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Phylogenetical aspects of gill development and proportions in basidiocarps

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Summery: From an evolutionary standpoint one of the chief factors in the survival of basidiocarps has been the advantage arising from successful reproduction with a relatively small investment of material and energy. Three-dimensional models of gill systems of increasing complexity predict optimum proportions of basidocarps in relation to their stability and the maximization of hymenophoral surfaces. The extent to which these models reflect the actual situation is examined.

Zusammenfassung: Als einer der Hauptfaktoren für die positive Selektion von Fruchtkörpertypen wird eine erfolgreiche Reproduktion bei relativ geringem Aufwand an Material und Energie angenommen. Dreidimensionale Modelle von Lamellensystemen zunehmender Komplexität lassen in Bezug auf eine Maximierung hymenophoraler Oberflächen und die Stabilität der Fruchtkörper optimale Proportionen erkennen. Es wird untersucht, inwieweit diese Modelle die tatsächlichen Verhältnisse widerspiegeln.

Introduction

The development of radially symmetrical lamellae systems of different complexity must obey geometrical laws. Special features of such systems were described by the present author in 1983. The studies were based on 3-dimensional models permitting the simulation or calculation of the surface increase of and material consumed by such hymenophores. An important factor in connection with maximization of the hymenophoral surface was considered to be the ratio of the pileus diameter to that of the stipe (in the case of free gills, to the correspondingly larger stipe diameter). Independent of the thickness and width of the lamellae, each system is characterized by a particular value at which surface increase reaches a maximum. For a system with two generations of lamellulae (l_2-system), probably the most commonly occurring system in nature, this value is 5.5. Basidiocarps with lamellar systems of higher complexity become increasingly unstable on account of their necessarily relatively thinner stipes.

In the present work we have tried to examine the extent to which these models reflect the actual situation. For that purpose we analysed the same source of data already used by Bond (1952, see also Ingold 1946 and 1971). Viz.

the illustrations of Lange (1935 - 1940). Ingold (1946) concluded that size and proportion of agaric basidiocarp are mutually determined by simple mechanical and functional principles involving proportional relationships between thae volume of the pileus and the cross sectional area of the stipe; i.e. the weight of the pileus will depend on the mechanical strength of support (the cube of the pileus diameter will be proportional to the square of the stipe width).

It is clear that the different forms of basidiocarps are based on such principles, at least in a wide sense. However, numerous exceptions, like large and slender basidiocarps (e.g. *Macrolepiota* sp.) or small stout ones (e.g. *Russula* sp.) cannot be explained readily by this hypothesis. Moreover, remarkable differences concerning qualitative and quantitative aspects of fungal tissues within various taxonomical groups (membranous caps, hollow or cartilaginous stipes etc.) are not adequately covered by the explanation mentioned above.

In the maximization of hymenophoral surface additional functional principles such as the optimization of the relationship between the diameter of pileus and the diameter of the hymenophore free zone ('stipe diameter') may be involved.

Methods

The measurements, made to the nearest millimeter, were taken from Lange's illustrations (1935 - 1940). Examples with an unsuitable fruitbody geometry (e. g. pleurotoid or conchate basidiocarps) were not taken into account. The diameter of the stipe was measured at the level of the insertion of the primary gills . In the case of 'free gills' a correspondingly larger value was noted. 756 individuals were recorded, representing approximately 600 species. For taxonomical and nomenclatorial reasons the exact number of species is difficult to establish.

Remark: We are not sure that Lange's illustrations represent the actual distribution pattern of large and small agarics in Europe. According to Moser (Moser, M., pers. comm. 1989) the number of small basidiocarps might be underrepresented. In the 'Kleine Kryptogamenflora' (Moser, 1983) a total number of about 3250 taxa (species and varieties) is registered. This number includes the members of Polyporales, Boletales and taxa of Agaricales with an unsuitable fruitbody geometry (in the sense of this investigation) like *Crepidotus* spp., *Hohenbuehelia* spp., *Resupinatus* spp., etc. Moreover, a clear definition of 'small' and 'large' agarics does not exist. A more detailed study on the latter topic will follow.

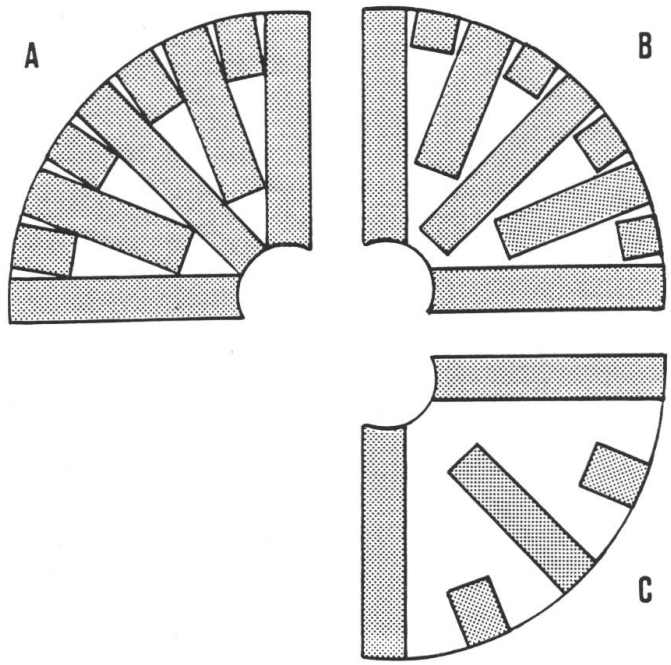


Fig. 1. A: Outline of a gill system with 2 generations of lamellulae (l_2-system) according to the basic theoretical model (Pöder, 1983). **B:** A slight shortening of gills in '**A**.' simulates a system with 3 generations of lamellulae (= pseudo-l_3-system). The loss of surface is less than 10%. **C:** Every second gill series of '**A**.' was removed. The resulting surface is about 50%.

Fig. 1. A: Schematische Darstellung eines Lamellensystems mit 2 Generationen von Zwischenlamellen (l_2-System) gemäss dem theoretischen Modell von 1983. **B:** Eine leichte Verkürzung der in 'A' dargestellten Lamellen simuliert ein System mit 3 Generationen von Zwischenlamellen (= Pseudo-l_3-System). Der Oberflächenverlust beträgt weniger als 10%. **C:** Jede zweite Lamellenserie von 'A' wurde entfernt (Oberfläche ca. 50%).

Results and discussion

An example of the theoretical arrangement of gills according to our model from 1983 is given in fig. 1 A. This represents a gill system with secondary and tertiary gills. In addition, two useful modifications of this basic model are shown (figs 1. B and C) which may represent a better fitting to actual configurations. For instance, the removal of every second gill series (fig. 1 C) means a simple division of the original numerical results by two. In this way, problems related to the 'safe distance' between gills are easily managed without additional complications of the basic algorhytm It is important to know, that such modifications do not change the positions of the graphs relative to each other in fig. 2. All variations reach their maximum of surface at the same ratio values (cap/stipe diameter) which are indicated by vertical

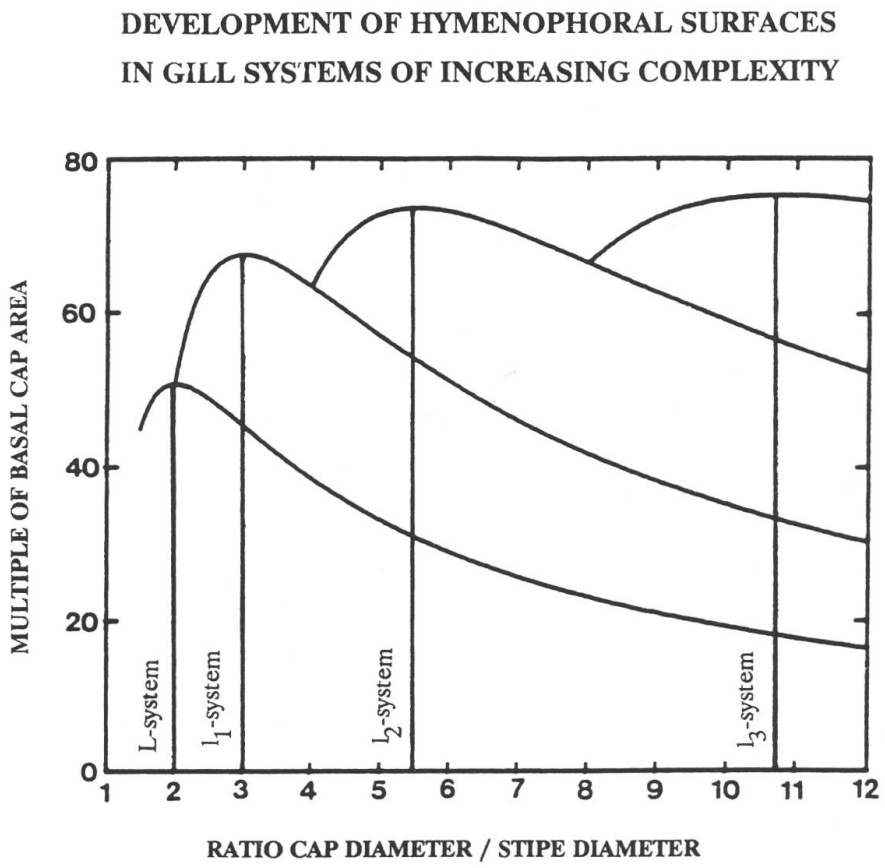


Fig. 2: The vertical lines indicate the ratio values where the different gill systems reach their surface maximum. Note that the relative gain of surface by the l_3-system can be nearly neglected in relation to the previous one (about 2%). Graphs based on the theoretical model from 1983.

Fig. 2: Die Proportionen bei welchen die jeweiligen Lamellensysteme ein Maximum an Oberfläche produzieren sind durch vertikale Linien gekennzeichnet. Der relative Oberflächengewinn durch das l_3-System (ca. 2% gegenüber dem l_2-System) kann nahezu vernachlässigt werden.

lines. Moreover, the graphs in fig. 2 suggest that the introduction of a further generation of lamellulae ('true' l_3-system) will not be very effective. The relative gain of surface is about 2%. Consequently, an even more complex gill system ('true' l_4-system) seems to be even more uneconomic, while the large caps with necessarily slender stipes would be mechanically unstable.

Our measurements show a good agreement with these predictions (see fig. 3). 70.8% of the measured proportions lay within the range covering the theoretical l_2-system. 7.4% show stout proportions (cap/stipe ratio less than 4) and 21.8% are slender (ratio greater than 8). In addition, large and small basidiocarps (cap diameters greater than 10 cm respectively about 1 cm) are

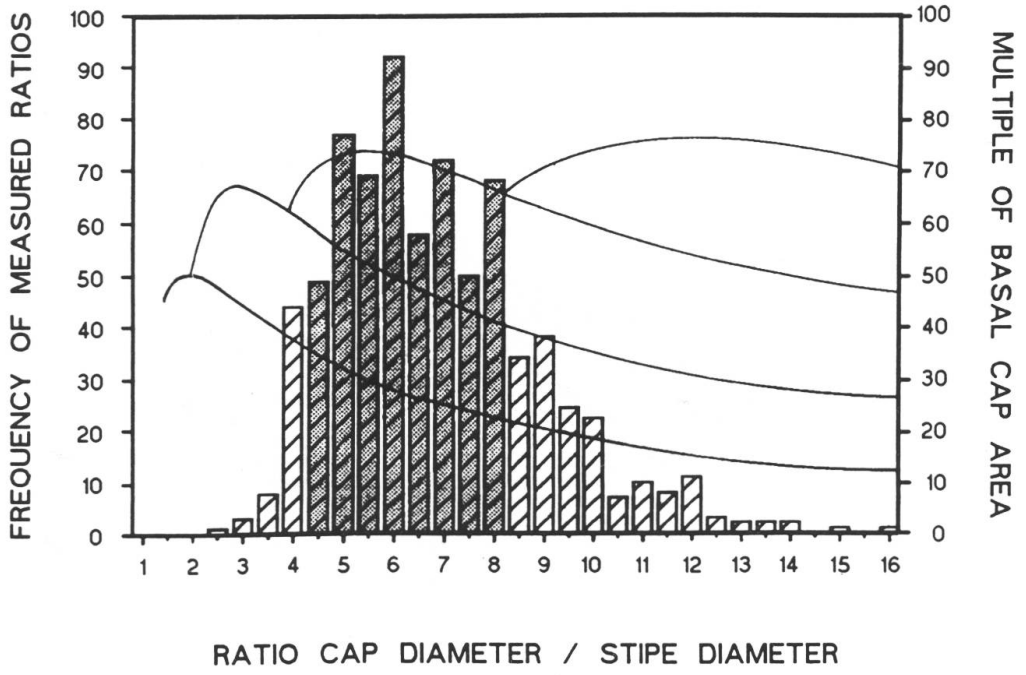


Fig. 3: Combination of fig. 2 and the frequency distribution of cap/stipe diameter relationships of 756 basidiocarps (representing more than 600 species). 70.8% (shaded area) of the measured ratios lay within the range covering the theoretical l_2-system. Fruitbodies of such proportions show a maximum of hymenophoral surface while the mechanical stability seems unaffected.

Fig. 3: Kombination von Fig. 2 und der Häufigkeitsverteilung der gemessenen Hut/Stiel-Verhältnisse von 756 Fruchtkörpern (mehr als 600 Arten). 70.8% (schattierte Fläche) der Werte liegen innerhalb jenes Bereiches, welcher das theoretische l_2-System abdeckt. Fruchtkörper dieser Proportionen entwickeln ein Maximum an hymenophoraler Oberfläche wobei deren Stabilität ungefährdet erscheint.S

found in all of these ratio ranges. The 3-dimensional graphs of the distribution of all measured values (figs 4 A, B and C) show a clear trend towards smaller and more slender basidiocarps. One of the possible interpretations of this phenomenon may be that three-dimensional features vary as the cube and two-dimensional ones as the square of linear measurements. That is, even for the most favourably sized basidiocarps (considered mechanically and fonctionally a mere proportional enlargement will produce an unfavourable 'cost/benefit relationship'. Additional considerations towards the problem and utility of being small will be the subject of further investigations. Moreover, the individual basidiocarp must be considered as a subsystem directed by the mycelium. Saving sterile material like stipe material lowers the cost for reproduction. Such a strategy must be accompanied by several architectural

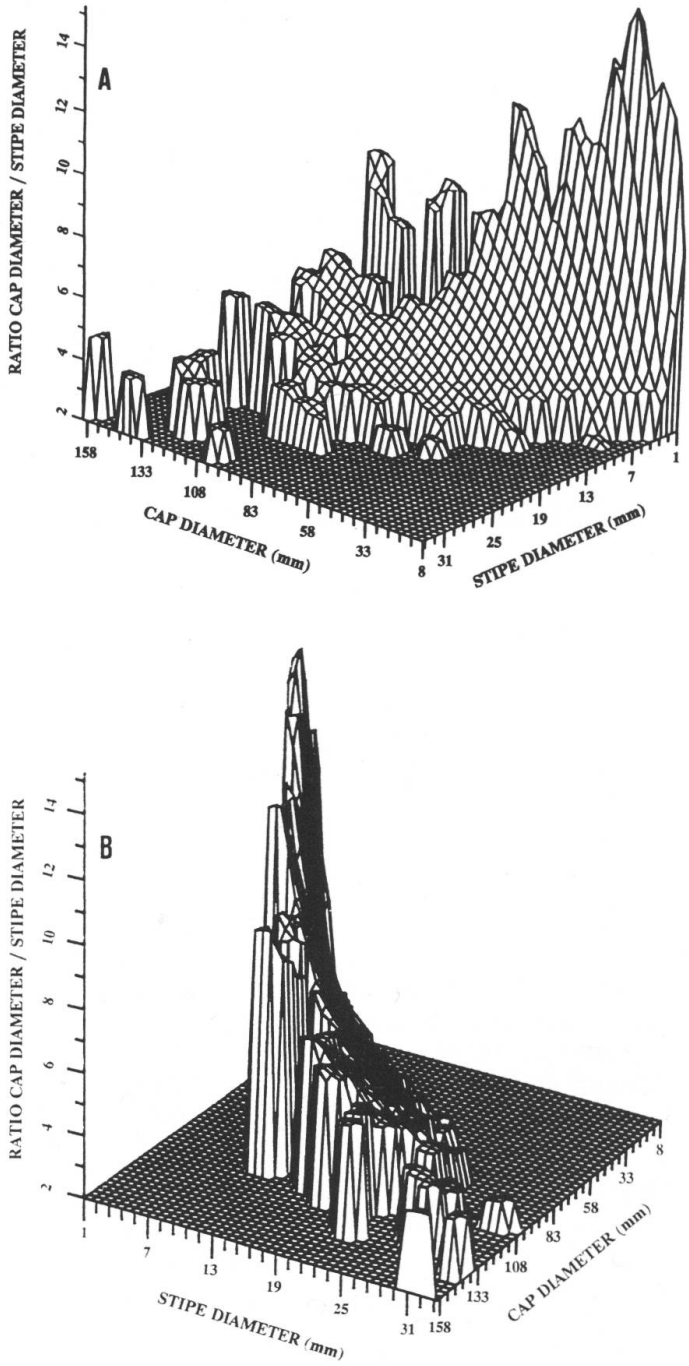
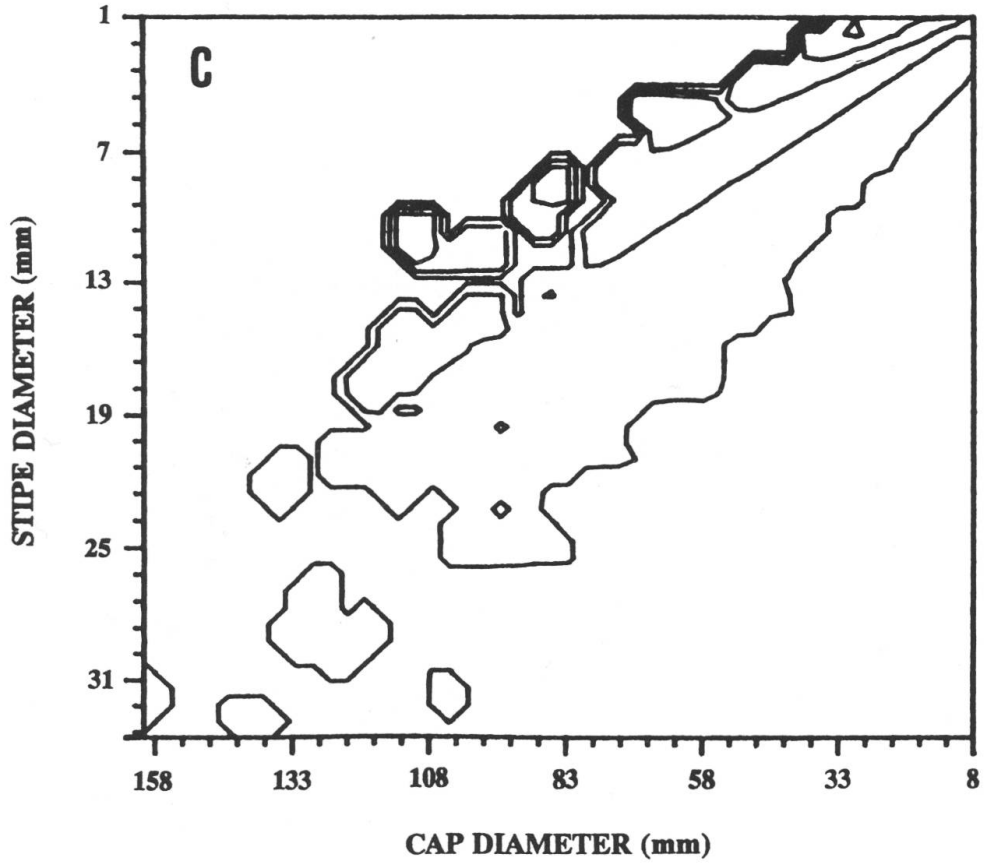


Fig. 4: The three investigated parameters are plotted against each other (3 different views of the same graph; **A**, **B** and **C**). A trend towards smaller basidiocarps is obvious and this is accompanied by an increasing cap/stipe ratio.

Fig. 4: Die drei untersuchten Parameter wurden gegeneinander aufgetragen (3 verschiedene Ansichten derselben Graphik; A, B und C). Ein Trend zu kleineren und gleichzeitig schlanker proportionierten Fruchtkörpern ist deutlich erkennbar.



improvements (e. g. the carrying capacity of hyphae, etc.) to guarantee function. The nature and the degree of such adaptions depend on different boundery conditions which are characterizing special life conditions. For surface maximization the hymenium, respectively the hymenophore may retract from the stipe (cf. Pöder, 1984).

Chiu & Moore (1990) studied the development of the basidiocarp of *Volvariella bombycina* in some detail and think that a co-ordinated activation of subroutines specifies the architecture of fruiting structure. One of their observations is that the distance between the central stipe and the hymenophore during early stages of development was increased to a fixed distance. Consequently, the future gills were free (see also Reijnders, 1963).

Statistical tests show that none of the three parameters is normally distributed (Kolmogorov-Smirnov-test; $p < 10^{-4}$). Such distributions are not well characterized by mean values. Nevertheless, the arithmetic mean value of cap diameters is 43.5mm (SD 25.2mm) and 7.6mm (SD 5.8mm) the mean stipe diameter (Bond 1952: 40.8 and 6.8 mm). The mean value of all the ratios is 6.7 (SD 2.1).

Summarizing our results we think that the process of maximizing hymenophoral surface influences the proportions of basidiocarps. Moreover,

characters like 'free gills' and collars may be understood as profitable adaptions.

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