# Larval shells of Tertiary *Cubitostrea* Sacco, 1897, with a review of larval shell characters in the subfamilies Ostreinae and Crassostreinae (Ostreoidea, Bivalvia)

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## Abstract

The characteristics of larval shells of some fossil Ostreoidea are described [*Cubitostrea sellaeformis, Cubitostrea* sp., *Cu.* ? *plicata*, ? *Crassostrea* sp., ? *Saccostrea* sp. (all Eocene), *Agerostrea* sp., *Flemingostrea cretacea, Pycnodonte* sp. 1 (Santonian, Campanian), *Pycnodonte* sp. 2 (Eocene), and *Exogyra ponderosa* and *E. cancellata/costata* (Campanian)] from the United States and France and current knowledge on larval shells of the Jurassic genus *Liostrea* and of Recent Crassostreinae and Ostreinae are reviewed.

A comparative study and evaluation and a tentative attempt towards a phylogenetic interpretation of the Ostreoidea have been made.

Shape (prodissoconch I+II), sculpture, length and height of left and right valves (P I+II), length of straigth hinge (P I), length of provinculum (P II), convexity (P II), shell proportions (P I+II), hinge dentition, and shape and dimensions of denticles have been studied in detail and a "formula" has been developed for the dentition. Measurements of "shoulders", angle of rotation of length axis, width of provinculum are included. Differentiations at the subfamily level are possible using shape and sculpture or the type of hinge dentition. The height to length ratio of the prodissoconch I (P I) and/or the hinge dentition often allow to recognize species.

Of phylogenetic importance is:

1) The P I of the fossil species studied herein is small suggesting (a) small egg size, (b) completely planktotrophic development, and (c) non-brooding mode of larval development.

2) The shapes and size relations of larval shells of Eocene species and the hinge dentition of American *Cubitostrea* show all characteristics of larval shells of Recent non-brooding Crassostreinae. This questions current concepts of the phylogeny of the Ostreidae and the subfamily definitions of the Ostreinae and Crassostreinae. If a small P I is the plesiomorphic character state for all oysters then *Cubitostrea* may be more closely related to the Ostreinae than to the Crassostreinae.

3) Shape and sculpture of two Cretaceous *Exogyra* species are very different from those of Pycnodonteinae, though both belong to the Gryphaeidae. The two Campanian and Eocene *Pycnodonte* species and the Kimmeridgian *Liostrea plastica* (Gryphaeidae and Ostreidae respectively) have the same sculpture of coarse growth crests on the P II, different from the generally smooth shells of all other species. Therefore possibly this '*Liostrea*' belongs to the Gryphaeinae, but insufficient information currently prevents a taxonomic evaluation.

4) Based on adult shell characters it is hypothesised that *Planostrea pestigris* (Hanley, 1846) and *Ostreola stentina* (Payraudeau, 1826) are Recent representatives of the genus *Cubitostrea*. Their larval shells, however, are not known.

**Key-words**: Larval shell characters, Ostreidae (Bivalvia), fossil and Recent.

## Résumé

Les coquilles larvaires de quelques Ostreoidea fossiles [*Cubitostrea sellaeformis, Cubitostrea* sp., *Cu.* ? *plicata*, ? *Crassostrea* sp., ? *Saccostrea* sp. (all Eocene), *Agerostrea* sp., *Flemingostrea cretacea*, *Pycnodonte* sp. 1 (Santonien, Campanien), *Pycnodonte* sp. 2 (Eocène), *Exogyra ponderosa* et *E. cancellata/costata* (Campanien)] des Etats-Unis et de France sont décrites. Les données connues concernant les coquilles larvaires appartenant au genre jurassique *Liostrea* et aux Crassostreinae et Ostreinae actuelles sont passées en revue.

Une étude comparative et un essai d'interprétation phylogénétique des Ostreoidea sont tentés.

Les caractères étudiés en détail sont: la forme (prodissoconche I+II), l'ornementation, la longueur et la hauteur des valves gauche et droite (P I+II), la longueur de la charnière rectiligne (P I), la longueur du provinculum (P II), la convexité (P II), les proportions de la coquille (P I+II), la dentition de la charnière, la forme et les dimensions des denticules. Une "formule" de dentition est établie. Les "épaules", l'angle de rotation autour de l'axe de la longueur, la largeur du provinculum ont été mesurés.

La distinction au niveau de la sous-famille est possible sur base de la forme, de l'ornementation et du type de dentition de la charnière.

Le rapport hauteur/longueur de la prodissoconche I (P I) et/ou la dentition de la charnière permettent, dans de nombreux cas, de séparer les espèces. Au point de vue phylogénétique, les conclusions importantes sont:

1. La P I des espèces fossiles étudiées ici est petite, suggérant (a) des oeufs de petite taille, (b) un développement exclusivement planctotrophe et (c) un développement larvaire sans "couvaison".

2. Les rapports de formes et de tailles des coquilles larvaires de l'Eocène et la dentition de la charnière des *Cubitostrea* d'Amérique sont caractéristiques des coquilles larvaires de Crassostreinae actuelles se développant sans "couvaison". Cela met en question les concepts habituels de la phylogénie des Ostreidae et les définitions des Ostreinae et Crassostreinae. Si une petite P I est le caractère d'un état plésiomorphe chez toutes les huîtres, alors *Cubitostrea* pourrait être plus étroitement apparentée aux Ostreinae qu'aux Crassostreinae.

3. La forme et l'ornementation de deux espèces d'*Exogyra* du Crétacé sont très différentes de celles des Pycnodonteinae, bien qu'elles appartiennent toutes aux Gryphaeidae. Les deux espèces de pycnodontes du Campanien et de l'Eocène et *Liostrea plastica* du Kimmeridgien (appartenant respectivement aux Gryphaeidae et aux Ostreidae) ont les mêmes côtes de croissance grossières sur la P II ce qui les distingue des autres espèces à coquille généralement lisse. En conséquence il est possible que cette "*Liostrea*" appartienne aux Gryphaeidae, mais les données actuelles insuffisantes empêchent toute évaluation taxinomique.

4. Les caractères des coquilles adultes laissent supposer que *Planostrea pestigris* (HANLEY, 1846) et *Ostreola stentina* (PAYRAUDEAU, 1826) sont des représentants actuels du genre *Cubitostrea*. Leurs coquilles larvaires ne sont pas connues.

**Mots-clefs**: Coquilles larvaires, Ostreidae (Bivalvia), fossiles et actuelles

## Introduction

Efforts to integrate living and fossil oysters into a con-

sistent classification and phylogenetic hypothesis face two major problems. First, the currently accepted supraspecific classification — Ostreoidea (Ostreidae (Ostreinae [brooding], Crassostreinae [non-brooding], Lophinae [brooding]), Gryphaeidae (Pycnodonteinae [non-brooding; inferred from soft body and larval shell characteristics])) — includes on the subfamily level the character ''brooding-non brooding'' (informally by STENZEL, 1971; and formally introduced by TORIGOE, 1981; HARRY, 1985). And second, fossil oysters are fit in the actualistic classification on the basis of adult shell characters only, thus implying a certain mode of larval development without evidence (see STENZEL, 1971; and critique in MALCHUS, 1990: 61, 80).

Characters of larval shells may help to resolve this problem, but they are insufficiently known from fossil taxa. For this reason Upper Cretaceous and Eocene sediments from the North American Gulf Coast were sampled and screened for larval oyster shells; further material of Jurassic, Late Cretaceous and Eocene age could be borrowed. Most specimens belong to the Palaeogene genus *Cubitostrea*. With the results presented here the genus becomes crucial with respect to oyster phylogeny because its adult shell characters suggest that it is a member of the Ostreinae (STENZEL, 1971; see Pls. 1 and 2, Figs. A-D: specimens from the Gulf Coast; Pl. 2, Figs. E-H: specimens from the Paris Basin) while their larval shells turn out to be typically crassostreinid. This contradiction indicates that the current classification is not consistent with ostreid phylogeny.

Figured specimens are deposited with the Institut royal des Sciences naturelles de Belgique, Bruxelles: IRSNB-MI 10638-10648 (Mesozoic); IRSNB-TI 6134-6171 (Tertiary). Most of the measured specimens will be found on the same SEM-stubs as the figured larval shells. The rest stays with the author for further examinations.

## Historical background

The larval development of oysters has been described and reviewed many times since HORST's (1883) detailed examination of the ontogeny of *Ostrea edulis* LINNÉ, 1758. However, only a number of these contributions is specifically related to the larval shell and thus to this paper. Concerning studies of the soft parts the reader is referred to GALTSOFF (1964) on *Crassostrea virginica* (GMELIN, 1791) and WALLER (1981) on *Ostrea edulis* and the literature cited therein. Additional information about the development of the larval shell in bivalves can be drawn from BANDEL (1988). According to BERNARD (1896) the earliest examinations of larval shells of bivalves and their hinge dentitions go back to LACAZE-DUTHIERS (1855) [of *Mytilus edulis* (GRAY, 1847)] and JACKSON (1890; of *Crassostrea virginica* among many other species). The latter also introduced the term ''prodissoconch''. But it was BERNARD himself who published the earliest comprehensive studies on bivalve prodissoconchs, including

*Ostrea edulis* and *Neopycnodonte cochlear* (POLI, 1795) and shells of fossil oysters mainly from the Eocene of the Paris Basin (BERNARD, 1898; and references therein). Nevertheless, his descriptions especially of fossil ostreoid species need verification and are therefore of limited use (see also STENZEL, 1971).

Subsequent important studies on larval shell morphology include the works of STAFFORD (1913), HORI (1933), ROUGHLEY (1933), RANSON (1939a,b; 1960; 1967a,b), WERNER (1939), KORRINGA (1941), CARRIKER (1951), LOOSANOFF & DAVIS (1963), and LOOSANOFF et al. (1966). RANSON (1960; 1967a,b) still represents the most extensive documentation of larval shells of extant oysters. Unfortunately, his generalised drawings (1960) and single photographs (of each species) (1967a,b) are not accompanied by measurements of size ranges or descriptions of ontogenetic stages of the hinge development of the larvae; also descriptions of the corresponding adults are missing. Thus, his primary claim that characters of larval oyster shells are species specific remained unproved, but it is now supported by more recent investigations of, e.g. FORBES (1967), PASCUAL (1971, 1972), DINAMANI (1973, 1976), DINAMANI & BEU (1981), DIX (1976), LE PENNEC (1978), BOOTH (1979), CARRIKER & PALMER (1979), CHANLEY & DINAMANI (1980), TANAKA (1980, 1981), WALLER (1981), LE BORGNE & LE PENNEC (1983), LE PENNEC & COATANEA (1985), VER (1986), FERNANDEZ CASTRO & LE PENNEC (1988), or HU et al. (1993 — with a determination key using characteristics of the larval and nepionic shells).

While there is abundant literature available on Recent species, fossil larval shells have rarely been examined (BERNARD, 1896; JABLONSKI & BOTTJER, 1983; PALMER, 1989). Of these, only PALMER's contribution about Jurassic *Liostrea* species (Liostreinae, Ostreidae) is of greater interest. Results of these works will be summarised and discussed later.

Ecological aspects of the larval life cycle of oysters are described in KORRINGA (1941) and CARRIKER (1951) (*Ostrea edulis* and *Crassostrea virginica*); experiments about the effects of food supply on adult oysters and their brood were carried out by LOOSANOFF & DAVIS (1963), HELM et al. (1973), HIS & ROBERT (1987), and CRISP (1974). *In vivo* observations on larval brooding in *Tiostrea chilensis* (PHILIPPI, 1845) have been recently described by CHAPARRO et al. (1993). Actualistic approaches to palaeoecology, palaeobiogeography, and to macro-evolution on marine larvae in general have been applied and reviewed by LUTZ & JABLONSKI (1978), JABLONSKI & LUTZ (1980, 1983), LUTZ (1985), and JABLONSKI (1986).

Important data on oyster evolution that are independent of larval shell morphology or larval development can be drawn from genetic investigations of AHMED (1975), BUROKER et al. (1979a,b), BUROKER (1983, 1985); FOLTZ & CHATRY (1986), REEB & AVISE (1990) and from cross-fertilisation experiments, which have been recently reviewed by GAFFNEY & ALLEN (1993). Investigations of the sperm ultrastructure of oysters as well appear to be promising for phylogenetic inferences but have not yet
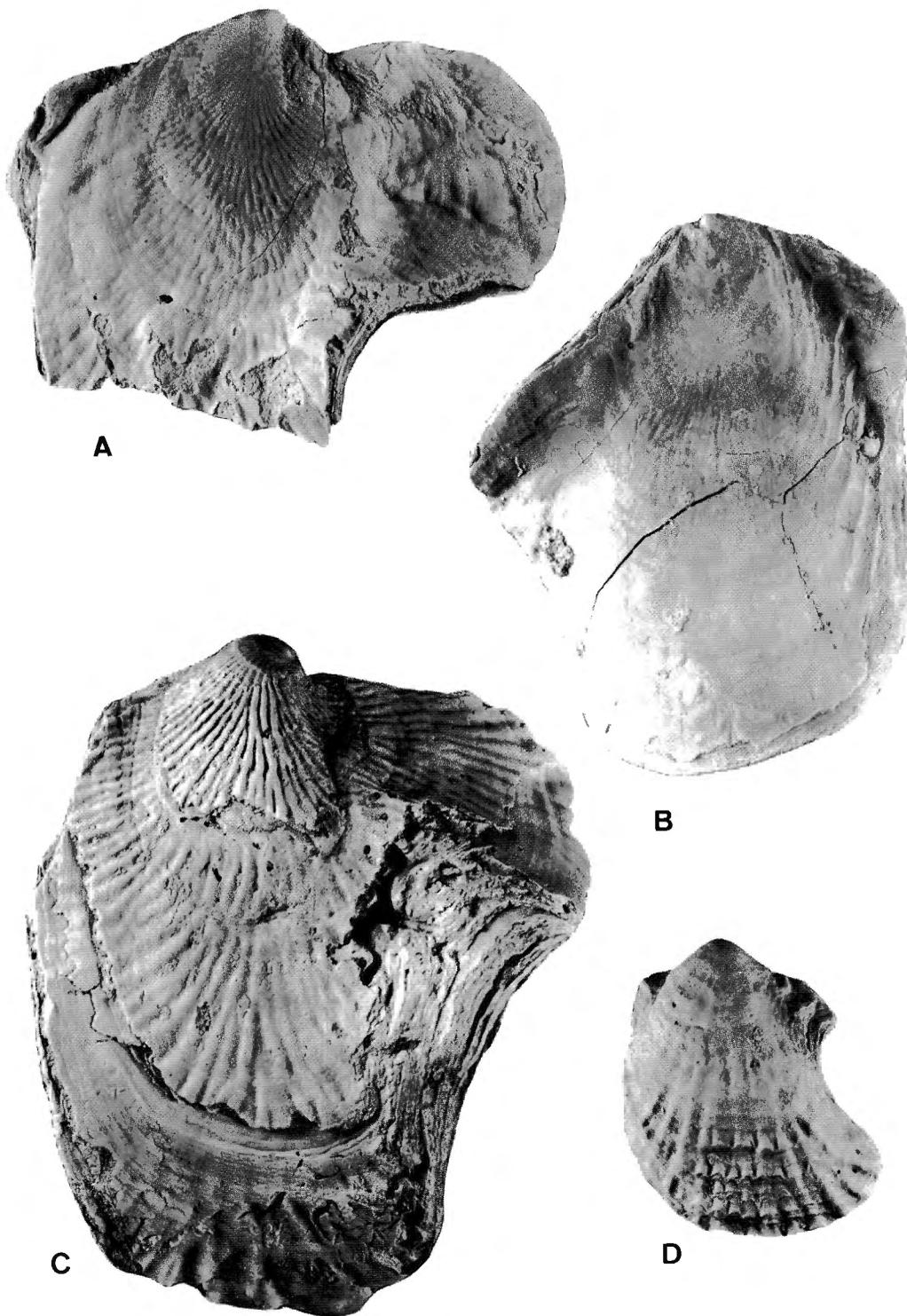
PLATE 1

All figures natural size

Figures A, B      — *Cubitostrea sellaeformis* (CONRAD), Middle Eocene, Lisbon Formation, Little Stave Creek, Alabama, 1st. sellaeformis bed (11891/1-4), A: LV, IRSNB-TI 6134, B: RV, IRSNB-TI 6135: Exterior of adult shells.

Figure C          — *Cu. sellaeformis*, Middle Eocene, Archusa Marl Member (Cook Mountain Fm.), Doby's Bluff, Mississippi, float (10891/4-float), IRSNB-TI 6136: LV, exterior. Note the large posterior flange of Figs. A-C, but the difference in convexity of earlier growth stages larnd sculpture in Figs. A and C.

Figure D          — *Cu. lisbonensis* (HARRIS), Middle Eocene, Lisbon Formation, Little Stave Creek, Alabama, 2nd. lisbonensis bed (11891/1-3), IRSNB-TI 6137: LV, exterior.
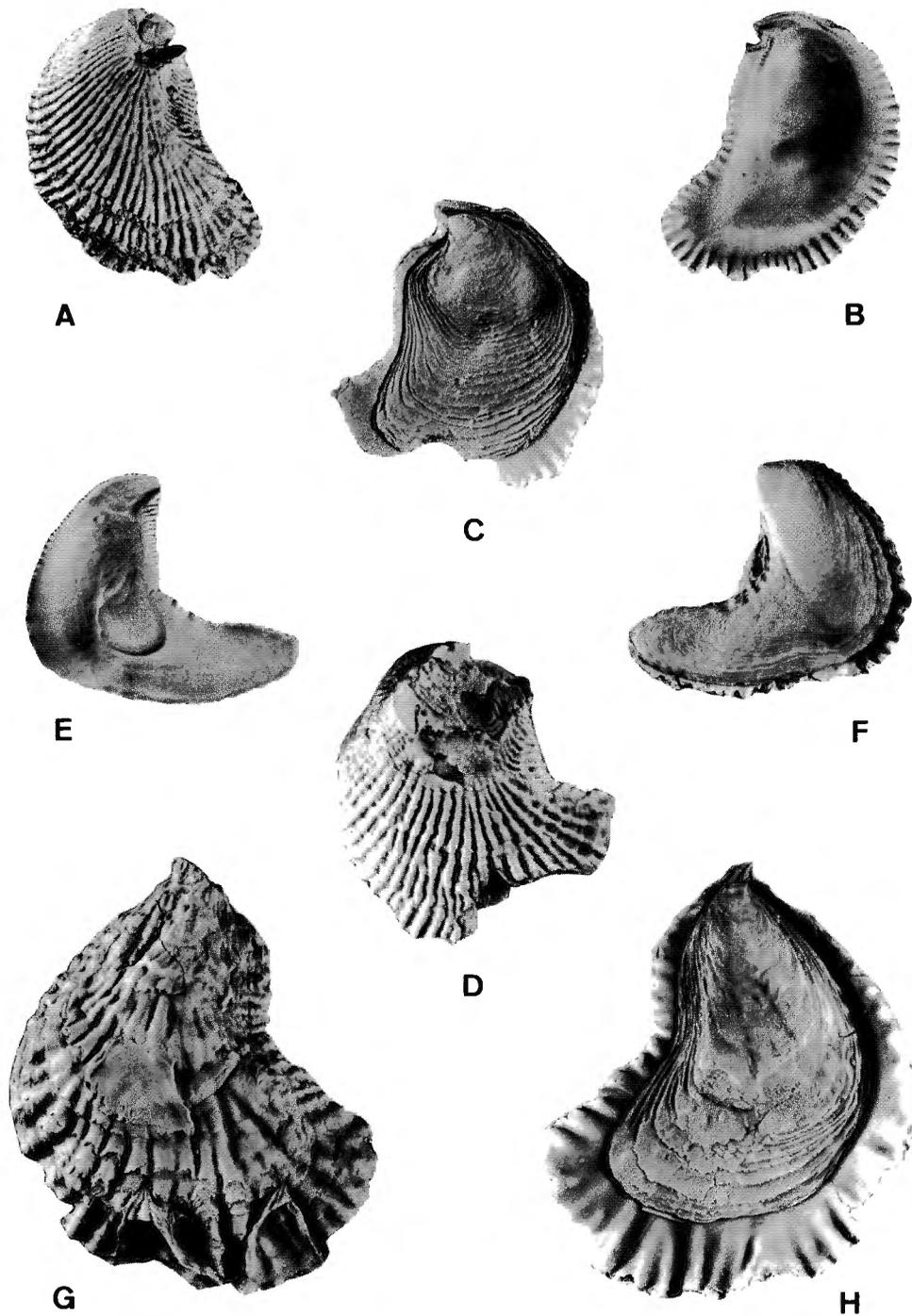
PLATE 2

Figures A, B and E-H natural size, C and D x 2

Figures A, B      — *Cubitostrea sellaeformis*, Middle Eocene, Lisbon Formation, Little Stave Creek, Alabama, 1st. sellaeformis bed (11891/1-4), LV, IRSNB-TI 6138. A, B: exterior and interior views of the same specimen.

Figures C, D      — *Cu. sellaeformis*, (11891/1-4), IRSNB-TI 6139: Articulated shell (x 2), C: RV, exterior, D: LV, exterior.

Figures E, F      — *Cu. cubitus* (DESHAYES), Eocene ("Auversien", Bartonian), Le Guépelle, France, (collection Dautzenberg), IRSNB-TI 6140. E: RV of articulated shell, interior, F: articulated shell seen from right valve exterior. Adult shells of *Cu. plicata* (SOLANDER *in* BRANDER) of which larval shells are described here are very similar to those of the type species *Cu. cubitus*.

Figures G, H      — *Cu. wemmelensis* GLIBERT, Eocene ("Wemmelien", Bartonian), from type locality Neder-over-Hembeek, Brabant, Belgium, IRSNB-TI 6141. G: LV of articulated shell, exterior, H: RV of articulated shell, exterior. Note the large free commissural shelf of the left valve.

yielded enough data (HEALEY & LESTER, 1991; on *Saccostrea commercialis*).

The supraspecific classification of oysters used here is mainly based on STENZEL (1971), HARRY (1985) and on my own studies (MALCHUS, 1990, and unpublished data). Most recent workers seem to have disregarded HARRY's classification scheme of living oysters (unfortunately without discussion). Although there may be some criticism of his interpretation, his examination of the soft body characters and those of the adult shell are thorough and worth considering.

## Development of the larval shell and shell characteristics: definitions and comments

### Development, growth stages, and shell shape

The process of shell forming which appears to be very similar in all bivalves has been recently reviewed by EYSTER (1986) and BANDEL (1988) (for oysters see also HORST, 1883; WALLER, 1981). A primary organic larval shell forms — at least in *Ostrea edulis* LINNÉ — during the early or middle trochophora-like stage (HORST 1883). According to BANDEL (1988) this organic hood is completely attached to and grows together with the mantle rudiment (shell gland, shell invagination field of authors) until it is large enough to cover the embryo. At this stage the cells of the mantle rudiment detach from the primary shell except for a small fringe near the inner edge and the interior of the shell is coated with an aragonitic mineral layer; the dorsal connection of the valves — the later hinge — remains uncalcified. Then the larva pulls the two mineralised halves towards each other which creates the functional bivalved calcified primary shell or **prodissoconch I** (P I). As soon as this has happened growth continues commarginal by means of specialised mantle cells thus giving rise to the second larval shell or **prodissoconch II**. (Views contrast about the existence of a "shell gland" in bivalves and about its role in shell formation; see, e.g., OCKELMANN, 1965; WALLER, 1981; EYSTER, 1986; BANDEL, 1988).

STENZEL (1964) and CARRIKER & PALMER (1979) showed that the entire larval shell is aragonitic, which is in contrast to the predominantly calcitic mineralogy of the post-metamorphic dissoconch.

Both the mineralised primary shell (P I) and the earliest stage of prodissoconch II are characteristically D-shaped because of the prominent straight line of the hinge. The animals at this stage are therefore often referred to as **"D-shape veligers"**. The term **"straight hinge veliger"** is less appropriate because the hinge remains straight throughout the larval phase. During further growth the umbo of the P II gets knobby (**"knobby umbo stage"**) and may finally grade into a **"skewed umbo stage"**. At advanced stages of the P II a foot and a coloured eye-spot develop (= **pediveliger, eye-spot larva** of authors). Further changes of the shape do not occur before metamorphosis.

### Shell structure and sculpture

The prodissoconch I (P I) appears smooth but has a characteristic ultrastructure (**"central pitted zone"** and **"outer stellate-radial zone"**; CARRIKER & PALMER, 1979; WALLER, 1981). The outer zone, in addition, shows a subordinate concentric ornament. This feature becomes predominant in the prodissoconch II and allows an easy distinction between the two growth stages. Nearly all Ostreidae have a smooth P II, with the exception of *Liostrea plastica* (TRAUTSCHOLD, 1860); pycnodonteinid oysters produce prominent concentric ridges (see WALLER, 1981; PALMER, 1989). Detailed examinations of the shell structure were not carried out here; it appeared to be very similar in all species investigated. But some additional remarks will be given on the sculpture.

### Shell size and shell proportions

The present study distinguishes seven characters related to shell size: the length, height and length of the straight hinge (D-line) of the P I and the length, height, convexity, and length of the provinculum of the P II. For more details see "Measurements" in the chapter "Methods and materials".

There exists a pronounced correlation in extant oysters between egg size, mode of larval development and the size of the prodissoconch I. The extent to which this fact can be used for phylogenetic interpretations requires some explanations. Eggs produced by living oysters generally fall into three size classes with diameters of (a) 35 to 60 (m, (b) 90 to 150 (m, and (c) 200 to 290 (m (see AMEMYA, 1926, on *Crassostrea angulata*; LOOSANOFF & DAVIS, 1963, on *Cr. virginica, Ostrea edulis, Ostreola lurida*; LE PENNEC, 1978, *Crassostrea gigas*; CHAPARRO et al., 1993, on *Tiostrea*; and review of BUROKER, 1985). Similarly, there are three size classes of the prodissoconch, i.e. of 50 to 85 (m (P I), 105 to about 185 (?200) (m (P I; very large values probably refer to early P II stages), and larger than 240 (m (P I; values larger than 400 (m certainly belong to P II stages). Small eggs and prodissoconchs I are characteristic of the oviparous Crassostreinae, while most species of the larviparous Ostreinae and Lophinae (RANSON, 1967b; HARRY, 1985) fall into the medium size class. Exceptions are the sponge oyster, *Cryptostrea permollis*, Ostreinae, with an egg size of 60 to 80 $\mu$m (BUROKER, 1985), and the two species of *Tiostrea*, Ostreinae, which define the third category.

A similar size distribution occurs throughout the class Bivalvia and has been generally related to planktotrophic, lecithotrophic, and direct modes of development, respectively (OCKELMANN, 1965; MACKIE, 1984). Nevertheless, most Ostreidae are planktonic and planktotrophic, at least for a period of several days (BUROKER, 1985), and *Tiostrea chilensis* (PHILIPPI, 1845) has been shown to feed on plankton while being brooded (CHAPARRO et al., 1993). Thus, the egg size and P I size of living oysters are primarily related to ovipary and larvipary, with the exception of *Cryptostrea permollis*. This species, however, is of an unusual small size for oysters (about 30 mm; HARRY, 1985: 144) which fits perfectly well with OCKEL-

MANN's (1965: 26) observation that "within a systematic group of bivalves, large species produce larger eggs than do small species, provided that both have the same type of development." In addition, even though the egg size is exceptionally small this does not apply to the size of P I (see Table 14).

The basic assumption in the present context is therefore that the P I size of fossil oysters gives a first hint towards their egg size and thus to ovipary or larvipary. This interpretation, of course, needs confirmation through similarities in other larval shell characteristics. The within-group comparison is supposed to be safer than comparisons with larval shell sizes or ratios between P I/P II of other bivalve groups (OCKELMANN, 1965; LABARBERA, 1974; JABLONSKI & LUTZ, 1983).

*Growth patterns*
The different shapes of larval oyster shells "straight hinge veliger", "knobby umbo stage", and "skewed umbo stage" represent successive steps of an allometric shell growth. The resulting pattern which is supposed to be genetically fixed and not influenced by the environment is reflected by changing size relations (proportions). Complete ontogenetic series which are necessary to analyse this pattern were not available for the fossil material and consequently the analysis refers to data from the literature.

*Intraspecific variability of absolute shell size*
"Variability" here is used for both genetic and ecological variability of a species. The term s. str. refers only to the genetic variability within a population and as such could rarely be applied to fossils. The analysis of some studies on Recent oysters allows one to get at least a rough idea of the type and range of the variability of shell size. This is desirable because FULLER et al. (1989) assumed that congeneric species (of bivalves) may differ by only 5% of their respective shell size. This is also the least range we have to assume for the relative error of measurements (see chapter on measurements).

HAGMEIER (1916) and KORRINGA (1941) observed that larvae of Ostrea edulis which belong to the second spawning period in August of the year have a smaller average and minimum size than do larvae of the first period in June. ERDMANN (1935) assumed that high water temperatures lead to a shortened period of incubation and thus to a smaller size of the liberated larvae (see also JABLONSKI & LUTZ, 1978). However, KORRINGA (1941) himself did not find hints that supported the "high temperature hypothesis". He concluded that the date of liberation may be of greater importance (which may be interpreted as "exhaustion" of the adult females during the second spawning season).

TANAKA (1954, *fide* LOOSANOFF et al., 1966) reported that larvae of Crassostrea gigas are, at times of metamorphosis, larger on southern coasts of Japan than on northern coasts, and LOOSANOFF & DAVIS (1963) experimentally demonstrated for Cr. virginica that a positive correlation exists between average growth rate of the larvae and temperature, i.e. 12 day old larvae measured only 77 $\mu$m in length when they developed at a temperature of 10°C, while larvae of the same age reached a length of 203 $\mu$m at a temperature of 33°C.

Feeding experiments with Cr. virginica by LOOSANOFF & DAVIS (1963) and with Ostrea edulis by HELM et al. (1973) showed that food supply is another important size-controlling factor. Twelve day old larvae of Cr. virginica which were offered supplementary food were, on average 169 $\mu$m long while the control group reached an average size of 96 $\mu$m. Supplemented adults of Ostrea edulis gave rise to larvae that exceeded those of a non-supplemented control group in size (by about 5%), neutral fat reserves and their initial rate of growth (see also Table 14: 19A, B respectively).

It is, at the moment, not possible to differentiate clearly between the genetical and ecological influence of size ranges. But, apparently, size is strongly affected by environmental factors and perhaps by the spawning season (1st or 2nd of a year). Considering all measurements of O. edulis the natural intra-specific variability in size of young larvae appears to be much higher than the experimentally produced ones although it could have been assumed that oyster spat growing under favourable conditions, e.g. in hatcheries, become larger on average. In general, the natural variability in absolute size may be estimated as being +/− 5 to 10%. The extreme differences in temperature as induced by LOOSANOFF & DAVIS (1963) may not correspond to naturally occurring conditions during spawning and larval growth. The value coincides more or less with the range of the relative error estimated for measurements in this study (see chapter "Measurements"). But, it is supposed here that proportions between the different size measurements are not affected.

*Hinge and hinge dentition*
The hinge (= provinculum of authors) is the (narrow) plate below the umbo around which the right and left valves rotate when opening/closing the shell. It contains the imaginary **pivotal axis** (= **hinge axis** or **hinge line**). Development of **hinge denticles** coincide with the broadening of the hinge plate itself which starts at or near the P I/II boundary. Initially the young hinge plate (of P I) contains a single row of minute irregular crenulations. The first denticles occur anterior and posterior of the central portion of the crenulated area. The central portion develops differently in oysters and has received various names such as **central apparatus** (both valves, HU et al., 1993) or **cardinal plateau** (right valve) and **cardinal socket** (left valve, CARRIKER & PALMER, 1979). In this study the terms **central platform** (both valves), **central ridge** (right valve) and **central socket** (left valve) are used. Detailed descriptions will be given further.

According to BERNARD (1898) oyster larvae possess a "demi-provinculum". He noticed that in oysters a ligament forms anterior of the hinge while it has a central position in other bivalve larvae (the problem is not yet solved, see below: "larval ligament"). Dysodont

"teeth" described by Bernard in the early dissoconch of ostreids are in fact crenulations of the adult shell margin (**chomata**). They form independently of larval denticles. Neither are they rudiments or vestiges of adult hinge denticles (Harry, 1983; Malchus, 1990).

*Formula of denticle arrangement*
Denticle arrangements are described here by using a "formula". It should be emphasised that it has nothing to do with the formula of Bernard & Munier-Chalmas (see Bernard, 1898) which is only applicable to post-metamorphic, heterodont bivalves. Numbers of pairs of denticles do not reflect the order of their appearance.

Description (Text-fig. 1, view inside an articulated shell from ventral to dorsal, left valve is lower valve): The central denticle (CP = central platform, CR = central ridge) of the upper right valve (RV) is regarded as number 1. Numbers 2a and 2p are the two anterior and posterior denticles of the left valve (LV) adjacent to number 1. Numbers 3a and 3p again belong to the RV, and so on. Thus the denticles of the RV receive odd, those of the LV even numbers. Poorly developed denticles are enclosed in brackets. Information about the size of the shell or growth stage should be added to allow safer comparisons between different ontogenetic stages of the same or different species.

The two formulas presented in Text-fig. 1 are different in two important aspects. First, in the ostreine species the central portion is not well developed (CP) while it is in the Crassostreinae (CR, CS), and second, it is characteristic of the Ostreinae that denticles 2 and 3 are very weakly separated from their central platforms (which rarely occurs in Crassostreinae). This is indicated by a hyphen.

Fernandez Castro & Le Pennec (1988) developed another denticle formula. Their method is not adopted here, first, because it was felt unsuitable for giving a clear image of the arrangement of the ontogenetic developmental steps as recognised in this study, and second, because it emphasises the importance of the denticle shape (quadrangular, round, and triangular) which is here regarded a subordinate character that obliterates the information of the denticle arrangement (Hu et al.,1993 use the same terminology and add the form type 'rectangular'; see comments in the comparative chapter).

*Larval ligament*
A larval ligament has been variously described for extant oysters with a position between or anterior to the hinge denticles (a.o. Bernard, 1898; Ranson, 1960; Tanaka, 1960; Stenzel 1971). Le Pennec (1978), however, denied the existence of a fibrous ligament in oyster larvae. But, as described by Waller (1981) there is a thickened periostracum in the P II of *Ostrea edulis* between the two valves dorsally of the hinge plate and denticles (Waller, 1981, fig. 139). It probably originates from the dorsal uncalcified part of the primary shell. This "larval ligament" is distinct in mineralogy, ultrastructure, and position from the adult ligament which forms at or only shortly in advance of metamorphosis (see also Pascual, 1972; Carriker & Palmer, 1979). Bernard (1898) perhaps observed the rudiment of the adult ligament or its socket (resilifer); the latter may also be visible at a late P II stage in fossils.

*Postero-dorsal notch*
The postero-dorsal notch is a minute recess of the postero-dorsal shell margin near the umbo. It leaves a marked growth track in the left valve while it is hardly visible in the right. It occurs first at the P I/P II boundary and disappears at the P II/dissoconch boundary. Waller (1981: 62) showed that this feature in *O. edulis* is related to a post-anal ciliary tuft of the P II stage veliger. As will be seen later the character seems to be shared by all oysters.

## Methods and materials

*Sampling, processing, and SEM preparation*

Sampling
Samples were collected from different fossil localities from East Texas to West Georgia. They comprise Latest Santonian to Late Eocene limestones, marls, and sands. Samples were taken from each horizon containing oysters. Free prodissoconchs (< 400 μm) and spat (500 to 2000 μm) were only found in loose silts and sands with aragonitic shells generally present and with the carbonate content nearly exclusively represented by shell fragments. Larval shells were not homogeneously distributed in a horizon but occurred locally concentrated.

| *Ostrea edulis* | | |
|---|---|---|
| size L x H | hinge dentition | |
| 167 x 180 | **R V**     5     3   — CP —   (3)     5 <br> p ——————————————————— a <br> **L V**     (6)     4   (2)– CP         4 | |

| *Saccostrea glomerata* | | |
|---|---|---|
| size L x H | hinge dentition | |
| early Pd II | **R V**     5     3     CR     3     5   (7) <br> p ——————————————————— a <br> **L V**     4     2     CS     2     4     6 | |

Text-fig. 1 — Two examples of denticle formula developed here for description and comparison of developmental steps of hinge formation of larval oysters (see "Formula of denticle arrangement").

PROCESSING

The mostly loose sands were kept in water (1 or 2 days) before sieving. Treatment with kerosene (or similar detergents) did not give better results. The use of hydrogen peroxide and ultrasonic treatment was counter productive.

Samples (from Little Stave Creek) were split into fractions between 0-90, −180, −250, −500, −1000 and −2000 µm by sieving them wet. Examination under a light microscope revealed that only three fractions — 0-180, −500, and −2000 µm respectively — contained prodissoconchs. In sample fractions smaller than 180 µm larval shells (no oysters) were very rare. Shells of oysters comprised a size range between 180-450 microns, already including early post-metamorphose stages.

The next size group was above 1 mm large leaving a wide gap in between. Larval shells on the tip of the umbo of these nepionic stages were rarely preserved.

Shells of the 180-500 micron fraction were concentrated by winnowing them out. Larger foraminifera and articulated shells of ostracods and bivalves floated on the water surface and were easily separated from the rest. Repeated careful winnowing of a small fraction of the sediment at a time in a large, shallow beaker gave a hardly visible residue, which, nevertheless, often contained several hundred shells per gram of larval oysters, other molluscs, foraminifera, and ostracods. Samples from other localities were first treated in the same way to choose the most promising size fractions, which varied from one locality to another.

PREPARATION FOR SEM

Specimens were picked a) distinguishing between different sizes and shapes and b) at random, using a low magnification light microscope (40x). Specimens were cleaned with distilled water or alcohol. Nearly all dirty shells that were treated with ultrasonic broke.

Specimens were mounted on stubs and coated with gold for examination under an SEM. Adhesive coal pads proved to be best for fixation. To avoid distorted images shells were oriented with the commissure plane parallel to the stub surface, with the interior facing up.

*Measurements*

DEFINITION OF MEASUREMENTS

The length (L) of the P I is defined as the maximum distance of the shell along a line parallel to the D-line (straight hinge, D). "D" marks the length of the straight hinge. The height (H) is measured normal to the length. The convexity of P I was not measured.

The length (L) of the P II is measured along a line parallel to the hinge axis (the D-line of P I and the hinge axis of P II diverge by a few degrees!). The height (H) is measured normal to L (of P II) (Pl. 3, Figs. A, B). The length of the provinculum (LP) is the maximum distance between the most distant anterior and posterior denticles and/or sockets distinguished (Pl. 3, Fig. E).

The convexity (C) is defined as the shortest distance between two imaginary lines, one drawn from the tip of the umbo to the highest point of the posteroventral edge of the shell, the other is the tangent (parallel to line one) through the most distant point of the shell exterior (Pl. 3, Fig. D). This definition is chosen because the commissure plane which is normally taken as the reference is non-euclidic (spherical) in many ostreid shells.

PLATE 3

| | |
|---|---|
| Figures A, B | — *Cubitostrea sellaeformis*, Middle Eocene, Little Stave Creek (11891/1-4), P II of RV, SEM No. 7/16-2, IRSNB-TI 6142. Interior view. A: Vertical lines define the length of the shell (= widest distance of shell points parallel to the hinge line), B: Vertical lines define the height of the shell (hinge line vertical). (Note that the image on the SEM screen was rotated for measurements, not the specimen itself.) |
| Figure C | — *Cu. sellaeformis*, (11891/1-4), P II of LV, SEM No. 6/11-1a, IRSNB-TI 6143: Exterior view. The two white crosses at the shell margin define the approximate shell length. Because the hinge line is not visible, there is less control for correct orientation of the shell. |
| Figure D | — *Cu. sellaeformis*, (11891/1-4), P II of LV, broad type B, SEM No. 7/16-7, IRSNB-TI 6144: Posterior view, umbo to the left. Note the spherical nature of the commissure plane. The upper horizontal grid line and the small white arrow in the lower left show how the shell's convexity was measured. |
| Figure E | — *Cu. sellaeformis*, (11891/1-4), P II of LV, thick type C, SEM No. 7/15-3, IRSNB-TI 6145: The two vertical lines define how the length of the hinge line was measured. Note that inclusion of the posterior and anterior sockets from the denticles of the right valve ensures that measurements from RV and LV produce comparable results. The denticle formula for this specimen is: p 4 2 CS 2 4 6 a. The right valve must have had a dentition of: p 5 3 CR 3 5 7 a. |
| Figure F | — *Cu. sellaeformis*, (11891/1-4), P II of LV, slender type A, SEM No. 6/11-1c, IRSNB-TI 6146. |
| Figures G, H, I | — *Cu. sellaeformis*, (11891/1-4), P II of LV, broad type B, SEM No. 6/1-1c, IRSNB-TI 6147. H: Close up of hinge dentition with: p (4) 2 CS 2 4 6 a, I: Close up of P I. |
| Figures K, N | — *Cu. sellaeformis*, (11891/1-4), P II of LV, broad type B, SEM No. 6/1-1b, IRSNB-TI 6148. N: Close up of hinge dentition with: p 4 2 CS 2 4 a. |
| Figures L, M | — *Cu. sellaeformis*, (11891/1-4), P II of LV, between slender and broad type A-B, SEM No. 6/11-2b, IRSNB-TI 6149. L: Close up of hinge dentition with p 2 CS 2 4 6 (8) a; denticle (8a) is doubtful. |
| Figures O, P | — *Cu. sellaeformis*, (11891/1-4), P II of LV, slender type A, SEM No. 6/11-2a, IRSNB-TI 6150. O: Close up of hinge dentition with: p 4 2 CS 2 4 6 a. |
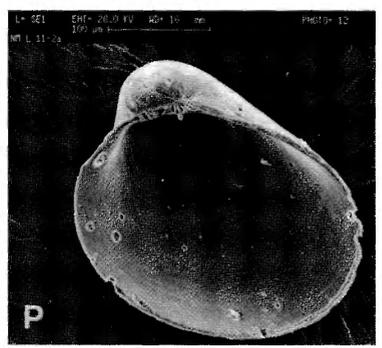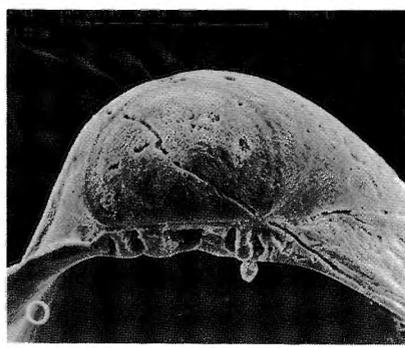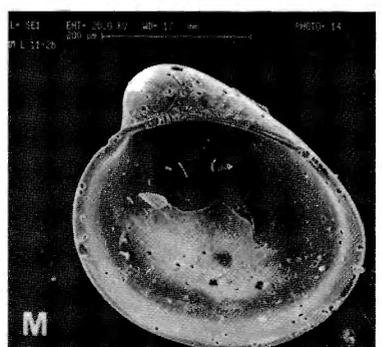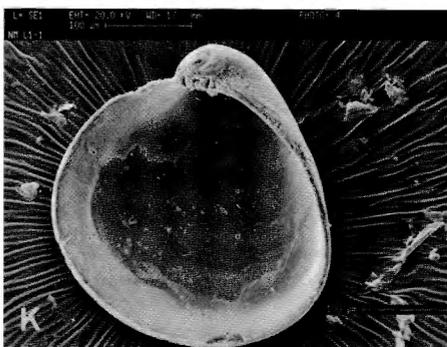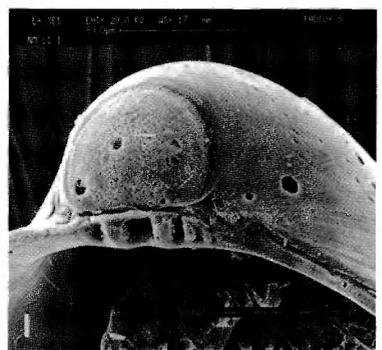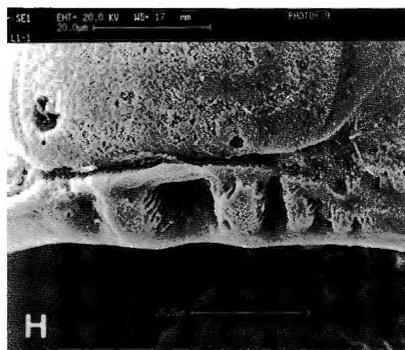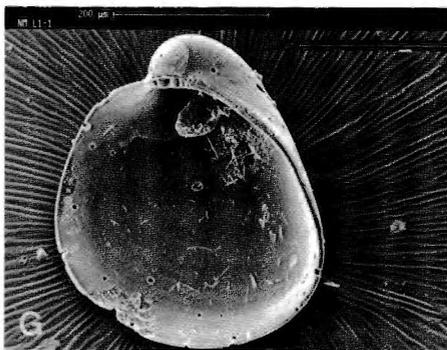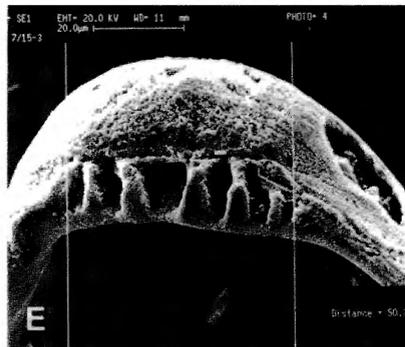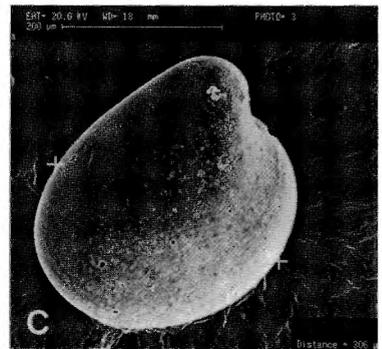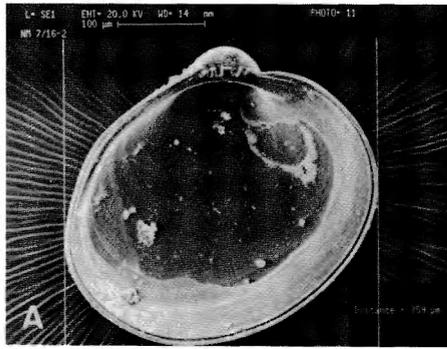
Other measurements not carried out here include: (a) those which describe the geometry of the dorsal half of the shell and the skewness of the umbo in more detail, especially the umbo length and height, the ''shoulders'' (posterior and anterior of the umbo), and the length of the posterior and anterior flanks of the shell (CHANLEY & DINAMANI, 1980: fig. 1; see also HU et al., 1993); (b) rotation angle of the length axis (FORBES, 1967: fig. 3; HU et al., 1993). The angle is defined by the converging length axes of the P I and P II (provided the length axis is defined by the most distant anterior-posterior points on the shell margin); (c) the width of the provinculum of the P II (HU et al., 1993), measured normal to its length. (d) the length of the central apparatus (HU et al., 1993). Where appropriate, results from these measurements are included in the text. A general evaluation will be found in the final chapter.

INACCURACIES OF MEASURING AND ERROR SOURCES

One source for errors is related to the instruments used. The resulting systematic errors are unidirectional, i.e. either positive or negative and can be determined or estimated. Measured values can generally be corrected by a factor. The systematic error of SEM-measurements accumulates from a number of influencing factors (FULLER et al., 1989). The unavoidable use of two different SEMs here adds minor errors. For the ''Stereoscan 360'' (''CAM'' in Appendix A) the systematic error was determined with a standard grid for working distances between 11 and 20 mm, an electron accelerating voltage (EHT) of 20 kV, an aperture of 20 $\mu$m, and magnifications of 500x and 1000x. Measurements were taken along the X-axis over about 3/4 of the monitor size (measurements of shell characters were well within these limits). The error was in the range of + 0.55 to 0.95% and increasing towards larger working distances and larger magnifications. In other words, the read-out in most cases was less than 1% smaller than the true value of the standard. Accordingly, values of 50.5 $\mu$m would become 51.0 $\mu$m or 320 $\mu$m correspond to 323.2 $\mu$m, respectively. Because this error is much smaller than the random error the values given in this study remain uncorrected. (According to E.-O. WOLF, pers. commun. 1993, the difference between measurements in X- and Y-directions of the Cambridge-SEM used can be neglected).

Measurements with the S 2700 (''HIT'' in Appendix A) were taken under similar conditions (but with an aperture of 50 $\mu$m). Values were measured on a second monitor using an automated image analysing system. Measurements in the Y-direction were smaller by 2.5% than those in the X-direction. Thus, values of the height were corrected by this factor. Five specimens were measured twice, once with each SEM. On average, length measurements with the S 2700 were smaller by a factor of 1.2% (ranging from − 3,6 to + 1%); corrected values of the Y-direction were still larger by 1,9% (from − 0,3 to +6,2%). The published values remained uncorrected with respect to these differences (in Appendix A it is indicated with which instrument specimens were measured).

A second source of errors is random in nature, i.e. sometimes positive and sometimes negative and will partly eliminate themselves (if enough measurements are made). Wrong measurements which fall in this category mainly occur: 1) if the two points, between which a distance is measured (e.g. dorso-ventral and anterior-posterior axes), do not lie in the X/Y-plane of the SEM, i.e. normal to its Z-axis and 2) if the shell axes (of L, H, C) are not exactly determined.

According to FULLER et al. (1989), the points of the outer edge of most bivalve shells lie more or less in one orthoclinal plane. Measurements will be best if this commissure plane is parallel to the X/Y-plane of the SEM. To achieve this FULLER et al. (1989) describe a time consuming procedure which was not possible to carry out with the SEMs used here. Furthermore, the commissure plane of many larval oyster shells is spherical (non-euclidic) and thus, the height (dorsal-ventral axis) and length (anterior-posterior axis) should be measured in two steps.

In order to minimise the error range in this study the position of the commissure plane was estimated. If, as explained above, the systematic error is small, the tilt between the imaginary commissure plane and the X/Y-plane becomes the main error source. A tilt results in a foreshortening of the measured distance between two points along the Y-axis (tilt was only possible in this direction). Thus, without tilt, the value will be at its maximum and nearest to the true value. The maximum was found by measuring at different tilts.

The height and length axes can be determined within a range of +/− 1/2 degree (of 360°), if the D-line (for L, H of P I) or the length of the provinculum (for L, H of P II) is used to control the orientation. The relative error then can be disregarded. From the exterior of the shell the position of the axes of the P II can only be estimated. Deviations of +/− 2-3° correspond to a relative error of +/− 5% or more (compare Table 3, Fig. C with A). The error range may be larger (+/− 7-10%) if the P II of an early dissoconch is measured. Reasons are a minor visual control of the tilt and the often only fragmentary preservation of the larval shell (Pl. 5, Fig. H, Pl. 6, Figs. D-P). Because of the allometric growth of the P II the error varies, depending on the axis measured, on the shape of the valve, i.e. whether it is the right or left valve, and, of course, also on the experience of the investigator. For measurements of the convexity (of the P II) a relative error of at least +/− 5-7% must be assumed.

It is obvious that the definition of length and height of the shell may vary from author to author. In CHANLEY & DINAMANI (1980) and HU et al. (1993), for example, the two measurements were not defined relative to the D-line/hinge line but instead were the largest diameters in (approximately) dorso-ventral and antero-posterior directions, respectively. Thus, size measurements given in this study may be smaller. In general, this depends on the size of the shell and on the degree of the 'rotation of the length axis' (sensu HU et al., 1993). In other words, in species with a more or less orthogyrate beak — e.g. Ostrea edulis — the difference is smallest, but it becomes larger with increasing allometric growth/rotation of length axis — as e.g. in Crassostrea gigas.

*Statistics*

A real statistical approach was beyond the scope of the present paper. Nevertheless, some descriptive and analytical statistics were carried out:

(a) Pearson correlation coefficient ''r'' (ranging from − 1 to + 1) which describes the degree of correlation between two interdependent variables (Table 3). Its calculation requires a (nearly) linear correlation. This is not exactly the case if all growth stages of the larval shell are included; minor breaks of linearity are related to an allometric growth. But, all specimens investigated here already passed the size at which these changes occur.

(b) Reduced major axis (RMA) which substitutes the normal least square regression where both variables are subject to error as the characters height and length. Unfortunately, statistical computer programmes do not include the calculation of the
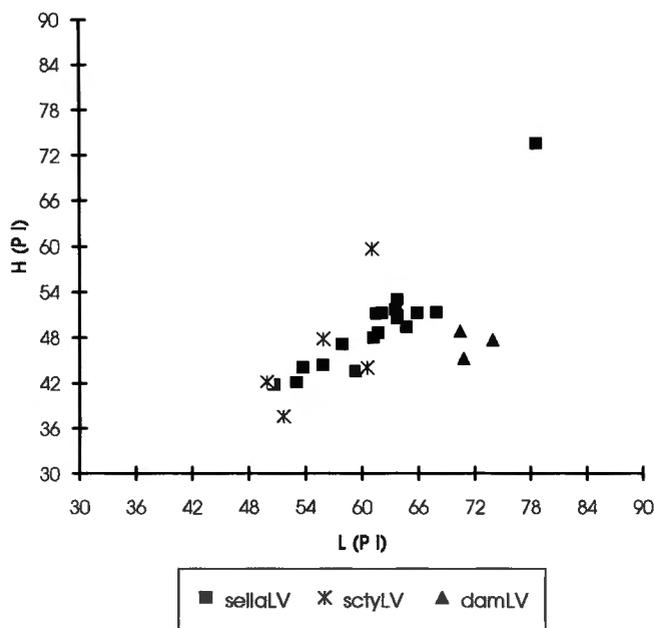
Text-fig. 2 — Height vs. length values of P I-LV's of *Cubitostrea sellaeformis* (sellaLV; Little Stave Creek), *Cubitostrea* sp. (sctyLV; Stone City Beds), and ? *Crassostrea* sp. (damLV, Damery). (Dimensions of both axes in μm.) The equation to fit (reduced major axis, RMA) for sellaLV is: $H = 1.10*L - 18.07$.
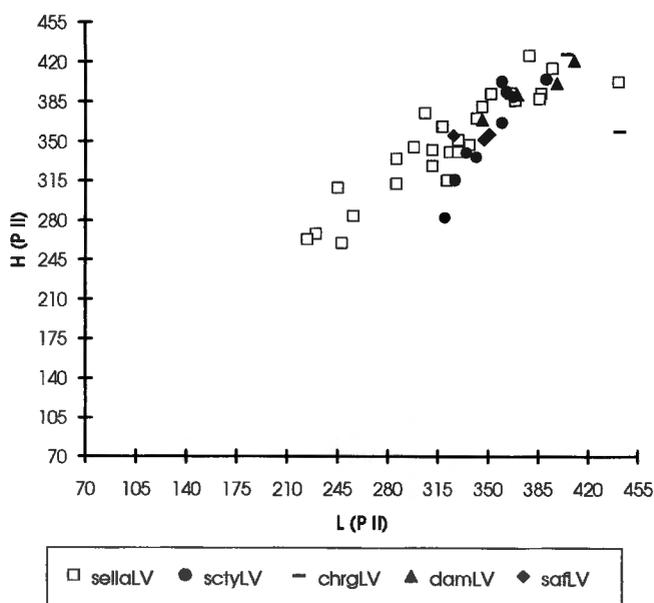


Text-fig. 4 — Height vs. length values of P II-LV's of *Cubitostrea sellaeformis* (sellaLV), *Cubitostrea* sp. (sctyLV), *Cu.?* *plicata* (chrgLV; Chateaurouge), ? *Crassostrea* sp. (damLV), and ? *Saccostrea* sp. (safLV). (Dimensions of both axes in μm.) RMA (sellaLV): $H = 0.85*L + 72.58$.
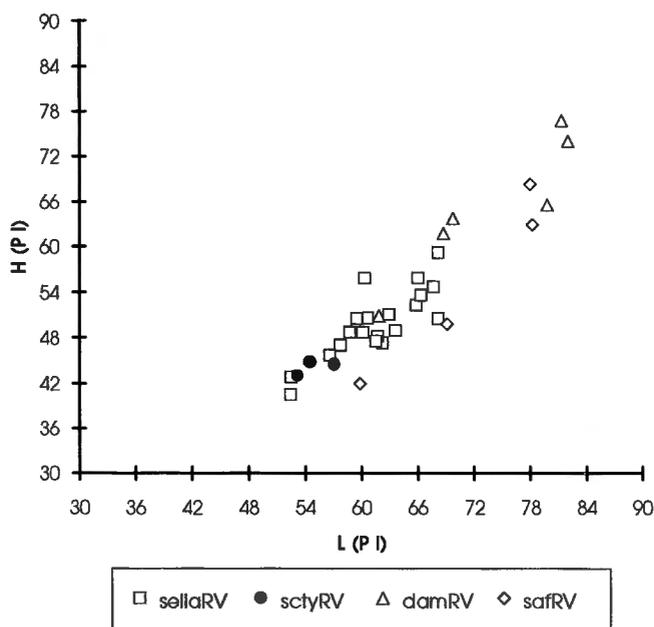


Text-fig. 3 — Height vs. length values of P I-RV's of *Cubitostrea sellaeformis* (sellaRV; Little Stave Creek), *Cubitostrea* sp. (sctyRV; Stone City Beds), ? *Crassostrea* sp. (damRV, Damery), and ? *Saccostrea* sp. (safRV; Saffré). (Dimensions of both axes in μm.) RMA (sellaRV): $H = 0.97*L - 9.78$.



Text-fig. 5 — Height vs. length values of P II-RV's of *Cubitostrea sellaeformis* (sellaRV), *Cubitostrea* sp. (sctyRV), *Cu.?* *plicata* (chrgRV; Chateaurouge), ? *Crassostrea* sp. (damRV), and ? *Saccostrea* sp. (safRV). (Dimensions of both axes in μm.) RMA (sellaRV): $H = 01.08*L - 32.1$.

RMA. Thus it was not plotted in Text-figs. 2 to 5 but only calculated for P I and II of the left and right valves of *Cubitostrea sellaeformis* following Davis (1986: 200).

(c) Box-and-whisker plots of means and standard deviations of the length and height values and of the ratio of H/L. The graphs allow estimates about the significance of the differences between populations (Text-figs. 8-13). Measurements were excluded from calculation if less than three height-length pairs were available for a population, and in Text-figures 11 to 13 if the P II measured less than 210 ($\mu$m in length. The latter condition ensured as far as possible that the compared groups contained comparable developmental stages, i.e. advanced P II veligers including the size at metamorphosis. (Compare smallest and largest P II's of *Cubitostrea sellaeformis* with the sizes of the pediveligers or eye-spot larvae of extant Crassostreinae in Table 9.)

(d) Kolmogorov-Smirnov two sample tests: This non-parametric test method shows whether size measurements of two populations are significantly different (Table 17). The tests are based on the same data as the box-and-whisker plots. They substitute a series of Anova (analysis of variance) *a priori* tests carried out earlier (see Sokal & Rohlf, 1969: 226, for details) which were not suitable because of significant differences in the distribution of size variances.

*Origin of material and determination of species*

Little stave creek

North of Jackson, Clarke Co., Alabama, (Geological Society of America locality 62). The site comprises sediments of Middle Eocene to Oligocene age (Toulmin, 1967, 1977; Mancini & Tew, 1989). Only the oyster beds of the Middle Eocene part were sampled: Upper Tallahatta Formation (Early Lutetian) with one horizon of *Cubitostrea perplicata* (Dall, 1898), Lisbon Formation (Lutetian to Bartonian), the lower part with two horizons of *Cu. lisbonensis* (Harris, 1919), the middle and upper parts together with six horizons containing *Cu. sellaeformis* (Conrad, 1832) (containing field no. 11891/1-4; the sixth horizon was not sampled), Gosport sand (Upper Bartonian) with pycnodonteinid oysters (field no. 11891/1-9; note that field numbers are personal locality and sample numbers, read: 11th. of August 1991/locality 1, sample 9). Only field no. 11891/1-4 (the first sellaeformis bed) contained considerable amounts of larval oyster shells. It was more rich in larval shells than any of the other sites visited. Thus, they form the basis of this study.

Although adult oyster shells of this horizon appear to represent a monospecific accumulation of *Cu. sellaeformis* four types of larval shells were found, three very similar types (types

Table 1 — Overview of the differences between means calculated for each of the seven larval shell characters of the populations studied here. For basic values see Appendix A.
* indicates that the value is based on less that 3 measurements (may be rounded), [1] field n° 141091/1-A, [2] field n° 141091/1-B (referring to the Stone City Beds).

| means | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) |
|---|---|---|---|---|---|---|---|---|
| *Cubitostrea sellaeformis* | LV | 61.8 | 49.3 | 44.8 | 319.3 | 342.1 | 131.6 | 55.5 |
| - Little Stave Creek (sella) | RV | 61.6 | 49.5 | 44.6 | 332.1 | 323.5 | 109.5 | 53.0 |
| - Doby's Bluff (sella) | RV | --- | --- | --- | 327.0 | 318.0 | --- | --- |
| *Cubitostrea* sp.[1] | LV | --- | --- | --- | 321.* | 315.* | --- | --- |
| - Stone City Bluff (scty) | RV | 58.* | --- | --- | 320.* | 282.* | --- | --- |
| *Cubitostrea* sp.[2] | LV | 55.8 | 46.3 | 38.1 | 359.9 | 375.3 | 135.3 | 48.6 |
| - Stone City Bluff (scty) | RV | 54.9 | 44.1 | 37.8 | 370.3 | 341.3 | 108.7 | 40.6 |
| *Cubitostrea ?plicata* | LV | 63.* | --- | --- | 424.* | 392.* | --- | --- |
| - Chateaurouge (chrg) | RV | --- | --- | --- | 456.* | 413.* | --- | --- |
| ? *Crassostrea* sp. | LV | 69.5 | 47.2 | --- | 381.0 | 395.5 | 167.0 | --- |
| - Damery (dam) | RV | 73.9 | 65.5 | 50.3 | 373.5 | 365.5 | --- | --- |
| ? *Saccostrea* sp. | LV | --- | --- | --- | 341.0 | 354.0 | --- | --- |
| - Saffré (saf) | RV | 71.3 | 55.8 | --- | 358.* | 380.* | 128.* | --- |
| *Agerostrea* sp. | LV | 62.* | 50.* | 46.* | 331.* | 330.* | --- | --- |
| - Chapelville (ager) | --- | --- | --- | --- | --- | --- | --- | --- |
| *Exogyra ponderosa* | LV | 50.* | --- | --- | 273.* | 336.* | 174.* | --- |
| - Chapelville (pond) | --- | --- | --- | --- | --- | --- | --- | --- |
| *Exogyra cancellata/cost.* | LV | --- | --- | --- | 304.* | 386.* | --- | --- |
| - Coon Creek (cost) | --- | --- | --- | --- | --- | --- | --- | --- |
| *Pycnodonte* sp. 1 | LV | 66.* | 47.* | 50.* | 303.* | 320.* | 160.* | --- |
| - Coon Creek (pyc1) | RV | 65.* | 52.* | 55.6 | 356.* | 337.* | 158.* | --- |
| *Pycnodonte* sp. 2 | LV | 82.* | 67.* | 57.* | 327.* | 337.* | 118.* | 73.* |
| - Little Stave Creek (pyc2) | RV | --- | --- | --- | --- | --- | --- | --- |

A, B, C) and one pycnodonteinid species. Unfortunately, the size class between 500-1000 $\mu$m did not contain nepionic specimens, and on larger specimens the prodissoconch was destroyed. Thus, none of the three types could be unambiguously assigned to *Cu. sellaeformis*. On the other hand, the Lisbon Formation and its equivalents from Mississippi to Texas are completely dominated by species of the genus *Cubitostrea*. It appears therefore safe to assume that the shells in question belong to this genus and not to *Crassostrea* or *Saccostrea*. Furthermore, it is not known whether the types A to C represent different species or only variants of a single species. For the time being they are all described as *Cubitostrea sellaeformis* types A, B, C.

### DOBY'S BLUFF

East bank of the Chickasawhay River south of Quitman, Clarke Co., Mississippi. The site comprises the Doby's Bluff tongue of the Kosciusko Formation and (above) the Archusa Marl Member of the Cook Mountain Formation (equivalent of the Upper Lisbon) which is truncated by Pleistocene terrace sands (DOCKERY, 1986).

The lower two thirds of the Archusa marl contain *Cu. sellaeformis*. Samples were taken from 50 cm and 150 cm above the Kosciusko/Cook Mountain contact (field nos. 10891/4-3, and /4-4). Larval shells are rare and not well preserved. Two groups may be distinguished: one is comparable to type B of *Cu. sellaeformis*; the other belongs to a pycnodonteinid oyster.

### STONE CITY BLUFF

South bank of Brazos River, at Texas highway 21 crossing the river, Burleson County, Texas, USA. Exposed at this site is the type section of STENZEL's Stone City Formation (STENZEL *et al.*, 1957; YANCEY & DAVIDOFF, 1991), including the lowest portion of the Crocket or Cook Mountain Formation of Middle Eocene age. Stratigraphically the main part of it is equivalent to the middle portion of the Lisbon Formation in Alabama.

Samples were taken from unit R of STENZEL *et al.* (1957) (about 150 cm and 15 cm below unit S, field nos. 141091/1-A and /1-B) and from the overlying unit S (= main glauconite of Stenzel, field nos. 141091/1-C, 1-D, 1-E; 2-A, 2-B). The first three samples and 1-E contain rare oyster larval shells. Adult shells were not found, but STENZEL *et al.* (1957) described *Cubitostrea petropolitana* STENZEL & TWINING, 1957, and *Crassostrea frionis* (HARRIS, 1919) from this locality (with the main glauconite being the most fossiliferous unit). Thus, the larval shells may belong to either of the two species mentioned.

### CHATEAUROUGE

Near Fercourt, Oise, Paris Basin, about 50 km N of Paris, France. Samples were taken by D. Nolf (IRScNB) from Middle Eocene sediments — Upper Lutetian, Lutetian IV, Zone of *Orbitolites complanatus* — (for locations in the Paris Basin see NOLF & LAPIERRE, 1979; MÉGNIEN, 1980).

Three early dissoconch oyster shells (left and right valves) with the larval shells more or less preserved could be investigated. At least the two left valves can be assigned to *Cubitostrea (?)plicata* (SOLANDER *in* BRANDER, 1766) (= *flabellula* DESHAYES, 1832), the right valve certainly belongs to the genus.

### DAMERY

Near Reims, Marne, Paris Basin, about 120 km ENE of Paris, France. Samples are from K. Bandel (University Hamburg)

Table 2 — Minima, maxima, and means of the ratio of height versus length (H : L) calculated for P I, P II, and left (LV) and right valves (RV). Note the strong similarities of the P I of the two North American species *Cubitostrea sellaeformis* (sella) and *Cubitostrea* sp. (scty) and their difference from the European ? *Crassostrea* sp. (dam) and ? *Saccostrea* sp. (saf). For P II differences are not well developed.

| H : L (P I) | min | max | mean |
|---|---|---|---|
| sella-LV | 0.73 | 0.93 | 0.80 |
| sella-RV | 0.74 | 0.92 | 0.81 |
| scty-LV | 0.73 | 0.98 | 0.82 |
| scty-RV | 0.78 | 0.82 | 0.80 |
| dam-LV | 0.64 | 0.69 | 0.66 |
| dam-RV | 0.82 | 0.94 | 0.88 |
| saf-LV | --- | --- | --- |
| saf-RV | 0.70 | 0.88 | 0.78 |
| **H : L (P II)** | **min** | **max** | **mean** |
| sellaLV | 0.90 | 1.26 | 1.08 |
| sella-RV | 0.89 | 1.20 | 0.99 |
| scty-LV | 0.89 | 1.13 | 0.99 |
| scty-RV | 0.88 | 0.93 | 0.91 |
| dam-LV | 1.01 | 1.07 | 1.04 |
| dam-RV | 0.89 | 1.05 | 0.99 |
| saf-LV | 1.01 | 1.09 | 1.04 |
| saf-RV | 1.05 | 1.07 | 1.06 |

from Eocene sediments of the surroundings of Damery (stratigraphic overview in MÉGNIEN, 1980).

A dozen early dissoconchs — five left and seven right valves — could be examined with their prodissoconchs partially preserved. According to characters of the post-metamorphic shells the specimens belong either to *Crassostrea* or *Saccostrea*. *Crassostrea raincourti* (DESHAYES, 1860) is described from the Upper Eocene in that area and may thus represent the correct determination.

### SAFFRÉ

Near Bois-Gouet and Epernais, Loire-Atlantique, France. Specimens were collected by K. Bandel from the uppermost Lutetian sediments (calcaire grossier, Middle Eocene).

A dozen early dissoconchs exist — six left and six right valves — of which some still carry remains of their prodissoconchs. Judging from their macroscopic appearance the specimens represent species of either *Saccostrea* or *Crassostrea*. With the SEM some few chomata are visible in two specimens. By genus definition only *Saccostrea* has chomata (which is true in Recent species, but it may prove wrong in the fossil record). VASSEUR (1881) mentioned *S. mutabilis* (DESHAYES, 1832) and COSSMANN (1904) *S. subelongata* (DUFOUR, 1881) from the Calcaire grossier at Bois-Gouet, thus one of them or both may represent the correct determination(s).

It is noteworthy that post-metamorphic shells of only a few mm. in size are extremely difficult (or perhaps impossible) to

identify on the species level if no larger specimens from the same horizon can be related to them. This is the case with the present material from the Paris Basin. DESHAYES (1824-1832, 1860, 1864) and GLIBERT & VAN DE POEL (1965) described a large number of species to choose from. Nevertheless, most of them can be attributed to the Crassostreinae, exclusive of *Cubitostrea* (personal data, unpublished).

COON CREEK
Old Dave Weeks farm, McNairy County, SW Tennessee, USA, about 6 km south of Enville, Chester Co., SW Tennessee; type locality of the Coon Creek Formation (latest Campanian, KENNEDY & COBBAN, 1993; or Early Maastrichtian, RUSSELL *et al.*, 1983; fauna was described by WADE, 1926). Samples are from K. Bandel, taken from the main fossiliferous sands above the "transitional clay".

Oyster spat with prodissoconchs partially preserved belong to *Exogyra costata* SAY, 1820 or *E. cancellata* STEPHENSON, 1914 and *Pycnodonte* sp. 1, probably *P. mutabilis* (MORTON, 1828) as these are typical of the section.

CHAPELVILLE
About 5 km E of Guntown, Lee County, NE Mississippi, USA; upper part of the Coffee Sands Formation (Campanian) (RUSSELL, 1975). Samples are from K. Bandel and myself.

Oyster spat, in part with prodissoconchs (badly preserved), can be assigned to *Exogyra ponderosa* ROEMER, 1852; *Agerostrea* sp., and *Pycnodonte* sp., though large specimens of the *Pycnodonte* are missing.

EAST CENTRAL ALABAMA
Russell County; Upper Eutaw Formation; latest Santonian or earliest Campanian (RINDSBERG, pers. commun., 1990). Material is from M. Puckett (Geological Survey Alabama, field nos. 901115/2a to 2c). See SMITH (1989) for an overview of the geology.

Oyster spat belongs to *Flemingostrea cretacea* (MORTON, 1834). Prodissoconchs are largely dissolved. Only their general shapes are visible, which are comparable to those of *Cubitostrea*, *Saccostrea* or *Crassostrea* (Pl. 6, Fig. K-M). Because of their poor preservation, larval shells will not be described in detail.

## Description of own material

*Cubitostrea sellaeformis*, Little Stave Creek, *Cubitostrea sp.*, Stone City Bluff, (Eocene)

GROWTH STAGE AND SHELL SHAPE
The shells belong to advanced P II veligers, many of them probably near metamorphosis. Their general outline is triangular, with a strongly skewed umbo, which is more pronounced in left valves (Pl. 3, Figs. G, K); right valves are less inflated.

Three types have been distinguished at Little Stave Creek. A slender type A (Pl. 3, Figs. F, P) in which the height exceeds the length of the shell by 20 or 30 $\mu$m, a broad type B (Pl. 3, Figs. G, K), which has a more round outline, and a thick shelled type C which has generally small and show relatively thick shell walls (Pl. 3, Fig. E; Pl. 4, Figs A-C). Distinction between types A and B, which are both common, is not clear. Type C is rare. Whether these differences are statistically significant remains to be tested. For the time being the three types are regarded as variants of the same species.

Only a few specimens could be examined from Doby's Bluff. Nearly all are filled with matrix and hinge structures are not visible. Their general appearance is that of type B of *Cu. sellaeformis*. Specimens from the different levels at Stone City Bluff are also comparable to the broad type B. But there are minor differences which will be discussed below.

PLATE 4

Figures A, B — *Cubitostrea sellaeformis*, Middle Eocene, Little Stave Creek (11891/1-4), P II of LV, thick type C, SEM No. 7/15-3, IRSNB-TI 6151. A: Posterior view, umbo left, B: Close up of hinge dentition.

Figure C — *Cu. sellaeformis*, (11891/1-4), P II of LV, thick type C, SEM No. 7/15-7, IRSNB-TI 6152: Close up of P I and hinge dentition.

Figures D, E, F — *Cu. sellaeformis*, (11891/1-4), P II of LV, broad type B, SEM No. 6/11-4a, IRSNB-TI 6153. D: Close up of P I and hinge dentition, E: Close up of shell anterior of the hinge (i.e. lower right corner) of Fig. D. It shows a fibrous prismatic structure which is interpreted as the rudiment of the socket (resilifer) for the adult ligament.

Figure G — *Cu. sellaeformis*, (11891/1-4), articulated P II, SEM No. 6/11-2c, IRSNB-TI 6154: Posterior view, umbo left. The growth track of the postero-dorsal notch is clearly visible in left valve causing a very faint inflection in right valve.

Figures H, I — *Cu. sellaeformis*, (11891/1-4), P II of LV, SEM No. 6/11-1-c, IRSNB-TI 6146. H: Shows the growth track of the postero-dorsal notch, I: Close up of granular-prismatic shell structure of the track. In cases where this structure is eroded the track appears concave (compare Fig. G).

Figures K, L — *Cu. sellaeformis*, (11891/1-4), P II of LV, broad type B, SEM No. 6/1-1a, IRSNB-TI 6155. K: External view, L: Close up of growth track of postero-dorsal notch, and micro-"borings".

Figures M, P — *Cu. sellaeformis*, (11891/1-4), P II of RV, SEM No. 6/11-4c, IRSNB-TI 6156. P: Close up of hinge dentition: p 3 CR 3 5 7 a. Note that in this figure the posterior is to the right.

Figures N, O — *Cu. sellaeformis*, (11891/1-4), P II of LV, SEM No. 6/2-2b, IRSNB-TI 6157. O: Close up of hinge dentition.
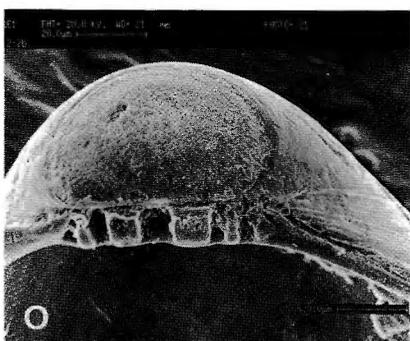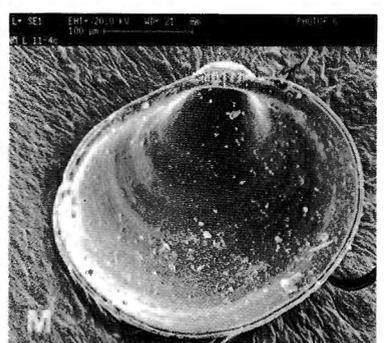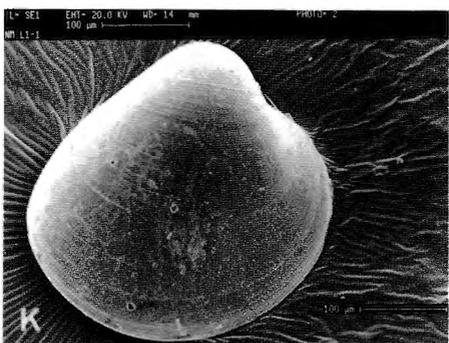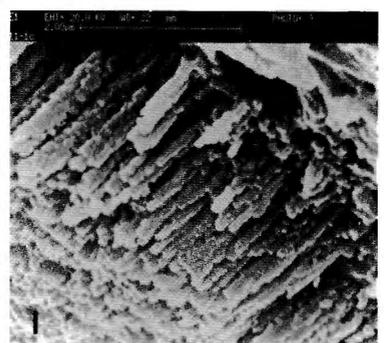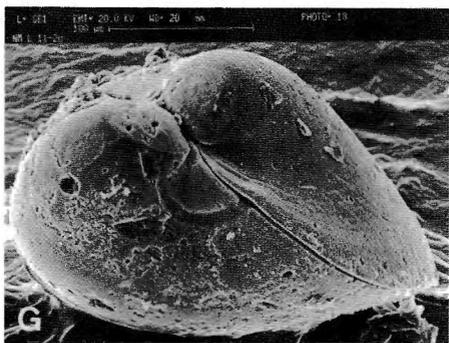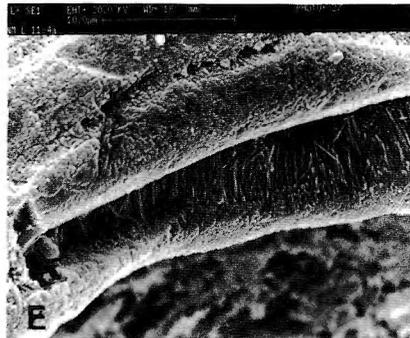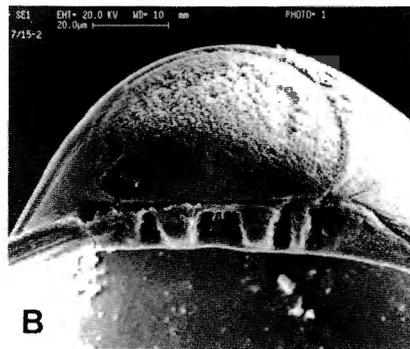
SCULPTURE

The exterior surface of the P II is smooth with fine concentric growth lines; coarser sculptural elements are missing. The largest distances between growth lines occur at mid-height of the shell. In *Cu. sellaeformis* this distance diminishes from around 20 μm at mid-height to 5 μm at the shell edge. Narrow bands may accumulate near the shell edge although this general tendency may be superimposed by an alternation of wide and narrow accretion bands. In a right valve of 360 x 334 μm from Stone City Bluff the last nine growth tracks diminish from about 17 to 9 μm.

SHELL SIZE AND PROPORTIONS

In *Cu. sellaeformis* dimensions of the P I are above 50 to nearly 80 μm long with the height always being smaller than the length, on average by 20% (Tables 1, 2, Text-figs. 2, 3, 12). The D-line measures about 45 μm. The convexity was not measured but may be roughly estimated as 15 to 30 μm in each valve (complete lists of all measurements of specimens are given in Appendix A).

All specimens larger than 80 μm belong to the prodissoconch II stage. But, as the smallest specimen found in the sediment measured 224 μm in length, size relations cannot be described for Ps' II smaller than that. The ratio of height to length is quite variable, ranging from 0.9 to 1.26 in left valves and from 0.89 to 1.2 in right valves. This proportion changes during growth of the P II, but on average the height is by 8% larger in left valves and by 1% smaller than the length in right valves (Table 2, Text-figs. 4, 5, 13).

Convexities of the P II cover a wide range between 100 to 164 μm (LV) and 88 to 138 μm (RV). Naturally, the convexity becomes continuously larger with shell growth and in left valves it is highly correlated with the growth of height and length (Table 3). In right valves the correlation

Table 3 — Correlation coefficients (r, Pearson) between the seven characters measured of *Cubitostrea sellaeformis*. Upper right of table (above "1") corresponds to LV, lower left to RV. Correlations are significant for most measurements within P I and P II respectively but are generally much higher in LV.

| characters | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) |
|---|---|---|---|---|---|---|---|
| L (P I) | 1 | 0.92 | 0.85 | 0.68 | 0.69 | 0.67 | 0.59 |
| H (P I) | 0.81 | 1 | 0.85 | 0.61 | 0.71 | 0.86 | 0.71 |
| D (P I) | 0.65 | 0.60 | 1 | 0.60 | 0.59 | 0.52 | 0.27 |
| L (P II) | -.03 | -.12 | 0.09 | 1 | 0.91 | 0.90 | 0.38 |
| H (P II) | -.37 | -.48 | 0.05 | 0.79 | 1 | 0.94 | 0.19 |
| C (P II) | -.03 | -.21 | -.07 | 0.64 | 0.44 | 1 | 0.48 |
| LP (P II) | 0.27 | 0.36 | 0.59 | -.05 | -.12 | -.07 | 1 |

PLATE 5

Figures A, B — *Cubitostrea sellaeformis*, (11891/1-4), P II of RV, SEM No. 6/11-4b, IRSNB-TI 6158. B: Close up of P I; the hinge dentition is not completely visible, but has at least: p 3 CR 3 5 7 a.

Figure C — *Cu. sellaeformis*, (11891/1-4), P II of RV, SEM No. 7/16-2, IRSNB-TI 6142: Close up of P I and hinge dentition with: p 3 CR 3 5 a.

Figure D — *Cu. sellaeformis*, (11891/1-4), P II of RV, SEM No. 6/2-1a, IRSNB-TI 6159.

Figure E — *Cu.? plicata*, Eocene, Chateaurouge, France, P II of RV, SEM No. 7/3-2, IRSNB-TI 6160: Close up of the 11 last growth steps, shell edge in lower left corner. See also Figs. G, H.

Figures F, I — *Cubitostrea* sp., Middle Eocene, Stone City Bluff, Texas (141091/1-A), P II of RV, SEM No. 7/15-3, IRSNB-TI 6161. I: Close up of P I and hinge dentition with: p 3 CR 3 a. See also Figs. L, M, and P.

Figures G, H — *Cu. ?plicata*, P II of LV, exterior, SEM No. 7/3-4, IRSNB-TI 6162. G: With view towards P I, H: The contact between the partly broken P II and the nepionic shell is very sharp.

Figure K — ? *Crassostrea* sp., Eocene, Damery, France, P II of RV on top of nepionic shell, exterior, SEM No. 7/5-2a, IRSNB-TI 6163. See also Figs. N, O.

Figures L, M — *Cubitostrea* sp., (141091/1-A), P II of LV, SEM No. 6/5-1b, IRSNB-TI 6164. L: Close up of P I and hinge dentition with: p 2 CS 2 4 a.

Figures N, O — ? *Crassostrea* sp., P II of LV on top of nepionic shell, exterior, SEM No. 7/6-2, IRSNB-TI 6165. N: Close up of growth increments, shell edge in lower left corner.

Figure P — *Cubitostrea* sp., (141091/1-A), P II of LV, SEM No. 6/5-1a, IRSNB-TI 6166.
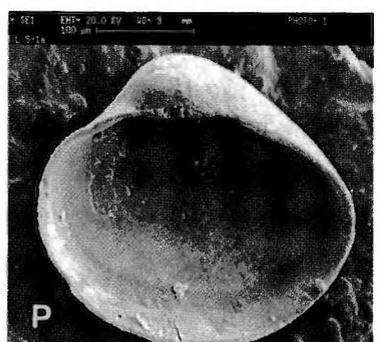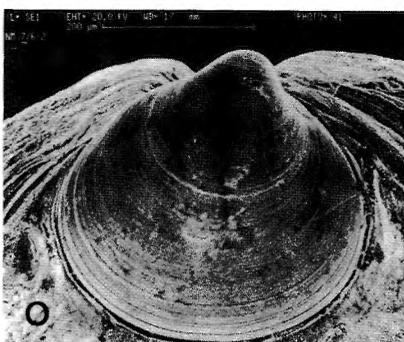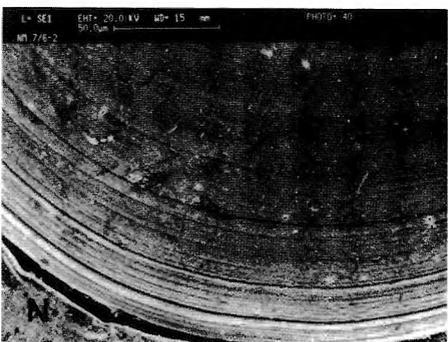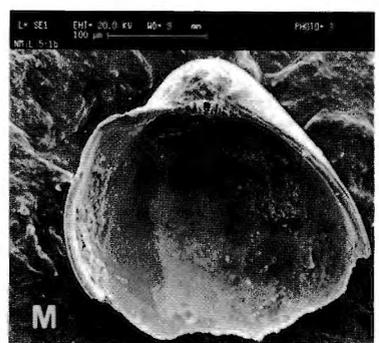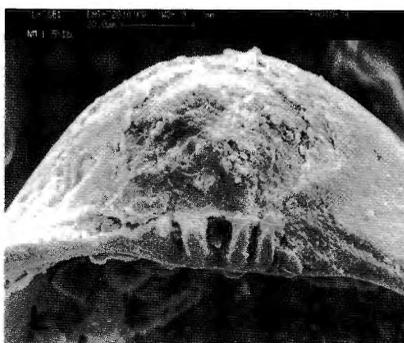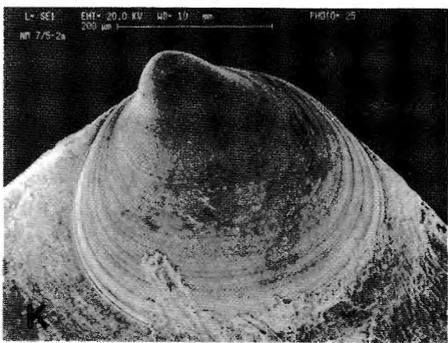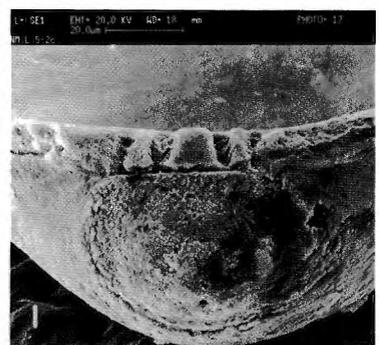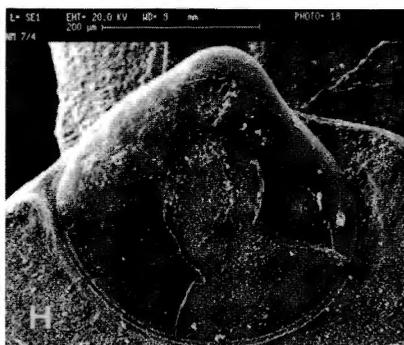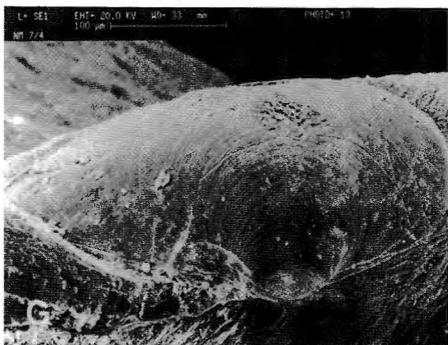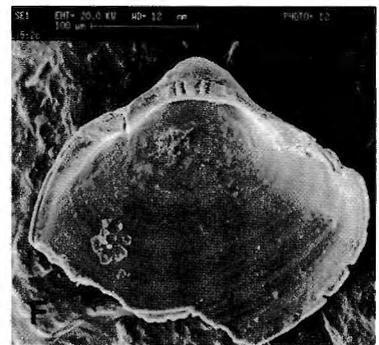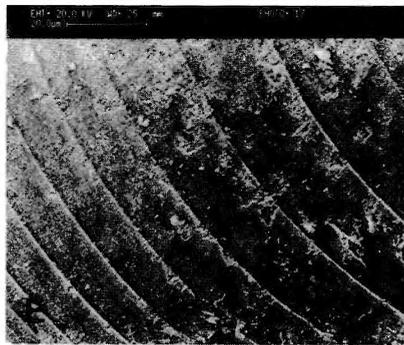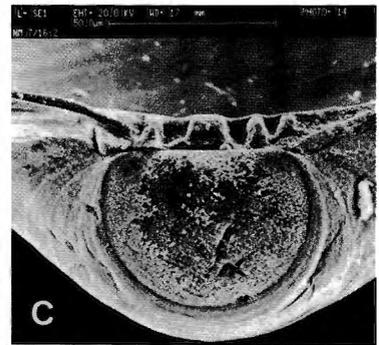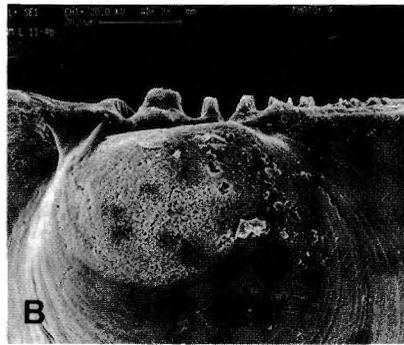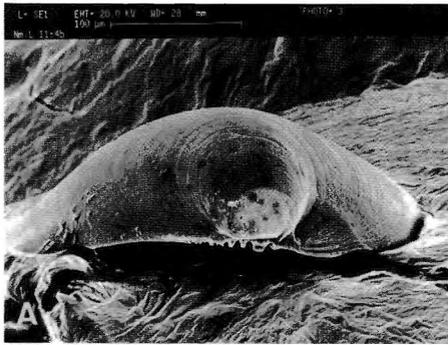
is much weaker. The length of the provinculum (LP) is generally a little larger than the D-line, but it may be smaller in fully developed specimens where denticles have already been strongly reduced (see description of hinge).

Relations between height and length of the P I + II and the other characters considered are shown as a matrix of correlation coefficients in Table 3. High positive correlations exist between length, height and D-line of the first prodissoconch and between the length, height and convexity of the second prodissoconch (upper right of matrix corresponds to LVs). Also, the correlation coefficient between H (P I) and LP (P II) is relatively high (r = 0.71), whereas the length of the provinculum (LP) is only weakly correlated with L, H and C of prodissoconch II. Intuitively, one would expect the LP to increase with increasing number of denticles formed during growth of the P II and with the length of the shell. But, firstly, as will be discussed below, reductions of the posterior denticles and development of new anterior denticles occur more or less at the same time resulting in an anterior shift of the hinge plate rather than in an extension in both directions, and secondly, there exists considerable variation in the shell size at which the hinge denticles are at their maximum development and at which final reductions occur.

The correlation indices for right valves (lower left in Table 3) offer the same tendency, but values are generally smaller. Positive correlations exist between L, H, and D of the P I and L, H, C, and LP of the P II respectively. The very low - positive or negative - correlations between P I and P II measurements reflect growth differences between left and right valves (see above).

In *Cubitostrea* sp. from Stone City Bluff (Pl. 5, Figs. F, I, L, M, P) dimensions of the P I and P II are very similar to those of *Cu. sellaeformis* (Text-figs. 2-5). But on average the P I inclusive of the D-line and the length of the provinculum of the P II are a little smaller (Tables 1, 2). Weak differences also exist in the H : L ratios of the P II.

HINGE AND HINGE DENTITION

As already stated above growth of the provinculum is weakly correlated with other measurements of the P II. The dentition itself shows the following characteristics (Tables 4, 5 for *Cu. sellaeformis*, Tables 6, 7 for *Cubitostrea* sp.):

1) The central apparatus of the hinge of left and right valves are clearly developed as central socket (CS) and central ridge (CS) respectively. Denticles 2a, p and 3a, p are also developed (LV: Pl. 3, Figs. E, H, L, N, O; Pl. 4, Figs. B, D, O; RV: Pl. 4, Fig. P; Pl. 5, Figs C, D).

2) Denticles 4a, p (LV) are normally developed, though smaller than 2a, p, in *Cu. sellaeformis* (Pl. 3, Fig. O; Pl. 4, Fig. O). In contrast the adjacent denticles 5a, p of the opposite valve are less developed (Pl. 5, Figs. C, D). In *Cubitostrea* sp. denticle 4a is generally better developed than 4p, and, accordingly, denticle 5a

Table 4 — The hinge dentitions of left valves of *Cubitostrea sellaeformis* show that there are less denticles developed on the posterior side than on the anterior (for RVs see Table 5).

| SEM no. | size L x H | hinge dentition LV [LP = 55.5 µm] | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 7/16-10 | 245 x 309 | (4) | (2) | CS | 2 | 4 | 6 | (8) |
| 7/16-11 | 248 x 259 | 4 | 2 | CS | 2 | 4 | | |
| 6/11-2a | 286 x 312 | 4 | 2 | CS | 2 | 4 | | |
| 7/16-12 | 311 x 328 | 4 | 2 | CS | 2 | 4 | 6 | |
| 6/11-3c | 311 x 342 | 4 | 2 | CS | 2 | 4 | | |
| 7/16-9 | 329 x 340 | 4 | 2 | CS | 2 | 4 | | |
| 6/11-4a | 329 x 351 | (4) | 2 | CS | 2 | 4 | 6 | |
| 6/2-2b | 337 x 346 | 4 | 2 | CS | 2 | 4 | | |
| 6/1-1b | 352 x 392 | 4 | 2 | CS | 2 | 4 | | |
| 6/11-2b | 379 x 425 | | (2) | CS | 2 | 4 | 6 | |
| 6/1-1c | 387 x 392 | (4) | 2 | CS | 2 | 4 | (6) | |

may be present while 5p is missing (Tables 6, 7; see also Pl. 5, Figs. I, L).

3) Denticle 6 is developed on the anterior side, if at all. Thus, fully developed hinges are not symmetrical, because the posterior side has fewer denticles (Pl. 3, Fig. E, Pl. 4, Figs. C, D, P).

4) Medial denticles (CR + 2a + 2p) of valves of *Cu. sellaeformis* are generally larger than posterior and anterior ones. Nevertheless, their sizes may vary (values for *Cubitostrea* sp. in brackets). Measurements for the RV are: denticle 1 (CR): 6.9 - 13.1 µm (8.5 µm) in length, 3a:

Table 5 — Hinge dentitions of right valves of *Cubitostrea sellaeformis* show the same asymmetry as the left valves (Table 4).

| SEM no. | size L x H | hinge dentition RV [LP = 53 µm] | | | | | |
|---|---|---|---|---|---|---|---|
| 6/12-1b | 268 x 260 | (5) | 3 | CR | 3 | 5 | |
| 7/13-10 | 296 x 305 | (5) | 3 | CR | 3 | 5 | |
| 7/13-7 | 309 x 313 | | 3 | CR | 3 | 5 | |
| 6/11-4b | 309 x 372 | | 3 | CR | 3 | 5 | 7 |
| 7/13-8 | 345 x 321 | (5) | 3 | CR | 3 | 5 | |
| 6/11-4c | 352 x 325 | (5) | 3 | CR | 3 | 5 | (7) |
| 6/2-1b | 367 x 348 | (5) | 3 | CR | 3 | (5) | |
| 7/13-11 | 419 x 374 | (3) | | CR | 3 | 5 | 7 |

Table 6 — The asymmetric growth of hinge dentitions is also present in left valves of *Cubitostrea* sp. (Stone City Beds, compare Tables 4, 5).

| SEM no. | size L x H | hinge dentition LV [LP = 48.6 µm] | | | | | |
|---|---|---|---|---|---|---|---|
| 8/1-4 | 335 x 339 | 4 | 2 | CS | 2 | 4 | (6) |
| 8/1-2 | 342 x 335 | 4 | 2 | CS | 2 | 4 | |
| 8/1-3 | 360 x 402 | (4) | 2 | CS | 2 | 4 | |
| 8/1-5 | 368 x 388 | (4) | 2 | CS | 2 | (4) | |
| 8/1-6 | 391 x 404 | (4) | 2 | CS | 2 | 4 | (6) |

Table 7 — Hinge dentitions of the right valves of *Cubitostrea* sp. show the same asymmetry as the left valves (see Table 6).

| SEM no. | size L x H | hinge dentition RV [ LP = 40.6 µm] | | | | |
|---|---|---|---|---|---|---|
| 6/5-2c | 320 x 282 | | 3 | CR | 3 | 5 |
| 8/1-8 | 379 x 351 | (3) | | CR | 3 | 5 |

4.2-6.3 µm, 3p: 3.3 - 6.3 µm (3a, p: 4.8 - 5.4 µm), 5a: 3.7-4.7 µm (6 µm), 5p: not complete enough to measure (not present). Measurements for the LV give the following results: 2a: 5.8 - 10.9 µm, and 2p: 7.0 - 9.2 µm (2a, p: 5-7.9 µm), 4a: 4.1 - 5.5, 4p: 3.7 - 6.5 (4a, p: 3.9 - 4.6 µm), 6a: 3.4 - 4.7 (4.7 µm), 6p: never complete enough to measure (not present).

Apart from CR the general shape of the denticles is rectangular, although quadrangular denticles may occur (denticles 2a, p; Pl. 4, Figs. B, O).

5) The maximum development of the dentition was perhaps reached at a length between 310 and 380 µm and a height of 320 to 400 µm. This statement needs verification by examination of younger P II stages, which were not available for this study.

6) Final reductions appear first on the posterior side of the shell (Pl. 3, Figs. E, H, L).

Main differences between *Cu. sellaeformis* and *Cubitostrea* sp. are that the latter develops less denticles (coinciding with a shorter provinculum) and that the central ones are smaller (on average) although the ranges of shell sizes largely overlap.

LARVAL LIGAMENT
There was no larval ligament observed between the denticles. The prismatic structure found in one large specimen of *Cu. sellaeformis* anterior of the hinge is interpreted as the rudimentary socket of the post-metamorphic ligament (Pl. 4, Figs. D, E).

POSTERO-DORSAL NOTCH
The growth track of a postero-dorsal notch is present in all left valves examined (Pl. 4, Figs. A, D, G, H, I, L); it is very weakly developed in some right valves (Pl. 5, Fig. A). In some specimens parts of the outer prismatic layer of the notch are eroded and its nodular internal structure becomes visible (Pl. 4, Figs. H, I).

*Cubitostrea ?plicata*, Chateaurouge (Eocene)

GROWTH STAGE AND SHELL SHAPE
The prodissoconchs were only found on early disso-

conchs; they thus represent full grown P II stages. The shells are quite broad in shape, even more than type B of *Cu. sellaeformis*, the umbo is less skewed (Pl. 5, Figs. G, H).

SCULPTURE
In general, the sculpture is comparable to that of the other species discussed so far, but near the ventral edge there exist low, widely spaced growth crests which are a little more prominent than in the specimens described before (Pl. 5, Fig. E).

SHELL SIZE AND PROPORTIONS
Because of the poor preservation of the shells, only a few dimensions could be measured. But, obviously the P I is small (L = 62.5 $\mu$m) (Pl. 5, Fig. G). Shells are quite large with more than 400 $\mu$m in length. The length exceeds the height in one left and one right valve. Whether this is a significant character of the species cannot be concluded from these data.

Structures of the hinge are obliterated by dissoconch shell material and cannot be described.

*?Crassostrea* sp., Damery, *?Saccostrea* sp.,
Saffré, (Eocene)

GROWTH STAGE AND SHELL SHAPE
Specimens are found on early dissoconchs and represent full grown P II stages. The shapes are very similar in the two samples. Right valves begin with a slender beak (P I and early P II). In later stages the shell broadens in length which creates an unusual (for RVs) strong knobby appearance of the early P II [Pl. 5, Fig. K (RV), O (LV); Pl. 6, Fig. F (RV)]. The knobby stage is more pronounced in the shells from Saffré than in those from Damery.

SCULPTURE
The sculpture is as described before. Distances between growth lines (specimens from Damery) vary strongly, e.g. from 18.8-11.8-25.4-30.9-17.2-12.4 (in $\mu$m) for the last six steps (Pl. 5, Figs. N, O) or from 11.0-11.6-10.7-9.5-9.8-8-92-5.6-2.7 (in $\mu$m) for the last nine steps (specimen 7/5-1b, RV, not figured). In between a number of subordinate growth lines occur.

SHELL SIZE AND PROPORTIONS
Sizes of the P I fall within the range of the other species described above. Their absolute sizes are larger than those of *Cu. sellaeformis* (Table 1; Text-figs. 2-5). As already stated for other species the length always exceeds the height in P I (Table 2). During the P II stage the height becomes weakly dominant in left valves (Table 2). This tendency is not obvious in right valves from Saffré. The convexity is quite high in one LV from Damery (C = 167 $\mu$m) and in two RVs from Saffré (C = 113 and 142 $\mu$m, Table 1). But these measurements may contain a relative error of more than +/-10%.

Structures of the hinge are hidden by shell material of the early dissoconch, and the postero-dorsal notch is not

PLATE 6

Figures A, B — ? *Crassostrea* sp., Eocene, Damery, France, nepionic RV, internal view, with one dorso-posterior and one dorso-anterior tubercle (= rudimentary chomata) and a preserved prodissoconch, SEM No. 7/5-2b, IRSNB-TI 6167. B: Close up of the P I.

Figure C — ? *Crassostrea* sp., prodissoconch on top of nepionic RV, SEM No. 7/5-3a, IRSNB-TI 6168: Close up of P I.

Figure D — *Liostrea plastica*, Kimmeridgian, Upper Kimmeridge Clay, S England, P II of RV, crashed, on nepionic shell, dorsal view, SEM No. 8/3-7, IRSNB-MI 10638: The strong growth crests are clearly visible and the size of P I can be estimated as being about 60 $\mu$m. See also Fig. G.

Figures E, F — ? *Crassostrea* sp., prodissoconch on top of nepionic RV, SEM No. 7/5-1a, IRSNB-TI 6169. E: Close up of P I.

Figure G — *Liostrea plastica*, P II of RV on nepionic shell, dorsal view, SEM No. 8/3-9, IRSNB-MI 10639: The strong growth crests are clearly visible, the size of the P I, although being partly destroyed, can be estimated. Compare Pl. 7, Figs. A-D.

Figures H, I — *Agerostrea* sp., latest Campanian, Coon Creek, SW Tennessee, P II of LV on top of nepionic shell, SEM No. 7/7-4, IRSNB-MI 10640. H: Close up of partly destroyed P I.

Figures K, L, M — *Flemingostrea cretacea*, latest Santonian, Upper Eutaw Formation, E Central Alabama, inner mould of P II of RV on nepionic shell, original larval shell largely destroyed, K: SEM No. 6/6-3, IRSNB-MI 10641, L: SEM No. 6/6-4, IRSNB-MI 10642: Flat area at umbo marks the position and approximate size of the P I. This phenomenon is commonly seen on early dissoconchs, M: SEM No. 6/6-2, IRSNB-MI 10643: Overview of young dissoconch with P II.

Figure N — *Exogyra ponderosa*, ? Late Campanian, Coffee Sand, E Mississippi, P II of LV on early dissoconch, SEM No. 7/9-2a, IRSNB-MI 10644: The P I of the tip is broken, but the size can be estimated as being between 50 and 70 $\mu$m.

Figure O — *Exogyra cancellata/costata*, latest Campanian, Coon Creek, SW Tennessee, P II of LV on early dissoconch, view from top, SEM No. 7/7-3, IRSNB-MI 10645.

Figure P — *Exogyra ponderosa*, P II of LV on early dissoconch, SEM No. 7/9-1a, IRSNB-MI 10646: View from top.
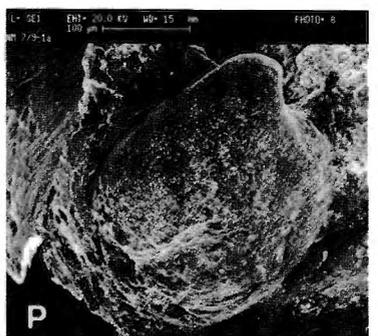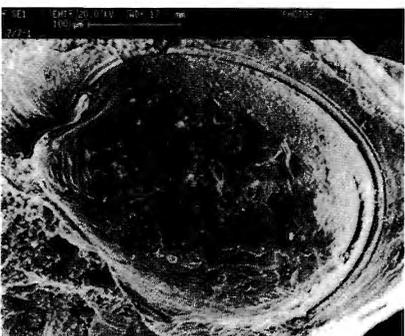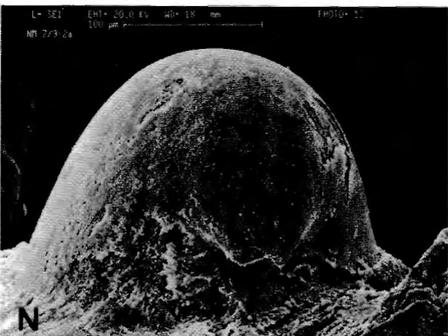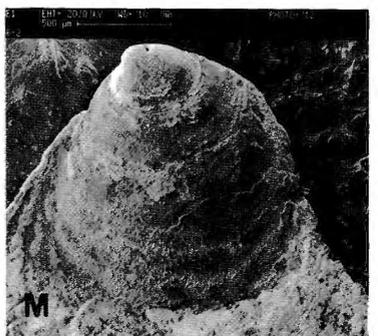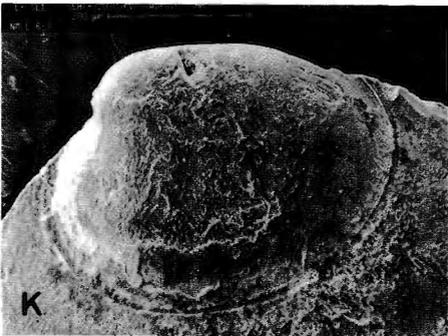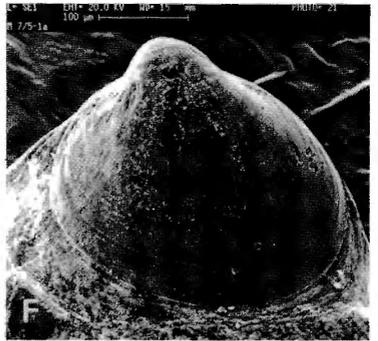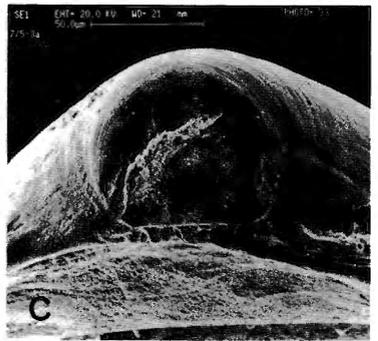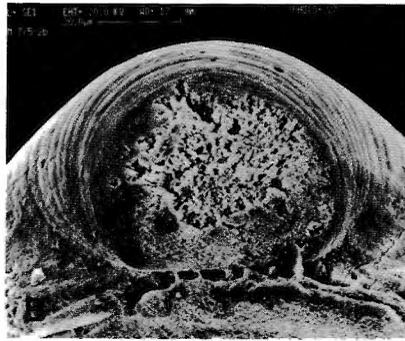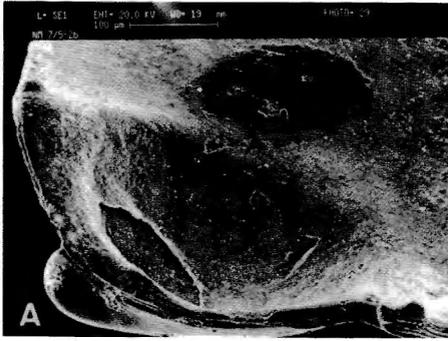
preserved. But, two chomata, one small bump on each side of the hinge (Pl. 6, Fig. A), are visible in one specimen from Damery. These are early structures of the dissoconch shell.

### *Agerostrea sp.*, Coon Creek (latest Campanian)

GROWTH STAGE AND SHELL SHAPE

Shells represent full grown P II veligers on early dissoconchs. They are characterised by a broad triangular outline and a skewed umbo. Their general appearance does not differ from other ostreid species described above (Pl. 6, Figs. H, I). (The same appears to be true of a single specimen of the Late Campanian *Agerostrea falcata* in JABLONSKI & BOTTJER, 1983: fig. 4.)

The sculpture is of the same type as in other ostreid species described above.

SHELL SIZE AND PROPORTION

A single specimen (LV) was found complete enough to measure. It has a small P I with the length exceeding its height; in P II length and height are equal (L = 331 μm, H = 330 μm; Table 1, Text-figs. 6, 7). The convexity was not measured because of a high error range.

Structures of the hinge are not visible. The posterodorsal notch is present (Pl. 6, Fig. H).
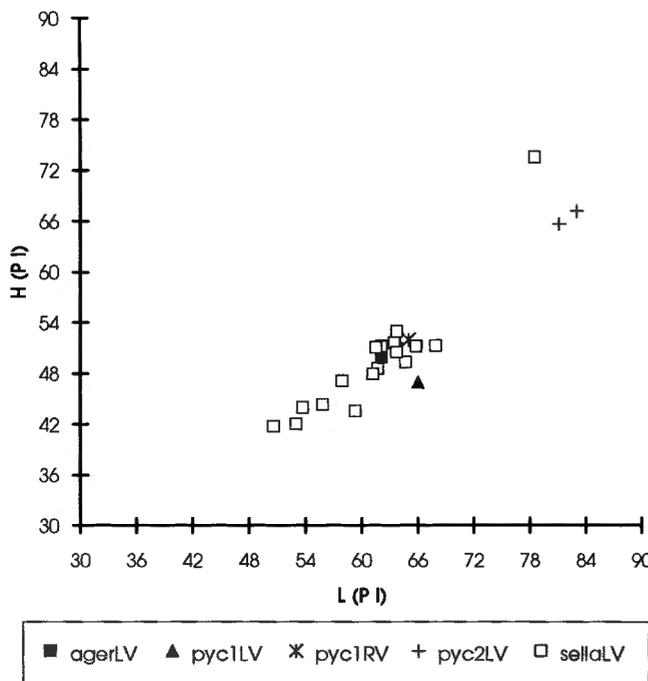


Text-fig. 7 — Height vs. length of P II-LVs of *Agerostrea* sp. (agerLV), of LV and RV of *Pycnodonte* sp. 1 (pyc1LV, pyc1RV), of LV of *Pycnodonte* sp. 2 (pyc2LV), and of LVs of *Exogyra ponderosa*, (pondLV, Chapelville), and *E. cancellata/costata*, (costLV, Coon Creek) in relation to LVs of *Cubitostrea ? sellaeformis* (sellaLV). (Dimensions of both axes in μm).

### *Exogyra ponderosa*, Chapelville (? Late Campanian), *E. cancellata/costata*, Coon Creek (latest Campanian)

GROWTH STAGE AND SHELL SHAPE

In both cases larval shells are from early dissoconchs. They are, therefore, full grown P II stages. As far as can be concluded from the poorly preserved specimens, the beak is slender, the outline triangular and the convexity high, thus giving the shell a conical appearance. The beak is deflected opisthogyrately and forms a steep angle with the commissure plane (Pl. 6, Figs. N, P: *E. ponderosa*, Fig. O: *E. cancellata/costata*). All these features will be found characteristic of the adult shells of this genus.

The sculpture appears to be of the same type as in other ostreids. Preservational conditions did not allow more detailed examinations.

SHELL SIZE AND PROPORTIONS

Measurements could not be carried out with accuracy; they should be regarded as estimates with an error range of +/- 10% or more. The size of the P I, although not directly visible, cannot be larger than the tip of the umbo (broken in Pl. 6, Fig. N). The length may be estimated as 50 to 70 μm. Assuming that the few measurements of L and H of the P II are representative, the height is considerably larger (by more than 60 μm) than the length.



Text-fig. 6 — Height vs. length of P I-LVs of *Agerostrea* sp. (agerLV, Chapelville), of LV and RV of *Pycnodonte* sp. 1 (pyc1LV, pyc1RV, Coon Creek), of LV of *Pycnodonte* sp. 2 (pyc2LV, Little Stave Creek) in relation to LVs of *Cubitostrea ?sellaeformis* (sellaLV). (Dimensions of both axes in μm).

The convexity may be larger by 20 to 30 $\mu$m than in ostreid species (Table 1; Text-fig. 7).

## Pycnodonte spp. 1 and 2, Coon Creek (latest Campanian) and Little Stave Creek (Eocene)

### GROWTH STAGE AND SHELL SHAPE

Specimens from Coon Creek are from early dissoconchs and thus represent full grown P II veliger shells, those from Little Stave Creek are advanced or full grown P II shells. The umbo is weakly skewed in an opisthogyrate direction in the Campanian specimens; in contrast, the corresponding early dissoconch exhibits a more pronounced deflection of the umbo (Pl. 7, Figs. A-C). The P II umbo is nearly orthogyrate in the Eocene species (Pl. 7, Figs. F, G). The outline of the shells is nearly round in specimens from both localities. The appearance of left and right valves is more or less hemispherical.

### SCULPTURE

The sculpture is characterised by pronounced growth steps with relatively sharp crests instead of fine lines as in ostreids. The crests are much stronger in the Coon Creek specimens (Pl. 7, Figs. A and D). Distances between the last 16 steps of a right valve are: 23.9-22.4-21.1-21.3-21.1-15.-10.-12.8-10.3-10.3-9.4-12.5-9.1-7.6-5 ($\mu$m; Pl. 7, Fig. A).

### SHELL SIZE AND PROPORTIONS

Sizes of the P I are in the range of the species discussed above, although the absolute size of the Eocene species is significantly larger with more than 80 $\mu$m in length (Table 1; Text-fig. 6; Pl. 7, Figs. D, E). As in the ostreid larvae the length of the P I exceeds its height. Whether this tendency changes during the P II cannot be concluded from the few measurements (Table 1; Text-fig. 7). In one specimen from Coon Creek the convexity of 160 $\mu$m (+/− 10 %) is considerably higher than usual, while it is much lower in the specimen from Little Stave Creek.

### HINGE AND HINGE DENTITION

Structures of the hinge are visible in the two specimens from Little Stave Creek. In one of them five rectangular denticles can be identified, the most distant anterior one being broken, a sixth posterior one is rudimentary (Pl. 7, Figs. D, E). The other specimen exhibits a row of 7 more or less equally sized denticles measuring between 6.6 and 4 $\mu$m (Pl. 7, Fig. H). The dentition may be described as in Table 8 (Pl. 7, Figs E, H).

Nevertheless, the formula is originally based on the recognition of a central apparatus. This cannot be clearly identified in the pycnodonteinid type of dentition and it will be necessary to examine the development of the hinge of pycnodonteinid oysters in more detail to test the above interpretation. It may be added that the denticles seen in Pl. 7, Fig. C are not larval denticles but chomata of the dissoconch shell (for explanations concerning chomata see STENZEL, 1971, or MALCHUS, 1990).

Table 8 — Dentition formulas of two specimens of the Eocene *Pycnodonte* sp. 2 (Little Stave Creek). The formulas are speculative because a real central socket (CS) — and thus central denticle (CR) of the right valve — does not exist.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 6/12-1c | 342 x 362 | | 4 | 2 | CS | 2 | 4 | 6 | |
| 7/12-10 | 311 x 312 | (6) | 4 | 2 | CS | 2 | 4 | 6 | 8 |

A second row of about ten smaller denticles which is found on the posterior shell edge of Recent species appears to be missing in the specimens investigated here (e.g. fig. 1, in RANSON, 1967a).

### POSTERO-DORSAL NOTCH

The notch is visible on the left valves from Little Stave Creek (Pl. 7, Figs. D, F, G).

## Description of material from the literature

### Fossil Liostreinae

Information about larval shells of fossil ostreids is very scarce and mostly not satisfying, the only exception being the description of *Liostrea irregularis* (MÜNSTER, 1833) from the Early Jurassic (Hettangian) and *L. plastica* (TRAUTSCHOLD, 1860) from the Upper Kimmeridge Clay by PALMER (1989) [see (1) in Tables 10, 11].

### GROWTH STAGE AND SHELL SHAPE

Larval shells of both species were found on early dissoconchs. They thus represent full grown P II stages. The general outline of their right valves is triangular with a marked skewed umbo stage. Left valves of *L. plastica* (very rare) are less skewed but more strongly convex than right valves. The general appearance of the shells is comparable to the Ostreidae described in previous chapters.

### SCULPTURE

The exterior of the P II of *L. irregularis* is smooth, but shells may be recrystallised. The P II of *L. plastica* is characterised by strong regularly spaced concentric ridges (Pl. 6, Figs. D, G). PALMER (1989) counted about 30 ridges over the entire shell.

### SHELL SIZE AND PROPORTIONS

PALMER (1989) estimated the size of the P I of *L. irregularis* as 60 $\mu$m across and the length of the P II as 500 $\mu$m.

Table 9 — List of Recent Crassostreinae discussed in this chapter (within each genus species are ordered alphabetically). Information is given about the original distribution of species and their proposed phylogenetic relationships, about the literature used here, and about the conditions (natural or artificial) of larval and post-larval growth. Key number 2 to 17 of authors' names refer to Tables 10-12 and 14-16. Abbreviations: artif. = artificial, lab(s) = laboratory(ies), lab or nat. cond. = laboratory or natural conditions, N Isl. = Northern Island (of New Zealand), popul. = population.

→
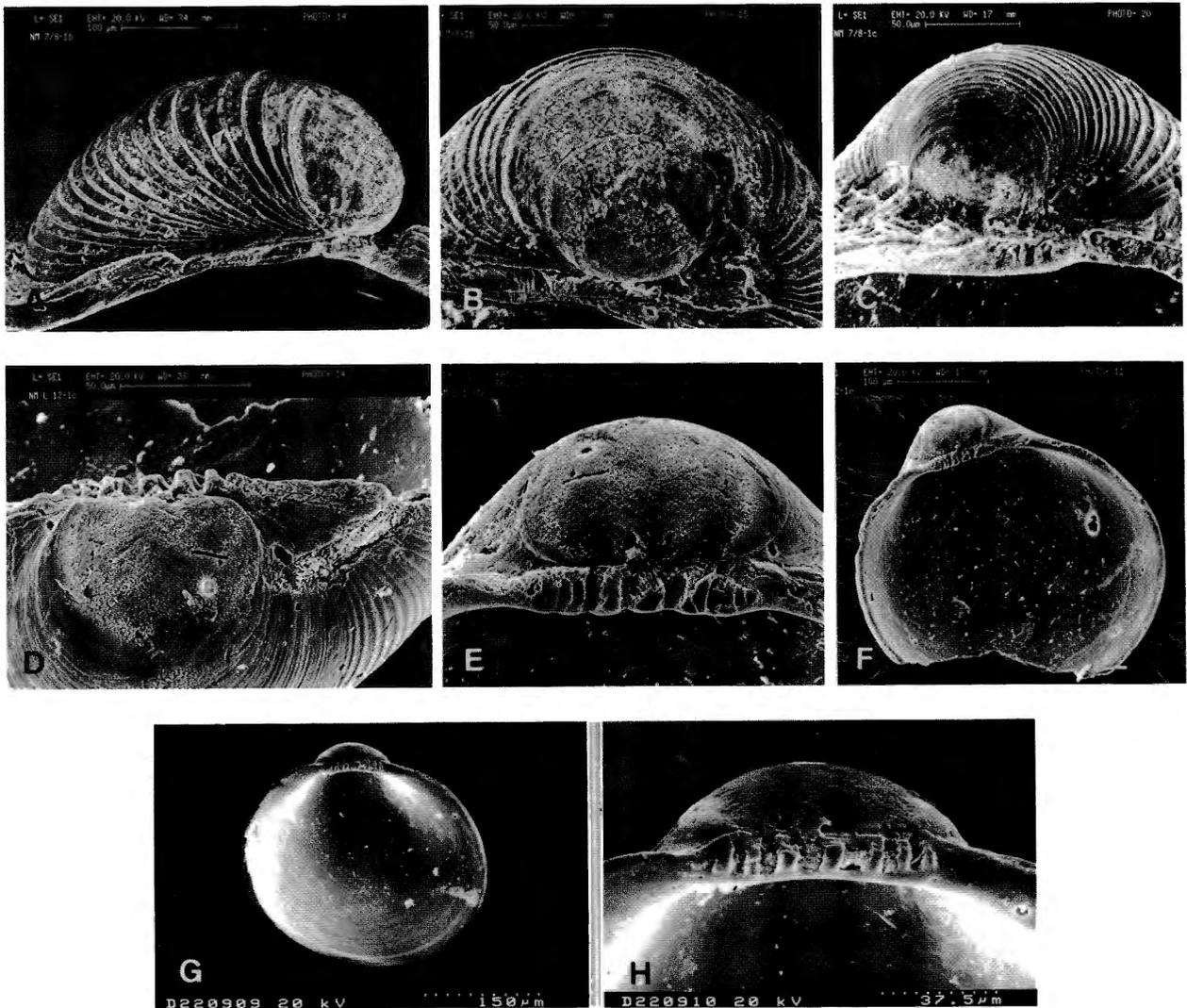


PLATE 7

Figures A, B — *Pycnodonte* sp. 1, latest Campanian, Coon Creek, SW Tennessee, P II of RV on top of nepionic shell, SEM No. 7/8-1b, IRSNB-MI 10647. A: Posterior view with umbo to the right, strong growth crests clearly visible, B: Dorsal view with P I.

Figure C — *Pycnodonte* sp. 1, P II of LV on top of nepionic shell, SEM No. 7/8-1c, IRSNB-MI 10648: Dorsal view with P I, the vertical indentations below P I are chomata and belong to the adult shell.

Figures D, E, F — *Pycnodonte* sp. 2, Middle Eocene, Little Stave Creek, Alabama, P II of LV, SEM No. 6/12-1c, IRSNB-TI 6170. D: Dorsal view with P I and hinge denticles and growth track of postero-dorsal notch of the P II, growth crests are clearly visible but less strong than in *Pycnodonte* sp. 1 (Figs. A-C), E: Close up of hinge dentition with: p 4 2 CS 2 4 6 a, F: Internal view of the whole shell.

Figures G, H — *Pycnodonte* sp. 2, P II of LV, SEM No. 7/12-10, IRSNB-TI 6171. G: Internal view, inflection of postero-dorsal notch (left of the hinge) proves that this is the left valve, the decision cannot be made with the hinge dentition, H: Close up of hinge dentition with: p (6) 4 2 CS 2 4 6 8 a.

### Crassostrea angulata (Lamarck, 1819)

E Atlantic; according to Harry (1985) one of four valid species of the genus, but Buroker et al. (1979a,b) stated on the basis of genetic studies that it is probably identical with the Japanese *C. gigas* (Thunberg. 1793). Thus, the two would represent geographically isolated populations of one species.

(2)  Dinamani (1976): SW Pacific, New Zealand, N Isl.; adults from labs, larvae lab conditions.

(3)  Pascual (1971): E Atlantic, Spain; natural cond.

### Crassostrea gigas (Thunberg, 1793)

Indo-West Pacific; see *C. angulata*

(2)  Dinamani (1976): larvae from labs outside N. Zealand

(4)  Chanley & Dinamani (1980): SW Pacific, N. Zeal., N Isl.; adults and larvae lab cond.

(5)  Hu et al. (1993): E Pacific, Washington. adults nat., larvae lab conditions

(6)  Le Pennec (1978): E Atlantic, NE France; lab conditions

(7)  Loosanoff. et al. (1966): E Pacific, California; larvae lab conditions

(8)  Miyazaki (1962): ? not known

(9a) Roughley (1933): data on shell sizes taken from Hori & Kusakabe (1926)

### Crassostrea iredalei (Faustino, 1932)

Indo-Pacific; according to Harry (1981) possibly identical with *C. gigas* (see also above); the view is indirectly supported by results from Ver (1986).

(10) Ver (1986): China Sea, Philippines; adults from experimental farms; adults and larvae lab conditions

### Crassostrea virginica (Gmelin, 1791)

W Atlantic; type of genus; according to Buroker et al. (1979b) perhaps a superspecies including *C. rhizophorae* (Guilding. 1827).

(2)  Dinamani (1976): larvae from labs outside N. Zealand

(5)  Hu et al. (1993): W Atlantic, New Jersey; adults natural, larvae lab conditions

(7)  Loosanoff. et al. (1966): E Pacific, California; larvae lab conditions

(9b) Roughley (1933): data on shell sizes taken from

Stafford (1913)

(11) Carriker (1951): W Atlantic, New Jersey; natural conditions

(12) Carriker & Palmer (1979): W Atlantic, Delaware; adults nat. popul., larvae lab cond.

(13) Chanley & Andrews (1971): W Atlantic, Virginia; larvae lab conditions

### Saccostrea commercialis (Iredale & Roughley, 1933)

SW Pacific. SE Australia; probably included in *S. cucullata* (Born. 1778) by Harry (1985); Buroker et al. (1979 b) stated that *S. cucullata* and *S. commercialis* are sister species; they also discuss a superspecies status of *S. cucullata* including *S. echinata and S. amasa*

(9c) Roughley (1933): S Pacific, E Austr.; larvae from nat. popul. and artif. fertilization

(14) Dinamani (1973): larvae from labs outside New Zealand

### Saccostrea echinata (Quoy & Gaimard, 1835)

Indo-Pacific; species accepted as valid by Torigoe (1981); because of strong similarities to *S. glomerata* (Gould. 1850) and *S. kegaki* Torigoe & Inabe (1981) Tanaka's (1960) designation may be erroneous; Le Pennec & Coatanea (1985) considered *S. echinata* a subspecies of *S. cucullata*; see also *S. commercialis* above.

(15) Le Pennec & Coatanea (1985): Central Pacific, French Polynesia; adults imported from New Caledonia; adults and larvae lab conditions

(16) Tanaka (1960): NW Pacific; ? conditions

### Saccostrea glomerata (Gould, 1850)

SW Pacific (origin. N. Zeal.); species probably included by Harry (1985) in *S. cucullata* (Born, 1778); recognised by Torigoe (1981) as a valid species; Buroker et al. (1979 b) regard it as a subspecies of *S. commercialis* perhaps included in a superspecies *S. cucullata*.

(2)  Dinamani (1976): SW Pacific, N. Zeal., N Isl.; larvae natural conditions

(4)  Chanley & Dinamani (1980): SW Pacific, N. Zeal., N Isl.; adults from natural populations. larvae lab conditions

(14) Dinamani (1973): SW Pacific, N. Zeal., N Isl.; adults natural popul., larvae lab conditions

(17) Booth (1979): SW Pacific, N. Zeal., N Isl.; larvae natural conditions

He did not measure sizes of the P I of *L. plastica*, but his figs. 1 and 2 of plate 2 indicate a size of approximately 60 μm (compare Pl. 6, Figs. D, G). Sizes of the P II of 50 right valves range from 360 to 520 μm (L) and 310 to 480 μm (H). Thus, on average the length exceeds the height.

POSTERO-DORSAL NOTCH

According to PALMER (1989) there is no evidence of a postero-dorsal notch. But on his pl.2, fig. 2 a weak mark in both valves (in the lower centre) corresponding in form and position to the growth track of the notch can be seen.

*Living Crassostreinae*

GROWTH STAGE AND SHELL SHAPE

Generally speaking, all developmental stages from initial shell formation to metamorphosis have been described in the literature. Most crassostreinid oysters — *Crassostrea* and *Saccostrea* — are characterised by the same steps of allometric growth resulting in a knobby umbo stage of the early P II and a skewed umbo at later stages (exception: *S. glomerata*). The general outline is triangular (broad or slender, depending on size relations between L and H, see below) (see Table 9 for species considered here).

SHELL SIZE, PROPORTIONS, PATTERNS OF GROWTH

The absolute length of the P I directly after its formation is about 50 μm to less than 80 μm and height is about 45 μm to less than 80 μm in all Crassostreinae. Larval shells of *Saccostrea glomerata* and *S. commercialis* are somewhat smaller than of the others (Table 10). Nevertheless, in both *Crassostrea* and *Saccostrea* length always exceeds height (H : L < 1).

Characteristic changes occur during the P II phase (Tables 10, 11). Apart from the earliest stage, in which a straight hinge is maintained, the young prodissoconch II is characterised by two phenomena: a) the direction of maximum growth changes, resulting in a height : length ratio larger than 1, except for *S. commercialis*, and b) the umbo gets a knobby appearance. Later, at a length of approximately 115 to 130 μm the direction of maximum growth shifts towards the postero-ventral to -lateral margin. Consequently, the ratio H : L becomes smaller again, although, on average, the height remains larger then the length, and the umbo becomes continuously more skewed.

This second change of the direction of maximum growth is well documented in figs. 26 and 29 in LOOSAN-

Table 10 — Size ranges and growth stages of the prodissoconchs of various Crassostreinae and Liostrea (Liostreinae) (from different sources; for authors see key numbers in Table 9). The numerous overlaps with Table 11 are due to the heterogeneity of information provided by different authors.

| species | author | size P I | | size D-shape veliger | | size early P II | | size advanced P II | | L = x * H in % | | | | convexity (both valves) | | 
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | length | height | length | height | length | height | length | height | P I | P II | P I | P II | P I | P II |
| *Liostrea plastica* | (1) | — | — | — | — | — | — | 360 - 520 | 310 - 480 | — | — | — | — | — | — |
| *Crassostrea angulata* | (3) | < 78 | 56 | 78 - 112 | ? < 90 | — | — | 310 | 285 | — | — | — | — | — | 53 - 250 |
| *Crassostrea gigas* | (4) | 70 | — | ? < 105 | — | — | — | 245 - 340 | — | — | — | 34 - 53 | — | — | — |
| | (5) | 72 - 77 | 65 | — | — | — | — | 285 - 335 | — | — | — | — | — | — | — |
| | (6) | 70 | 60 | — | — | 90 - 120 | 90 - 120 | 210 - 350 | 210 - 330 | — | — | — | — | — | — |
| | (7) | 70 | — | — | — | — | — | — | — | — | — | L - 35/40 | — | — | — |
| | (8) | — | — | — | — | — | — | — | 310 / 310 | — | — | — | — | — | — |
| *Crassostrea iredalei* | (10) | 69 | 60 | 64 - 84 | 65 - 80 | > 85 | > 81 | — | — | max 115 | — | 41 - 61 | — | — | 62 - 220 |
| *Crassostrea virginica* | (11) | 62 - 77 | 55 - 77 | 82 | 77 | < 144 | < 144 | 153 - 284 | 157 - 273 | — | min 9⟨ | — | — | — | — |
| | (12) | 60 | 60 | 90 - 100 | 90 - 100 | 85 - 125 | — | 248 - 400 | — | — | — | — | — | — | — |
| | (13) | 50 - 70 | — | ? > 80 | — | — | — | — | 195 - 325 | — | — | — | — | — | — |
| | (5) | 70 - 77 | — | — | — | — | — | 294 - 335 | — | — | — | — | — | — | — |
| | (7) | 68 - 75 | 55 - 67 | — | — | — | — | — | — | — | — | — | — | — | — |
| *Saccostrea commercialis* | (14) | 50 - 60 | 45 - 50 | — | — | — | — | 320 - 330 | 350 - 360 | — | — | — | — | — | — |
| *Saccostrea echinata* | (9c) | < 75 | < 58 | — | — | — | — | — | — | — | — | — | — | — | — |
| | (16) | 74 - 76 | — | — | — | — | — | 320 - 350 | 370 | — | — | — | — | — | — |
| | (17) | — | 57 | — | — | ? 111 | ? 101 | 260 - 330 | — | — | 89 | — | — | — | — |
| *Saccostrea glomerata* | (4) | 70 | — | — | — | — | — | 226 - 337 | — | 102 - 120 | 95 - 112 | 45 - 73 | 74 - 210 | — | — |
| | (14) | 50 - 60 | 45 - 50 | 70 - 90 | 68 - 90 | 110 - 120 | — | 270 - 330 | 290 - 360 | — | — | — | — | — | — |

| species | author | changes of ratio H:L | umbo becomes apparent/knobby[1] | | umbo becomes skewed[1] | | size of pediveliger or eye-spot larva[2] | | size of P II at metamorphosis | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | length | height | length | height | length | height | length | height |
| Liostrea plastica | (1) | H < L (large P II) | — | — | — | — | — | — | 360 - 520 | 310 - 480 |
| Crassostrea gigas | (4) | at L > 170: H > L | 90 | — | 150 -200 | — | 245 - 270 | — | — | — |
| | (6) | at L >80, >120, <190 | 80 - 90 | 80 - 90 | > 120 | > 120 | 205 | 210 | ?205, 300 | 350 - 400 |
| | (7) | at L > 85 - 90, >122 | < 95 | < 92 | > 125 | > 135 | — | — | 300 | > 300 |
| Crassostrea iredalei | (10) | at L > 85 - 90 | 100 - 110 | — | > 150 | — | 210 - 275 | 240 - 305 | > 274 | > 328 |
| Crassostrea virginica | (11) | at L > 82: H > L | — | — | — | — | 262 - 284 | 262 - 273 | — | — |
| | (12) | — | 85 - 125 | — | — | — | — | — | 248 - 400 | — |
| | (13) | at L = 90: H < or = L | — | — | — | — | — | — | 310 - 350 | — |
| | (5) | at L > 240: H < L | — | — | — | — | — | — | — | — |
| | (7) | at L = 85, = 120 | 85 - 90 | — | > 115 | — | — | — | 275 - 355 | — |
| Saccostrea commercialis | (14) | at L > 300: H > L | — | — | — | — | — | — | 320 - 330 | 350 - 360 |
| | (9c) | at L > 300: H > L | — | — | — | — | — | — | 333 | — |
| Saccostrea echinata | (16) | H always > L | — | — | — | — | — | — | — | — |
| Saccostrea glomerata | (17) | at L > 120 - 175: H > L | 95 - 110 | — | 180 -185 | — | 270 | — | 260 - 330 | — |
| | (4) | at L > 120: H > L | — | — | — | — | — | — | 300 - 330 | — |
| | (14) | — | 110 | — | — | — | 270 | 290 | 320 - 330 | 350 - 360 |

[1] Most Crassostreinae develop "knobby" and "skewed" umbos, an exception is Saccostrea glomerata.
[2] The foot seems to develop before the eye-spot, but the literature is not always that specific (see references for details).

OFF et al. (1966) for *Crassostrea virginica* at a size of L = 120 and H = 131 $\mu$m and for *Cr. gigas* at L = 122 and H = 134 $\mu$m. The skewed umbo stage becomes well defined between 150 - 200 $\mu$m of length (CHANLEY & DINAMANI, 1980; figs. 25, 28, in LOOSANOFF et al., 1966). The growth pattern in *Saccostrea glomerata* differs in so far as the umbo does not become skewed (DINAMANI, 1976: figs. 18, 19). Nevertheless, the length : height diagram in DINAMANI (1976: fig. 18) also documents changes of the growth direction at sizes of (approximately) 120 x 130 $\mu$m and 240 x 250 $\mu$m.

The obliqueness of the umbo is also expressed by the angle of the rotation axis. For *Crassostrea virginica* FORBES (1967) measured an angle of 33.6° +/− 6.62°. This is not in accordance with the 20-30° measured by HU et al. (1993). In *Cr. gigas* the angle was determined as being 30-40° (HU et al., 1993).

In all Crassostreinae under discussion an eye-spot and the foot developed at lengths of 245 to 284 $\mu$m. A corresponding size of 205 $\mu$m measured for specimens of *Cr. gigas* (see LE PENNEC, 1978) seems to be exceptional. Metamorphosis in most larvae of *Cr. gigas* occurred within a size range of 270 to 335 $\mu$m in length. Other sizes appear to be extremes.

An estimate for the convexity of the P I of articulated shells is 34 to 73 $\mu$m (CHANLEY & DINAMANI, 1980: fig. 1), i.e. 17 to 37 $\mu$m for a single valve. The higher values may already belong to early P II-stages (compare table 2 in CHANLEY & DINAMANI, 1980). In P II stages the convexity of articulated valves is 53 to 250 $\mu$m (in this case simple division by 2 is not possible, because left valves are more strongly convex than right valves). According to CARRIKER & PALMER (1979) the convexity of shells of *Cr. virginica* is about 90 to 100 $\mu$m smaller than the length which should correspond to 148 to 300 $\mu$m.

Measurements of the length of the straight hinge (here: D-line) are rare. STAFFORD's (1913) values for the D-line of *Cr. virginica* are: 48 $\mu$m for shells of 69 (P I) to 103 (P II) $\mu$m in length, and 55 $\mu$m for specimens of 117 to 179 $\mu$m, and CARRIKER (1951) for the same species: 38-44 $\mu$m for specimens 62 to 75 $\mu$m long. (It should be noted that STAFFORD's measurements are unusually high and their correctness was doubted by LOOSANOFF et al., 1966). CHANLEY & DINAMANI's (1980) values for *Cr. gigas* are: 51 to 60 $\mu$m (with L = 66-93 $\mu$m), and for *Saccostrea glomerata*: 41 to 53 $\mu$m (with L = 68-111 $\mu$m).

Values for the length of the provinculum are generally missing in the older literature, but are given by HU et al. (1993) for *Crassostrea gigas* (50-61 m) and *Cr. virginica* (45-55 m), They also measured the width of the provinculum: 10-11 $\mu$m for *Cr. gigas* and 13-17 $\mu$m for *Cr. virginica* (HU et al., table 2).

Table 11 — Relations between growth sizes of prodissoconchs and developmental phases of various Crassostreinae and *Liostrea* (Liostreinae) (for authors see key numbers in Table 9).

Size differences between left and right valves were generally not considered, but LE PENNEC (1978) mentioned that the dimensions of a left valve of a *Cr. gigas* are 190 x 195 $\mu$m, whereas the corresponding right valve measures 190 x 150 $\mu$m. In some cases length values of disarticulated valves measured by HU *et al.* (1993, figs. 2, 6, 10, 14) are not identical. These differences probably reflect minor errors of measurement. The length must be the same in the two valves of a single specimen.

HINGE DENTITION

Several sources were used to demonstrate how denticles develop in left and right valves (Table 12). The most characteristic features are:

1) The central parts of the hinge are developed as central socket (CS) in the left valve and central ridge (CR) in the right valve. Denticles 2a, p and 3a, p are also developed (in a full grown hinge). But, in early P II stages of *Crassostrea gigas* and *Cr. virginica* denticles 2a, p are

Table 12 — Ontogenetic development of the hinge dentition of various Crassostreinae (reconstructed from published photographs; for authors see key numbers in Table 9). Distribution of the denticles is first symmetrical but becomes asymmetrical with age (or size) of larvae. Posterior denticles are reduced before the anterior ones.

*Crassostrea angulata*

| author | size L x H | hinge dentition (LV + RV) [LP = ?] |
|---|---|---|
| (3) | 78 - 112 | **5 3 CR 3 5** / **4 2 CS 2 4** |
| (3) | L = 85 | **5 3 (CR) 3 5** / |
| (3) | L = 131 | **5 3 CR 3 5** / **6 4 2 CS 2 4 6** |
| (3) | L = 131 | **5 3 CR 3 5** / **6 4 2 CS 2 4** |
| (3) | L = 163 | **5 3 CR 3 5** / **6 4 2 CS 2 4 6** |
| (3) | 163 x 142 | / **4 2 CS 2 4** |
| (3) | L = 250 | **5 3 CR 3 5** / **(6) 4 2 CS 2 4** |
| (3) | L = 263 | / **(4) (2) CS 2 4 (6)** |
| (2) | late pediveliger | **(5) 3 CR 3 5** / |
| (2) | L = 290 | / **CS 2 4 (6)** |
| (3) | 310 x 285 | / **CS 2 4 (6)** |

| (3) | L = 315 | / **(4) (2) CS 2 4** |
|---|---|---|
| (2) | post larval | / **(4) (2) CS 2 4** |

*Crassostrea gigas*

| author | size L x H | hinge dentition (LV + RV) [LP 50-61 micron, (4), (5)] |
|---|---|---|
| (6) | 90 x 90 | **5 3 (CR) 3 5** / **(6) 4 2 (CS) 2 4 (6)** |
| (6) | 130 x 140 | **5 3 CR 3 5** / **(6) 4 2 CS 2 4 (6)** |
| (4) | early Pd II | **5 3 CR 3 5** / **(6) 4 2 CS 2 4 (6)** |
| (6) | 210 x 210 | **5 3 CR 3 5** / **4 2 CS 2 4** |
| (6) | 240 x 240 | **5 3 CR 3 5** / **4 2 CS 2 4 6** |
| (6) | 300 x 270 | **(5) 3 CR 3 5** / **4 2 CS 2 4** |
| (4) | late pediveliger | **(5) (3) CR 3 5** / **(4) (2) CS 2 4 (6)** |
| (2) | late pediveliger | **(5) 3 CR 3 5** / |

(2)   L = 310

$$\frac{}{\text{(2) CS 2 (4)}}$$

(6)   350 x 330

$$\frac{\text{(CR) 3 5}}{\text{(CS) 2 4}}$$

(6)   550 x 600 (post-larval)

$$\frac{\text{(3) (5)}}{\text{(2) (4)}}$$

## *Crassostrea iredalei*

| author | size L x H | hinge dentition (LV + RV) [LP = ?] |
|---|---|---|
| (10) | 89 x 83 | $\dfrac{\text{(5) 3 (CR) 3 (5)}}{\text{6 4 (2)-(CS)-(2) 4}}$ |
| (10) | 214 x 236 | $\dfrac{\text{5 3 CR 3 5}}{\text{4 2 CS 2 4 6}}$ |

## *Crassostrea virginica*

| author | size L(LV/RV) | hinge dentition (LV + RV) [LP = 45-55 micron, (5), (12)] |
|---|---|---|
| (5) | 72/72 | $\dfrac{\text{5 3 CR 3 5}}{\text{4 (2)- CS -(2) 4}}$ |
| (5) | 110/110 | $\dfrac{\text{5 3 CR 3 5}}{\text{(6) 4 CS 4 (6)}}$ |
| (5) | 161/161 | $\dfrac{\text{5 3 CR 3 5}}{\text{4 2 CS 2 4 (6)}}$ |
| (5) | 237/230 | $\dfrac{\text{5 3 CR 3 5}}{\text{4 2 CS 2 4 (6)}}$ |
| (2) | late Pd II | $\dfrac{\text{5 3 CR 3 5}}{\text{4 2 CS 2 4 (6)}}$ |
| (2) | L = 250 | $\dfrac{}{\text{4 2 CS 2 4}}$ |
| (5) | 296/290 | $\dfrac{\text{5 3 CR 3 5}}{\text{4 2 CS 2 4}}$ |
| (5) | 350/337 | $\dfrac{\text{3 5}}{\text{2 4}}$ |

## *Saccostrea echinata*

| author | size L x H | hinge dentition (LV + RV) [LP = ?] |
|---|---|---|
| (15) | 90 x 80 | $\dfrac{\text{(5) (3) (CR) 3 5}}{\text{4 (2)-(CS) 4}}$ |
| (15) | 140 x 120 | $\dfrac{\text{5 3 (CR) 3 5}}{\text{4 (2) (CS) (2) 4}}$ |
| (15) | 180 x 180 | $\dfrac{\text{5 3 (CR) 3 5}}{\text{4 (2) (CS) (2) 4 6}}$ |
| (15) | 260 x 230 | $\dfrac{\text{5 3 CR 3 5 7}}{\text{4 2 CS 2 4 (6)}}$ |
| (15) | 260 x 260 | $\dfrac{\text{5 3 3 5}}{\text{4 2 2 4 6}}$ |
| (16) | L = 340 | $\dfrac{}{\text{2 CS 2 4}}$ |
| (16) | L = 340 | $\dfrac{\text{(7) 5 3 CR 3 5 7}}{\text{6 4 2 CS 2 4 6}}$ |

## *Saccostrea glomerata*

| author | size L x H | hinge dentition (LV + RV) [LP = ?] |
|---|---|---|
| (2) | L = 150 | $\dfrac{\text{5 3 CR 3 5}}{\text{4 2 CS 2 4 (6)}}$ |
| (14) | L = 180 | $\dfrac{}{\text{4 2 CS 2 4 6}}$ |
| (4) | early Pd II | $\dfrac{\text{5 3 CR 3 5 (7)}}{\text{4 2 CS 2 4 6}}$ |
| (2) | L = 290 | $\dfrac{}{\text{4 2 CS 2 4 (6)}}$ |
| (14) | L = 300 | $\dfrac{}{\text{4 2 CS 2 4 (6)}}$ |
| (2) | L = 300 | $\dfrac{\text{5 3 CR 3 5}}{\text{(6) 4 2 CS 2 4 (6)}}$ |
| (4) | late Pd II | $\dfrac{\text{(5) 3 CR 3 (5)}}{\text{4 2 CS 2 4}}$ |

less developed than denticles 4a, p! (see LE PENNEC, 1978: pl. 25; HU *et al.*, 1993: figs 3, 7). 2) Denticles 4a, p and 5a, p are generally well developed and are already visble in specimens only 78 μm long.

3) Denticles 6a, p occur well developed in *Cr. angulata* (L = 131 to 163 m) while denticles 7a, p are missing. In *Cr. gigas* denticles 6a, p are rudimentary (at L = 130 m), in *Cr. virginica* only denticle 6a may be developed as a rudiment (not enough small specimens available for confirmation). A specimen of *Saccostrea echinata* (with L = 340 m) is extraordinarily large with denticles 6a, p, 7a and 7p (as a rudiment) developed, and finally, in *S. glomerata* denticle 6a and 7a (as a rudiment) may occur at an early P II stage (exact size not known).

4) Denticle 1 (= CR) is generally much larger thàn denticles 3a, p, 4a, p which are — later joined by 2a, p — more or less equal in size. These relations may be seen in HU *et al.* (1993: figs. 3, 7). Nevertheless, exact measurements only exist for denticle 1: 17-23 μm and 13-20 μm respectively in *C. gigas* and *C. virginica* (HU *et al.*, 1993). The dominant denticle shape is rectangular; irregularly shaped or triangular denticles may be found in the most distant positions.

5) The maximum development of the hinge was reached at a length of 130 to 160 μm in *Cr. angulata* and *Cr. gigas* (or 90-160 μm according to LE PENNEC, 1978), for *Cr. virginica* between lengths of 110-237 μm (HU *et al.*, 1993, fig. 7). It cannot be reconstructed from the available data for *Saccostrea echinata*, although the large number and symmetrical arrangement suggests that the maximum development may have been reached (or was still present) at the size of 340 μm. In *S. glomerata* the size may be estimated as being between 110 and 150 μm.

6) Final reductions of the denticles in all species occur first on the posterior side of the hinge. The corresponding shell sizes vary, probably depending on the individual size at metamorphosis. Nevertheless, the two *Saccostrea* species seem to reduce their denticles somewhat later than species of *Crassostrea*. Note that the interpretation of denticles as representing 2a, p (LV) and 3a, p (RV) respectively may be ambiguous if they are not well developed as is the case in early prodissoconchs (e.g. *Saccostrea echinata* in LE PENNEC & COATANEA, 1985: pl. 1; interpretation in Table 12). Further irregularities in the formula may occur if one valve clearly shows a socket where the other valve lacks a denticle. Reasons for this may be that the denticle broke during preparation, or that the two compared valves do not belong to the same specimen, or that the photograph is too bad for an unequivocal description (compare pairs of figs 2, 3 and 4, 5 of plate 1 of LE PENNEC & COATANEA, 1985; in figs. 10 and 11 left and right valves appear exchanged). Such a "missing" denticle is nevertheless added in the formulas.

*Living Ostreinae*

GROWTH STAGE AND SHAPE

Species of the Ostreinae are larviparous. In consequence,

the earliest growth stages examined by most authors are those directly after release. They already belong to the earliest P II. The still existent D-shape at this stage is similar to that of the Crassostreinae, but it is generally larger by a factor of 1.3 to 3. The knobby umbo appears more blunt; a skewed umbo stage is not developed. The overall aspect of a full grown larva is more globular than triangular (Table 13 lists species considered here; for description of the shell structure and sculpture see WALLER, 1981).

SHELL SIZE, PROPORTIONS, PATTERNS OF GROWTH

According to WALLER (1981) and HU *et al.* (1993) the size of the prodissoconch I of *Ostrea edulis* is about 160 to 173 μm long and 160 μm high. Commonly, young larvae of this species directly after their release are between 165 and 185 μm long. Specimens smaller than 160 μm have been considered premature and not viable (LOOSANOFF *et al.*, 1966). Altogether, measurements range from 130 to 199 μm. In contrast, the size of the P I of *Ostreola equestris* is considerably smaller with a length between 113 to 129 μm [Table 14, no. (5)]. Sizes of freshly released D-stage veligers of *Ostreola stentina*, *Ostrea* (*Eostrea*) *puelchana*, *O.*? (*E.*) *aupouria*, and *Cryptostrea permollis* suggest that this is also true for these species. Species of *Tiostrea* are exceptionally large (see discussion below).

Shells generally retain their D-shape until they reach a size of about 200 μm after which it changes to a knobby umbo shape. The height : length ratio which has already been below 1 during earlier stages decreases even more between a length of 200 to 240 μm. In larger specimens it

Table 13 — Living species of the Ostreinae discussed in this chapter (listed alphabetically). Information is given about the original distribution of species and their proposed phylogenetic relationships, about the literature used here, and about the conditions (natural or artificial) of larval and post-larval growth. In Tables 14 to 16 authors' names are replaced by numbers (2-27). Abbreviations: artif. = artificial, lab(s) = laboratory(ies), lab or nat. cond. = laboratory or natural conditions, N Isl. = Northern Island (of New Zealand), popul. = population.

*Ostrea (Ostrea) denselamellosa* Lischke, 1869

NW Pacific; according to Harry (1985) one of the two species of the subgenus.

(18) Le Borgne & Le Pennec (1983): ? NW Pacific; adults transferred to France, larvae lab conditions

*Ostrea (Ostrea) edulis* Linné, 1758

E Atlantic; see Harry (1985) for systematics.

(5)  Hu et al. (1993): W Atlantic, Maine; adult nat., larvae lab conditions

(6)  Le Pennec (1978): E Atlantic, NE France; lab conditions

(7)  Loosanoff et al. (1966): E Pacific, California; larvae lab conditions

(19) Helm et al. (1973): England; lab conditions

(20) Korringa (1941): North Sea, Oosterschelde, Netherlands; natural conditions

(21) Pascual (1972): E Atlantic, Spain; larvae from natural population, lab conditions

(22) Waller (1981): W Atlantic, N.Y.; lab condit.

### *Ostrea (Eostrea) puelchana* D'Orbigny, 1841

SW Atlantic, Argentina, type of subgenus *O. (Eostrea)* Ihering (1907); according to Harry (1985) *O.(E.) angasi* Sowerby, 1871, *O. (E.) chilensis* Philippi, 1845, and *O. (E.) lutaria* Hutton, 1873, are junior synonyms. For the last two species Chanley & Dinamani considered a new genus: *Tiostrea* (see below).

(23) Fernandez Castro & Le Pennec (1988): SW Atlantic, San Matias Gulf; adults natural, brooding and larvae lab conditions

### *Ostrea ?(Eostrea) angasi* Sowerby, 1871

S hemisphere (between latitudes 35 and 50°); Harry (1985) regards the name a junior synonym of *O. (E.) puelchana* (see above).

(24) Dix (1976): S Australia, Tasmania; adults natural, larvae lab conditions

### *Ostrea ?(Eostrea) aupouria* Dinamani, 1981

SW Pacific, New Zealand; Booth (1979) and Chanley & Dinamani (1980) independently described an *Ostrea* sp. which was later described as a new species - *O. aupouria* - by Dinamani (in Dinamani & Beu, 1981). The new species was compared neither with the Australian *O. ?(E.) angasi* nor with the Argentinian *O. (E.) puelchana* (see above). It is here tentatively put within the same subgenus.

(4)  Chanley & Dinamani (1980): SW Pacific, New Zealand, N Isl.; adults nat. population, larvae lab conditions

(17) Booth (1979): SW Pacific, New Zealand, N Isl.; adults and larvae natural condition

(25) Dinamani & Beu (1981): data on larvae based on Chanley & Dinamani (1980)

### *Ostreola equestris* (Say, 1834)

W Atlantic, from N Carolina to Argentina; according to Harry (1985) a valid separate species of the genus, with *Ostrea spreta* d'Orbigny, 1841 as a junior synonym.

(5)  Hu et al. (1993): W Atlantic, N Carolina; adults natural, larvae lab conditions

### *Ostreola lurida* (Carpenter, 1864)

E Pacific; according to Harry (1985) this species is a junior synonym of *Ostreola conchaphila* (Carpenter, 1857).

(7)  Loosanoff et al. (1966): E pacific, California; larvae lab conditions

(8)  Miyazaki (1962): ?, not known.

(26) Hori (1933): adults from E Pacific (Wash. St.), larvae lab conditions

### *Ostreola stentina* (Payraudeau, 1826)

Mediterranean (Corsica), E Atlantic (probably not N of 40° N); type species of *Ostreola* Monterosato, 1884 (see Harry, 1985).

(22) Pascual (1972): E Atlantic, Spain; larvae from natural population, lab conditions

### *Cryptostrea permollis* (Sowerby, 1871)

W Atlantic, from N Carolina to E Gulf of Mexico; type species of *Cryptostrea* Harry, 1985.

(27) Buroker (1985): cites Forbes (1962, 1964, 1966; not seen); specimens probably from W Atlantic, ?Florida (see Harry, 1985: 144f)

### *Tiostrea chilensis* (Philippi, 1845)

SW Atlantic, S Chile; according to Harry (1985) a jun. synonym of *Ostrea (Eostrea)* Ihering (1907) *puelchana* (d'Orbigny, 1841) (see above); one of two species of *Tiostrea* Chanley & Dinamani (see below).

(4)  Chanley & Dinamani (1980): SW Atlantic, S Chile; adults from nat. popul., larvae lab conditions

### *Tiostrea lutaria* (Hutton, 1873)

SW Pacific, New Zealand; type of genus *Tiostrea* Chanley & Dinamani (1980); according to Harry (1985) a junior synonym of *Ostrea (Eostrea)* Ihering (1907) *puelchana* (d'Orbigny, 1841).

(4)  Chanley & Dinamani (1980): Pacific, New Zealand, N Isl.; adults from natural popul., larvae lab condions

Table 14 — Size ranges and growth stages of the prodissoconchs of various Ostreinae (from different sources; for authors see key numbers in Table 13). The numerous overlaps with Table 15 are due to the heterogeneity of information provided by different authors.

| species | author | size P I / earliest P II [1] | | size D-shape veliger [1] | | size early P II [1] | | size advanced P II | | L = x * H in % | | convexity (both valves) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | length | height | length | height | length | height | length | height | P I | P II | P I | P II |
| O. (O.) denselamellosa | (18) | 150 | --- | ?160 -170 | --- | --- | --- | 260 - 270 | --- | --- | --- | --- | --- |
| Ostrea (Ostrea) | (19) A | 166 - 168 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| edulis | (19) B | 171 - 175 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | (20) | 165 - 185 | --- | --- | --- | --- | --- | 260 - 300 | --- | --- | --- | --- | --- |
| | (21) | --- | --- | --- | --- | --- | --- | 213 - 280 | --- | --- | --- | --- | --- |
| | (22) | 170 | 160 | --- | --- | --- | --- | 265 - 360 | 250 - 300 | --- | --- | 90 - 100 | 250 |
| | (5) | 162 - 173 | --- | --- | --- | --- | --- | 313 - 340 | --- | --- | --- | --- | --- |
| | (6) | 130 | 124 | 170 | 160 | --- | --- | 300 - 320 | 300 - 320 | --- | --- | --- | --- |
| | (7) | 142 - 199 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| O. (Eostrea) puelchana | (23) | 105 - 155 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| O. ?(Eostrea) angasi | (24) | 192 - 204 | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| O. ?(Eostrea) | (17) | --- | --- | --- | --- | --- | --- | 218 - 291 | 240 - 320 | 90 | --- | --- | --- |
| aupouria | (4) | 125 - 155 | --- | --- | --- | --- | --- | 230 - 320 | --- | --- | --- | 73 - 94 | --- |
| Ostreola equestris | (5) | 113 - 129 | --- | 135 - 160 | --- | --- | --- | 300 - 315 | --- | --- | --- | --- | --- |
| Ostreola | (26) | 178 | 157 | 193 | 172 | 205 | 183 | 300 - 340 | 230 - 310 | --- | --- | --- | --- |
| lurida | (7) | 160 - 185 | 150 | --- | --- | 205 | --- | --- | --- | --- | --- | --- | --- |
| | (8) | --- | --- | --- | --- | --- | --- | 320 | 310 | --- | --- | --- | --- |
| Ostreola stentina | (21) | 139 | 123 | --- | --- | 177 - 193 | 163 - 177 | 237 - 259 | 226 - 248 | --- | --- | --- | --- |
| Cryptostrea permollis | (27) | 108 - 127 | --- | --- | --- | --- | --- | 290 | --- | --- | --- | --- | --- |
| Tiostrea chilensis | (4) | 416 - 514 | 318 - 372 | --- | --- | --- | --- | 416 - 514 | 318 - 372 | --- | 120 - 143 | --- | 200 - 243 |
| Tiostrea lutaria | (4) | 444 - 521 | 348 - 405 | --- | --- | --- | --- | 444 - 521 | 348 - 405 | --- | 118 - 141 | --- | 212 - 264 |

[1] Measurements of ostreine larvae normally refer to freshly released larvae, i.e. earliest P II stages; exceptions are Waller (1981) and Hu et al. (1993) [see no. (22) and (5), this Table] who measured the P I proper. As well, authors' terminology is often not very precise and the measurements of the subsequent columns (marked [1]) overlap.

increases again and reaches a degree similar to the first ratio (see LOOSANOFF *et al.*, 1966: fig. 20 for *O. edulis*, and fig. 23 for *Ostreola lurida*). Because new shell material accretes on both the anterior and posterior shell edge at a similar rate in the two species, a skewed umbo stage never develops. Nevertheless, for *Ostreola equestris*, HU *et al.* (1993) determined an angle of rotation (obliqueness) of 20-25°.

Eye-spot and foot develop at a length of 260 to 300 μm. At the time of metamorphosis most specimens measure between 260 and 320 μm (340 μm being rare). Specimens of *Ostreola stentina* appear to metamorphose at smaller sizes (Table 15).

Data about the convexities of shells are rare and those available were taken from closed valves (Table 14). The convexity of shells during the P I stage are higher than in crassostreinid species, while it is more or less the same at the P II stage.

Lengths of the provinculum were measured for *Ostrea edulis* (80-95 m) and *Ostreola equestris* (70-79 m) (HU *et al.*, 1993) and for *O.* ?(*E.*) *aupouria* (64 to 78 m) (CHANLEY & DINAMANI, 1980, for shells 132 to 157 μm long). There are no data given for the widths of the provinculum.

The larval developments of *Tiostrea chilensis* and *T. lutaria* are exceptional in many respects. Both P I and P II are compressed and hinge denticles are either rudimentary (RANSON, 1960, figs. 133, 135) or not at all developed (CHANLEY & DINAMANI, 1980: fig. 10D). Because larvae lack a real planktonic phase, their shells also lack knobby umbo or skewed stages so characteristic of the other species (see CHANLEY & DINAMANI, 1980; CHAPARRO *et al.*, 1993 for reviews). These differences are interpreted here as a result of their extraordinary long brooding phase (further discussion in the final chapter).

## HINGE DENTITION

Characteristic features of the hinge dentition in the Ostreinae are (compare Table 16):

1) The central part of the hinge is mostly an ill defined platform in both valves (CP) from which the adjacent denticles 2a, p of the left valve are barely separated. Denticles 3a, p of the right valve are often well developed. The first true denticle may already occur at a size of 110 μm (LE PENNEC, 1978). The hinge of a 130 μm long *Ostrea edulis* may bear 3 "laterals" in the right and 4 in the left valve.

2) At its maximum development denticles 4a, p, and 5a, p are well established.

3) Sometimes denticle 6p is developed in *O. edulis*, while denticle 6a never occurs. Both denticles are missing in *O.* ? (*Eostrea*) *aupouria* and *Ostreola stentina*.

Table 15 — Relations between growth sizes of prodissoconchs and developmental phases of various Ostreinae (for authors see key numbers in Table 13).

| species | author | changes of ratio H : L | umbo becomes apparent / "knobby"[1] | | umbo becomes prominent / "skewed"[1] | | size of pediveliger or eye-spot larva[2] | | size of P II at metamorphosis | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | length | height | length | height | length | height | length | height |
| *O. (O.) denselamellosa* | (18) | --- | --- | --- | 200 | --- | 260 - 270 | --- | 275 - 300 | --- |
| *Ostrea (Ostrea)* | (20) | --- | --- | --- | --- | --- | 260 - 300 | --- | 260 - 315 | --- |
| *edulis* | (21) | --- | 213 | --- | --- | --- | --- | --- | --- | --- |
| | (5) | H always < L | 200 | --- | 280 | --- | --- | --- | --- | --- |
| | (6) | --- | 210 | 205 | --- | --- | 300 | 300 | 320 | 320 |
| | (7) | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *O. ?(Eostrea) aupouria* | (4) | --- | 155 - 200 | --- | > 230 | --- | < 280 | --- | 300 - 320 | --- |
| *Ostreola equestris* | (5) | at L > 280: H < L | 160 - 170 | --- | > 280 | --- | --- | --- | --- | --- |
| *Ostreola* | (26) | --- | 205 | 183 | 300 | 230 | 280 | --- | 320 - 340 | 310 |
| *lurida* | (7) | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *Ostreola stentina* | (21) | H always < L | 177 - 193 | 163 - 177 | --- | --- | --- | --- | 240 - 275 | --- |
| *Cryptostrea permollis* | (27) | --- | --- | --- | --- | --- | --- | --- | 290 | --- |
| *Tiostrea chilensis* | (4) | H always < L | umbo | flat | umbo | flat | --- | --- | --- | --- |
| *Tiostrea lutaria* | (4) | H always < L | umbo | flat | umbo | flat | --- | --- | --- | --- |

[1] In Ostreinae the umbo rarely becomes knobby [example: *Ostreola equestris*, fide Hu et al., 1993, no (5), this Table]; it is never really skewed as in Crassostreinae.
[2] The foot seems to develop before the eye-spot, but the literature is not always that specific (see references for details).

Table 16 — The table demonstrates ontogenetic steps of the development of the hinge dentitions of several ostreine species (reconstructed from published photographs; for authors see key numbers in Table 13). Well developed dentitions are often symmetrical, but the central denticles generally remain ill-defined. Reductions occur first on the anterior side.

### Ostrea edulis

hinge dentition (LV + RV) [LP approx. 90 micron, (6)]

| author | size (L x H) | hinge dentition (LV + RV) |
|--------|--------------|---------------------------|
| (6) | 130 x 115 | (5) 3 ℗ 3 / 4 (2) ℗ (2) 4 |
| (21) | 159 x 174 | 5 (3) — ℗ — (3) 5 / 4 ℗ 4 |
| (21) | 167 x 180 | 5 3 — ℗ — (3) 5 / (6) 4 (2)- ℗ 4 |
| (6) | 200 x 180 | 5 3 ℗ 3 (5) / 4 (2)- ℗ -(2) 4 |
| (21) | 206 x 227 | / 4 (2)- ℗ -(2) 4 |
| (6) | 210 x 220 | 5 3 ℗ 3 5 / 4 (2)- ℗ -(2) 4 |
| (21) | 214 x 234 | 5 3 ℗ — (3) 5 / |
| (6) | 250 x 220 | 5 3 ℗ (3) / 6 4 (2)- ℗ -(2) |
| (21) | 257 x 279 | / 4 (℗)-(2) |
| (21) | 263 x 301 | / 6 4 (2)- ℗ |
| (21) | 270 x 288 | 5 3 — ℗ / 4 (2)- ℗ -(2) |
| (21) | 315 - 320 | 5 3 — ℗ — 3 / (6) 4 (2)- ℗ (4) |
| (6) | 350 x 330 | 5 3 ℗ / 6 4 (2)- ℗ |
| (6) | 400 x 370 | 5 3 (℗) / 4 (2)-(℗) |

### Ostrea ?(Eostrea) aupouria

hinge dentition (LV + RV) [LP = ?]

| author | size (L x H) | hinge dentition (LV + RV) |
|--------|--------------|---------------------------|
| (4) | early Pd II | 5 (3) — ℗ / 6 4 ℗ 4 6 |
| (4) | ? late Pd II | 5 3 — ℗ / 4 (2)- ℗ |

### Ostreola equestris

hinge dentition (LV + RV) [LP = 70 - 79 micron, (5)]

| author | size (L x H) | hinge dentition (LV + RV) |
|--------|--------------|---------------------------|
| (5) | 135 x 135 | (5) 3 ℗ 3 (5) / 4 ℗ 4 |
| (5) | 156 x 158 | 5 3 ℗ 3 5 / 4 ℗ 4 |
| (5) | 172 x 172 | 5 3 ℗ 3 5 / 4 ℗ 4 |
| (5) | 187 x 185 | 5 3 ℗ 3 5 / 4 (2)- ℗ -(2) 4 |
| (5) | 196 x 200 | 5 3 ℗ 3 5 / 4 (2)- ℗ -(2) 4 |
| (5) | 245 x 250 | 5 3 ℗ (3) (5) / 4 (2) ℗ (4) |
| (5) | 288 x 300 | 5 3 ℗ / 4 (2)- ℗ |

### Ostreola stentina

hinge dentition (LV + RV) [LP = ?]

| author | size (L x H) | hinge dentition (LV + RV) |
|--------|--------------|---------------------------|
| (21) | L = 140 | 5 (3) — ℗ (3) 5 / 4 ℗ 4 |

(21)    L = 170    $\dfrac{5 \quad 3 \quad\quad CP \quad\quad 3 \quad 5}{4 \quad (2)- \quad CP \quad -(2) \quad 4}$

(21)    177 x 163    $\dfrac{5 \quad 3 \quad\quad CP \quad\quad 3 \quad 5}{4 \quad (2)- \quad CP \quad -(2) \quad 4}$

(21)    196 x 185    $\dfrac{5 \quad 3 \quad\quad CP \quad\quad 3 \quad 5}{4 \quad (2)- \quad CP \quad -(2) \quad 4}$

(21)    237 x 226    $\dfrac{5 \quad 3 \quad - \quad CP}{4 \quad (2)- \quad CP}$

4) The central platforms are much larger than the following denticles (qualitative statement, measurements were not given by authors). Denticles are generally quadrangular in shape except for the most distant ones which may be triangular. According to FERNANDEZ CASTRO & LE PENNEC (1988: table 1) "rounded" denticles occur in *Ostreola stentina* and *Ostrea* (*Eostrea*) *puelchana*. But the diagnostic character of the round shape is doubted here (see last chapter).

5) The maximum development occurs at a size of 167 x 180 μm. Denticle 6p normally occurs later, at sizes larger than 250 x 220. These hinges already show reductions of anterior denticles.

6) Final reduction always affect anterior denticles first.

It was already noted for the Crassostreinae that the interpretation of denticles as representing 2a, p (LV) and 3a, p (RV) respectively may be ambiguous. This is even more so for the Ostreinae because of the generally less developed central apparatus (see above point 1).

## Comparison (Ostreidae)

The present chapter focuses on a statistical comparison of the height and length measurements (of P I and P II) of the ostreids described before and on a comparison of the larval hinge dentitions. A general evaluation of all characters will be given in the next chapter.

HEIGHT, LENGTH, AND THE RATIO H : L

There can be no doubt that the prodissoconchs I of both the inspected fossil ostreids and the Recent Crassostreinae belong to the smaller size class, i.e. of 50-80 μm, and thus that they are distinct from the group of living Ostreinae (Tables 1, 10, and 14). It did, however, not become obvious whether the other size differences between the populations in question are significant. Means and standard deviations of heights, lengths, and H : L
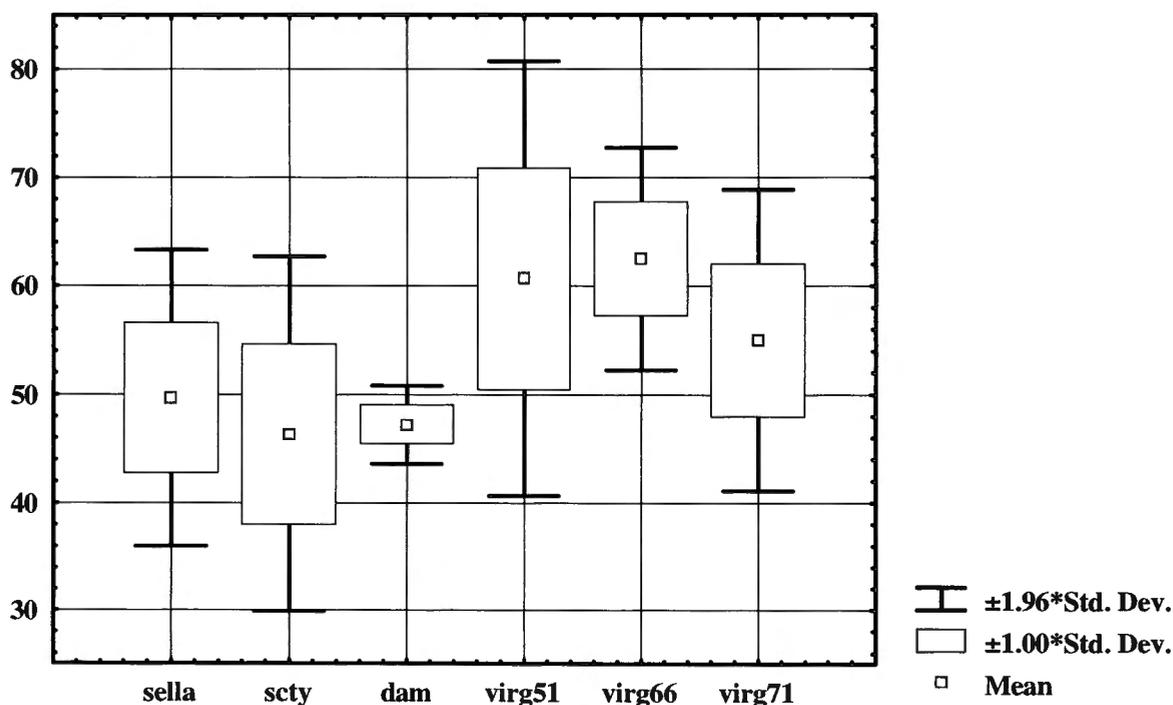


Text-fig. 8 — Box-and-whisker plot showing the means and standard deviations (std. dev.) of height values of P I - LV of *Cubitostrea sellaeformis* (sella), *Cubitostrea* sp. (scty), ? *Crassostrea* sp. (dam) and of three populations of *Cr. virginica* (virg51, virg66, and virg71). (Dimension of vertical axis in μm.) The standard deviations and thus the variances are very heterogeneously distributed, but although the ranges of standard deviations overlap widely the first three populations exhibit slightly smaller height values.
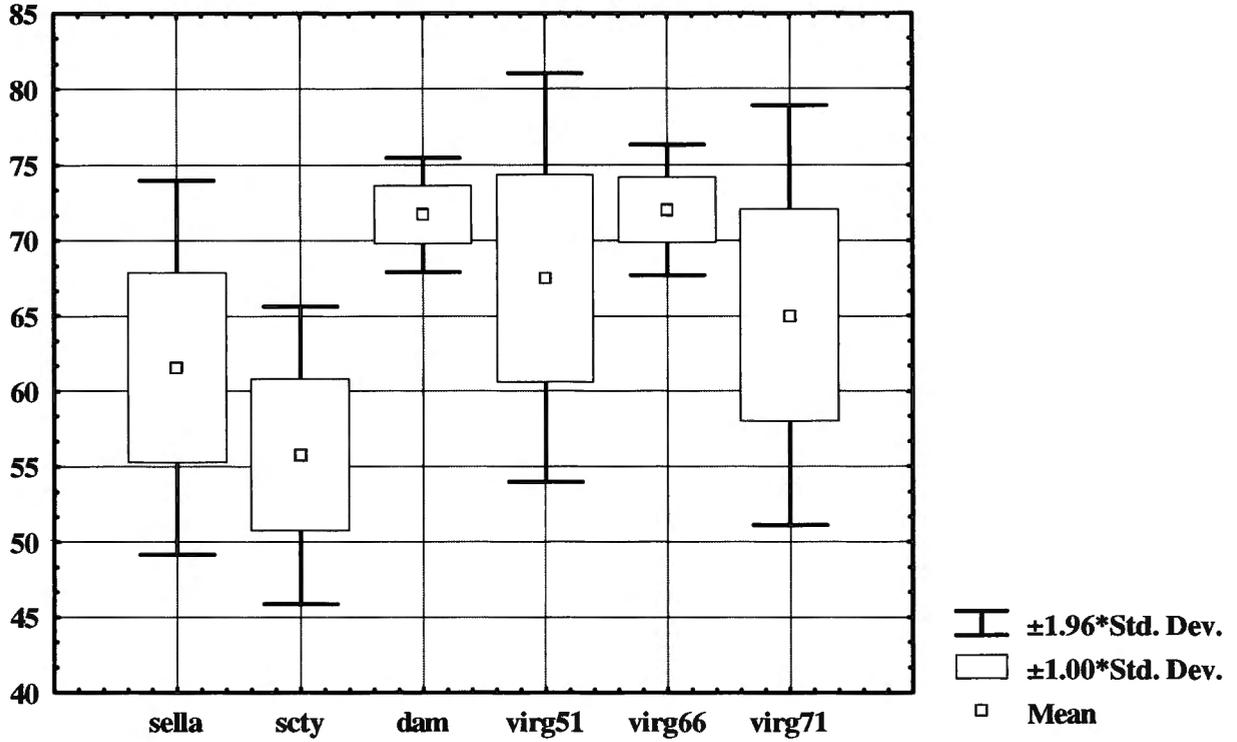
Text-fig. 9 — Box-and-whisker plot showing the means and standard deviations (std. dev.) of length values of P I-LV (populations as in Text-fig. 10; dimension of vertical axis in $\mu$m). Note that ? *Crassostrea* sp. (dam) is completely indistinguishable from *Cr. virginica* (virg).
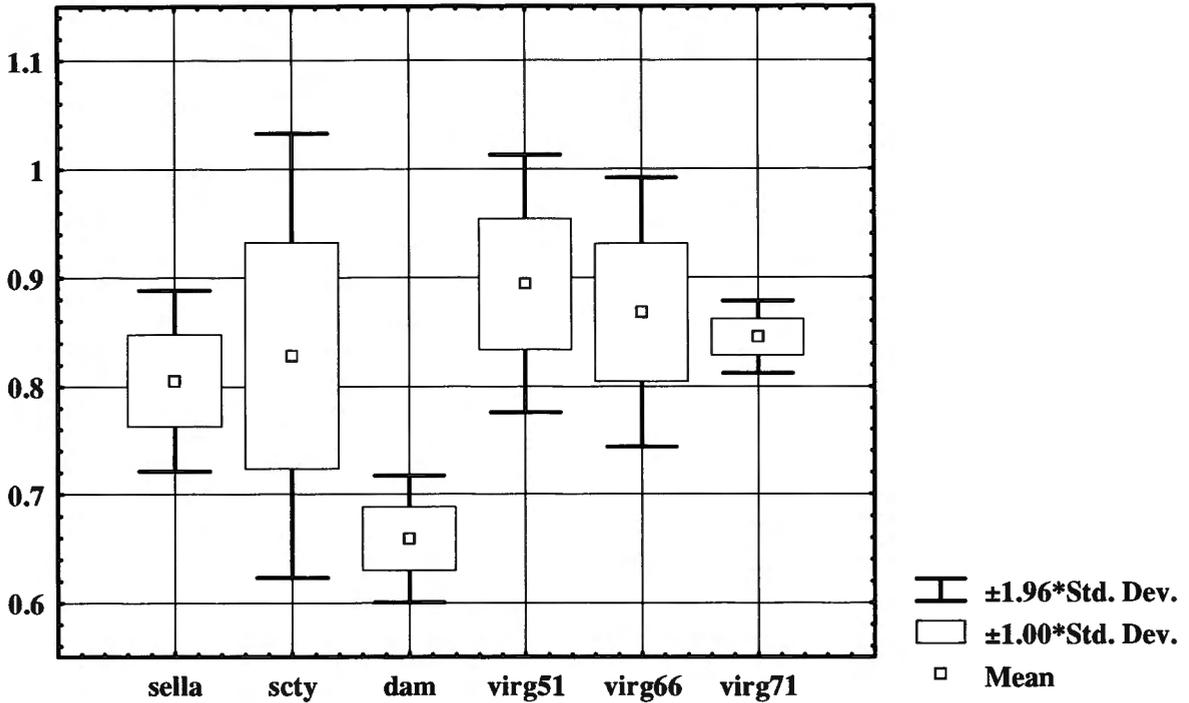


Text-fig. 10 — Box-and-whisker plot showing the means and standard deviations (std. dev.) of the ratio of H: L (without dimension) of populations of Text-figs. 8, 9. Note that only ? *Crassostrea* sp. (dam) is clearly separated from *Cr. virginica* (virg).
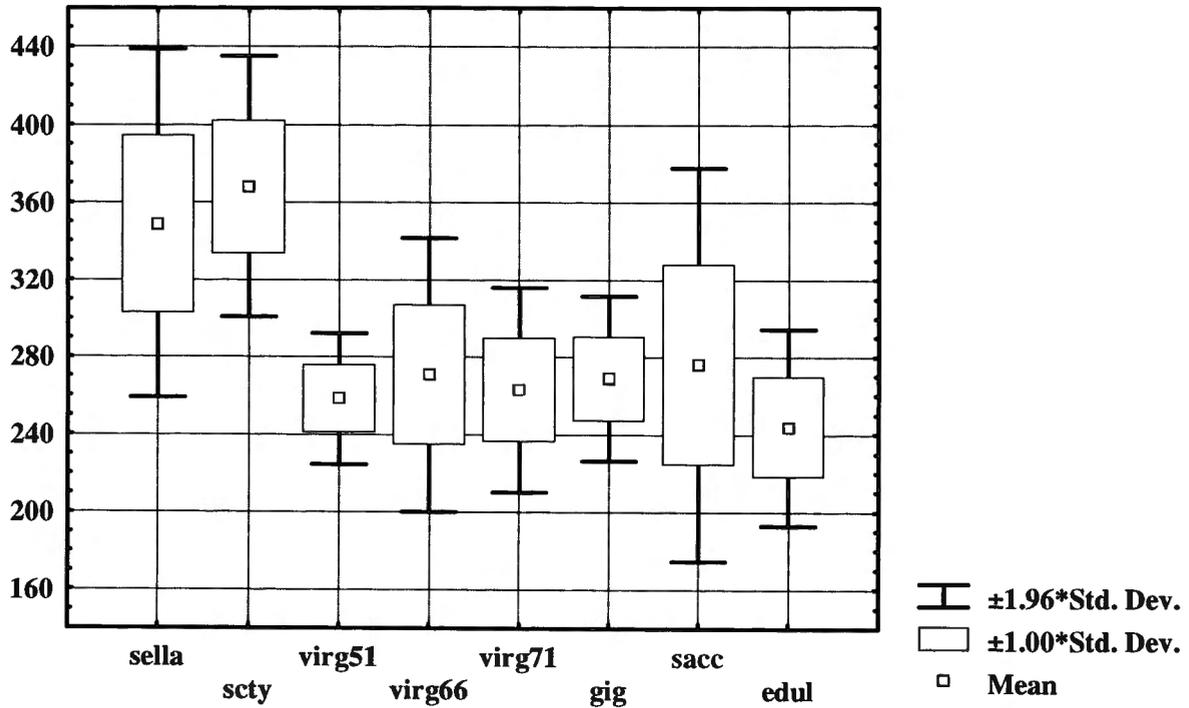
Text-fig. 11 — Box-and-whisker plot showing the means and standard deviations (std. dev.) of height values of P II - LV of eight populations. (Dimension of vertical axis in $\mu$m). Note that the fossil *Cubitostrea sellaeformis* (sella) and *Cubitostrea* sp. (scty) are separated from the extant *Crassostrea virginica* (virg51, virg66, and virg71), *Cr. gigas* (gig), *Saccostrea commercialis* (sacc), and *Ostrea edulis* (edul).
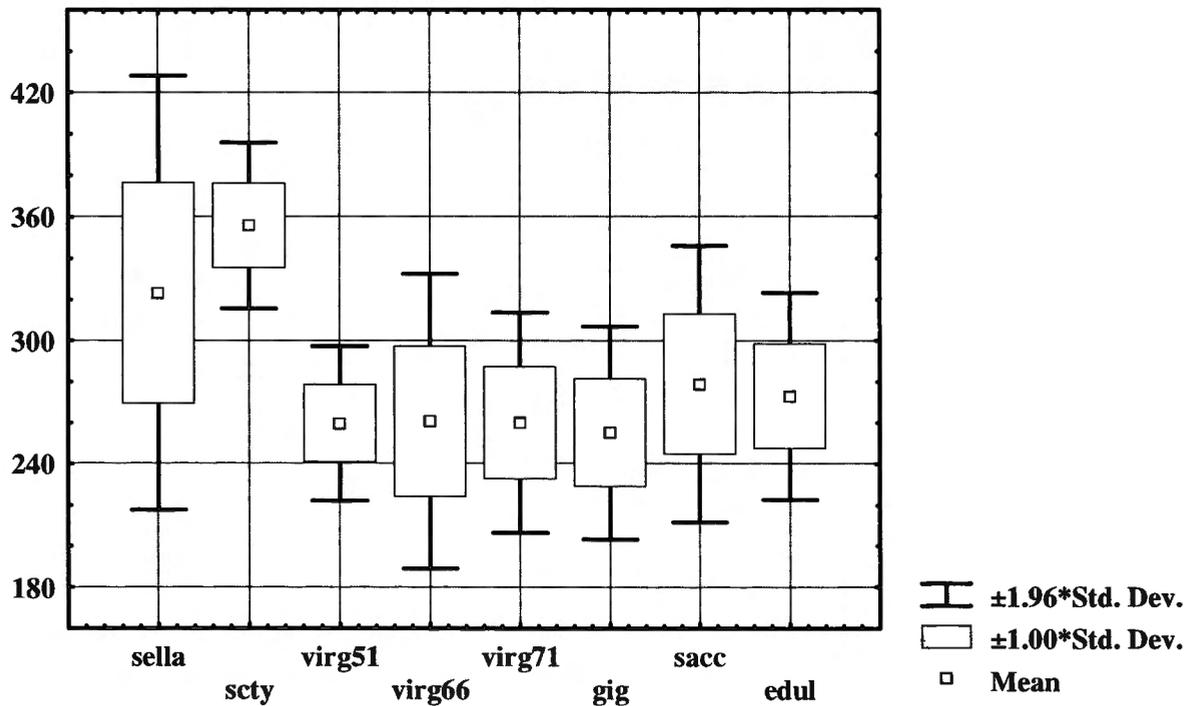


Text-fig. 12 — Box-and-whisker plot showing the means and standard deviations (std. dev.) of length values of P II-LV of the populations of Text-fig. 11. (Dimension of vertical axis in $\mu$m). The plot reveals the same tendency as in Text-fig. 11.
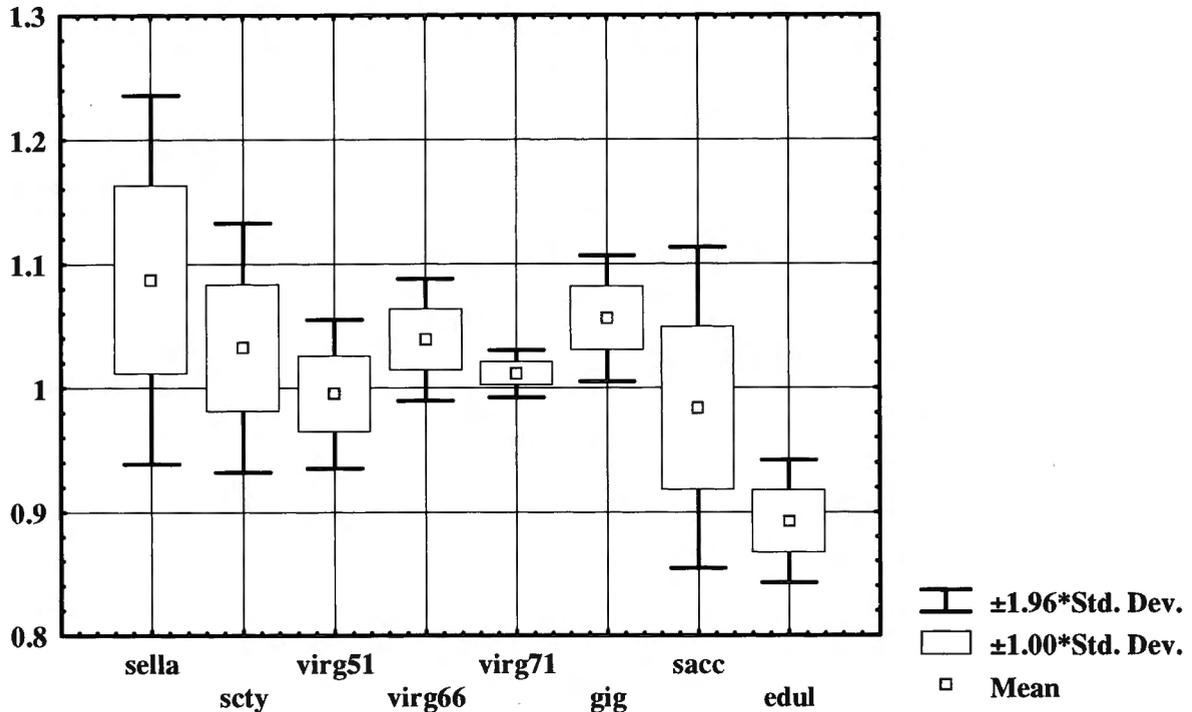
Text-fig. 13 — Box-and-whisker plot showing the means and standard deviations (std. dev.) of the ratio of H: L (without dimension) of populations of Text-figs. 11 and 12. Only the far ends represented by *Cubitostrea sellaeformis* (sella) and *Ostrea edulis* (edul) appear to be clearly distinct from each other.

ratios of a number of fossil and Recent populations can be inferred from Text-figs. 8 to 10 (P I, left valves) and 11 to 13 (P II, left valves). More generally, the figures reveal a heterogeneous distribution of variances (the square of standard deviations) and wide overlaps of the standard deviations themselves. Weak grouping patterns appear in all figures, but they are not constantly developed and their interpretation may be erroneous.

Nevertheless, these patterns coincide with the results from Kolmogorov-Smirnov tests carried out for various groupings of populations (Table 17). Most importantly, two *a priori* tests reveal significant differences between fossil and Recent groups, i.e. for P I between *Cubitostrea sellaeformis* (sella), *Cubitostrea* sp. (scty), and ? *Crassostrea* sp. (dam) vs. *Cr. virginica* (virg51, 66, 71), and for P II between "sella" and "scty" vs. "virg51, 66, 71", *Cr. gigas* (gig), *Saccostrea commercialis* (sacc), and *Ostrea edulis* (edul). This is true for all three characters: height, length, and the ratio of H : L. In contrast, no differences whatsoever were found between *Cubitostrea sellaeformis* (sella) from Alabama and *Cubitostrea* sp. (scty) from Texas. The two populations, however, differ in length (and thus also in H : L) from the fossil ? *Crassostrea* sp. (dam) (*a priori* and *a posteriori* tests for P I). Surprisingly, significant differences were also found for the ratio H : L between two of three populations of *Cr. virginica* (virg51 vs. virg66; P II, *a priori* test). These differences may at least in part be due to the way in which data had to be extracted from the literature (i.e. from

graphical presentations). The tests suggest significant differences between and within fossil and Recent groups. However, it should be kept in mind that the amount of data available for each population ranged from three (dam) to 27 (sella) pairs of length/height values. In addition, it is not known how large sample sizes should be for such comparisons. For an estimate of this value one would need to know the standard deviations for these characters in natural populations of, e.g. *Cr. virginica* or *Ostrea edulis*.

It may be noted that the ratio H : L occasionally remains 'not significant' although the p-levels for height and length values are significant (e.g. P I and P II *a posteriori* tests, Table 17, see also Table 18). This happens because length and height are highly correlated and although the values may be much larger (or smaller) in one population the quotients in both samples may be very similar. It may also happen that the original values are not significant while the ratio H : L is (see P II *a priori* tests, Table 17). Here the ranges of each character of two populations are insignificantly different but a height value occurring in both groups must be connected to two different length values (or vice versa). Nevertheless, this situation may be restricted to small sample sizes. Finally, as a rule H : L is always decisive if either length or height is (Table 18). It is obvious from this accessory note that the quotient of height and length may furnish results that would otherwise be missed. It should therefore be included in significance tests.

Table 17 — Results of Kolmogorov-Smirnov two-sample tests (non-parametric) carried out for various groupings of fossil and extant populations. Variables used are height, length, and H : L of P I and P II respectively, of left valves. In analogy to ANOVA the tests are divided into *a priori* and *a posteriori* tests. Most groupings show significant differences in at least one variable. Exceptions are "sella vs. scty" (for both P I and P II) and "virg51 vs. virg66 vs. virg71" (for P I). Abbreviations: dam = ? *Crassostrea* sp. (fossil); edul = *Ostrea edulis* (extant); gig = *Crassostrea gigas* (extant); sacc = *Saccostrea commercialis* (extant); scty = *Cubitostrea* sp. (fossil); sella = *Cu. sellaeformis* (fossil); virg51, virg66, virg71 = *Crassostrea virginica* (extant, different populations); n.s. = not significant; p-value = level of significance, p is significant if p < 0.05, vs. = versus.

| groups | | | p - level | | |
|---|---|---|---|---|---|
| **Prodissoconch I, Left Valve** | | | | | |
| A priori tests | | | Height | Length | H : L |
| sella + scty + dam | vs. | virg51 + virg66 + virg71 | p < 0.001 | p < 0.05 | p < 0.001 |
| sella + scty | vs. | dam | p = n.s. | p < 0.05 | p < 0.05 |
| sella | vs. | scty | p = n.s. | p = n.s. | p = n.s. |
| virg51 + virg66 | vs. | virg71 | p = n.s. | p = n.s. | p = n.s. |
| virg51 | vs. | virg66 | p = n.s. | p = n.s. | p = n.s. |
| A posteriori tests | | | | | |
| sella | vs. | dam | p = n.s. | p < 0.05 | p < 0.05 |
| scty | vs. | dam | p = n.s. | p < 0.05 | p < 0.05 |
| sella | vs. | virg51 + virg66 + virg71 | p < 0.001 | p = 0.01 | p < 0.001 |
| scty | vs. | virg51 + virg66 + virg71 | p < 0.05 | p < 0.01 | p = n.s. |
| dam | vs. | virg51 + virg66 + virg71 | p < 0.05 | p = n.s. | p < 0.05 |
| **Prodissoconch II, Left Valve** | | | | | |
| A priori tests | | | | | |
| sella + scty | vs. | virg51 + virg66 + virg71 + gig + sacc + edul | p < 0.001 | p < 0.001 | p < 0.001 |
| sella | vs. | scty | p = n.s. | p = n.s. | p = n.s. |
| virg51 + virg66 + virg71 + gig | vs. | sacc + edul | p = n.s. | p = n.s. | p < 0.001 |
| virg51 + virg66 + virg71 | vs. | gig | p = n.s. | p = n.s. | p < 0.05 |
| virg51 + virg66 | vs. | virg71 | p = n.s. | p = n.s. | p < 0.05 |
| virg51 | vs. | virg66 | p = n.s. | p = n.s. | p < 0.001 |
| sacc | vs. | edul | p = n.s. | p = n.s. | p < 0.001 |
| A posteriori tests | | | | | |
| sella + scty | vs. | virg51 + virg66 + virg71 + gig + sacc | p < 0.001 | p < 0.001 | p < 0.001 |
| sella + scty | vs. | virg51 + virg66 + virg71 + gig | p < 0.001 | p < 0.001 | p < 0.001 |
| sella + scty | vs. | sacc | p < 0.01 | p < 0.01 | p < 0.01 |
| sella | vs. | virg51 + virg66 + virg71 + gig | p < 0.001 | p < 0.001 | p < 0.001 |
| scty | vs. | virg51 + virg66 + virg71 + gig | p < 0.001 | p < 0.001 | p = n.s. |

Table 18 — The "paradox" outcome of significance of the ratio H : L if both height (H) and length (L) are either significant (s.) or not significant (n.s.). For explanation see text.

| | L = s. | L = n.s. |
|---|---|---|
| H = s. | H : L = ? | H : L = s. |
| H = n.s. | H : L = s. | H : L = ? |

*Hinge dentition*

THE CRASSOSTREINID TYPE

The hinge dentitions of the two American *Cubitostrea* species and the Recent Crassostreinae have the following characters in common:

1) Denticle 1 (= CR) is developed as a prominent central ridge which fits into a pronounced socket (CS) of the other valve. Therefore, denticles 2a, p and 3a, p are generally well developed.

2) Equally, denticles 4a, p and 5a, p are normally present.

3) Denticle 6a is commonly present.

4) The prevailing shape of the denticles is rectangular; the most distant denticles may be triangular.

5) Final reductions start on the posterior side of the hinge.

Differences are:

1) Denticle 1 is larger in (at least) the two Recent *Crassostrea* species described by HU *et al.* (1993) than in *Cubitostrea*.

2) Denticles 2a, p of *Crassostrea* are generally a little smaller than denticles 3a, p and 4a, p. In *Cubitostrea* denticles 2a, p are the larger ones.

3) Denticles 2a, p in *Cubitostrea* can be quadrangular. This was not observed in Recent species.

4) Denticle 6p was only found in Recent species.

5) Denticle 7a seems to occur more often in *Cubitostrea ?sellaeformis* than in Recent species (compare *Saccostrea echinata*).

THE OSTREINID TYPE:

Ostreinae differ from the above group by:

1) an ill defined central platform (= CP) in both valves, which in general is much longer than the central ridge of the Crassostreinae.

2) Denticles 2a and 2p are often rudimentary in which case they are only weakly separated from the central apparatus. The same sometimes applies to denticles 3a, p.

3) Denticle 6a never occurs.

4) Denticles are dominantly quadrangular in shape, triangular denticles seem to be common; and round denticles are known only from two species.

5) Final reduction affects anterior denticles prior to the posterior ones.

Apart from these differences, Crassostreinae and Ostreinae share some characters in which they differ from *Cubitostrea*.

1) The central apparatus is larger.

2) Denticles 2a, p may be weakly separated from the central apparatus.

3) Denticle 6p is sometimes present.

## Conclusions

*Evaluation of larval shell characters*

SHELL SHAPE

The shape of P I is subspherical and equivalve, but slightly inequilateral, in all groups but *Tiostrea*. According to our present knowledge the character appears to be of very limited use for determinations or phylogenetic interpretations.

The shell shape of advanced veliger stages (P II), in contrast, is characteristic for the following groups:

1) extant Ostreinae and probably also Lophinae (*sensu* MALCHUS, 1990);

2) extant Crassostreinae, the Eocene *Cubitostrea* (? Crassostreinae, ? Ostreinae), the Late Cretaceous *Agerostrea* (Liostreinae), and perhaps also Jurassic *Liostrea*

(questionable because of insufficient data; Cretaceous Liostreinae in general as described in MALCHUS (1990) may be added because they include the stem groups of all extant Ostreidae;

3) Pycnodonteinae,

4) Cretaceous Exogyrinae.

Nothing is known about the fossil Gryphaeinae, Gryphaeostreinae, Jurassic Exogyrinae, Palaeolophinae, or Tertiary Lophinae (this statement also applies to the characters discussed below).

The fact that all fossil oysters investigated here — with the exception of the Pycnodonteinae and Exogyrinae — are characterised by a *Crassostrea*-like P II shape suggests in combination with the hinge dentition that this represents the phylogenetically older type among the Ostreidae (not Gryphaeidae, to which the Pycnodonteinae and Exogyrinae belong).

SHELL STRUCTURE

The ultrastructure was not investigated in this study. But WALLER (1981) assumed that the structure should be the same in all oysters and probably even in most bivalves. It may thus be regarded a plesiomorphic character of the group.

SCULPTURE

Nearly all living Ostreidae (Ostreinae, Crassostreinae, Lophinae), the Eocene ostreids, the Late Cretaceous *Agerostrea*, *Flemingostrea*, the two studied *Exogyra* species, and perhaps the Early Jurassic *Liostrea irregularis* (MÜNSTER) are characterised by a smooth exterior of the P II. The sculpture of the extant *Crassostrea margaritacea* (LAMARCK), *Ostrea futamiensis* SEKI, *Dendostrea frons* (LINNE) (see RANSON, 1967b), and *Saccostrea echinata* (see TANAKA, 1960) are perhaps stronger. But growth increments may be overemphasised in RANSON (1967b) because the photographs were taken under a light microscope where specimens are transparent, and in TANAKA (1960) because the illustration is a drawing.

Significantly different from those above are the sculptures of fossil and Recent Pycnodonteinae and of the Kimmeridgian *Liostrea plastica* (TRAUTSCHOLD). Both exhibit strong concentric ridges. But while this character is found in Cretaceous, Tertiary, and Recent Pycnodonteinae (and thus is probably characteristic of the whole subfamily) it occurs only in one (of three known) species of *Liostrea* which, otherwise is more similar in shape to the Crassostreinae. Thus, currently, this character allows distinctions on the (sub)family level from Cretaceous times onward.

Apart from the fact that the evolutionary path of the sculpture cannot be evaluated properly at the moment, with more knowledge it may prove valuable for phylogenetic reconstructions. Because the Gryphaeinae are the stem group of the Pycnodonteinae and probably also of the Exogyrinae (MALCHUS, 1990), it is very likely that the Gryphaeinae and the earliest Exogyrinae had the same sculpture.

ABSOLUTE SIZE OF THE P I

The absolute size of the P I is probably diagnostic for species or genera as is demonstrated in Table 17 (see also "Relative shell sizes", below). More investigations are needed to test this interpretation, however.

In addition, the size of P I can be interpreted phylogenetically. It could be demonstrated that a small P I is characteristic of fossil and Recent representatives of different phylogenetic lineages such as the Campanian, Eocene, and Recent Pycnodonteinae, Campanian Exogyrinae (Gryphaeidae), Hettangian, Kimmeridgian, and Campanian Liostreinae, different Eocene ostreids (i.e. *Cubitostrea*, ? *Saccostrea*, ? *Crassostrea*), and Recent Crassostreinae (Ostreidae). No fossil species was found with a large P I. It appears, therefore, rather safe to argue that a small P I is the plesiomorphic character for the Ostreidae, Gryphaeidae, and probably also Palaeolophidae. (The three families together form the superfamily Ostreoidea; MALCHUS, 1990.)

Furthermore, because all Recent species with a small P I also have a small egg size, it is suggested that this also applies to the majority of fossil species with a small P I. A small egg size in Recent Ostreidae (and very likely also Pycnodonteinae) corresponds to a relatively long planktonic, planktotrophic larval stage and to a non-brooding mode of development in all species but *Cryptostrea permollis*. This is an exceptional case among Recent oysters, however, and it is suggested that P I sizes — in conjunction with other shell characters — should also be diagnostic of the mode of development of fossil species. (It may become doubtful if the P I measures between 90 and 100 $\mu$m in length.). CHANLEY & DINAMANI's (1980: 118-119) interpretation that incubation should be the more primitive character in oysters is therefore rejected here (see also "hinge dentition" and "Questions of phylogeny").

ABSOLUTE SIZE OF THE P II

The maximum size of the P II is very similar in all extant species except for those of *Tiostrea*. Nevertheless, it seems that in the fossil species examined here it grew larger than in Recent ones. Recalling the correlation between growth rate, shell size, and temperature in *Crassostrea virginica* (see LOOSANOFF & DAVIS, 1963), it may be speculated that — among other unknown factors — higher average temperatures were responsible for this difference. This interpretation would be consistent with Tertiary palaeotemperature curves (a.o. ADAMS *et al.*, 1990; GLADENKOV, 1994; WOLFE, 1994). However, it contrasts with the evidence from other bivalve studies revealing a reciprocal relation between larval shell size and temperature (see LUTZ & JABLONSKI, 1978). A phylogenetic value of the absolute P II size is not known.

RELATIVE SHELL SIZES

The ratio of height to length appears to be significant for both P I and P II on the level of species and perhaps also of genera. In most cases this is correlated with the significance of either length or height values (Tables 17, 18).

It is, of course, necessary to compare entities of the same growth stage. Whether there is any phylogenetic tendency cannot be concluded from the data base.

LENGTH OF D-LINE (P I)

According to the available data — for two *Cubitostrea* spp., three crassostreine and one ostreine species, and two fossil pycnodonteinid species – the D-line tends to be longer in Ostreinae than in Crassostreinae and *Cubitostrea*, with the Pycnodonteinae in between. Measurements may even be characteristic on the species level. But, due to an insufficient data base this could not be tested statistically. In addition to its presumed taxonomic value, it has the advantage of being more clearly defined than other characters. Measurements from different studies are more reliably compared, therefore. Concerning the Pycnodonteinae more data are needed to confirm the measurements presented here.

The 'length of D-line' is correlated with other growth measurements of the P I and does not serve as an independent argument for phylogenetic relationships (see "Relations between characters", below).

LENGTH OF HINGE LINE (P II)

Measurements exist from two crassostreine, two ostreine, two *Cubitostrea* and one *Pycnodonte* species. What has been stated about the 'length of D-line' is also correct here.

CONVEXITY

Convexities of the P I of Crassostreinae and Ostreinae show the same tendency as the other characters of the P I, i.e. values are generally smaller in the former subfamily. During the P II stage convexities are very similar in all groups, although the highest values were measured on the left valve of an *Exogyra*. But again, more data are needed for confirmation. Currently, phylogenetic conclusions cannot be drawn.

As the convexity is strongly correlated with the length and height of the shell, comparisons of different taxa must consider shells of the same size interval. Unfortunately, the character is difficult to measure which results in a high error range. In addition, there exists no standard procedure of how to measure convexity.

DISTANCE BETWEEN GROWTH LINES OF THE P II

Up to the present, growth lines have not been measured of larval shells of ostreid species. (But, according to LE PENNEC, pers. commun., 1994, measurements have been recently carried out for some Teredinidae, Veneridae, and for *Placopecten magellanicus*.) The sporadic measurements taken in this study do not reveal any hint as to their usefulness for determination or phylogenetic interpretation.

OTHER MEASUREMENTS

The following measurements allow distinctions on the species level (see CHANLEY & DINAMANI, 1980, tables 2, 3; HU *et al.*, 1993: table 2).

Rotation angle: The angle between the length axes of the P I and P II is a measure of the skewness of the umbo, provided the length axis is defined by the most distant anterior-posterior points on the shell margin (see FORBES, 1967: fig. 3). The character allows distinctions between subfamilies (Crassostreinae and Ostreinae/Lophinae) and species (*Crassostrea virginica*, *Cr. gigas*) (FORBES, 1967: table 1; HU *et al.*, 1993: tables 1, 2). Whether there exists a phylogenetic pattern within each subfamily remains to be tested.

Width of provinculum: The widths of the provincula of *Crassostrea virginica* and *Cr. gigas* differ considerably (HU *et al.*, 1993: table 2). Thus, it seems a good character for determination. But since corresponding measurements in other oysters are lacking this result cannot be generalised. For the same reason its phylogenetic value remains undetermined.

Central apparatus: The value (see HU *et al.*, 1993) is discussed under 'length of denticles' (see below).

These characters are undoubtedly correlated with the growth measurements described above and are in part represented by the rotation angle. Thus, they do not provide independent data for taxonomic determinations or on phylogenetic patterns. In addition, these measurements are time consuming and probably (not tested) contain a broad relative error range.

RELATIONS BETWEEN MEASURED CHARACTERS

Most size characters are strongly correlated with each other (Table 3). This is not surprising, but the consequences may not always be appreciated. Graphs or tables referring to different combinations of correlated growth characters do not represent independent characteristics of the shell. Growth patterns may be described by comparing height, length and H : L, although other combinations may show the same characteristics more clearly.

HINGE DENTITION

The Recent Crassostreinae, Ostreinae (+ Lophinae) and Pycnodonteinae are each characterised by a typical hinge dentition (RANSON, 1960, 1967). Furthermore, the two genera *Crassostrea* and *Saccostrea* (Crassostreinae), *Cr. gigas* and *Cr. virginica*, and different species of *Ostrea*, *O.* (*Eostrea*), and *Ostreola* can be differentiated with the help of the hinge dentition (DINAMANI, 1976; FERNANDEZ CASTRO & LE PENNEC, 1988; HU *et al.*, 1993; and references therein).

Here, for the first time, detailed descriptions of the dentitions of fossil species are presented and the dentitions of Recent ones are discussed. The results can be summarised as follows:

1) The two Eocene species *Cubitostrea* ? *sellaeformis* and *Cubitostrea* sp. possess a typical crassostreinid type of dentition. Nevertheless, each of these species has unique characteristics (number, shape, length or developmental stage of denticles) not shared by the other or by modern Crassostreinae.

2) The Tertiary *Pycnodonte* sp. 1 has a dentition typical for Recent Pycnodonteinae, but at the same time

has more provincular denticles and lacks the lateral row of small denticles which characterise living representatives (RANSON, 1960: figs. 1-16). The two points support the diagnostic value of the hinge dentition.

3) The generalisation "two denticles on each side of the central apparatus" for Crassostreinae is an over-simplification because it only applies to a certain growth interval, though a fairly long-lasting one (Tables 4-7, 12). Likewise, this is true of the descriptions of the ostreine type of hinge (Table 16).

4) In most modern Ostreinae and sometimes also Crassostreinae, denticles 4a, p are earlier and more strongly developed than denticles 2a, p and 3a, p. It seems that many investigators — although occasionally describing these rudiments — did not count them when referring to the number of denticles (e.g. RANSON's schematic drawings, 1960).

5) The shape of incompletely developed denticles, that were not recognised as such, might be thought characteristic for single species or genera. "Rounded" denticles were reported from *Ostrea* (*Eostrea*) *puelchana* and *Ostreola stentina* (FERNANDEZ CASTRO & LE PENNEC, 1988: table 1). FERNANDEZ CASTRO & LE PENNEC (1988, pl. 3, figs. C,E, and F) show for a pre-release, early P II stage of *O.* (*E.*) *puelchana* that the round denticles are rudiments of 2a, p and are still part of the central apparatus (RMF there; compare point 4, above). According to the authors the species "has fully developed denticles at the time of release". This may not be the case because the species has a planktonic larval phase (not studied by the authors) suggesting that the "rounded" denticles will develop further into (quadrangular) denticles. Equally, round denticles of *Ostreola stentina* are restricted to early developmental stages (PASCUAL, 1972: 299, 301, and fig. 4).

"Triangular" denticles are another example of incompletely developed denticles. A closer look reveals that only the most distant denticles may be triangular (sometimes also irregular or round), where the provinculum meets the shell margin. Obviously, the shape simply reflects a lack of space. It is therefore not surprising that they are not restricted to the Ostreinae as has been supposed before; they also occur in Crassostreinae (see chapter "Comparison").

At present only the rectangular and quadrangular denticle shapes remain valuable for taxonomic purposes (and phylogenetic, see below), while "rounded" and "triangular" shapes have to be studied in more detail before they may prove useful.

6) Measurements of the length of denticles did not show any significant pattern within the *Cubitostrea* stock. Comparable measurements in Recent oysters only exist for the central apparatus of *Crassostrea gigas* and *Cr. virginica* showing that it is larger in the former, which corresponds to its longer provinculum. The lengths of denticle 1 of *Cubitostrea sellaeformis* comprise a larger size spectrum, but tends to be smaller on average (not tested statistically).

Although there is no direct proof of a phylogenetic tendency the few data in combination with the ontoge-

netic hinge development seem to hint towards an evolution of denticle 1 from a small well defined central apparatus (CA, of *Cubitostrea*) to a larger, still mostly well defined CA (of the Crassostreinae), to an even larger but ill defined CA (Ostreinae). It seems promising to study this character in more detail (see also point 7).

7) It is tempting to assume that the arrangement of equally sized, rectangular denticles in the Pycnodonteinae represents a model of the original (plesiomorphic) state of hinge dentition. The crassostreinid type may have developed from a similar arrangement in older representatives of the Liostreinae by merging of a few central denticles. Further merging then led to the broad central



Text-fig. 14 — Five reconstructions of possible phylogenetical relations between the Lophinae (Lo), Ostreinae (Os), *Cubitostrea* (Cu), Striostreini (St), and Crassostreini (Cr) (all Ostreidae). "St" and "Cr" together represent the subfamily Crassostreinae. The character 'brooding' is indicated as an apomorphy.
1) considers *Cubitostrea* as the sister taxon of the Ostreinae, and;
2) of the Crassostreinae.
In both cases the Lophinae are the sister taxon of both Ostreinae and Crassostreinae. In the dashed line version of 1) they form the sister taxon of the Ostreinae and *Cubitostrea*.
3) and 4) consider the Lophinae and Ostreinae s.str. as sister taxa.

platform of the Ostreinae (Text-fig. 15). This hypothesis is based on several independent observations:

(a) Pycnodonteinae, *Cubitostrea*, and Crassostreinae generally share the same denticle shape (rectangular), except for CR in the latter two,

(b) in the Pycnodonteinae all denticles are more or less of the same size, while *Cubitostrea* has a larger CR; the central apparatus is even larger in modern Crassostreinae and Ostreinae,

(c) denticles 2a, p in *Cubitostrea* are well defined and larger than the external ones suggesting that they were already well developed in early ontogenetic stages (this could not be proved because of the lack of small growth stages); in contrast, they may be ill defined in early ontogentic stages of Crassostreinae and become even more so in the Ostreinae; furthermore, they occur clearly after the development of denticles 4a, p, i.e. interior, towards the central ridge (CR).

Obviously, the idea has to be based on and tested by further examinations. One related question that arises is whether the edentulous hinge of the species of *Tiostrea* should be considered a final result of a phylogenetic trend (as described above), or whether it simply is a consequence of long brooding and thus very short free swimming period of the veliger, which makes the possession of hinge denticles unnecessary, or whether the two phenomena are functionally related to each other.

LARVAL LIGAMENT
This character cannot be evaluated properly at the moment. As explained in the introductory chapter on larval shell characters, the time of its appearance and position during ontogeny are discussed controversially in the literature. It seems to be a plesiomorphic character of the Crassostreinae and Ostreinae.

POSTERO-DORSAL NOTCH
According to PALMER (1989) this character might not be present in *Liostrea plastica*. But, apparently it occurs in all other oysters examined while it has not been described for other bivalves. Thus, it may be an autapomorphic character of the whole group, an hypothesis which remains to be tested.

*Questions of phylogeny*

CUBITOSTREA, CRASSOSTREINAE, OSTREINAE, LOPHINAE
Until the present study there was little doubt expressed about the systematic position of the Palaeogene genus *Cubitostrea* among the Ostreinae because its adult shell characters are typically ostreinid. In contrast, its larval shells are crassostreinid in all aspects suggesting a closer relationship to the Crassostreinae and thus, rendering *Ostrea*-like adult shell characters inadequate to distinguish between the two subfamilies. The results from this study, however, also suggest that the Ostreinae evolved from species with crassostreinid larval shells. *Cubitostrea* may therefore be the sister taxon of the Ostreinae, or it may contain its stem species. Three possible phylogenies

representing this case are shown in Text-figs. 14-1 and 14-3. Text-figs. 14-2 and 14-4 present *Cubitostrea* as sister taxon of the Striostreini and Crassostreini (Crassostreinae).

The dashed line in the *Cubitostrea* lineage indicates that the genus may have survived even until today (own unpublished data). Younger representatives are probably the Miocene ? *Cu. latimarginata* (VREDENBURG, 1908) from Asia and Saudi Arabia and ? *Cu. coxi* (GARDNER, 1945) from Florida (the two being closely related taxa or even the same species), and perhaps also the Recent Indo-West Pacific *Planostrea pestigris* (HANLEY, 1846) and the Mediterranean *Ostreola stentina* (PAYRAUDEAU, 1826). (The genus is distributed in the East and West Atlantic and in the East Pacific). The latter species broods its larvae (HARRY, 1985). Unfortunately, nothing is known about their larval shells.

MALCHUS (1990) supposed — on the basis of comparisons of microstructures of the adult shell — that the Crassostreinae, Ostreinae, and Lophinae developed during the Palaeogene. Thus, all *Lopha*-shaped groups occurring from the Triassic to the Cretaceous are excluded from the Lophinae (see e.g. STENZEL, 1971 for a contrasting view). Text-figs. 14-1 and 14-2, therefore, show the subfamily Lophinae as sister taxon of the Ostreinae, *Cubitostrea*, and Crassostreinae, or only of the Ostreinae and *Cubitostrea* (dashed line in Text-fig. 14-1). In Text-fig. 14-3 and 14-4 the Lophinae are the sister taxon of the Ostreinae. This possibility is the most parsimonious solution based on the fact that both subfamilies share the ostreinid type of larval shell and brooding mode. On the other hand, the Ostreinae and Crassostreinae share soft body and adult shell characters not observed in the Lophinae (e.g. two loops of the intestine instead of one as would be typical of the Lophinae and Pycnodonteinae; see TORIGOE, 1981; HARRY, 1985; Text-figs. 14-2, 15). This suggests that the larval shell and brooding are convergent autapomorphies of the Ostreinae and Lophinae. Currently, there is no solution to this problem.

Text-fig. 15, finally, presents *Cubitostrea* as the sister taxon of all other extant Ostreidae with the monophyla Lophinae-Ostreinae and Crassostreinae. The supposed common ancestor is to be found within the ''Liostreinae'' (see next chapter). But, as just explained the Lophinae should perhaps be excluded. The Gryphaeidae, of which only the Pycnodonteinae are considered here, form the outgroup.

Text-fig. 15 leaves the subfamily definitions (including the character brooding/non-brooding) valid. This would probably not be the case if *Cubitostrea* were included in the Ostreinae because the presented data suggest that this fossil genus was non-brooding. It may be added that the taxon Striostreini (*Saccostrea, Striostrea*) remains without an autapomorphy. They differ from the Crassostreini (= *Crassostrea*) only by their generally strong (plesiomorphic) chomata (MALCHUS, 1990). This character is completely reduced in *Crassostrea*. However, *Crassostrea* species exhibit larger genetic distances between themselves than species of *Saccostrea*. The former genus

was therefore considered to be phylogenetically older (BUROKER *et al.*, 1979a,b). Unfortunately, the study did not include species of *Striostrea*. I expect their study would not conflict with the palaeontological data.

''LIOSTREINAE''

This subfamily was established by MALCHUS (1990) mainly on the basis of adult shell microstructures. It comprises species from the earliest representatives of *Liostrea* in the Triassic to Cretaceous genera such as *Flemingostrea* and *Agerostrea*. Late Cretaceous Liostreinae are supposed to contain the stem species of living Ostreidae. Because of a phylogenetically gradual change of microstructures from liostreinid to ostreinid (MALCHUS, 1990), the boundary between Liostreinae and following taxa must be drawn artificially. Also, there may be more than one stem species for modern oysters; therefore, the taxon as currently defined is probably polyphyletic.
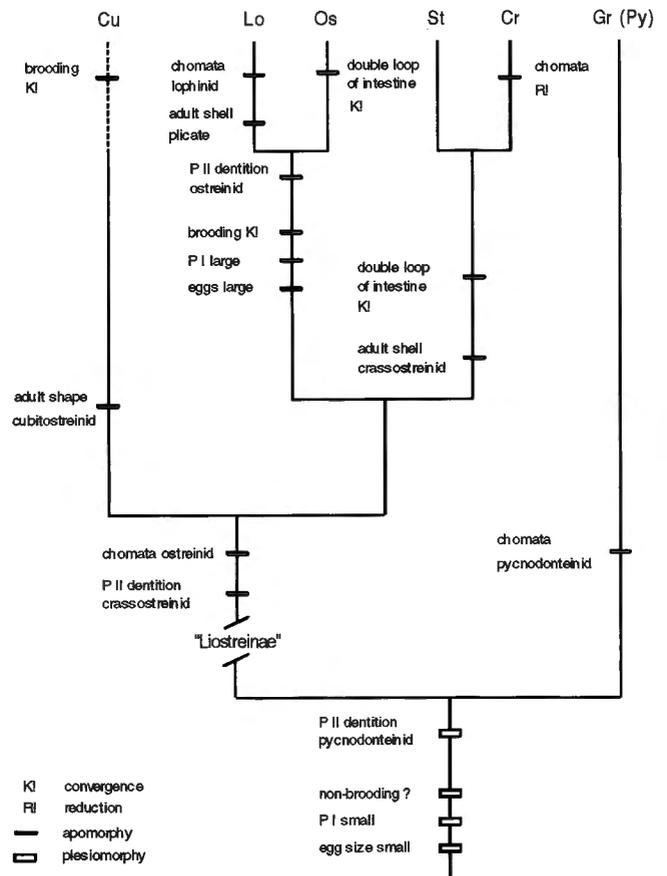


Text-fig. 15 — The phylogenetical reconstruction regards *Cubitostrea* (Cu) to be the sister taxon of a monophylum composed of [Lophinae (Lo) + Ostreinae (Os)] and [Striostreini (St) + Crassostreini (Cr) (= Crassostreinae)]. All together represent the Ostreidae. The Gryphaeidae — Gr (Py) — are chosen as outgroup. For simplicity only characters of the Pycnodonteinae are shown. The ''Liostreinae'' are probably polyphyletic. Note that the Striostreini (St) remain without autapomorphies.

Nevertheless, the shapes of the larval shells of two Jurassic *Liostrea* species, and of the Late Cretaceous *Agerostrea* sp. and *Flemingostrea cretacea* are crassostreinid. The problem posed by the sculptured larval shell of *Liostrea plastica* was already discussed. It may be added that the early dissoconchs of PALMER's material were also investigated for the present study. They revealed a strong growth of the ligamental area (in relation to the shell thickness), and the existence of a round, postero-dorsal adductor muscle scar (of one specimen). Both characters would be typical of adult gryphaeinid species. The result may indicate that *L. plastica* belongs to the Gryphaeinae.

PYCNODONTEINAE AND EXOGYRINAE

The Pycnodonteinae developed from the Gryphaeinae during the latest Jurassic to earliest Cretaceous. Adult shells can be easily identified by a large number of characters, reviewed in MALCHUS (1990). The same applies to the larval shells of the two pycnodonteinids (Cretaceous and Tertiary) examined here. They are very similar to each other and to extant representatives with respect to their shape, sculpture and hinge dentition. This combination of shell characters appears to be restricted to this subfamily (or perhaps also Gryphaeinae) and confirms their monophyletic origin.

The Exogyrinae arose probably early in the middle Jurassic. It has been suggested both, that the subfamily evolved from the Liostreinae (STENZEL, 1971) or from the Gryphaeinae (MALCHUS, 1990; based on microstructures of adult shells). Nevertheless, larval shells of the two Upper Cretaceous species of *Exogyra* have a shape and sculpture completely different from the Pycnodonteinae (the hinge dentition is not known); the shape is also different from the Ostreidae. These findings support neither of the two hypotheses.

The present paper may have demonstrated that the examination of fossil larval shells can offer new insights to the evolutionary pathways of oysters. Nevertheless, currently it originates more questions than answers. It will be necessary to fill some of the apparent gaps before a consistent phylogenetic hypothesis can be proposed on the basis of larval shell characters. Certainly, genetic studies of species of *Striostrea*, the Lophinae and extant Pycnodonteinae will be most illuminating.

For the sake of better comparability of larval shells the following recommendations are made:

1) Provide basic measurements, not only of length and height but also of the D-line and length of the central apparatus of the hinge,

2) refer to the shell stages "prodissoconch I and II" if measurements are made,

3) define standard procedures to measure characters such as the convexity, and

4) use *Crassostrea virginica* and *Ostrea edulis* as reference species in order to standardise comparisons. There are perhaps enough basic data accessible of these two species to determine population parameters (e.g. of length and height), and to estimate adequate sample sizes for comparisons.

## Acknowledgments

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# Appendix A (own material)

*Cubitostrea sellaeformis*, LV, Little Stave Creek, Alabama

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 6/1-1a | B, broad | --- | --- | --- | 369 | 385 | --- | --- | 11891/1-4 | HIT |
| 6/1-1b | B, broad | 62.1 | 51.3 | 49.0 | 352 | 392 | --- | 54.0 | ~ | ~ |
| 6/1-1c | B, broad | 63.7 | 50.9 | 49.5 | 387 | 392 | --- | 52.7 | ~ | ~ |
| 6/2-2a | ? | 53.7 | 44.1 | 38.5 | 298 | 344 | --- | --- | ~ | ~ |
| 6/2-2b | ? | 65.8 | 51.3 | 47.4 | 337 | 346 | --- | 57.1 | ~ | ~ |
| 6/11-1a | A, slend. | --- | --- | --- | 306 | 375 | --- | --- | ~ | CAM |
| 6/11-1c | A, slend. | --- | --- | --- | 286 | 334 | --- | --- | ~ | * |
| 6/11-2a | A, slend. | 59.3 | 43.6 | --- | 286 | 312 | --- | --- | ~ | * |
| 6/11-2b | A, slend. | 78.5 | 73.5 | --- | 379 | 425 | --- | --- | ~ | * |
| 6/11-3a | B, broad | --- | --- | --- | 321 | 315 | --- | --- | ~ | * |
| 6/11-3b | B, broad | --- | --- | --- | 441 | 402 | --- | --- | ~ | HIT |
| 6/11-3c | B, broad | 63.7 | 53.0 | --- | 311 | 342 | --- | --- | ~ | ~ |
| 6/11-4a | B, broad | 61.7 | 48.6 | --- | 329 | 351 | --- | --- | ~ | ~ |
| 6/13-1 | ? | --- | --- | --- | --- | 284 | --- | --- | ~ | ~ |
| 7/15-3 | C, thick | 55.8 | 44.4 | 41.2 | 230 | 268 | 100 | 50.6 | ~ | ~ |
| 7/15-4 | B, broad | 63.5 | 51.7 | 44.9 | 395 | 414 | 164 | 56.3 | ~ | ~ |
| 7/15-6 | B, broad | 64.1 | | 49.7 | 342 | 370 | 138 | 56.5 | ~ | ~ |
| 7/15-7 | C, thick | 62.5 | | 46.7 | 224 | 263 | 112 | 58.5 | ~ | ~ |
| 7/15-8 | B, broad | 61.5 | 51.1 | 47.8 | 323 | 340 | 144 | 60.8 | ~ | ~ |
| 7/15-9 | B, broad | 60.4 | --- | 46.0 | 318 | 363 | --- | 54.4 | ~ | ~ |
| 7/15-12 | B, broad | --- | --- | 45.0 | 386 | 387 | --- | --- | ~ | ~ |
| 7/16-7 | B, broad | 67.9 | 51.3 | 49.7 | 366 | 392 | 150 | 53.9 | ~ | ~ |
| 7/16-8 | B, broad | 61.2 | 48.0 | 45.6 | 346 | 380 | 149 | 54.0 | ~ | ~ |
| 7/16-9 | B, broad | 64.7 | 49.4 | 46.1 | 329 | 340 | --- | 57.1 | ~ | ~ |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 7/16-10 | A, slend. | 57.9 | 47.2 | 42.0 | 245 | 309 | 134 | 56.3 | ~ | ~ |
| 7/16-11 | B, broad | 53.0 | 42.1 | 41.1 | 248 | 259 | 109 | 46.4 | ~ | ~ |
| 7/16-12 | B, broad | 63.7 | 50.5 | 42.5 | 311 | 328 | 140 | 60.8 | ~ | ~ |
| 7/16-13 | ? | 50.6 | 41.8 | 38.8 | 256 | 284 | 120 | --- | ~ | ~ |

## *Cubitostrea sellaeformis*, RV, Little Stave Creek, Alabama

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 6/2-1a | RV | 57.7 | 47.0 | 41.4 | 381 | 377 | --- | 39.6 | 11891/1-4 | HIT |
| 6/2-1b | RV | 65.8 | 52.3 | 47.2 | 367 | 348 | --- | 49.0 | ~ | ~ |
| 6/11-4b | RV | 52.4 | 40.5 | --- | 309 | 372 | --- | --- | ~ | CAM |
| 6/11-4c | RV | 60.1 | 48.7 | --- | 352 | 325 | --- | --- | ~ | * |
| 6/12-1a | RV | --- | --- | --- | 326 | 342 | --- | --- | ~ | * |
| 6/12-1b | RV | --- | --- | --- | 268 | 260 | --- | --- | ~ | * |
| 7/13-1 | RV | --- | --- | --- | 340 | 355 | --- | --- | ~ | * |
| 7/13-2 | RV | 62.2 | 47.3 | 49.7 | 372 | 358 | 119 | --- | ~ | * |
| 7/13-3 | RV | 60.6 | 50.6 | 45.6 | 354 | 329 | 116 | 51.6 | ~ | * |
| 7/13-4 | RV | 68.1 | 50.5 | 46.9 | 363 | 353 | 126 | 55.5 | ~ | * |
| 7/13-5 | RV | 61.7 | 48.2 | 40.5 | 319 | 305 | 110 | 47.5 | ~ | * |
| 7/13-6 | RV | 63.6 | 49.0 | 40.0 | 312 | 309 | 114 | 49.7 | ~ | * |
| 7/13-7 | RV | 67.6 | 54.7 | 45.6 | 309 | 313 | 91 | 46.1 | ~ | HIT |
| 7/13-8 | RV | 66.3 | 53.6 | 45.6 | 345 | 321 | 123 | 60.0 | ~ | ~ |
| 7/13-9 | RV | 66.0 | 55.9 | 46.4 | 299 | 293 | 120 | 49.0 | ~ | ~ |
| 7/13-10 | RV | 60.3 | 55.9 | 41.4 | 296 | 305 | 90 | 52.4 | ~ | ~ |
| 7/13-11 | RV | 59.5 | 50.5 | 41.0 | 419 | 374 | 138 | 49.0 | ~ | ~ |
| 7/13-12 | RV | 58.7 | 48.7 | 44.0 | 309 | 310 | 113 | --- | ~ | ~ |
| 7/16-2 | RV | 62.9 | 51.0 | 47.2 | 367 | 366 | 111 | 54.9 | ~ | CAM |
| 7/16-3 | RV | 56.6 | 45.7 | 42.4 | 336 | 339 | 107 | 46.8 | ~ | * |
| 7/16-4 | RV | 61.5 | 47.6 | 42.2 | 324 | 325 | 88 | 51.5 | ~ | * |
| 7/16-5 | RV | 52.5 | 42.8 | 39.7 | 347 | 344 | 110 | 59.4 | ~ | * |
| 7/16-6 | RV | 68.1 | 59.2 | 55.9 | 336 | 325 | 95 | 69.1 | ~ | * |

## *Cubitostrea* sp., LV + RV, Stone City Bluff, Texas

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 6/5-1a | LV | --- | --- | --- | 327 | 315 | --- | --- | 141091/1A | CAM |
| 6/5-1b | LV | --- | --- | --- | 314 | --- | --- | --- | ~ | * |
| 6/5-2c | RV | 57.6 | --- | --- | 320 | 282 | --- | --- | ~ | * |
| 8/1-1 | LV | --- | --- | --- | 363 | 393 | --- | --- | 141091/1B | * |
| 8/1-2 | LV | 61.0 | 59.7 | 35.4 | 342 | 335 | 122 | 43.7 | ~ | * |
| 8/1-3 | LV | --- | --- | --- | 360 | 402 | 128 | 46.4 | ~ | HIT |
| 8/1-4 | LV | 49.9 | 42.2 | 34.0 | 335 | 339 | 142 | 51.4 | ~ | CAM |
| 8/1-5 | LV | 51.6 | 37.6 | 38.8 | 368 | 388 | 155 | 52.4 | ~ | HIT |
| 8/1-6 | LV | 60.5 | 44.1 | 44.3 | 391 | 404 | 148 | 49.0 | ~ | ~ |
| 8/1-7 | LV | 55.8 | 47.9 | --- | 360 | 366 | 117 | --- | ~ | ~ |
| 8/1-7 | RV | 57.1 | 44.5 | --- | 360 | 334 | 102 | --- | 141091/1B | ~ |
| 8/1-8 | RV | 54.5 | 44.8 | 38.8 | 379 | 351 | 117 | 46.9 | ~ | ~ |
| 8/1-9 | RV | 53.2 | 42.9 | 36.7 | 372 | 339 | 107 | 34.3 | ~ | ~ |
| 8/2-4 | LV | 60.5 | 46.7 | 44.3 | --- | --- | --- | --- | 141091/1E | ~ |

## *Cubitostrea ?plicata*, LV + RV, Chateaurouge, France

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/3-1 | LV | --- | --- | --- | 442 | 358 | --- | --- | Nolf | CAM |
| 7/3-4 | LV | 62.5 | --- | --- | 405 | 426 | --- | --- | ~ | * |
| 7/3-2 | RV | --- | --- | --- | 456 | 413 | --- | --- | ~ | * |

### ?*Crassostrea*, LV + RV, Damery, France

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/6-1 | LV | --- | --- | --- | 346 | 369 | --- | --- | Bandel | CAM |
| 7/6-2 | LV | 62.7 | --- | --- | 410 | 421 | --- | --- | ~ | * |
| 7/6-3a | LV | 70.4 | 48.8 | --- | --- | --- | --- | --- | ~ | * |
| 7/6-3b | LV | 73.9 | 47.7 | --- | 370 | 391 | 167 | --- | ~ | * |
| 7/6-4 | LV | 70.8 | 45.2 | --- | 398 | 401 | --- | --- | ~ | * |
| 7/5-1a | RV | 68.7 | 61.8 | 44.6 | 329 | 345 | --- | --- | ~ | * |
| 7/5-1b | RV | 82.0 | 74.0 | 52.0 | 421 | 374 | --- | --- | ~ | * |
| 7/5-2a | RV | 79.8 | 65.6 | 58.6 | 382 | 390 | --- | --- | ~ | * |
| 7/5-2b | RV | 61.8 | 50.9 | 44.1 | --- | --- | --- | --- | ~ | * |
| 7/5-3a | RV | 81.3 | 76.7 | 54.5 | --- | --- | --- | --- | ~ | * |
| 7/5-3b | RV | 69.7 | 63.8 | 48.0 | 362 | 353 | --- | --- | ~ | * |

### ?*Saccostrea* sp., LV + RV, Saffré, France

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/2-2b | LV | --- | --- | --- | 326 | 355 | --- | --- | Bandel | CAM |
| 7/2-3a | LV | --- | --- | --- | 351 | 356 | --- | --- | ~ | * |
| 7/2-4a | LV | --- | --- | --- | 347 | 351 | --- | --- | ~ | * |
| 7/1-1a | RV | --- | --- | --- | 378 | 400 | --- | --- | ~ | * |
| 7/1-2a | RV | 69.1 | 49.8 | --- | --- | --- | --- | --- | ~ | * |
| 7/1-2b | RV | 59.8 | 42.0 | --- | 367 | 387 | --- | --- | ~ | * |
| 7/1-3 | RV | 78.2 | 63.0 | --- | --- | --- | 113 | --- | ~ | * |
| 7/1-4b | RV | 78.0 | 68.3 | --- | 330 | 353 | 142 | --- | ~ | * |

### *Agerostrea* sp., Chapelville, Mississippi

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/7-4 | LV | 62.1 | 50.0 | 45.5 | 331 | 330 | --- | --- | Bandel | CAM |

### *Exogyra ponderosa*, Chapelville, Mississippi

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/9-1a | LV | 50.0 | --- | --- | 273 | 336 | --- | --- | Bandel | CAM |
| 7/9-2a | LV | --- | --- | --- | --- | --- | 174 | --- | ~ | * |

### *Exogyra cancellata/costata*, Coon Creek, Tennessee

| 7/7-3 | LV | --- | --- | --- | 304 | 386 | --- | --- | Bandel | CAM |
|---|---|---|---|---|---|---|---|---|---|---|

### *Pycnodonte* sp. 1, Coon Creek, Tennessee

| SEM No. | type | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) | C (P II) | LP (P II) | field.no | SEM |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/8-1c | LV | 66.0 | 47.0 | 50.0 | 303 | 320 | 160 | --- | Bandel | CAM |
| 7/8-1a | RV | --- | --- | --- | 380 | 356 | --- | --- | ~ | * |
| 7/8-1b | RV | 65.0 | 52.0 | 55.6 | 332 | 317 | 158 | --- | ~ | * |

### *Pycnodonte* sp. 2, Little Stave Creek, Alabama

| 6/12-1c | LV | 81.10 | 65.70 | --- | 342 | 362 | --- | --- | 11891/1-4 | CAM |
|---|---|---|---|---|---|---|---|---|---|---|
| 7/12-10 | LV | 83.00 | 67.20 | 57.0 | 311 | 312 | 118 | 72.6 | ~ | HIT |

## Appendix B

### *Crassostrea gigas,* see Hori and Kusakabe (1926), fide Roughley 1933), r = 0,99 (n = 15)

| Num. | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) |
|---|---|---|---|---|---|
| 1 | | | | 80 | 68 |
| 2 | | | | 90 | 80 |
| 3 | | | | 95 | 94 |
| 4 | | | | 100 | 107 |
| 5 | | | | 110 | 120 |
| 6 | | | | 120 | 132 |
| 7 | | | | 125 | 140 |
| 8 | | | | 143 | 160 |
| 9 | | | | 165 | 185 |
| 10 | | | | 180 | 200 |
| 11 | | | | 200 | 220 |
| 12 | | | | 220 | 240 |
| 13 | | | | 250 | 265 |
| 14 | | | | 270 | 280 |
| 15 | | | | 280 | 290 |

### *C. virginica,* see Carriker (1951)

| Num. | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) |
|---|---|---|---|---|---|
| 1 | 62 | 55 | 40 | | |
| 2 | 62 | 52 | 40 | | |
| 3 | 62 | 52 | 38 | | |
| 4 | 67 | 59 | 40 | | |
| 5 | 75 | 69 | 44 | | |
| 6 | 77 | 77 | | | |
| 7 | | | | 82 | 77 |
| 8 | | | | 88 | 88 |
| 9 | | | | 91 | 94 |
| 10 | | | | 95 | 91 |
| 11 | | | | 99 | 105 |
| 12 | | | | 117 | 124 |
| 13 | | | | 124 | 126 |
| 14 | | | | 127 | 127 |
| 15 | | | | 132 | 135 |
| 16 | | | | 134 | 138 |
| 17 | | | | 140 | 145 |
| 18 | | | | 144 | 144 |
| 19 | | | | 153 | 157 |
| 20 | | | | 153 | 163 |
| 21 | | | | 175 | 175 |
| 22 | | | | 185 | 200 |
| 23 | | | | 196 | 203 |
| 24 | | | | 217 | 234 |
| 25 | | | | 220 | 220 |
| 26 | | | | 224 | 224 |
| 27 | | | | 252 | 252 |
| 28 | | | | 252 | 266 |
| 29 | | | | 262 | 266 |
| 30 | | | | 270 | 266 |
| 31 | | | | 262 | 262 |
| 32 | | | | 260 | 266 |
| 33 | | | | 266 | 270 |
| 34 | | | | 273 | 266 |
| 35 | | | | 270 | 252 |
| 36 | | | | 280 | 273 |
| 37 | | | | 284 | 273 |

### *C. virginica,* see Loosanoff et al. (1966);

the irregular numbers of the 1st. column refer to numbers of specimens measured by the authors

| Num. | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) |
|---|---|---|---|---|---|
| 12 | 70 | 55 | | | |
| 137 | 70 | 60 | | | |
| 4 | 70 | 65 | | | |
| 38 | 74 | 60 | | | |
| 61 | 74 | 65 | | | |
| 72 | 74 | 70 | | | |
| 1 | | | | 210 | 210 |
| 11 | | | | 210 | 214 |
| 13 | | | | 210 | 220 |
| 8 | | | | 210 | 224 |
| 2 | | | | 210 | 229 |
| 2 | | | | 231 | 229 |
| 6 | | | | 231 | 235 |
| 15 | | | | 231 | 240 |
| 7 | | | | 231 | 245 |
| 3 | | | | 231 | 250 |
| 21 | | | | 236 | 244 |
| 21 | | | | 239 | 247 |
| 20 | | | | 257 | 266 |
| 15 | | | | 276 | 286 |
| 13 | | | | 291 | 303 |
| 1 | | | | 300 | 301 |
| 4 | | | | 300 | 307 |
| 10 | | | | 300 | 310 |
| 3 | | | | 300 | 316 |
| 2 | | | | 310 | 316 |
| 1 | | | | 310 | 323 |

### *C. virginica,* see Chanley and Andrews (1971)

| Num. | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) |
|---|---|---|---|---|---|
| 1 | 60 | 50 | | | |
| 2 | 70 | 60 | | | |
| 3 | | | | 80 | 73 |
| 4 | | | | 90 | 86 |
| 5 | | | | 100 | 100 |
| 6 | | | | 110 | 114 |
| 7 | | | | 120 | 128 |
| 8 | | | | 130 | 140 |
| 9 | | | | 140 | 150 |

| | | |
|---|---|---|
| 10 | 150 | 159 |
| 11 | 160 | 170 |
| 12 | 170 | 180 |
| 13 | 180 | 190 |
| 14 | 190 | 195 |
| 15 | 200 | 205 |
| 16 | 210 | 215 |
| 17 | 220 | 225 |
| 18 | 230 | 235 |
| 19 | 240 | 240 |
| 20 | 250 | 250 |
| 21 | 260 | 265 |
| 22 | 270 | 275 |
| 23 | 280 | 283 |
| 24 | 290 | 290 |
| 25 | 300 | 303 |

| | | |
|---|---|---|
| 11 | 226 | 208 |
| 12 | 233 | 216 |
| 13 | 242 | 226 |
| 14 | 250 | 233 |
| 15 | 258 | 242 |
| 16 | 266 | 250 |
| 17 | 275 | 258 |
| 18 | 283 | 275 |
| 19 | 292 | 283 |
| 20 | 300 | 300 |
| 21 | 308 | 318 |
| 22 | 312 | 346 |
| 23 | 325 | 345 |
| 24 | 333 | 366 |

*Ostrea edulis*, see Loosanoff et al. (1966),
r = 0,99 (n = 12)

| Num. | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) |
|---|---|---|---|---|---|
| 1 | | | | 158 | 138 |
| 2 | | | | 162 | 140 |
| 3 | | | | 168 | 145 |
| 4 | | | | 173 | 152 |
| 5 | | | | 247 | 209 |
| 6 | | | | 247 | 221 |
| 7 | | | | 247 | 226 |
| 8 | | | | 269 | 235 |
| 9 | | | | 269 | 241 |
| 10 | | | | 296 | 268 |
| 11 | | | | 300 | 278 |
| 12 | | | | 309 | 272 |

*Saccostrea commercialis*, see Roughley (1933),
r = 0,98 (n = 23)

| Num. | L (P I) | H (P I) | D (P I) | L (P II) | H (P II) |
|---|---|---|---|---|---|
| 1 | 75 | 58 | 50 | | |
| 2 | | | 75 | 145 | 133 |
| 3 | | | 75 | 158 | 142 |
| 4 | | | 83 | 166 | 145 |
| 5 | | | | 175 | 159 |
| 6 | | | | 182 | 166 |
| 7 | | | | 192 | 175 |
| 8 | | | | 200 | 182 |
| 9 | | | | 208 | 192 |
| 10 | | | | 216 | 200 |