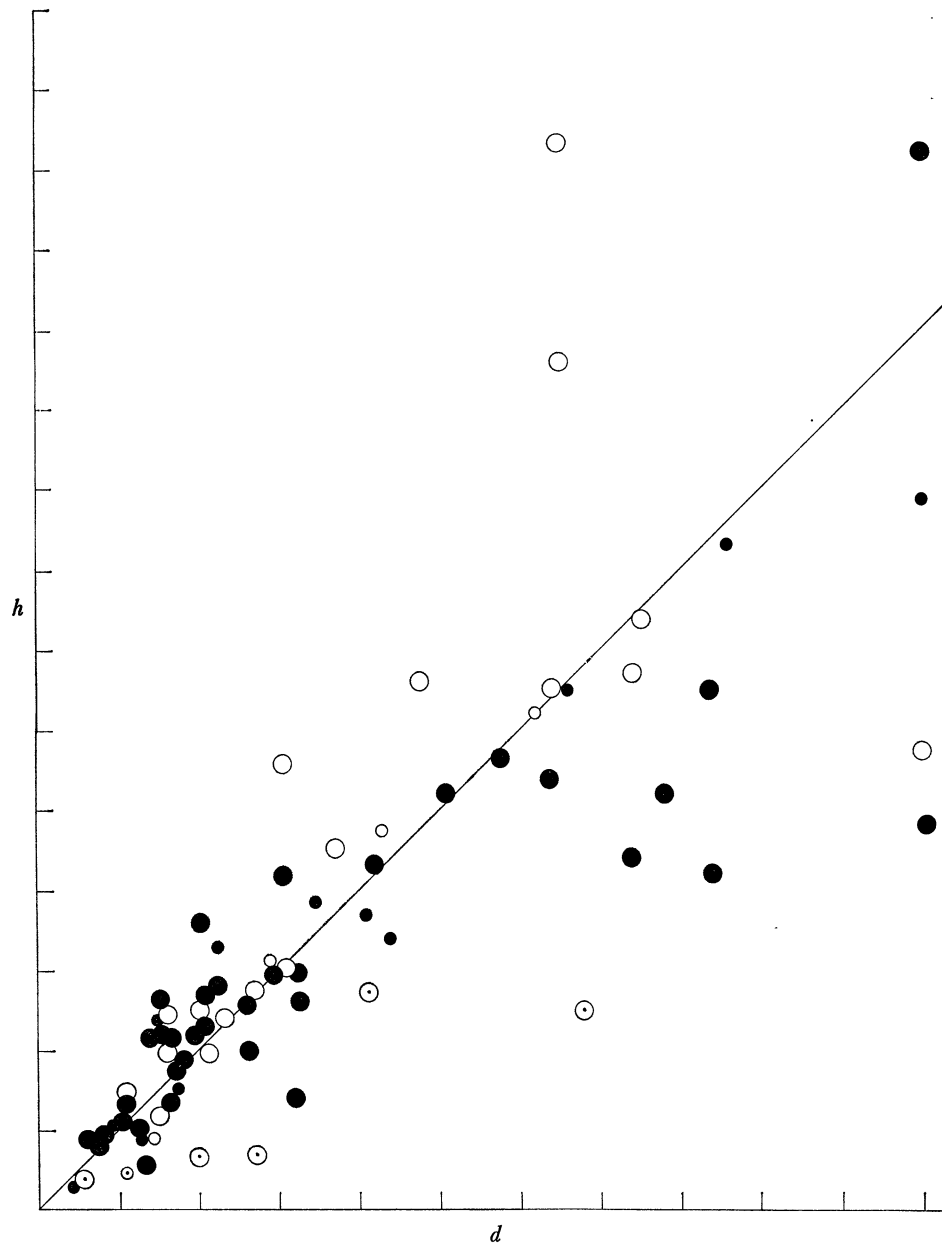

FIGURE 31. Archaeogastropods and related forms of the Jurassic.

Devonian), and among doubtful archaeogastropods the Pseudophoracea (Ordovician and Silurian) and the Craspedostomatacea, had some or many flattened forms in the Palaeozoic.

In figure 36, the bisector on the previous diagrams corresponds roughly to spire angles of between 60° and 90°, which are indicated in this figure on the x axis of each separate distribution. The wide spread of true archaeogastropods in the early Palaeozoic can be seen to narrow down considerably later, with only sporadic occurrences of very high-spired or low-spired shells. Naturally, far more genera and subgenera are known for the Recent than from the Palaeogene or Neogene, but, making allowance for the difference in numbers, there is little change in the distribution after the end of the Palaeozoic.
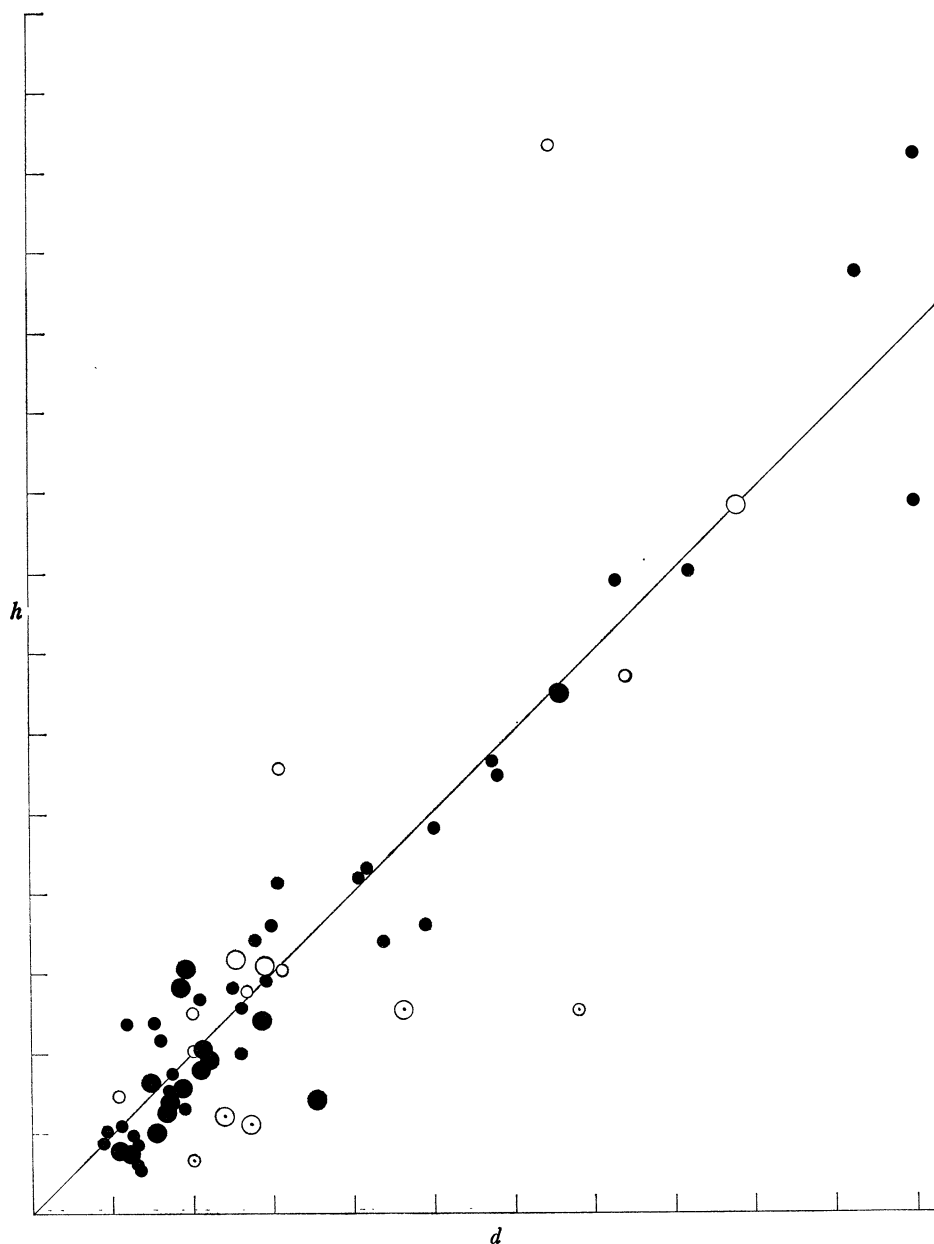

FIGURE 32. Archaeogastropods and related forms of the Cretaceous.

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In the same figure, the Murchisoniines are shown with stippled squares, and the Palaeozoic caenogastropods with circles below the x-axis; their predominantly very small values of θ' are in contrast to those of the true archaeogastropods and extend the distributions markedly to the left. As can be seen from figure 35, this effect would be much more marked in the post-Palaeozoic if the data were available. Again it seems that when the Murchisoniines and caenogastropods flourished the archaeogastropods were reduced in variation away from high-spired forms towards equidimensional ones; their withdrawal from the other limit of variation coincided with the decrease in flat shells generally remarked on above, which is evident in the present prosobranch fauna (figures 17–23).
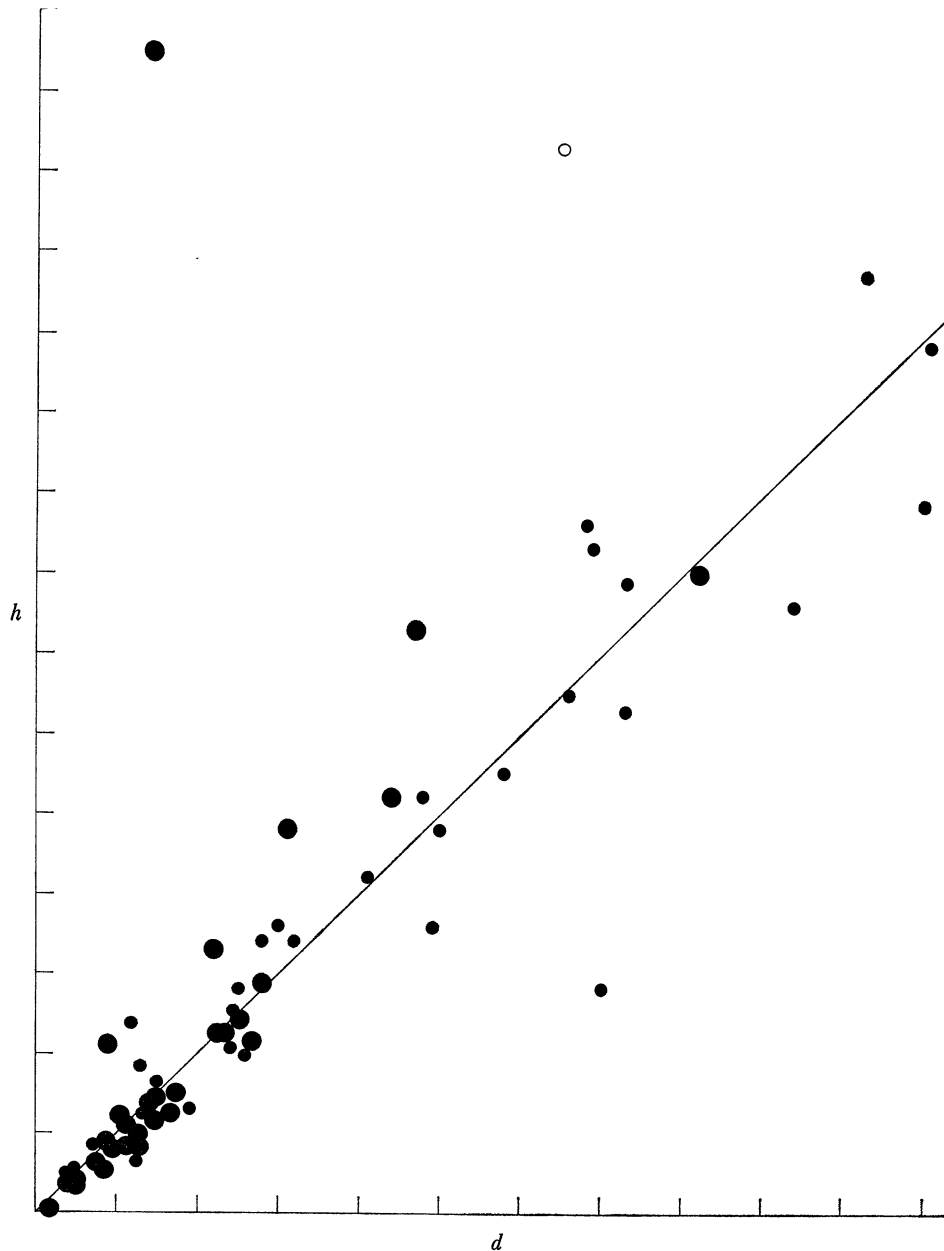

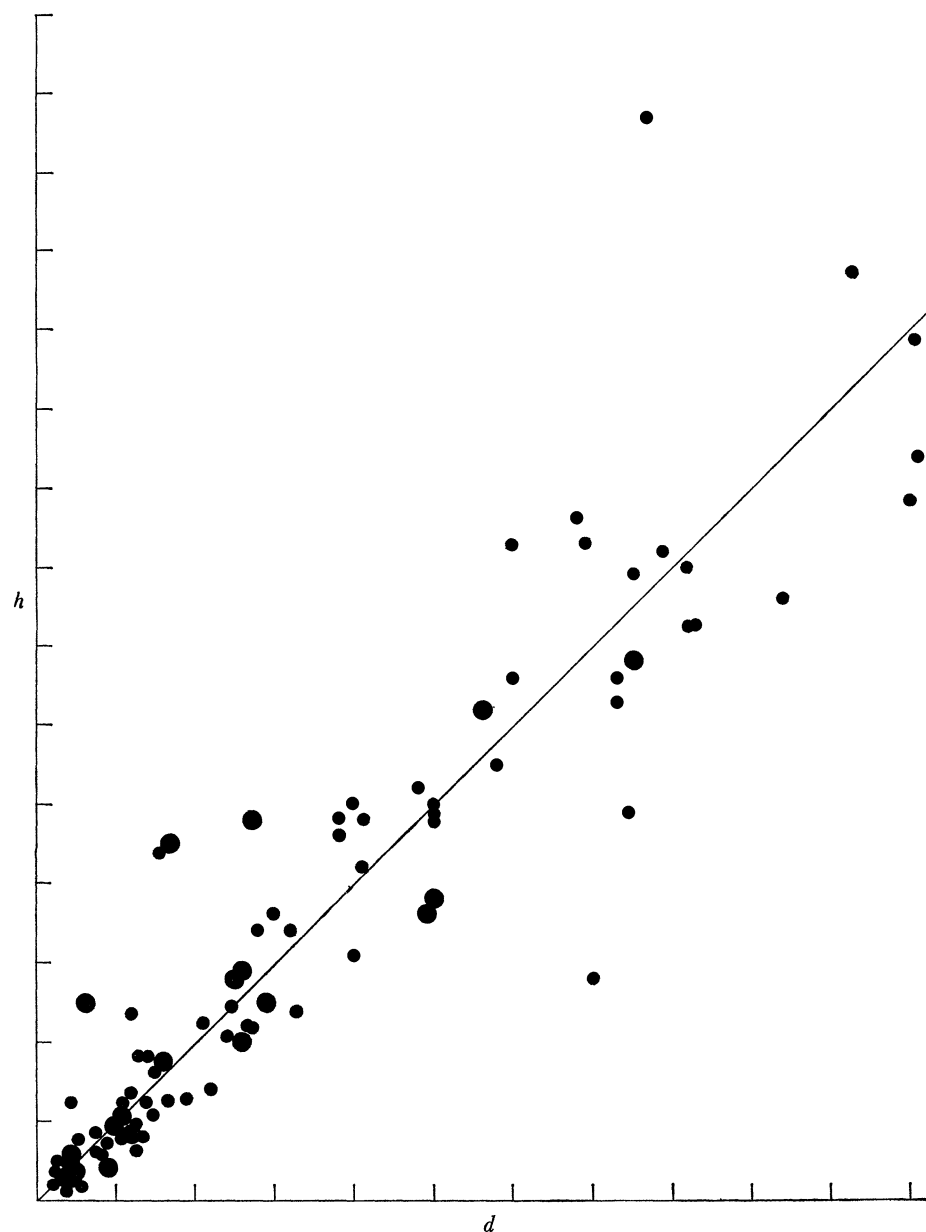FIGURE 33. Archaeogastropods and related forms of the Palaeogene.

FIGURE 34. Archaeogastropods and related forms of the Neogene.

8. DISCUSSION

(a) The distributions and selection

The foregoing diagrams have shown that (i) the distribution of h/d, (and of θ' where it has been investigated) is far from random within a fauna, (ii) it is often characteristic of major taxonomic groups although widely different values of h/d can occur in most of them, (iii) these variations can occur within major or minor taxonomic groups, and (iv) if all holocleid, free-crawling polygyres are taken together, almost any value of h/d may be found. Moreover (v) there is some evidence from fossils that the range of h/d of the archaeogastropods may have

been restricted when the mainly high-spired caenogastropods arose but (vi) there seems to have been a general reduction in planorboid marine shells after the Permian. These findings are sufficiently obvious from the diagrams, even though the data used are not properly comparable throughout.

The striking non-randomness of the distributions can only be produced by natural selection, which could be primarily external, related to features of the ecologies of different forms, or primarily internal, determined by mechanical or physiological considerations dictated by the

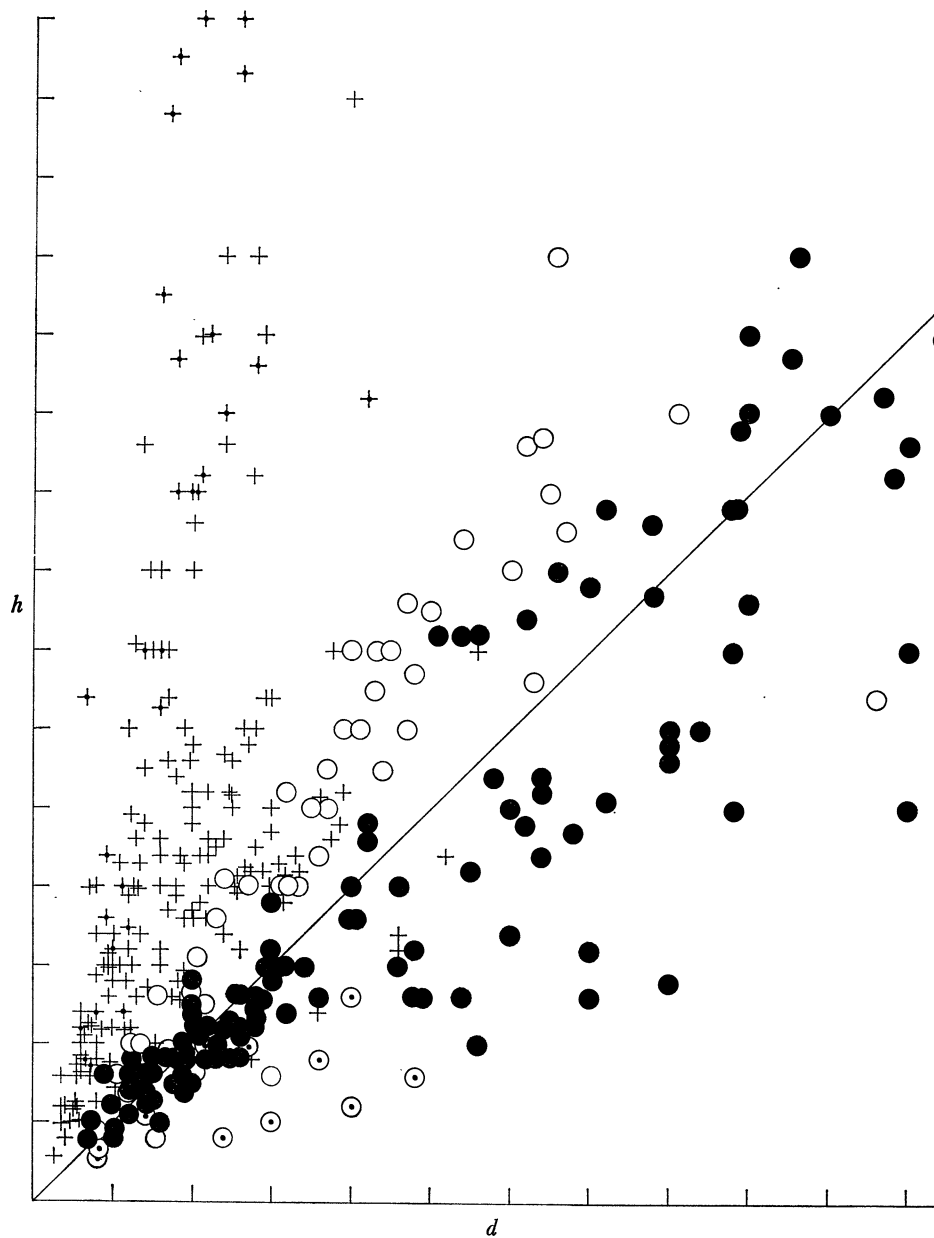FIGURE 35. All prosobranchs from the Inferior Oolite of England, data from Hudleston, plus Nerineacea, cross with central black spot. Other symbols as in figures 24–34. (Plain crosses below the bisector are Xenophoridae.) All measurements of those mesogastropods (Aporrhaids, etc.) with spines or flanges are of the body of the shell only, and correspond to the adjusted measurements of figure 19.
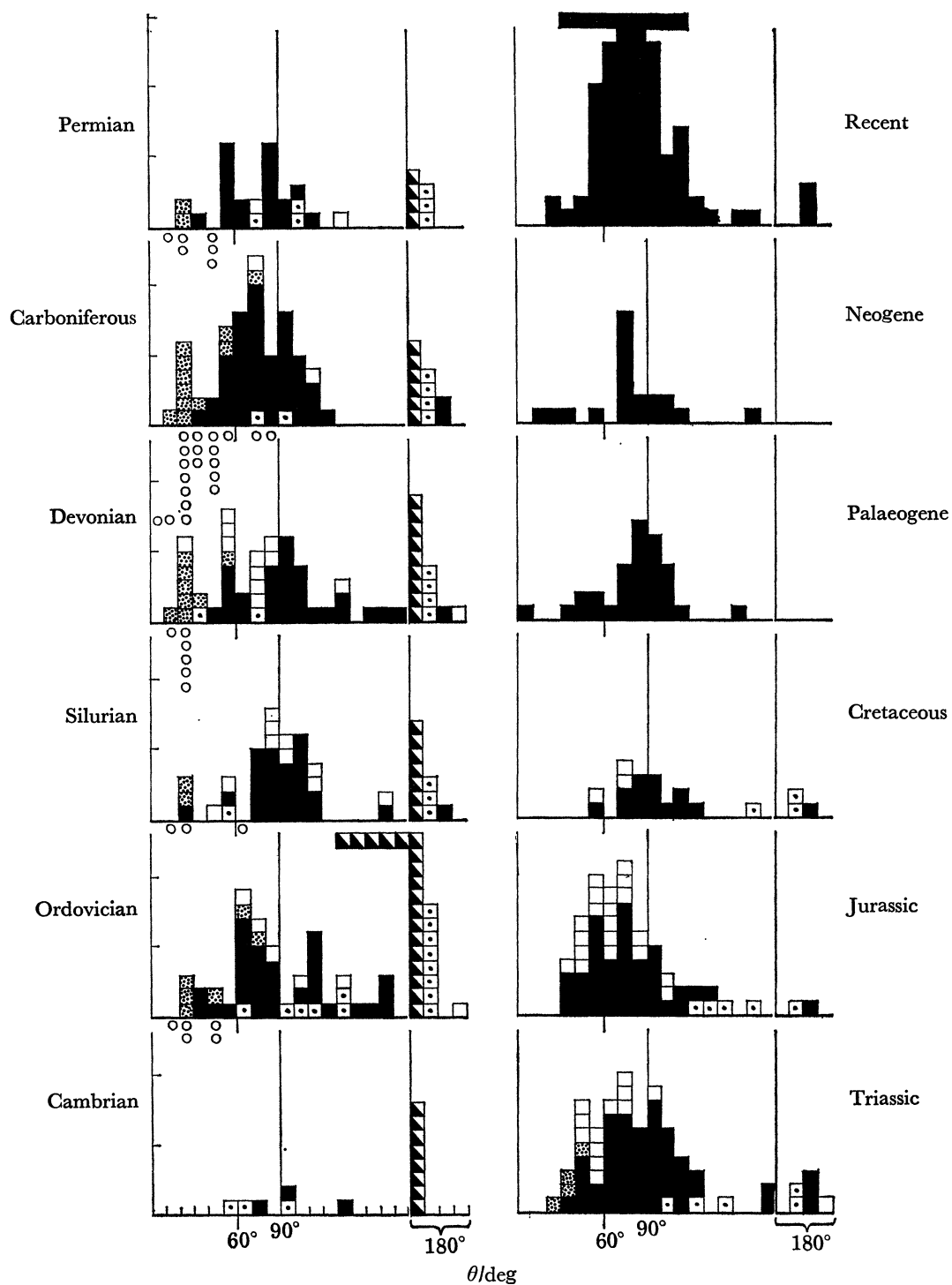
FIGURE 36. Frequency of spire angle of all subgenera in figures 24–34, plus Recent forms, data from illustrations in the *Treatise*. Shells with $\theta' = 180°$ on the right of each diagram; caenogastropod species (Palaeozoic only) given in the *Treatise*, circles below the x-axis. ◨, Bellerophontina; ⊡, Macluritina; ■, true archaeogastropods; □, dubious archaeogastropods; ▨, Murchisoniina.

organization of the animal irrespective of wide variation in ecology. This second possibility is ruled out by the nature of the variation found; although, as already said, certain ranges of h/d may be characteristic of large taxa, there are quite enough exceptions to show that there is no necessary relationship between being (say) an archaeogastropod, a helicelline, or a urocoptid, to take only these few examples, and having a particular shape of shell. But if there is no necessary relationship, then what keeps the shape within narrow limits in the majority of archaeogastropods, or all the neogastropods, or Clausiliids must be external selection.

It is not possible to attribute the characteristic distributions in the land-snails (for example) to historical events; it would not be easy to find a historical explanation producing the same effect on the faunas of Europe, North America, Puerto Rico, and New Caledonia. Even if one postulated that faunas before the glaciations of the Pleistocene showed a much more uniform spread of spire index (which is certainly not true), and that extinction was highly selective, or that extinction was near-total, and subsequent immigration was highly selective, the characteristic distribution would be produced by selection, not by history *per se*.

Equally, if it were thought that the present distribution of h and d for archaeogastropods were produced by historic events in the Permian, a time when there was vast extinction in many marine groups, it would be necessary to explain the remarkable constancy of that distribution ever since, about 200 million years, *plus* the sporadic appearance of very high-spired and low-spired shells. The assertion of total neutrality of shell characters, however, would not explain the characteristic distributions of h and d, repeated in different taxonomic groups and faunas, of the land snails.

(b) Broad ecological deployment

There is nothing in the broad ecological deployment of those gastropods considered here to suggest a reason for shell shape. For so many marine forms nothing is really known of their ecology, but the land-snails are more open to investigation. On the hot sand dunes of the Mediterranean coast near Montpellier, I have collected within a few feet of each other the high-spired *Cochlicella acuta*, the trochoid *Helicella pyramidata* and the flat *Helicella explanata*; on dunes in the west of Ireland one finds *C. acuta* again, the near-globular *Cepaea nemoralis* and *Helicella itala* or *caperata*, both with depressed shells. Under the same stones in wet rather acid areas of the western Pennines, the only shells not minute are the high-spired *Cionella* (= *Cochlicopa*) *lubrica* and the disk-like *Discus rotundatus*. Associations of species characterized by Germain (1930) as hygrophile, xerophile, of wet meadows, of sand-dunes, of rocks exposed to the sun, of dry meadows and of woodlands, all contain both high-spired and low-spired species. Habitats favourable to snails (highly calcareous) have more species than others, but even in the inimical habitats of the semi-acid Pennines both a flat and a high-spired species occur.

It is of course true that most species of snail when active are nocturnal or at least crepuscular, while conchologists are largely diurnal. Perhaps it is true that when they emerge from under their stones *Cionella lubrica* and *Discus rotundatus* betake themselves to different foods or feeding places. There seems no great differences between long thin shells and flat broad ones when it comes to lurking under a stone, and both species appear to be non-specialist feeders, although not enough is known about their food in the wild. But if the shell shape produces either a preferred mode of locomotion, or a preferred type of surface (e.g. horizontal as against vertical) on which to move, or the one leads to the other, it might well be that in difficult environments only snails of markedly different shell shape can coexist. It is possible to imagine species competing for available calcium, but since shells of any shape can be thickwalled or thin, hardly for

shell shape. If, however, shell shape predisposes to places of locomotion and therefore food, one can believe that species with shells of very different shape (or size) may come less into competition than those with similar ones.

If there is or has been some competition between species with shells of similar shape and size, then among those of similar diet (excluding food specialists) there should be some mutual exclusion of h/d or $(h+d)$ values. This can be tested properly only on data produced by taking random samples of all shells (or all those of a certain broad size-range) in numerous localities each so restricted that the species are certainly together in an ecological sense and could compete; some exclusion could then be found. The data for this do not exist. However, an approach can be made, less satisfactorily, via figures 6, 7 and 8.

Since in figures 3 and 4 the two clusters are continuous along their respective groups of radii, the same bimodality holds at all observed heights of shell, and we can discuss minute shells, medium-sized ones, or large ones, with the same results in this context. Some taxa contribute to the continuity of each distribution not along a radius but across a broad arc. Thus the larger European Helicines (figure 6, open circles) spread right across the lower distribution and even cross the bisector (compare also figure 7, large open circles). The Tacheocampylinae (figure 6, circles with a vertical bar) and Murellinae (figure 7, stippled circles) also tend to show an arclike rather than a radial distribution. Sometimes, one family continues the distribution of another outwards or inwards radially. In figure 6 the Chondrulines and then the Pupillids successively continue the upper distribution downwards, and the Vertiginids (figure 8 circles with a horizontal bar) bring it even closer to the origin. The Endodontids show a discontinuity of distribution like those of the Helicellines and Helicigonines, but along a single distribution (figure 8, black circles); the small ones (*Punctum*) are those of the lower distribution nearest the origin, partly overlapping with Valloniines, and the large ones (*Discus* and *Goniodiscus*) are scattered among Zonitines and Fruticicolines. In several cases, taxa run along nearly adjacent radii without obvious overlap; for example in figure 6 the Clausiliids (large crosses), and Enines (circles with a cross) in the upper distribution, and to a large extent, although with a little overlap, the Zonitines (small cross) and Helicellines (circle with central dot) in the lower distribution. A few groups are largely coincident, for example the Fruticicolines (figure 7, circle with vertical bar) and Helicellines (figure 6, circle with central dot), or the Helicodontines (figure 7, circles with central dot) and some of the Zonitines (figure 6, small crosses). Similarly in the upper distribution the Chondrulines overlap to some extent with the Clausiliids and Enines (figure 6), and the three Cionellids and the orculids extensively with several families.

Nevertheless, considerable areas in all three diagrams are characterized by symbols consistently of one type. If we take the actual pairs and values of h and d and assign them by random numbers to the same numbers of species of each family and subfamily, we get a far more spotty distribution, with very little consistency in areas, and far more representation of the larger taxonomic groups in both distributions, than is actually seen in the west European fauna.

It is also worth noting that of the Helicid subfamilies that overlap extensively, the helicodontines are largely high-mountain forms, the helicellines forms of very short vegetation, usually hot and dry, and the fruticicolines somewhat intermediate; a close ecological scrutiny might show that they overlap seldom ecologically.

In the North American lower scatter there is a much greater degree of overlap than in the western European. However, the area and ecological diversity of the United States is far greater

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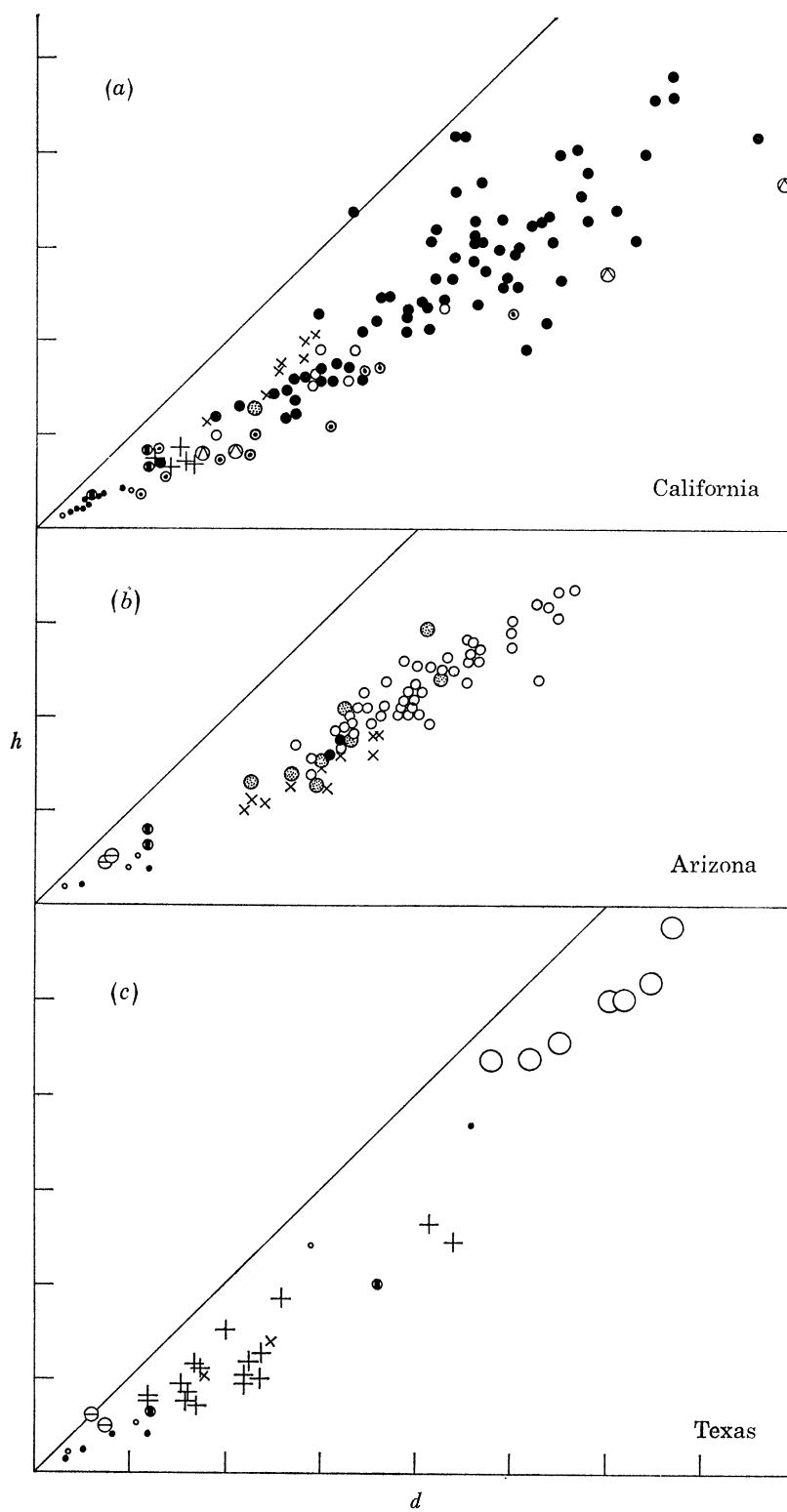
FIGURE 37 (*a–c.*) For description see opposite.
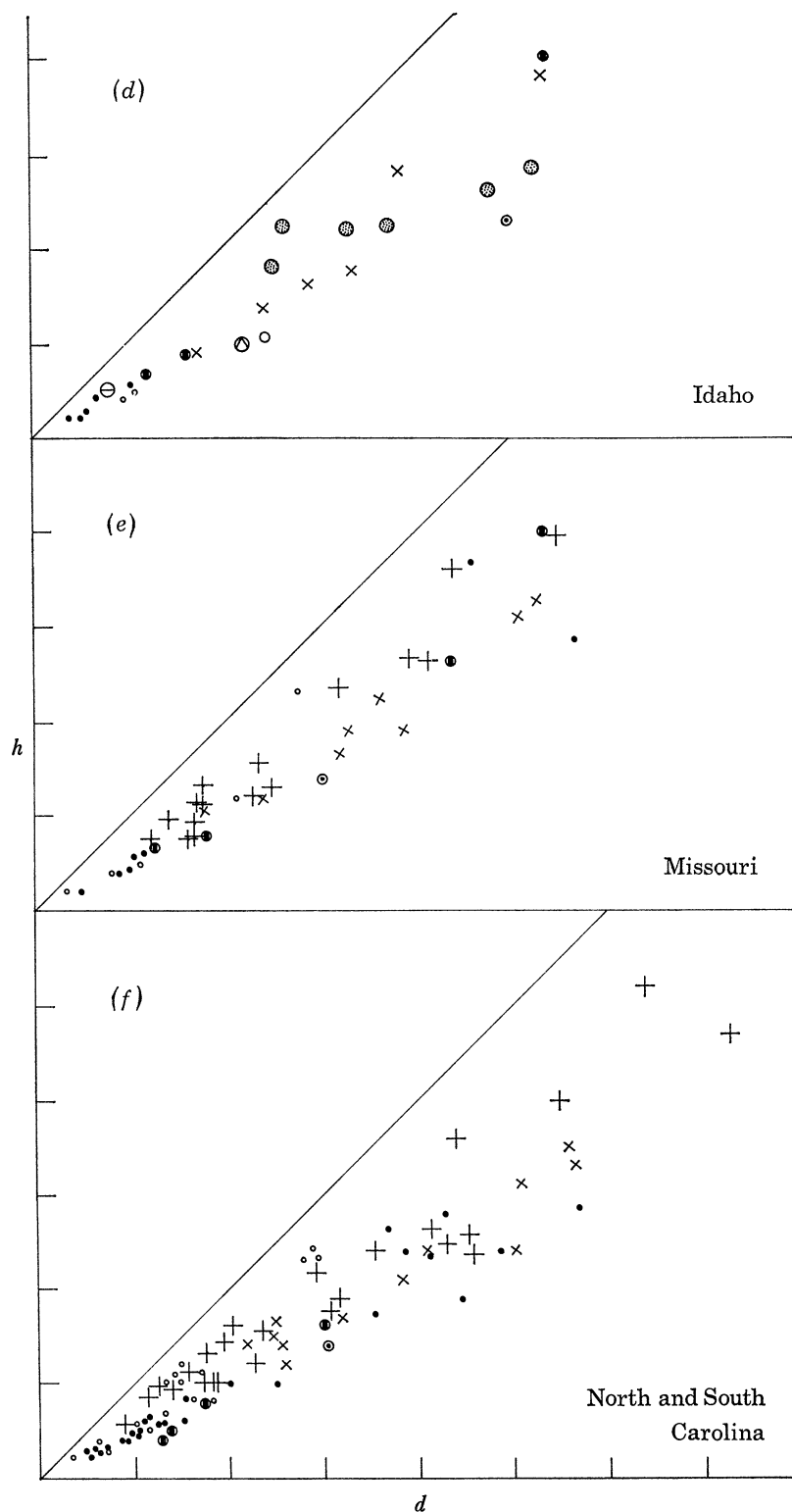
FIGURE 37. Taxonomy of the lower cluster of terrestrial stylommatophorans of North America, by states; (a) California; (b) Arizona; (c) Texas; (d) Idaho; (e) Missouri; (f) North and South Carolina. ●, Zonitinae; o, Gastrodontinae; ●, Helminthoglyptinae; ○, Sonorellinae; ○, Humboldtianinae; ◑, Endodontinae; ⊙, Haplotrematidae; ◉, Oreohelicidae; ⬡, Ammonitellidae; ⊖, Thysanophoridae; +, Polygyrinae; ×, Triodopsinae. The very small Valloniinae, Helicodiscinae and Punctinae, which are common to all, are omitted, as are the equally tiny Euconulidae and Strobilopsinae of all but the far west. These form a small scatter almost at the origin.

than that of the British Isles, France and Germany, and it might well be that some of the overlap in the overall diagram is caused by geographical representation. Accordingly, the states of California, Washington, Texas, Missouri, Wisconsin, and Florida, and the groups North and South Carolina and Massachusetts and New Hampshire and Maine were chosen as geographically separate and sampling the ecological diversity; to these were added Idaho, Wyoming, Colorado, Arizona and New Mexico to give a better representation of the faunas of the mountain states. The data were taken, again, from Pilsbry, and this time, if there seemed to be a marked trend in size and shape of shell within a species from one state to another, different values for h and d were taken from the *Monograph*; only one pair of values, however, was used for each state, even though it might contain several subspecies. In several states it is likely that the fauna is still not well known, especially the smaller species; attention has been concentrated therefore on shells with one or other measurement greater than 10 mm.

Much of the overlapping is removed by concentrating on one state at a time, especially in the south and southwest (figure 37). Thus a great deal of the lower cluster is made up from helminthoglyptines in California (*a*), from sonorellines in Arizona (*b*), from oreohelicines in Idaho (*d*), Wyoming and Colorado, from polygyrines and humboldtianines in Texas (*c*), from polygyrines in Florida, from zonitines, triodopsines and polygyrines in the Carolinas (*f*). In these last, there is again some suspicion of ecological separation, with the zonitines principally in the mountains. New Mexico is close to Arizona, but with a much larger representation proportionally of triodopsines. Intermediate states and groups show a very considerable mixture and overlap (Wisconsin; Missouri, *e*) as do Washington (into which the Columbia River Valley is well known to bring a proportion of eastern forms), and the Massachusetts–New Hampshire–Maine group, which appears to have been colonized by a mixture from the states to the south. These findings are in good agreement with the accepted biogeography and present climatic zones of the U.S.A. It is probable therefore that those states or groups with mixtures have a mixture of habitats and local climates to correspond, and that overlapping elements will again be found not to overlap extensively when their habitats are determined with more accuracy. The rather scanty data in Pilsbry hardly allow of further analysis, but do suggest that this is the case.

(c) *Size*

While variation in shell shape may indicate a different mode of progression, variation in size can hardly do so. Yet, as shown above, whole families may replace one another in size along a cluster. Here, the question of lurking-places may be of importance: a Vertiginid a millimetre long may be able to find a hiding-place (and a humid surface to feed on) where a Clausiliid 20 mm long is fully exposed and often dry. Conversely, a rather similar size-range is filled up in the lower cluster in different states of the U.S.A (figure 37) and in western Europe (figure 3). In the non-specialist Helicids, and probably in other groups too, a large radula moved by a powerful buccal mass may be able to erode material hardly affected by a small one; and since the sizes of eggs of snails are roughly proportional in size to adult shell size, at all times in the life-history there could be a size differential of ecological importance between different species in the same habitat.

Since in seasonal climates there will tend to be a time suitable to many species for egg-laying or producing live young, and since the size of eggs laid is roughly proportional to the size of the adult snail (when different species are compared) a size differential will tend to be preserved through the period of growth, thus reducing interspecific competition at earlier stages as well.

In the North American fauna, the taller shells (Bulimulidae, Urocoptidae, Spiraxidae, Pupillidae, Vertiginidae, etc.) show a much greater size-range in North America than in western Europe, where the only large high-spired form is the Mediterranean *Rumina decollata*. If one were to extend south into Africa, however, various achatinids would appear; and it is noticeable that large high-spired forms are nearly all very southern in the U.S.A. as well. Orthalicids (*Orthalicus*, *Liguus*) and bulimulids (*Bulimulus*) occur in Florida, bulimulids (*Drymaeus*) and the carnivorous spiraxid *Euglandina* in Texas, one extending northeastwards to Missouri and South Carolina. The medium-sized Urocoptids are also southern, and show considerable geographical separation, with a urocoptine and the microceramines in Florida, and a single Floridan microceramine and all the holospirines in Texas, New Mexico and Arizona. In both continents, therefore, large high-spired land shells appear only in the south. Medium-sized ones are southern in North America (but absent, remarkably, from California). They are much more general in Europe (Clausiliids) but are less well represented in the north; there is probably a parallel here too. The larger shells with low spires, however, are more widely distributed in both continents; but they also decrease in size in the north. Large landsnails of both clusters are more abundant in the tropics.

It would appear, then, that there are overall regularities governing the range of size of both high-spired and low-spired shells, but within the ranges to be expected, a considerable variation in size is actually found, and is largely irrespective of taxonomic position.

(d) The mechanics of carrying the shell

Several large marine shells, taken at random from an ornamental collection were examined. They included a large fasciolariid, a tonnid with very short spout, and a large muricid with spines and long spout. A piece of tape was affixed to the columellar wall of each, as far up inside as could be reached, to act as a columellar muscle. On suspending each shell from its tape, all three, although markedly different in dimensions and h/d, hung with the columellar axis approximately vertical, the tape lying along the spout, where present. This is a position of stability; correspondingly, if the shells are lying on a smooth surface and the tape is pulled, they align with the columellar axis as a prolongation of the tape. It follows that for pulling the shell along, the single columellar muscle is all that is necessary, and that if the shell is displaced, the minimum effort is required to bring it into line. All these shells were somewhat to very high-spired (except that the muricid, if notionally deprived of the spout and spines would have been a little below the bisector). Large discoidal or near-discoidal shells are not easily found; the corresponding observations were made on a full-grown *Zonites algirus* and a large unidentified shell collected by Professor B. C. Clarke at Angkor Vat. In both of these, when suspended, the columellar axis was markedly out of the vertical, and the substitute columellar muscle was pressed against the edge of the mouth. Correspondingly, when the shell was drawn along on a smooth surface, it tended to swing round, pressing the edge of the mouth against the 'muscle'.

A high-spired shell, therefore, can be dragged along the substrate by a single columellar muscle, and will tend to correct automatically for deviations as the animal proceeds. A discoidal shell will need some force to offset the tendency for the mouth to rotate across the pedicle, but can also correct for deviations when pulled by the columellar muscle. Furthermore, if tilted, the raised part will help to counter the depressed one. The most difficult shell to adjust would be a nearly globular one attached by a thin pedicle to a narrow foot. To raise it above the foot, or

so that it rests on it, the whole weight must be counteracted. It is certainly true that in such snails as *Natica* the foot tends to be broad, with extensions upwards and around the shell which effectively sits in a shallow basin on the top of the foot, in a position of near-stability, and this is even more marked in many forms which approximate to being slugs. A detailed examination of many species with various values of h/d and breadth of foot and pedicle is now necessary. The foot is narrow and the pedicle thin in both the extremely high-spired Clausiliids and the very flat planorbids. It should be broader, or the pedicle much larger proportionally in cross section in the more globular helicids and similar forms.

Jones (1971, 1975) and Dale (1973, 1974a, b) have shown that, in the species of land and fresh-water snails they investigated, the pedicle is inflated with blood and kept distended by blood-pressure. Correspondingly, the blood-pressure is much higher, and the ventricle more muscular, in land than in fresh-water species, and intermediate in *Lymnaea pereger*, which is somewhat amphibious. In aquatic forms, the pedicle can in fact on occasion be seen to be carrying the shell well away from the body at right angles to the action of gravity when the animal is climbing a vertical surface, and therefore to be stiffened by the blood. Simple twists of the shell on the pedicle will then be immediately corrected as the pedicle is restored to its normal shape by internal pressure. Large deviations, which might buckle the pedicle, can be removed by contraction of the columellar muscle as long as the foot is firmly anchored to a solid substrate. High-spired shells that are raised and not actually dragged along the substrate (as are clausiliid shells, for example) will require an expenditure of energy to maintain them in position when they are raised above the foot but lying more or less horizontal as the animal creeps over a horizontal surface. The weight of the shell and combined viscera projecting backwards will produce a torque tending to elongate the columellar muscle. The distribution of viscera of different specific gravity inside the shell may help to compensate, as may variations of thickness of the shell from mouth to apex. While the long narrow shell will not lie easily on the upper side of the foot, the broad flat one may well do so. It is highly unlikely that shells of very different shapes will be exactly equivalent for all attitudes and substrates, but only a detailed investigation of how they are actually carried in the wild will determine what selection pressures act on them.

Appendix A

The classification used in this paper is given below in outline, with groups not used and the reasons why. For easy checking against Taylor & Sohl and the *Treatise* the number of families in each superfamily not mentioned in the present paper is given in addition to the names of those mentioned. Genera mentioned in the paper are given in capitals to facilitate finding the systematic position. A dagger marks extinct groups. l. marks limpetlike forms, s. slugs with no external shell or unable to retract fully, v. (vermetid) distorted sedentary forms, p. modified parasites, f. (floating) pelagic. Subfamilies are inserted only if specially mentioned in the text; all families mentioned are italicized.

CLASS GASTROPODA

Subclass STREPTONEURA

Order   ARCHAEOGASTROPODA
Suborder †Bellerophontina
Superfamilies †Helcionellacea 2. †Bellerophontacea, *Bellerophontidae* except Ptero-
thecinae (l.) +2.
Suborder †Macluritina
†Macluritacea, *Onychochilidae* SINISTRACIRSA, *Macluritidae*. †Euompha-
lacea, *Euomphalidae* ANISOSTOMA, +3.
Suborder Pleurotomariina
Pleurotomariacea, †*Raphistomatidae* DIRACHOPEA, †*Lophospiridae* LOXO-
PLOCUS, +18 extinct families and 2 extant, excluding Haliotidae (l.) †Tro-
chonematacea (l.). Fissurellacea omitted (l.).
Suborder Patellina all omitted (l.)
(Patellacea 5. Cocculinacea 2.)
Suborder Trochina.
†Platyceratacea 2 (only Ordovician and Silurian Platyceratidae used,
rest v.).
†Microdomatacea 2. †Anomphalacea 1. †Oriostomatacea, *Tubinidae* SEMI-
TUBINA, +1. Trochacea, *Trochidae*, *Calliostomatinae* SINZOWIA, *Halistylinae*
HALISTYLUS, †*Velainellidae* VELAINELLA, Turbinidae ASTRAEA +1
extinct, and 4 living families.
Suborder Neritopsina
Neritacea *Neritidae* THEODOXUS, *Helicinidae*, +4 extinct and 2 living
families; omitting Titiscaniidae (s), Phenacolepadidae (l.) and *Septaria*, etc. (l.)
in Neritidae.
?ARCHAEOGASTROPODA
Suborder †Murchisoniina
†Murchisoniacea *Murchisoniidae* BRILONELLA, +1.
?ARCHAEOGASTROPODA, suborder doubtful
†Clisospiracea Clisospiridae omitting *Procrucibulum* (l. – perhaps all should
be omitted). †Pseudophoracea, 2. †Craspedostomatacea *Codonocheilidae* SCO-
LIOSTOMA, *Crossostomatidae*, +1. †Palaeotrochacea *Palaeotrochidae* WES-
TERNA, +1. †Amberleyacea *Cirridae* CIRRUS, +3.
?ARCHAEOGASTROPODA †suborder and family doubtful.
Burdikinia, Leptorima, Ozarkina.

Order   MESOGASTROPODA.
Superfamilies Cyclophoracea *Cyclophoridae, Poteriidae, Cochlostomatidae* OPISTHO-
STOMA, +2. Viviparacea, *Viviparidae* +1. Valvatacea, *Valvatidae*. Littorinacea,
†*Purpurinidae, Pomatiasidae* Chondropomidae, +2. Rissoacea, *Hydrobiidae* POTA-
MOPYRGUS. Bithyniidae *Assimineidae, Aciculidae* (= Acmaeidae), +16.
(Many truncatellids omitted as neither definitely marine nor terrestrial). †Sub-
ulitacea, 2. †Loxonematacea, 6. †Pseudomelaniacea, 2. Architectonicacea,

Architectonicidae (= Solariidae), + 1. Cerithiacea, *Mathildidae, Pleuroceridae*, + 13 and 3 extinct. *Vermetidae* (v.) and Vermiculariinae (v.) of Turritellidae omitted, also Caecidae (not polygyre) Epitoniacea (= Scalacea), 1, Janthinidae (f.) omitted. Eulimacea, 2, Paedophoropodidae (s) and Stiliferidae (p.) omitted. Strombacea *Aporrhaidae* + 2 + 1 extinct. Hipponicacea, 2, Hipponicidae (l.) omitted. Calyptraeacea, *Xenophoridae* + 1, Capulidae (l.) and Calyptraeidae (l.) omitted. Lamellariacea, 2, Pseudosacculidae (s), Ctenosculidae (s.) and Asterophilidae (p) omitted. Cypraeacea, 2. Atlantacea 3 all omitted (f). Naticacea *Naticidae* NATICA (many not fully retractile, omitted). Tonnacea, 5.

Order   NEOGASTROPODA
    Suborder Stenoglossa
        Muricacea *Muricidae* COLUMBARIUM, Magilidae
    (= Coralliophilidae) omitted (v). Buccinacea, 7. Volutacea 6.
    Suborder Toxoglossa
        Mitracea, 1. Conacea (= Terebracea), Conidae CONUS, Terebridae + 1.

Subclass EUTHYNEURA

Order   ENTOMOTAENIATA.
        †Nerineacea, 4. Pyramidellacea, *Pyramidellidae* CYCLOSTREMELLA, + 1 extinct. *Note:* the Architectonicacea and the Mathildidae (Cerithiacea), both in the Mesogastropoda are likely to belong here; some other mesogastropod families (Rissoacea) may also be here (Taylor & Sohl, note 12).

Order PARASITA omitted (p.).

Order CEPHALASPIDEA
        Acteonacea, *Acteonidae* ACTAEON, *Ringiculidae*, + 1 extinct. (The rest of this superfamily and the superfamilies Philinacea, Diaphanacea, Bullacea and Cylindrobullacea are omitted, – all s.)

Orders ACOCHLIDIOIDEA, PHILINOGLOSSOIDEA, THECOSOMATA omitted, all s.

Order BASOMMATOPHORA
        Siphonariacea 2 + 1 extinct, all l. Amphibolacea, 1. Ellobiacea (= Actophila), omitted as of doubtful ecology or l. (Otinidae). Chilinacea (*fide* Franc, 1968) 1 (Latiidae omitted, l.) Acroloxacea, 1 omitted, l. Lymnaeacea, *Lymnaeidae* LYMNAEA, Acroloxidae and Lancidae omitted, both l. Ancylacea *Planorbidae* (including *Bulininae*) PLANORBIS, BULINUS = (Bullinus, Isidora), *Physidae*. Ancylidae omitted, l.

Order   STYLOMMATOPHORA
    Suborder Orthurethra
        Achatinellacea *Achatinellidae* + 1. Cionellacea *Cionellidae* CIONELLA (= Cochlicopa), + 1. Pupillacea, *Pyramidulidae, Vertiginidae* COLUMELLA, *Orculidae, Pupillidae Pupillinae, Chondrinidae, Valloniidae Valloniinae, Acanthinulinae* ACANTHINULA, *Strobilopsinae, Enidae* (= Buliminidae) *Eninae, Chondrulinae, Cerastuinae*.

Suborder Mesurethra

Clausiliacea, Ceriidae (= Cerionidae) CERION, Clausiliidae Neniinae, Clausiliinae, Cochlodininae, +1 and 1 extinct. Corillacea 1. Strophocheilacea, 2

Suborder Heterurethra

Succineacea 2, omitted as largely amphibious. Athoracophoracea, 1, omitted, s.

Suborder Sigmurethra

Infraorder Holopodopes

Achatinacea, Ferussaciidae, Subulinidae Obeliscinae RUMINA, Achatinidae, Spiraxidae EUGLANDINA. Streptaxacea, Streptaxidae. Rhytidacea, Haplotrematidae, Rhytididae (= Paryphantidae), +1. Chlamydephoridae s. Bulimulacea, Bulimulidae BULIMULUS, DRYMAEUS, Orthalicidae ORTHALICUS, LIGUUS, Urocoptidae Urocoptinae, Microceraminae, Holospirinae HENDERSONIELLA, +2 and 1 extinct.

Infraorder Aulacopoda

Endodontacea Endodontidae Helicodiscinae, Endodontinae DISCUS, GONIODISCUS Punctinae PUNCTUM, +1. (Arionidae, Philomycidae both s, omitted). Zonitacea, Vitrinidae (several genera not fully retractile). Zonitidae Gastrodontinae, Zonitinae ZONITES, +1, (Parmacellidae, Milacidae, Limacidae, Trigonochlamydidae all s.). Ariophantacea Euconulidae, Helicarionidae, (Cystopeltinae s.), +2. (Urocyclidae s.). Testacellacea 1, all s.

Infraorder Holopoda

Polygyracea Thysanophoridae, Ammonitellidae, Polygyridae Triodopsinae ASHMUNELLA, TRIODOPSIS, Polygyrinae POLYGYRA. Oleacinacea, Oleacinidae, Sagdidae. Helicacea, Oreohelicidae, Camaenidae, Bradybaenidae (= Eulotidae) EULOTA, Helminthoglyptidae Cepoliinae, Helminthoglyptinae HELMINTHOGLYPTA, MONADENIA, Sonorellinae, Humboldtianinae. Helicidae, Helicinae HELIX CEPAEA, Tacheocampylinae, Murellinae, Leptaxinae, Helicigoninae ISOGNOMOSTOMA, ARIANTA, CYLINDRUS, Helicodontinae, Fruticicolinae, Thebinae, Helicellinae COCHLICELLA, HELICELLA, LEUCOCHROA.

Orders SACOGLOSSA, ANASPIDEA, GYMNOSOMATA, NOTASPIDEA, NUDIBRANCHIA and SOLEOLIFERA all s.

?Class GASTROPODA

Superfamily †Pelagiellacea, †Pelagiellidae PELAGIELLA

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