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Notes on the morphometry and anatomy of some Pisidium and Sphaerium species (Bivalvia, Sphaeriidae)

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The intraspecific and interspecific variation in the morphometry of *Pisidium* (25 recent and 11 fossil populations of 17 species) and *Sphaerium* (2 fossil populations of 2 species) was studied. Two simple indices, height index (100 height/length) and roundness index (100 diameter/height) were calculated and plotted against shell length.

Both indices show a linear correlation with shell length: in the case of the roundness index the correlation is almost always positive but in the height index the correlation coefficient is lower and the correlation again usually positive but negative in 5 species. These kinds of morphometric index give an additional quantitative character which could be more widely used in identification. The effect of environment on shell shape and the possible relation between fecundity and shell shape are discussed. The length of the pre-siphonal suture in *P. casertanum* and *P. subtruncatum* were measured and shown to be c. 10 % and 20—25 % of shell length, respectively. The tissue around the foot slit was clearly thickened in *P. subtruncatum* and could be used in species identification in case of material in which the hard shells are totally corroded e.g. after preservation in formalin.

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1. Introduction

The identification of *Pisidium* is mainly based on shell morphology: shape, size and texture of the shell and the hinge plate. In addition, the anatomy of soft parts, the presence or absence of a branchial opening, the length of the foot slit etc. can be used in some cases.

The general shape of the *Pisidium* shell is species specific. Kuiper (1947, 1949) was first to quantify the shape by indices calculated from shell length, height and diameter, and to use the indices as a taxonomical tool in species identification.

The shape of the Sphaeriid shell has, however, been reported to show high variation between different populations of the same species, or the shape is probably governed not only by genotype but also by environment (Thiel 1926, Brodniewicz 1960, Meier-Brook 1963, 1970, Wilbur & Owen 1966). Moreover, the shape usually shows a gradual change during an individual's life (e.g. Thiel 1926, Kuiper 1949, Meier-Brook 1963, Wilbur & Owen 1966, Alimov 1981).

In this paper the intraspecific and interspecific variation in the shape of the Sphaeriid shell is studied with the aid of two simple indices using recent and fossil material. In addition, a note is given on the length and anatomy of the foot slit in *P. casertanum* and *P. subtruncatum.*

2. Material and methods

2.1. Technique

Shape indices based on measurements of 1511 individuals from 25 recent and 11 fossil populations in 17 species of *Pisidium* and 303 individuals from 2 fossil populations in 2 species of *Sphaerium* are given. The measurements were made by eyepiece micrometer under stereomicroscope to an accuracy of 0.01—0.04 mm; some of the values were taken directly from the literature.

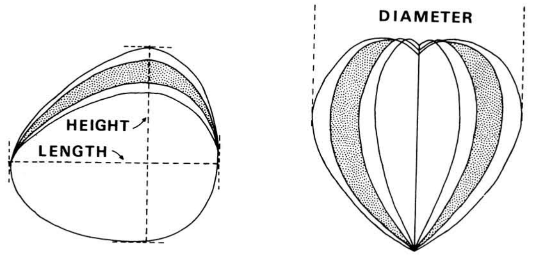

Fig. 1. A schematic diagram of a Sphaeriid shell to show the normal (stippled) and extreme variation in shell shape. The normal variation in height stays between index values of 75 to85 % and that of diameter between 100 D/H values of 55 to 80 %. The shape corresponding to the extreme values of 70 and 90 % (height index) and 40 and 100 % (roundness index) are also given.

The shape of the shell is indicated by the *height index* (100 H/L) or the percentage proportion of height (H) over the length (L), and the roundness or convexity index (100 D/H) or the percentage proportion of diameter (D) over the height (H) (Fig. 1, Kuiper 1947, 1949). In the case of fossil material the diameter values refer to one valve only and the latter index is used in the form 100 D/2H (Kuiper 1975). These indices are inverse values of those used by Meier-Brook (1963): 100 L/H and 100 H/D.

The values of the indices given here are plotted against respective shell lengths and a linear regression line of form $y = a + bx$, where y is the index, x is shell length and a, b are constants, was fitted to the data. The statistical significance of some differences was tested by covariance analysis. The pictures showing the soft parts of two species are of specimens mounted in Euparal on slides after removal of the hard shells.

2.2. Sampling localities

Sites of fossil material

1. *Eindhoven.* A boring to periglacial deposits of the latest glaciation near the city of Eindhoven, Netherlands. (Kuiper 1974a).
2. *Kallo.* The basal deposit of a holocene gully in a construction pit for a tunnel at Kallo, municipality of Beveren, Belgium. The material was collected and measured by A. W. Janssen, Rijksmuseum van Geologie en Mineralogie, Leiden.
3. *Tövelde Klint.* A holocene deposit in a former small lake at Tövelde Klint, southern coast of the island of Möen, Denmark (Schlesch 1943, 1947).
4. *White Bog.* Pleistocene deposits in the White Bog, Co. Down, Northern Ireland, U.K. (Stelfox et al. 1972).

Sites of recent material

1. *Esrom.* A eutrophic lake in Denmark (Jónasson 1972).
2. *Juis de Fora.* Muddy bottom of slow running drainage ditch at Minas Gerais, Brazil (Meier-Brook 1967).
3. *Mekrijärvi.* An oligotrophic and polyhumic lake situated in Ilomantsi municipality, eastern Finland. A shallow lake (max 2 m) with soft bottom.
4. *Naardermeer.* A swampy nature reserve in the centre of the Netherlands (Kuiper 1947, 1949).
5. *Nömmen.* A clear, oligotrophic lake in Björkö, Småland, Sweden (Odhner 1940).
6. *Pääjärvi.* An oligotrophic and mesohumic lake in southern Finland (Ruuhijärvi 1974, Holopainen 1979).
7. *Quelle am Sattel.* A spring in the mountains of High Vosges (1200 m above sea level). Population no. 11 in Meier-Brook (1963 p. 13).
8. *Siilaisenpuro.* A small river in the town of Joensuu, eastern Finland. The samples were collected from the soft bottom near the mouth of the river.
9. *Soesterveen.* A peat bog in the Netherlands.
10. *Stensjön.* A lake near Lake Nömmen (above), Sweden.
11. *Stautümpel Urberg-Höll.* A pond in the mountains of the High Black Forest. Population no. 7 in Meier-Brook (1963, p. 13).
12. *Stautümpel unter Quelle.* A spring pond in the mountains of High Vosges. Population no. 10 in Meier-Brook (1963, p. 13).
13. *Suomunjärvi.* An oligotrophic and mesohumic lake in eastern Finland (Viljanen & Holopainen 1982).
14. *Tümpel im Ursee Moor.* A pond in the mountains of the High Black Forest. Population no. 13 in Meier-Brook (1963, p. 13).
15. *Varangerhalbinsel.* Lake Buetjörni and Stjernevandet in the Varanger Peninsula, northern Norway (Kuiper 1975).
16. *Vålåsjöen.* A lake near Dombås, southern Norway (Hinz 1974).
17. *Windgfällweiher.* A lake in the High Black Forest (Elster 1955, Meier-Brook 1963).

3. Results

P. casertanum (Poli)

Shape of shell. Six recent populations from different shallow-water habitats, one from lake profundal (Esrom) and one fossil population are included in this study (see Fig. 2 and A1—A4 in Appendix). The values of height index of the recent populations do not show any clear differences between populations. The average change (c. 79—84 %) in any population during growth is linear and is positively correlated with shell length until a length of c. 4 mm, and constant thereafter. However, the form *P. c. ponderosum* (subfossil material) shows a clearly higher height index (87—95 %, Fig. A4). The roundness index shows a greater change (55—75 %) during the life of the individual and also correlates positively with shell length. In the three populations with material of comparable size structure, the difference between two littoral populations (Pääjärvi, Windgfällweiher) was not significant but

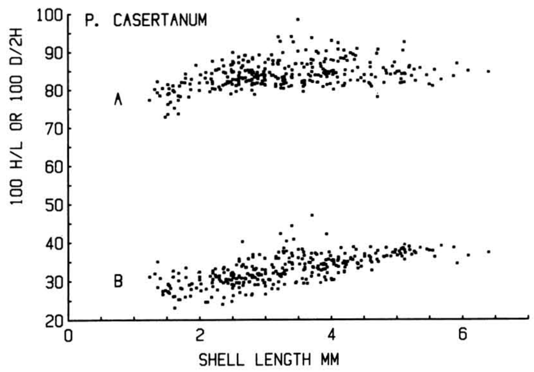

Fig. 2. The two shape indices plotted against shell length in eight populations of *Pisidium casertanum*. A = 100 H/L and B = 100 D/2H.

both differed ($P < 0.001$) from the profundal population (Esrom), which had clearly lower values of roundness index (Fig. A1).

The big individuals (4—6 mm) from a pool (Tümpel im Ursee-Moor, Fig. A3) show exceptionally low values of roundness index and also of regression coefficient; the two populations from springs seem to show wider variation in roundness index than normal, even in the very restricted size class (3—4 mm, Fig. A2, A3).

This species is a habitat generalist (e.g. Valle 1927, Boycott 1936, Feldmann 1971, Ellis 1978, Holopainen & Hanski 1979) and is also described as the most variable in shape and other shell characteristics among *Pisidium* species (e.g. Woodward 1913, Ellis 1962, Meier-Brook 1963, 1970, 1975, Zeissler 1971). Consequently many forms or variations have been described, usually with some reference to the environment typically inhabited by the form. For example, the form *ponderosum,* one of the best known varieties, is said to inhabit "favourable habitats, such as large rivers and canals" (Ellis 1978) or lotic environments in rivers and lake littorals (Meier-Brook 1975). This form is high (trigonal) with a high height index. Meier-Brook (1963) divided the 12 populations of *P. casertanum* from the High Black Forest and High Vosges into 3 form-groups with respective mean height indices of c. 82, 85 and 88 % in large animals.

However, the "highest" form (88 %) in his material was from the profundal of Lake Schluchsee. In Lake Washington the profundal population of *P. casertanum* was also described as a high or "shorter form" (Thut 1969). The population from the profundal of Lake Esrom can be interpreted to be highest (highest height index) in our recent material, but the difference between it and the littoral population of Lake Pääjärvi (Finland) was not significant, and it is far from being as high as the fossil *ponderosum* from Belgium. However, the low roundness index in our profundal population seems to be more marked (Fig. A1).

Foot slit and pre-siphonal suture. The foot slit in *P. casertanum* is long and consequently the pre-siphonal suture is short (Fig. 3 and e.g. Odhner 1929, Meier-Brook 1963, 1978). The length of the presiphonal suture was measured from two populations (Esrom, Windgfällweiher) and the values fall close to each other (Fig. 4B). The difference between populations is, however, statistically significant ($P < 0.01$) and the suture seems to be shorter in the littoral population if judged from this very small material. The length of the suture is linearly correlated with the shell length and is c. 10 % of it.

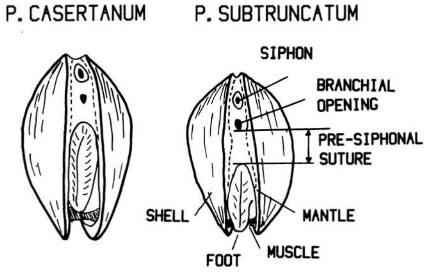

Fig. 3. In *P. casertanum* the foot slit is longer and the pre-siphonal suture shorter than those of *P. subtruncatum.*

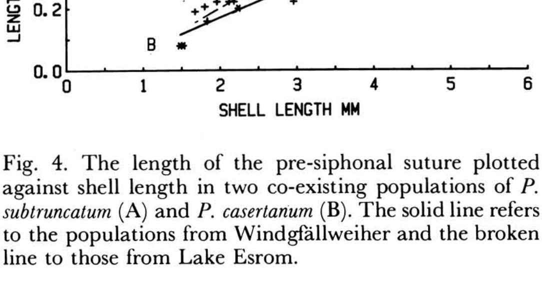

Fig. 4. The length of the pre-siphonal suture plotted against shell length in two co-existing populations of *P. subtruncatum* (A) and *P. casertanum* (B). The solid line refers to the populations from Windgfällweiher and the broken line to those from Lake Esrom.

P. subtruncatum Malm

Shape of the shell. The height indices (85—80 %) of the two populations studied (Esrom, Windgfällweiher) differed significantly from each other ($P < 0.05$), but both showed a negative linear correlation with the shell length — the clams grew "lower" or "longer" in shape during their life (Figs. 6 and A5). The roundness index showed a high change (60—80 %) in linear correlation with shell length, and the difference between populations was not significant.

As *P. casertanum*, this species is usually characterized as a euryoecious generalist, capable of inhabiting a great variety of water bodies (Valle 1927, Boycott 1936, Meier-Brook 1975) and again a lot of forms or varieties are described (Ellis 1962, Zeissler 1971). According to the material of Meier-Brook (1963) the mud-inhabiting populations are composed of specimens longer in shape than those from sand bottoms. His mean values for height index of large specimens varied between 85 and 89 % and those of roundness index between 68 and 77 % in different populations. In general, his populations — most of which came from sand bottoms — seemed to be shorter in shape than those in this study, which therefore further supports his statement of the shell shape in relation to bottom type. The bottom in the profundal of Lake Esrom is soft mud, but that in the littoral of Windgfällweiher is sandy, and again the latter population was "shorter" (Fig. A5).

Foot slit and pre-siphonal suture. The foot slit of *P. subtruncatum* is short and the pre-siphonal suture correspondingly long (e.g. Odhner 1929, Meier-Brook 1963, 1978). The length of the pre-siphonal suture was measured from two populations (Esrom, Windgfällweiher) which did not differ significantly from each other. The length of the suture showed a positive linear correlation with the shell length, being c. 20—25 % of it (Fig. 4A). In all corresponding size classes the length was c. twice that in *P. casertanum.*

In *P. subtruncatum* the part of the mantle which forms and surrounds the foot slit is clearly thickened (Fig. 5). In the case of old *Pisidium* material from the profundal of Lake Esrom, in which the hard shells had totally corroded and the soft parts darkened during storage of more than twenty years in formalin, this thickening was clearly visible and gave an easy and quick method for distinguishing between even very small specimens of *P. subtruncatum* and *P. casertanum.* In *P. milium* this thickening was even more pronounced, but the soft parts of this species could be easily identified from the long anterior muscle scar (see figure in Odhner 1929).

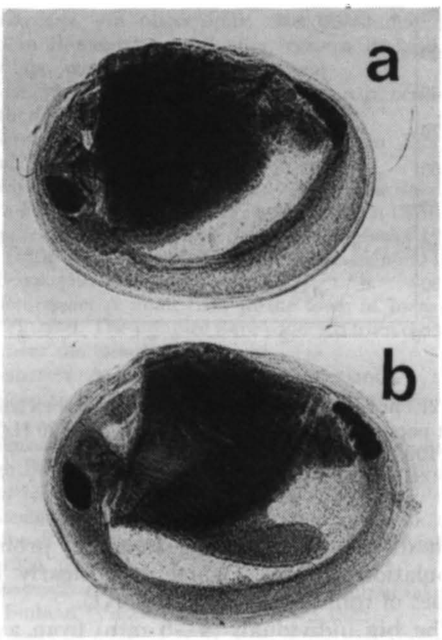

Fig. 5. The thickening of the mantle tissue around the foot slit is typical of the species with a short foot slit. a = *P. subtruncatum*, b = *P. casertanum.*

P. henslowanum (Sheppard)

Without the umbonal fold this species would resemble *P. lilljeborgi* in Lake Pääjärvi: the regression lines of both indices are parallel with these of the other species (Fig. 6). However, the values of both indices retain significantly lower values ($P < 0.01$) in *P. henslowanum.*

In comparison with *P. subtruncatum,* the height indices seem to be identical, but the roundness index is much lower in *P. henslowanum.*

This species is said to favour running water and big lakes with at least a moderate amount of calcium (Boycott 1936, Ellis 1962, Zeissler 1971, Meier-Brook 1975). Some variations have been described, and the disappearance of the umbonal fold is said to be not infrequent (Kuiper 1968) and to correlate with higher relative height (Odhner 1929).

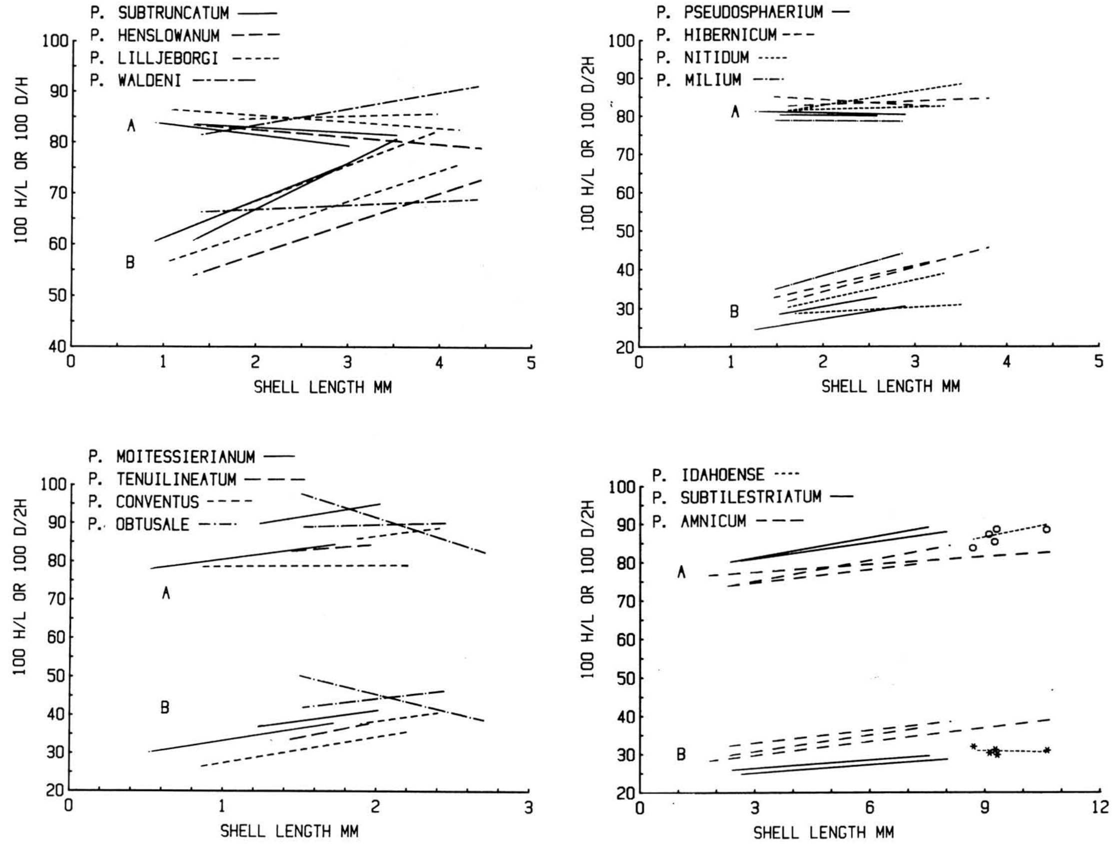

Fig. 6—9. The lines of regression between the two shape indices and shell length of several species are plotted together to allow comparison. A = 100 H/L and B = 100 D/H or 100 D/2H. For more exact data of each population see figures in Appendix.

P. lilljeborgi Clessin

The height index (c. 85 %) of this species seems to show negative correlation, but the roundness index (65—80 %) positive linear correlation with shell length. The values of height index were not different between populations, but the roundness index of the population from the muddy bottom of the polyhumous Lake Mekrijärvi (Finland) was significantly higher ($P < 0.001$) (Fig. A7).

This species is usually described as a stenoecious species inhabiting mostly sandy littorals of northern or mountain lakes (Boycott 1936, Ellis 1962, Bagge 1968, Zeissler 1971, Kuiper 1974, Meier-Brook 1975). The variation in shape is considerable, even though it is reported to be less than e.g. in the two species described above (e.g. Meier-Brook 1963, 1978, Zeissler 1971). The mean height and roundness indices for three populations given by Meier-Brook (1963) are 91.5, 87.6, 87.0 % and 69.5, 64, 63.9 %, respectively. The values of his height indices are all higher than those in the present study but his roundness indices fall near the values from Lake Pääjärvi.

P. waldeni Kuiper

The measurements were taken directly from Kuiper (1975) in order to compare them with those of *P. lilljeborgi*, which this species was said to resemble when older. The indices of *P. waldeni* and *P. lilljeborgi* from Pääjärvi did not differ significantly from each other, but this is probably because of the small amount of material and large variation in the values of *P. waldeni* (Fig. A8). In contrast to *P. lilljeborgi* the height index of *P.*

waldeni shows a clear positive correlation with shell length and the regression coefficient of the roundness index is lower.

P. moitessierianum Paladilhe

One population from the littoral of a southern Finnish lake and one subfossil from Belgium are included (Fig. A9). Both the height index (c. 77—84 %) and the roundness index (60—75 %) show clear positive correlation with shell length.

This is one of the smallest European species and inhabits both lakes and rivers (Zeissler 1971, Meier-Brook 1975, Ellis 1978).

Brodniewicz (1960) has studied the morphometry of recent and fossil populations of this species in Poland. Her studies show that this species grows bigger and might have a slightly higher height index in rivers than in lakes (Fig. A9). The differences in height index between her populations are not very conspicuous, and fall inside the variation shown by the fossil population from Belgium. However, the values seem to be higher than those of the southern Finnish population included here.

P. tenuilineatum Stelfox

The measurements of this small species, which inhabits both lakes and running waters (Zeissler 1971, Meier-Brook 1975, Ellis 1978), are of the form *suecicum* (Odhner 1940). Both indices of this small sample fall very close to those of *P. moitessierianum* from Lake Pääjärvi. However, the roundness index seemed to be slightly lower (Figs. 8, A7 and A10). Small individuals of *P. subtruncatum* might be of similar shape, too (Figs. A5 and A10).

P. milium Held

The only population included here is a fossil one from Tövelde Klint (Fig. A11). The height index was constant (c. 80 %) throughout life, but the roundness index showed a slightly positive correlation with shell length (100 D/2H = 35—45 %).

This species usually lives in the shallow water of small water bodies and has been considered to be among the least variable species in the genus (Ellis 1978); only the arctic areas are inhabited by the form *unioides,* which has prolonged anterior end and straight, lower margin (Kuiper 1968). The mean height index for large individuals in six populations from Central Europe given by Meier-Brook (1963) was 80.4 % (78.2—81.8 %) and that for five fossil individuals from White Bog, Ireland (Stelfox et al. 1972) was 80.0 % (75.0—84.0 %). The roundness index (D/H) of this small material from White Bog varied between 73 and 95 % (mean 86.5 %).

P. nitidum Jenyns

Two fossil populations are included (Figs. A12 and 7). That from Tövelde Klint shows almost constant height index (c. 83 %) throughout life and the roundness index shows positive linear correlation with shell length (100 D/2H: 30—40 %). The other population from White Bog shows higher height index and positive correlation with shell length, and constant roundness index with lower values. This species prefers large water bodies, both running and standing (Meier-Brook 1975, 1978) and is morphologically variable (Ellis 1978, Meier-Brook 1978). According to Meier-Brook (1978) this species has round, thick shells in running water (f. *crassa*) and is strongly striated in sand bottoms (f. *arenicola*).

P. hibernicum Westerlund

Two fossil populations are again included, one from Tövelde Klint and the other a small sample of the large form *portentosa* from White Bog (Figs. A13 and 7). The height indices of both populations seem to be constant (c. 85 %), whereas the roundness indices are in clearly positive correlation with shell length (100 D/2H: 32—42 %). The differences in indices between populations are not significant. This species is said to show great variability of form (Kuiper 1966a), but is also considered to have only low regional variation (Meier-Brook 1978). It inhabits small water bodies as well as lakes (Zeissler 1971, Ellis 1978).

In the 11 populations measured by Meier-Brook (1963) the height index varied from 83 to 87 % (mean 85.5 %), and did not show any correlation with the degree of latitude (from the island of Öland, in southern Sweden, to Bodensee).

P. pseudosphaerium Schlesch

Kuiper (1947, 1949) has used the roundness index to demonstrate the difference in the diameter of shell between populations of *P. pseudosphaerium* and *P. milium* from the same habitat.

Here we give the indices for two populations of *P. pseudosphaerium* (Fig. A14), one from a peat-bog in the Netherlands (Soesterveen) and the other a fossil population from Alleröd deposit in Tövelde Klint, Möen, Denmark (Kuiper 1947, Schlesch 1947). The height indices of both populations are identical and stay constant (c. 80 %) throughout life. The roundness indices both show positive linear correlation with shell length. The diameter of the fossil shells has been measured from one valve only and, to allow comparison, that of the recent population has been divided by two (Figs. A14 and 7). The fossil population shows a significantly higher ($P < 0.001$) roundness index than the recent, but both values stay well below those of *P. milium* ($P < 0.001$) (Fig. 7). There was no difference in the height index between *P. pseudosphaerium* populations, but the values were significantly higher than those of *P. milium*. This species is confined to standing water rich in vegetation (Kuiper 1947, 1949, 1972) and shows very little variation in its morphology (Kuiper 1972).

P. conventus Clessin

The height index (c. 79 % in all size classes) in Lake Pääjärvi is lower than the mean (82.9 %) from Lac de Longemer (23 m, Meier-Brook 1963), but the roundness indices, 50—75 % in Lake Pääjärvi and 64.6 % as mean in Lac de Longemer, seem to fit each other (Fig. A15). Meier-Brook (1963) states: "*P. conventus* variiert etwas im Höhen-Längen-Verhältnis, behält jedoch seine charakteristischen Formenmerkmale an allen Fundstellen bei".

The three fossil shells from the Netherlands (Kuiper 1974a) show higher values of both indices (Fig. A15) and the one large fossil individual from White Bog has higher height index, too ($L = 2.9$ mm, $100\ H/L = 86.2$ %, $100\ D/H = 72.0$ %).

This species is a habitat specialist, inhabiting, in temperate climates, the deep profundal areas of northern and pre-alpine lakes only, but in subarctic areas it lives in the littoral as well (e.g. Odhner 1923, Valle 1927, Heard 1963, Kuiper 1974a, b, Holopainen & Hanski 1979). Our knowledge of morphometric variation is not complete but at least a "deep-water form" has been separated: "A form from deep water is rhomboidal, dwarfed and depauparate with a very narrow hinge" (Piaget 1912, J. Conchyl. 60: 227; cited after Ellis 1978).

P. obtusale (Lamarck)

The measurements are based on material collected by Dr. W. Hinz (Duisburg, FRG) from southern Norway and on fossil material from White Bog (Figs. A16 and 8). Both the height and roundness indices are between 80 and 100 %, and the clams are spherical in general appearance. In contrast to the recent population, the fossil one shows higher variation between individuals and clearly negative correlation with shell length in both indexes. However, even if those samples belonged to the same population, the variation is not too high, and no further conclusions can be drawn because of the small size of the sample.

This species is typical of small waterbodies rich in plants or dead plant material but inhabits larger waterbodies, too (Valle 1927, Ellis 1962, Zeissler 1971). The shape of the shell is usually round and is particularly so in populations living in small waterbodies (Meier-Brook 1978) and in subarctic and arctic areas (the form *lapponicum*, e.g. Odhner 1951, Ellis 1962, Zeissler 1971). In extreme forms the height and roundness indices can both rise to 100 % or even more.

P. forense Meier-Brook

This is a species described from slowly running water in Brazil (Meier-Brook 1967). Both the high height index (c. 88—93 %) and the roundness index (c. 71—74 %) show slightly positive correlation with shell length, but the latter shows very wide variation between individuals (Fig. A17). From the species included in this study both indices of this species fall closest to *P. waldeni* but with somewhat higher values (c. 4 %), which make the difference statistically significant ($P < 0.001$).

P. amnicum (O. F. Müller)

In addition to the fossil population from Belgium, two recent populations of this large species are included, one from a small river in eastern Finland (Siilaisenpuro) and one from a lake near the mouth of a river (southern Finland) (Fig. A18). Both the height indices (75—85 %) and the roundness indices (60—75 %) are in positive linear correlation with shell length and both indices show significant difference between populations ($P < 0.01$).

According to Starobogatov (1977) the height index of *P. amnicum* falls between 73 and 80 %, and that of his species *P. inflatum* (Muhlfeld in Porro,

1838) 81—86 %. One specimen of *P. inflatum* from Lake Peipus with a length of 6.92 mm had a height index of 86.1 % and a roundness index (D/H) of 63.8 %. Timm (1975) gives an H/L value of 78 % and a D/L (diameter/length) of 50 % for *P. amnicum* and 82 % and 54 % as the respective figures for *P. inflatum*. The latter is said to favour sandy bottoms in Lake Võrtsjärv.

This species usually inhabits shallow areas of running waters, living both in sandy (Meier-Brook 1975, 1978) and muddy bottoms (both the recent populations in this study). The morphological variation is reported to be high, with the result that many forms have been described (Ellis 1962, Zeissler 1971).

P. idahoense Roper

This large species from North America is morphologically very near to *P. subtilestriatum* (see below). The height index values of the few very large specimens (*P. i.* f. *indianense*) used in this study fall between *P. subtilestriatum* and *P. amnicum* (Fig. 9) and could be interpreted to fit both of these. On the other hand, the roundness index is far from that of *P. amnicum* but equals the values of *P. subtilestriatum*. Mackie et al. (1980) give an H/L ratio of 0.86 or more to this species. Actually, *P. idahoense* and *P. subtilestriatum* have been regarded as identical (Kuiper 1966b, p. 65). Before final approval, this apparent synonymy should, however, be the object of closer examination in order to eliminate the possibility of convergence so common in Pisidia.

P. idahoense is said to favour cool water in large lakes, mountain regions and the far North (Herrington 1962) and to be a good indicator of mesotrophy in lakes (Clarke 1979). Long, slim specimens which resemble *P. amnicum* in shape have been found in Great Slave Lake, North-West Territories (Herrington 1962).

P. subtilestriatum Lindholm

Two populations are again included, one from a lake in eastern Finland and one from southern Sweden (Figs. A19 and 9). Both the morphometric indices used show only slight differences between populations, even though the difference in roundness indices is statistically significant ($P < 0.01$), and both show positive linear correlation with shell length. In comparison with *P. amnicum*, the values of height index are much higher, and those of roundness index much lower.

This species was described from Lake Baikal by Lindholm (1909), and is identical with *P. carelicum* described by Odhner (1926) from lakes north of Lake Ladoga (Odhner 1940). The previously known distribution in Europe is restricted to the Karelian lakes (in USSR and Finland, Valle 1927, Koli et al. 1964) and to some lakes in southern Sweden (Odhner 1940).

Sphaerium corneum (Linnaeus)

The height index of the fossil population from Kallo shows slightly negative linear correlation with shell length (H/L: 82—78 % between lengths of 2.5 mm and 12 mm) but the roundness index again showed clear positive linear correlation with shell length (D/2H: 26—43 %) (Fig. A20). The same indices in a population from Elbe as measured by Thiel (1926) fall very close to those above: the height index seems to stay rather constant (between 81 and 84 %) over the lengths measured (3.5 to 9.2 mm) but the roundness index (D/2H) increases from 25 to 35 %. Thiel (1926) also discussed the variation in relative measures of shells from different populations (habitats) and demonstrated the change in the direction of the marginal growth as the process behind the change in form (see Fig. 10 and discussion below).

Alimov (1967) gives the following allometric relations between shell length *(L)*, height *(H)* and diameter *(D)*: $H = 0.578\ L^{1\cdot18}$ and $D = 0.465\ L^{1\cdot18}$. According to these, both H/L and D/2H show positive linear correlation with shell length, reaching values of 77 % (at 5 mm) to 90 % (12 mm) and 34 % (5 mm) to 46 % (12 mm), respectively.

S. corneum is a common and widespread species inhabiting most kinds of freshwater and is said to be "a useful indicator of pretty good molluscan conditions" (Boycott 1936). It is also stated to exhibit considerable variation in form, like most other Sphaeriids.

Sphaerium solidum (Normand)

One fossil population from Kallo is included (Fig. A21). The height index of this species shows positive linear correlation with shell length and in small individuals it is clearly lower (c. 73 %) than that of *S. corneum*. The roundness index is approximately five percentage units higher than that of *S. corneum* but has a similar relation to shell length.

S. solidum inhabits soft bottoms of larger rivers in Eastern and Central Europe (Ellis 1978, Glöer et al. 1978).

According to Alimov (1967) the relationship between shell height and length in this species is of the form $H = 0.624\ L^{1\cdot1}$, which again gives positive linear correlation between height index and shell length with values from 73 % at 5 mm to 80 % at 12 mm. This gives a parallel line with values approximately three percentage units lower than those from Kallo. The relation between diameter and length was $D = 0.585\ L$, or D/2H had a constant value of 29.3 %, which is clearly lower than that from Kallo (33—40 %).

4. Discussion

In the populations studied both the morphometric indices show a linear relationship with shell length. In *P. casertanum* the combined height index data was, however, better described by a bent line and the same possibly holds true for the roundness index of *S. corneum.* In the other populations the material is not abundant enough to permit such conclusions to be drawn. The linear correlation with shell length is always positive (with the exception of the fossil *P. obtusale*) in the roundness index, as is the case with height index for most species. In the latter index, however, the regression coefficient is usually low (nearly horizontal line or isometric relation), or then the index shows negative correlation with shell length, as in populations of *P. subtruncatum, P. henslowanum, P. lilljeborgi,* the fossil *P. obtusale* and *S. corneum.* The linearity suggests a single allometric or isometric relation between the shell values during growth (cf. Wilbur & Owen 1966, Alimov 1967). In most species the diameter increases faster in relation to height (the clam grows rounder or "thicker") and the height usually increases a little faster or stays constant in relation to shell length (the clams tend to grow higher or "shorter"). However, the four exceptional species mentioned above grow lower or "longer".

The growth of the Sphaeriid shell mostly takes place in the lateral and ventral margins of the shell and the variable relative growth rate of the lateral and ventral part during life can cause the typical "growth interruptions" or changes in the direction or marginal growth (Thiel 1926, Wilbur & Owen 1966, see Fig. 10).

In general the two indices used here are widely overlapping and too simple to describe the shape of *Pisidium* well enough if used alone, and their construction is usually too time-consuming for practical species identification. However, they give an additional quantitative character, which has already occasionally been used in identification keys (Starobogatov 1977, Mackie et al. 1980) or in demonstration of the differences in relative values of the shell, especially in species which closely resemble each other (Kuiper 1947, 1949).

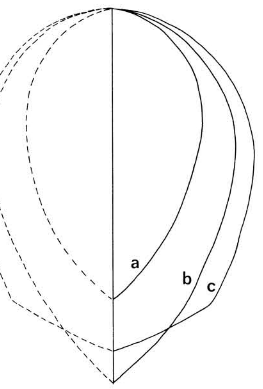

Fig. 10. The change in the direction of marginal growth can cause a clear change in shell shape. An equal length increment of the shell margin (b, c) from the same starting point (a) is shown. Adapted from Thiel (1926).

These kinds of index can also be useful in the quantification of shape for ecological as well as taxonomical purposes (e.g. Wilbur & Owen 1966). The relative roundness or thickness, for example, has been shown to demonstrate interesting relationships with the ecology of some bivalves. Thiel (1926) demonstrated the change in shape of *Sphaerium corneum* as a result of change in direction of margin growth. This change was induced by transfer from the original polluted habitat to clean water, or experimentally by increased oxygen content of the water. In addition to the increase in relative thickness, the species produced more embryos in clean water. Thiel (1926) suggested the clean water with higher oxygen content but lower food production to be a less favourable environment for *S. corneum* and consequently that the survival of the population required more effective reproduction. The higher number of embryos was suggested to need more room and to cause change in the direction of growth of the shell margin with consequent thickening of the parent.

A similar relationship between relative thickness and the number of embryos can be seen here by comparing two populations of *P. casertanum* from different habitats (Fig. A1): those in the littoral of Lake Pääjärvi are rounder or "thicker" and produce a higher number of embryos than the "thinner" specimens living in the profundal of Lake Esrom (Holopainen 1979, Holopainen & Jónasson 1982). Some observations on Unionids, too, suggest that populations with thicker individuals produce more glochidia (and have a shorter life-span) than the others (T. Hakala, unpubl.).

In *Pisidium* the number of eggs laid is usually higher than the number of young reaching birth size (Meier-Brook 1970, 1977, Holopainen 1979). This makes it possible to adjust the actual number of young produced according to environmental (physical, chemical and biological) conditions. The suggestion of Thiel (1926) assumes the number of young produced to be at least in part limited by the volume of the mantle cavity.

In our opinion these relationships are perhaps best understood in that the space limitation is true in very favourable environments only and selection favours thicker individuals with the highest reproductive capacity. The transplantation of individuals into more favourable environments might be thought to cause an increase in the number of young produced and also a change in growth direction, but the causality between them is at least improbable.

The study of the relationships between the morphology and ecology of recent species is one way to throw light on the ecology of fossil populations, too.

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References

Alimov, A. F. (Алимов, А. Ф.) 1967: Особенности жизненного цикла и роста пресноводного моллюска Sphaerium corneum (L.). (Summary: Peculiarities of the life cycle and growth of Sphaerium corneum.) — Zool. žurnal 46: 192—199.

—»— 1981: Функциональная экология прссноводных двустворчатых моллюсков. — Trud. Zool.Inst. AN SSSR 96: 1—248.

Bagge, P. 1968: Ecological studies on the fauna of subarctic waters in Finnish Lapland. — Ann. Univ. Turkuensis, Ser. A II, 40: 32—83.

Boycott, A. E. 1936: The habitats of fresh-water mollusca in Britain. — J. Anim. Ecol. 5: 116—186.

Brodniewicz, I. 1960: Pisidium moitessierianum Paladilhe (Lamellibranchiata) i porównanie jego populacji wspólczesnej z plejstoceńska (Summary: A comparison of the recent and pleistocene populations of Pisidium moitessierianum Paladilhe (Lamellibranchiata). — Acta Palaeontol. Polonica 5: 349—365.

Clarke, A. H. 1979: Sphaeriidae as indicators of trophic lake stages. — The Nautilus 94: 178—184.

Ellis, A. E. 1962: British freshwater bivalve molluscs with keys and notes for the identification of the species. — Linn. Soc. London, Synopses of the British Fauna 13: 1—92.

—»— 1978: British freshwater bivalve mollusca. Keys and notes for the identification of the species. — Linn. Soc. London, Synopses of the British Fauna (N. S. 11: 1—109.

Elster, H.-J. 1955: Beiträge zur Limnochemie der Hochschwarzwaldseen I. — Arch. Hydrobiol., Suppl. 22: 1—64.

Feldmann, R. 1971: Die Kleinmuscheln (Sphaeriidae) des mittleren Ruhrtales. — Decheniana 123: 27—47.

Glöer, P., Meier-Brook, C. & Ostermann, O.: Süsswassermollusken. — 73 pp. DJN. Hamburg.

Heard, W. H. 1963: The biology of Pisidium (Neopisidium) conventus Clessin (Pelecypoda: Sphaeriidae). — Papers Michigan Acad. Sci. Arts Lett. 48: 77—86.

Herrington, H. B. 1962: A revision of the Sphaeriidae of North America (Mollusca: Pelecypoda). — Misc. Publ. Mus. Zool. Univ. Michigan 118: 1—74.

Hinz, W. 1974: Molluskenfauna und -siedlungsdichten in einigen Gebirgsgewässern der Umgebung von Dombås (Südnorwegen). — Norw. J. Zool. 22: 221—229.

Holopainen, I. J. 1979: Population dynamics and production of Pisidium species (Bivalvia, Sphaeriidae) in the oligotrophic and mesohumic lake Pääjärvi, southern Finland. — Arch. Hydrobiol., Suppl. 54: 466—508.

Holopainen, I. J. & Hanski, I. 1979: Annual energy flow in populations of two Pisidium species (Bivalvia, Sphaeriidae), with discussion on possible competition between them. — Arch. Hydrobiol. 86: 338—354.

Holopainen, I. J. & Jónasson, P. M. 1982: Long-term population dynamics and production of Pisidium (Bivalvia, Sphaeriidae) in the profundal of Lake Esrom. — Manuscript.

Jónasson, P. M. 1972: Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. — Oikos, Suppl. 14: 1—148.

Koli, L., Keynäs, K. & Aho, J. 1964: Einige für Finnland neue Pisidium-Arten (Pelecypoda). — Ann. Zool. Fennici 1: 77—79.

Kuiper, J. G. J. 1947: Bijdrage tot de kennis der zoetwaterweekdieren van het natuurmonument Naardermeer. — Basteria 11: 2—53.

—»— 1949: Pisidium pseudosphaerium Favre in England. — J. Conchol. 23: 27—32.

—»— 1966a: The status of Pisidium hibernicum Westerlund. — J. Conchol. 26: 42—46.

—»— 1966b: Les espèces africaines du genre Pisidium, leur synonymie et leur distribution. — Ann. Mus.

Roy.Afr. Centr. Tervuren 151: 1—78.

—»— 1968: Die spätpleistozänen Pisidien des ehemaligen Ascherslebener Sees. — Arch. Moll. 98: 23—38.

—»— 1972: Neue Erkenntnisse über die Verbreitung von Pisidium pseudosphaerium. — Basteria 36: 7—20.

—»— 1974a: Een pleistocene vondst van Pisidium conventus Clessin in Nederland en de huidige geografische verspreiding van deze soort in Europa. — Basteria 38: 27—40.

—»— 1974b: Die Pisidien der Hochalpengewässer. — Arch. Moll. 104: 1—27.

—»— 1975: Zwei neue boreale Pisidium-Arten: P. hinzi und P. waldeni. — Arch. Moll. 106: 27—37.

Lindholm, W. A. 1909: Mollusken des Baikalsees. — Зоод. исслед. озера Бяикала 4: 1—104.

Mackie, G. L., White, D. S. & Zdeba, T. W. 1980: A guide to freshwater molluscs of the Laurentian Great Lakes with special emphasis on the genus Pisidium. — EPA Rep. 600/3: 1—143.

Meier-Brook, C. 1963: Über die Mollusken der Hochschwarzwald- und Hochvogesengewässer. — Arch. Hydrobiol., Suppl. 28: 1—46.

—»— 1967: Pisidium forense, a new species from Brazil (Mollusca; Eulamellibranchiata; Sphaeriidae). — Arch. Hydrobiol. 64: 63—68.

—»— 1970: Untersuchungen zur Biologie einiger Pisidium-Arten (Mollusca, Eulamellibranchiata, Sphaeriidae). — Arch. Hydrobiol., Suppl. 38: 73—150.

—»— 1975: Der Ökologische Indikatorwert mitteleuropäischer Pisidium-Arten (Mollusca, Eulamellibranchiata). — Eiszeitalter u. Gegenwart 26: 190—195.

—»— 1977: Intramarsupial suppression of fetal development in Sphaeriid clams. — Malacol. Review 10: 53—58.

—»— 1978: Gattung Pisidium. In: Glöer, P., Meier-Brook, C. & Ostermann, O.: Süsswassermollusken. — 73 pp. DJN, Hamburg.

Odhner, N. H. 1923: Pisidium conventus Clessin (P. clessini Surbeck, partim.). — Rep. Sci. Norwegian Exp. Novaya Zemlya 1921 (6): 1—6.

—»— 1926: two fresh water mussels from Carelia and notes on some forms of Sphaerium. — Arkiv Zool. 18A (28): 1—13.

—»— 1929: Die Molluskenfauna des Tåkern. — Sjön Tåkerns Fauna och Flora (Stockholm) 8: 1—129.

—»— 1940: Über Pisidien aus Südschweden. — Arkiv Zool. 32 (11): 1—16.

—»— 1951: Swedish high mountain mollusca. — In: Brinck, P. & Wingstrand, K. G. (eds.): The mountain fauna of the Virihaure area in Swedish Lapland. — Lunds Univ. Årsk., N.F. (Avd. 2) 46 (2): 26—50.

Ruuhijärvi, R. 1974: General description of the Lake Pääjärvi, southern Finland, and the ecological studies on it. — Ann. Bot. Fennici 11: 95—104.

Schlesch, H. 1943: Zur Molluskfauna Möens. — Arch. Molluskenk. 75: 165—186.

—»— 1947: The Pisidia of the Tövelde Klint. — Proc. Malacol. Soc. London 27: 137—140.

Starobogatov, Ya.I. (Старобогатов Я. И.) 1977: Класс двустворчатые моллюски Bivalvia. — In: Kutikova, L. A & Starobogatov, Ya.I. (eds.) (Кутикова, Л. А. & Старобогатов Я. И.) определитель пресноводных беспозвоночных европейской части СССР. Gidrometeoizdat. Leningrad.

Stelfox, A. W., Kuiper, J. G. J., McMillan, N. F. & Mitchell, G. F. 1972: The late-glacial and post-glacial Mollusca of the White Bog, Co. Down. — Proc. Irish Acad. 72 B: 185—207.

Thiel, M. E. 1926: Formwachstumsversuche an Sphaerium corneum. — W. Roux'Arch. Entwicklungsmechanik 108: 87—137.

Thut, R. N. 1969: A study of the profundal bottom fauna of Lake Washington. — Ecol. Monogr. 39: 79—100.

Timm, V. 1975: The Pisidiinae and the Euglesinae of Lake Vörtsjärv. — In: Productivity of Estonian Water Bodies. p. 201—261. Tartu 1975.

Valle, K. J. 1927: Ökologisch-limnologische Untersuchungen über die Boden- und Tiefenfauna in einigen Seen nördlich vom Ladoga-see. — Acta Zool. Fennici 2: 1—180.

Viljanen, M. & Holopainen, I. J. 1982: Population density of Perch (Perca fluviatilis L.) at egg, larval and adult stages in the dysoligotrophic Lake Suomunjärvi. — Ann. Zool. Fennici 19: 39—46.

WIlbur, K. M. & Owen, G. 1966: Growth. — In: Wilbur, K. M. & Yonge, C. M. (ed.), Physiology of Mollusca I: 211—242.

Woodward, B. B. 1913: Catalogue of the British species of Pisidium (Recent and Fossil) in the collections of the British Museum (Natural History) with notes on those of western Europe. — 144 pp + 30 plates. London.

Zeissler, H. 1971: Die Muschel Pisidium. Bestimmungstabelle für die Mitteleuropäischen Sphaeriaceae. — Limnologica (Berlin) 8: 453—503.

Appendix

Fig. A1—A21. The shape indices (A = H/L and B = D/H or D/2H) against shell length are plotted separately for each population, and the equations for regression lines are shown. When the measurements are taken directly from the literature, the reference is shown.

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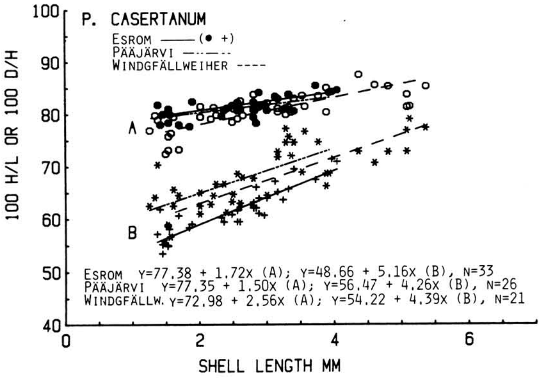

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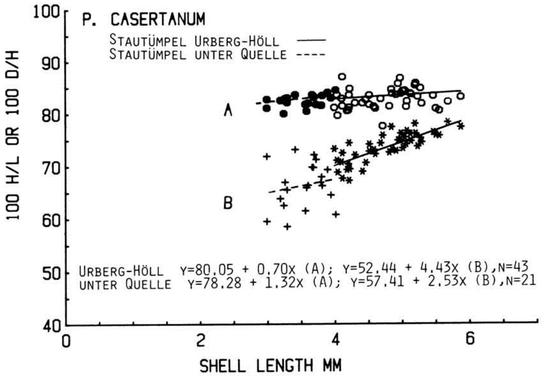

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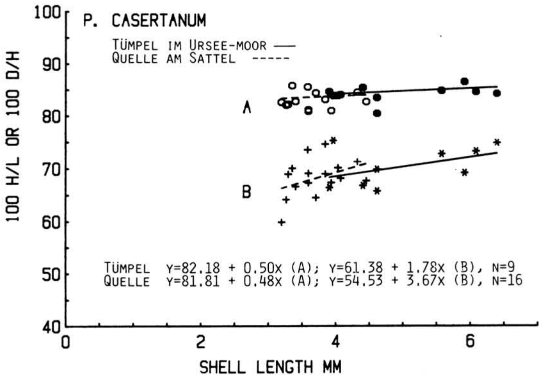

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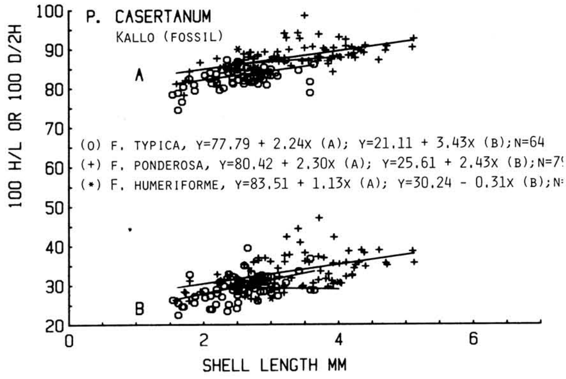

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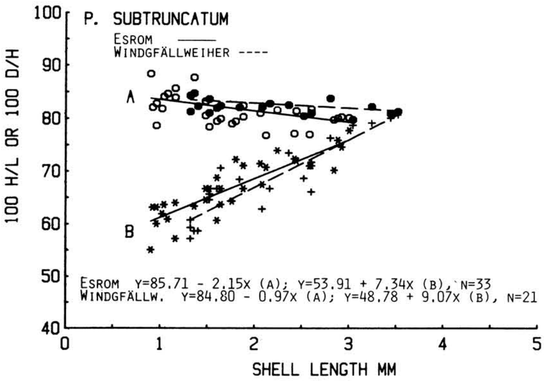

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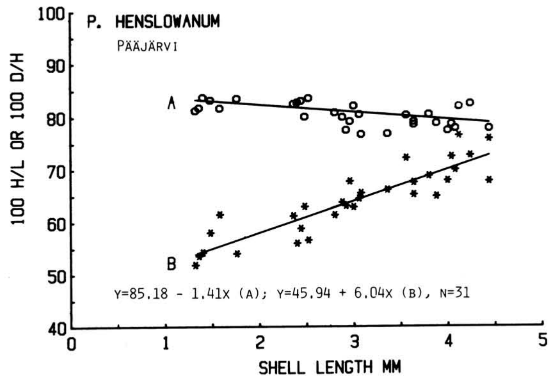

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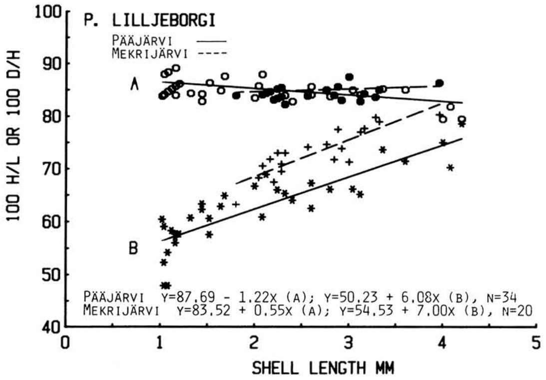

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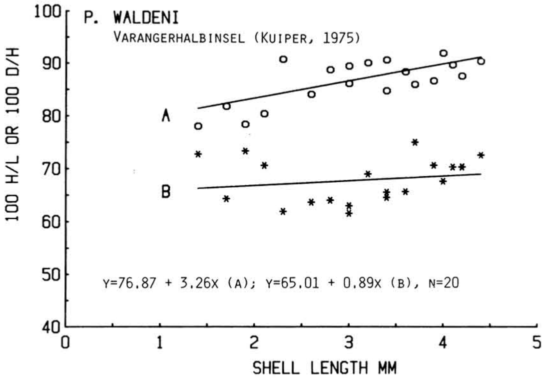

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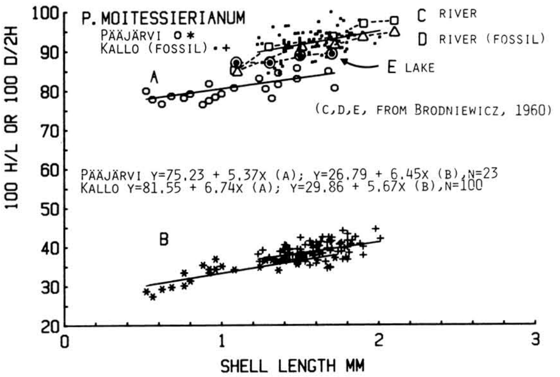

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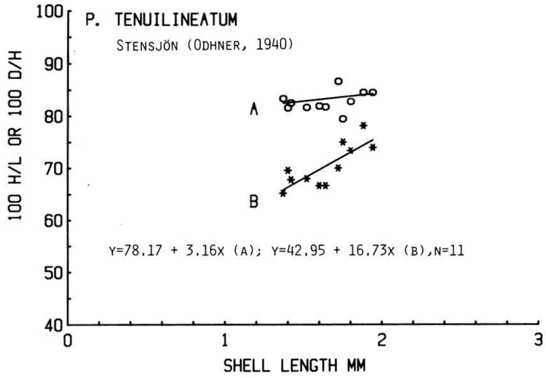

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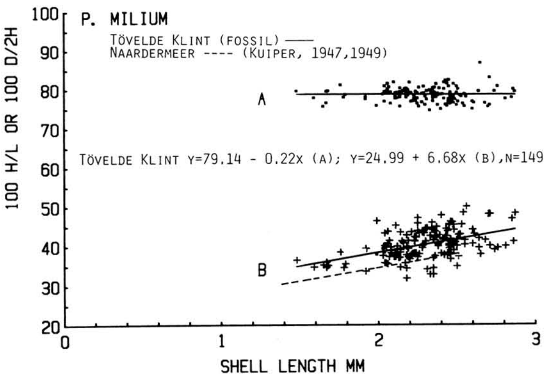

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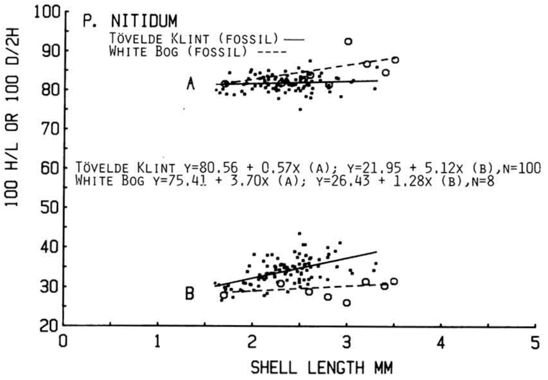

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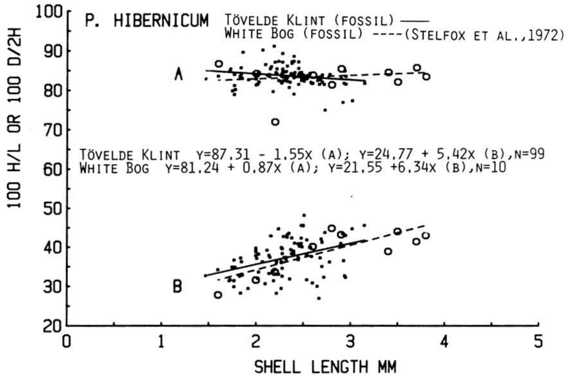

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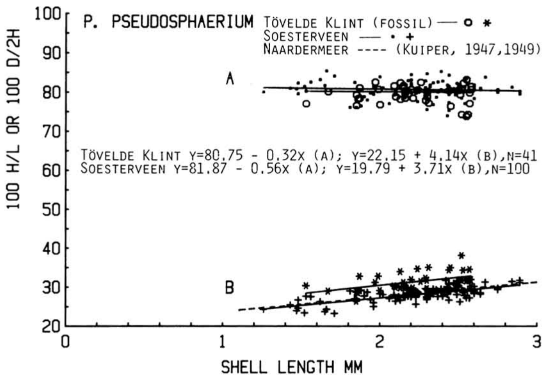

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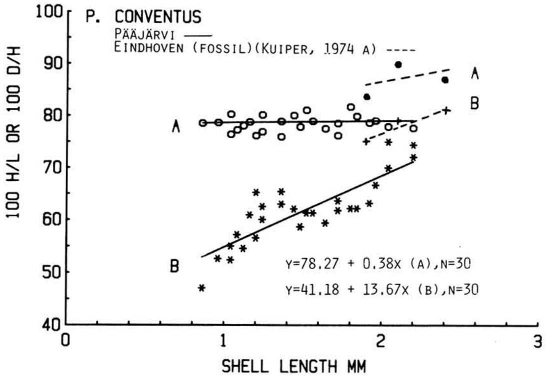

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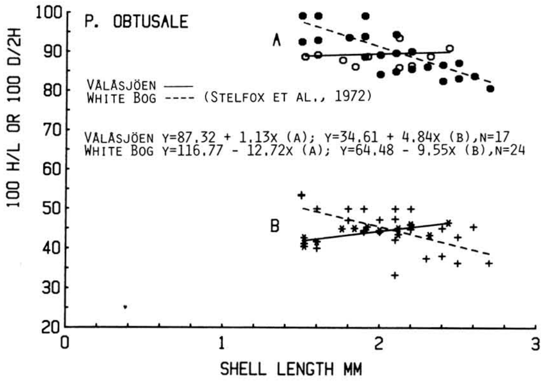

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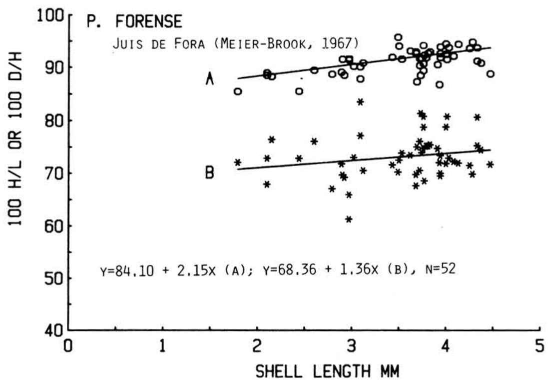

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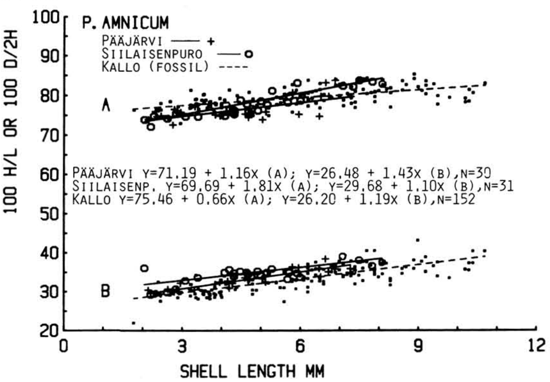

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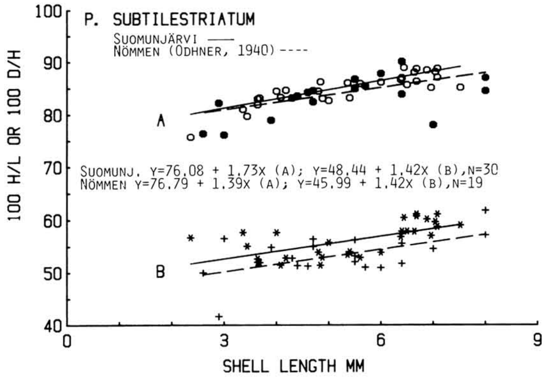

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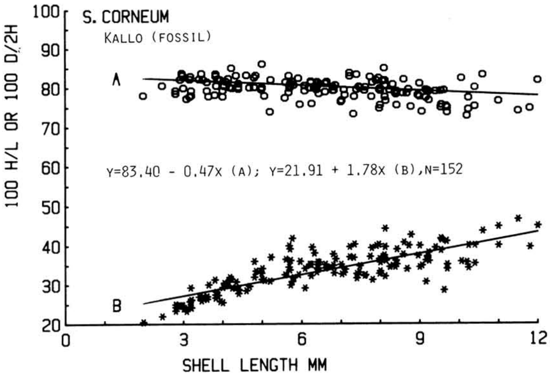

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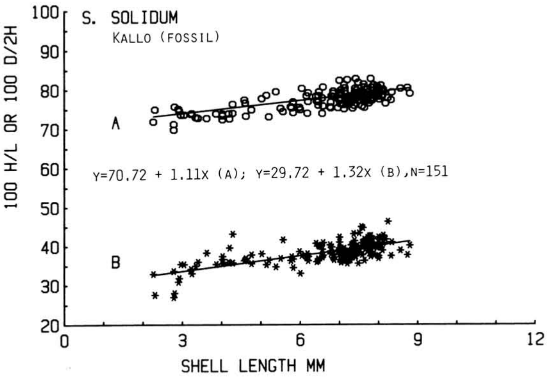

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