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Age determination by sclerite numbers, and scale variations in six fish species from the Central Amazon (Osteichthyes, Characoidei)

by

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Abstract

The scales of 6 different species of three families (*Brycon* cf. *melanopterus* (Characidae), *Semaprochilodus theraponura* (Curimatidae), *Semaprochilodus taeniurus* (Curimatidae), *Prochilodus nigricans* (Curimatidae), *Curimata* cf. *rutiloides* (Curimatidae), *Colossoma macropomum* (Serrasalmidae)) from the Central Amazon are described with regard to their size, shape, and number of sclerites originated from different parts of the body. For each species the body area is defined from which standard scales should be taken, and age determination is conducted by the sclerite method after WERDER (1983).

Keywords: **Age determination, scales, sclerites, Characoidei.**

1. Introduction

Scales for age determination of fish from temperate climate zones are preferably taken from the most protected body areas (EINSELE 1943), where chances are best to encounter original scales which carry all "yearmarks" (HOFFBAUER 1898) of the past. However, additional reabsorbtion marks have been described to occur in various areas, giving the impression of real yearmarks, thus complicating age determination. BLACKBURN (1951) and LIEDER (1959) have connected these marks with temporary reductions of girth-width, and the necessity to adapt the scales' shape to this. Other authors attribute their formation to growth-stagnation (FRASER 1917; HELLAWELL 1974; LINFIELD 1974; MOREAU 1977; etc.), or to Ca^{++}-reabsorption during gonadal maturation (LEE 1912; GARROD & NEWELL 1958; GODOY 1959; FLEMING et al. 1964; MUGIYA &

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WATABE 1977). Moreover the number of annuli may vary in the different body regions (DANNEVIG & HØST 1931), and sometimes not all scales from all body areas are in possession of yearmarks (BLACKBURN 1951; LIEDER 1959; BILTON & LUDWIG 1966). Consequently, if taken from the wrong area, the number of yearmarks is likely to be misinterpreted, and the age of a fish would be determined incorrectly. Therefore so-called "standard scales" can not be defined for all fish in general (DANNEVIG & HØST 1931), as well as the "standard method" for age determination by yearmarks cannot be applied to any species without defining the most appropriate body area for scale sampling first (MONASTUIRSKY 1926). Still many investigators do not seem to be aware of this.

Due to the lack of seasonal temperature changes tropical fish do not form classical yearmarks, from which McLARNEY (1973) deduced that scales taken from *Brycon guatemalensis* could not be used for age determination. He instead proposed the application of size-frequency analysis for this species, but the results are little convincing. CHOATE (1964) used tetracycline marking of bones under experimental conditions, but not in the field. WORTHMANN (1980) was able to apply PANNELLA's (1971) otolith method of counting daily rings to *Plagioscion monti* and *P. squamosissimus,* two Amazonian fresh-water species. He found the otoliths of many other species, including *Brycon* cf. *melanopterus,* useless for age determination, especially because of their small size and irregular shape (pers. comm.). Recently, WERDER (1983) proposed a new method for age determination in juvenile *Brycon* cf. *melanopterus*, which in regard to its accuracy is comparable to the otolith method, but by far more handy. It is based on the finding that sclerites on scales of this species are formed rhythmically, whereby in fish up to one year of age two days are needed for the formation of one sclerite. Since reabsorptioneffects (WALLIN 1957) brought on by limited food availability (FRASER 1917; BILTON 1974; MOREAU 1977; WERDER 1983) can reduce the number of sclerites, it is obvious that for tropical fishes the problem of selecting the right scales for age determination becomes more prominent than for fish from temperate climates. While in the latter ones only bands of sclerites are to be counted, every single sclerite becomes important in fast growing tropical fish. Consequently the best scales should be those with undisturbed sclerite patterns, which makes necessary a new definition of "standard" scales for each species to be investigated. Also, it is highly important to select the oldest scales of a fish, because they are not all formed on the same day (SCHNAKENBECK 1955; FISHELSON 1966).

The object of the present investigation is to test, in how far the sclerite method established for *Brycon* cf. *melanopterus* can also be applied on other tropical species. For this purpose the location of standard scales of 6 commercially important species from the Central Amazon is defined by examining the size-distribution of scales, and the number of sclerites in 6 selected body areas of these fish.

It is also tested, whether the calculated birth dates correlate with rainfall and rising water level, which are known to influence the onset of spawning in many fish (IHINGRAN 1959; KAMAL 1969; WELCOMME 1975; HANUMANTHARAO 1976; RAO 1976), especially in Amazonian species (GEISLER et al. 1971).

2. Materials and Methods

Juvenile specimens of Matrinchã (*Brycon* cf. *melanopterus*; N = 14), Jaraqui escame grossa (*Semaprochilodus theraponura*; N = 20), Jaraqui escame fina (*Semaprochilodus taeniurus*; N = 15), Curimatá (*Prochilodus nigricans*; N = 18), and Branquinha (*Curimata* cf. *rutiloides*; N = 8) were collected with seine nets in the floodplain of the Ilha de Marchantaria, an island in the Rio Solimões, about 5 km above the junction with the Rio Negro near the city of Manaus, Brazil. Additionally, fry of Tambaqui (*Colossoma macropomum*; N = 3) were obtained from a hatchery*).

The standard length of the fish was measured in mm. With reference to DANNEVIG & HØST (1931), the body of one fish of each species was subdivided into 6 areas (Fig. 1), from which scales were taken for defining the region in which standard scales occur.

Following the recommendations of THOMSON (1904), EINSELE (1943), and CASSIE (1956), approximately 6 - 10 scales were taken from each of these areas for analysis. After washing them in 70 %-ethanol, they were mounted under glass cover in "Kaisers Glyceringelatine" (Fa. Merck, Art. 9242).

One fish of each species was chosen for the description of the variation of shape and size of the scales in the different body regions (Fig. 2 - 7), and also for demonstrating the variation of the orad scale radius and the number of sclerites (Fig. 8). 3 specimens of every species were used for determining the body area, in which the highest sclerite numbers were found (Fig. 9). The same individuals served for age determination by the number of sclerites after WERDER (1983).

The orad scale radius (mm) and the number of sclerites were determined microscopically, and photographs were taken with a Pentax K2 camera.

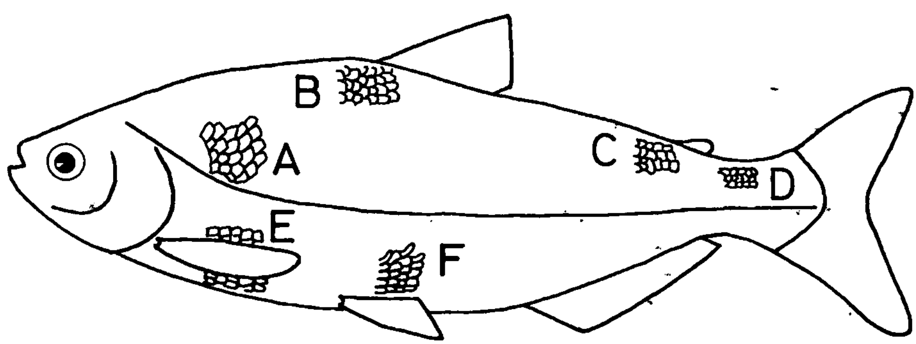

Figure 1:
Body areas from which scales were taken for analysis
A: above lateral line; B: beneath/in front of dorsal fin; C: beneath/in front of adipose fin;
D: caudal peduncle above lateral line; E: beneath pectoral fin; F: above pelvic fin

*) We are especially obliged Dr. Amauri Bezerra da Silva from DNOCS, Fortaleza, Brazil, for making available this material.

3. Results

3.1. Variation in scale-shape and -size from different body regions

Figures 2 to 7 show typical scales from the different body areas of all 6 species. The given scale refers to the original size of the scales. Enlargement is the same for all scale pictures, which allows a direct comparison of the size of scales in the different body areas of each specimen, and also among the species. The standard length of each specimen is also listed.

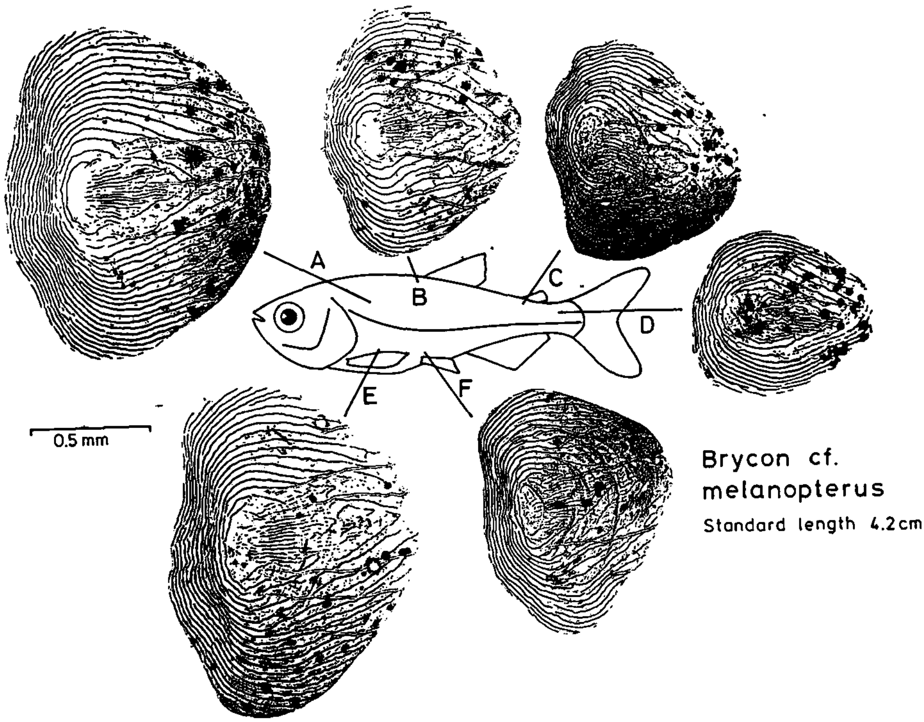

Figure 2:
Scale-size and -shape: *Brycon* cf. *melanopterus*

The scales of *Brycon* vary considerably in regard to shape and size in the different body areas.

The orad radius can be as small as 12 % - 20 % of the scale's length, and the sclerites are very closely packed here. The distance between the sclerites ranges from 10.0 to 18.1 x 10^{-3} mm (see fig. 8). In all cases, the nucleus i. e. the first visible sclerite, is easy to recognize, which permits a quick microscopic determination of the orad radius. The scales from region A, B, E, and F are dorsally and ventrally especially enlarged, and the distances between the sclerites are substancially greater here. This can be attributed to the allometric growth of the fish in these parts of the body at this early stage of development. Scales from the trunk and from beneath the adipose fin are little influenced by this, since growth in height of the fish is less pronounced in these regions.

Scales of region A are most regular and most uniform in shape, and thus appear to be particulary suited for age determination. All other scale-shapes are adapted to their specific position on the body, with great irregularities in form and large variations of sclerite numbers (Fig. 8, 9).

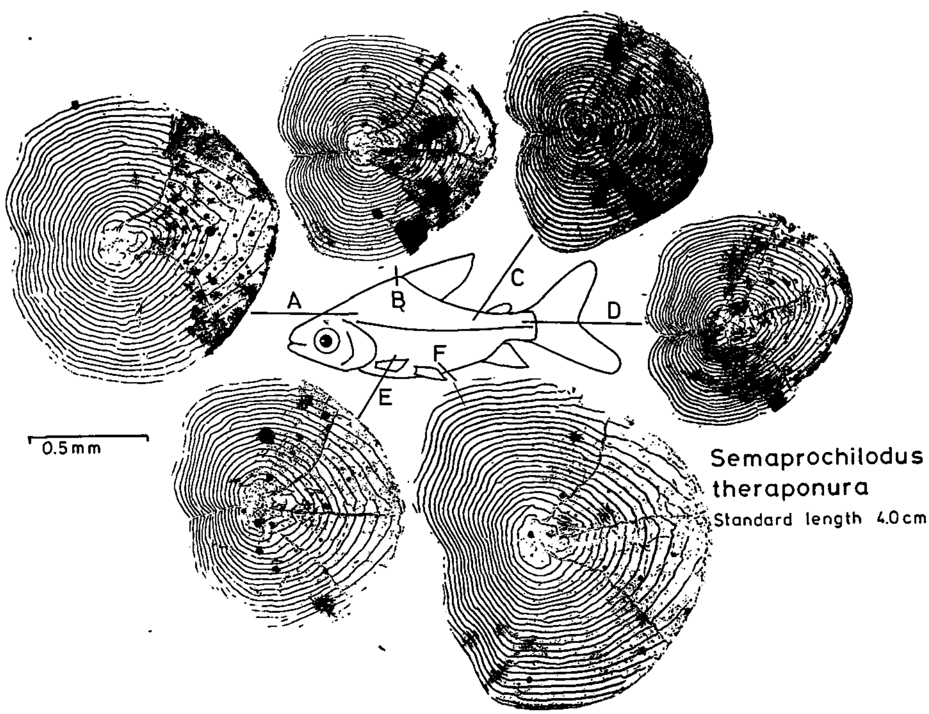

Figure 3:
Scale-size and -shape: *Semaprochilodus theraponura*

The most uniform sclerite patterns are found on scales from region A and region E. No interruptions along the orad radius are observed here, which is the case for all other scales. The first sclerites are easy to detect, and counting is simplified, as they are well separated. The variation of the average distances (10.0 - 17.0 mm x 10^{-3}) is almost the same as in *Brycon.* Regions A and E appear to be best suited for age determination.

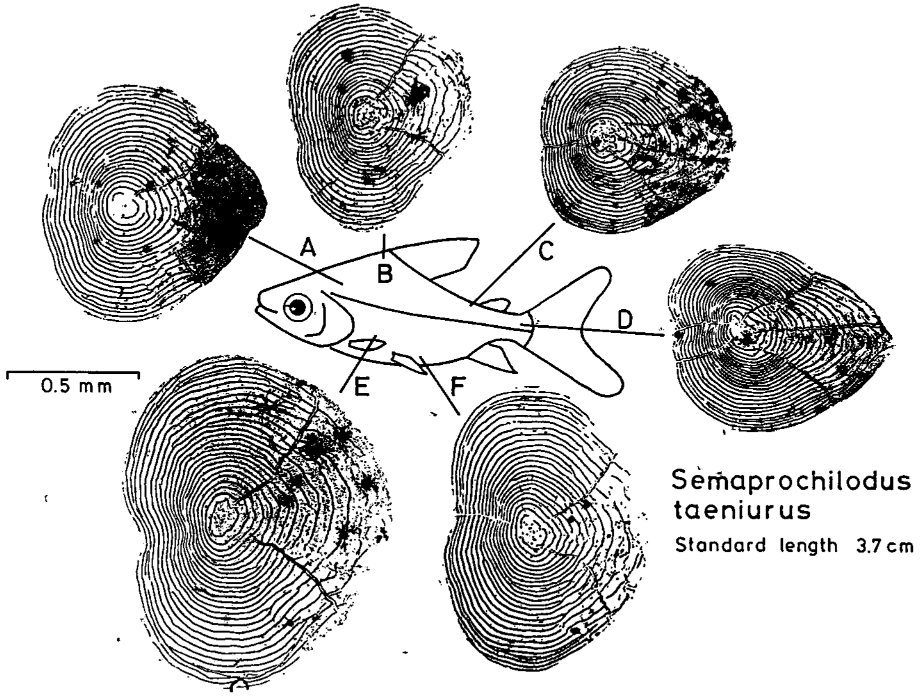

Figure 4:
Scale-size and -shape: *Semaprochilodus taeniurus*

This species, as already indicated by its local name "escama fina", which means small-scaled, possesses smaller scales than its close relative "escama grossa" (*Semaprochilodus theraponura*). Scales vary less in shape and size than in the former species, and the closely packed sclerites (8.6 - 14.0 mm x 10^{-3}) are clearly distinguishable in all regions of the body. The orad radius of scales from the trunk region is relatively large, but the sclerite pattern is disturbed by one or two incisions, which also accounts for the regions C and F. Still, no "unreadable" scales are found, making it hard to decide which area is the best for scale sampling. As for the size, scales from region E and F are the most suitable.

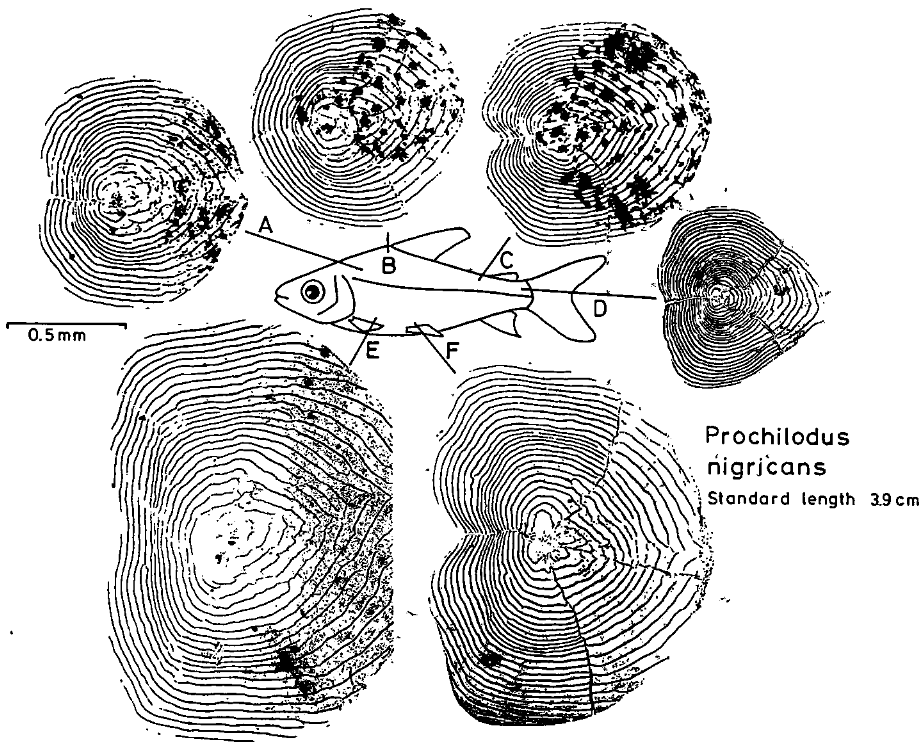

Figure 5:
Scale-size and -shape: *Prochilodus nigricans*

P. nigricans, more than the aforementioned species, exhibits a very strong variation with respect to the size of the scales from different body areas: The largest are encountered in region E and region F, but their shapes are quite irregular. It is not always easy to define the first sclerite, and the measurement of the radius may be complicated because of the indentations in the oral field of most scales. Sclerite distance is between 10.0 and 18.9 mm x 10^{-3}, the maximum value being slightly higher than in *Brycon* and *Semaprochilodus theraponura*, but generally in the same order as in these two species. With the exception of region B, C, and D all other areas, A, E, F, appear to be suited for scale-sampling.

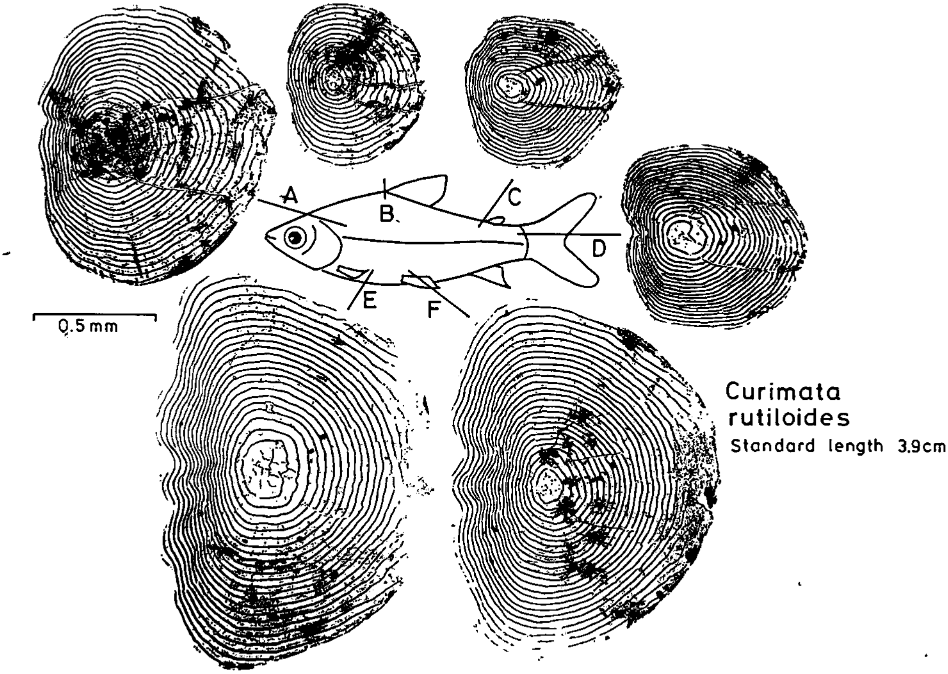

Figure 6:
Scale-size and -shape: *Curimata* cf. *rutiloides*

Despite being congruent with respect to shape, the scales of this species differ considerably in size. Scales from the areas B, C, and D are very small in comparison to the other regions, and the sclerite-density is much higher. Also, the distances between sclerites show a higher variability than any of the other species mentioned before (8.8 - 17.1 mm x 10^{-3}). With respect to size, constancy in shape and readability, areas A, E, and F carry the best scales for age determination.

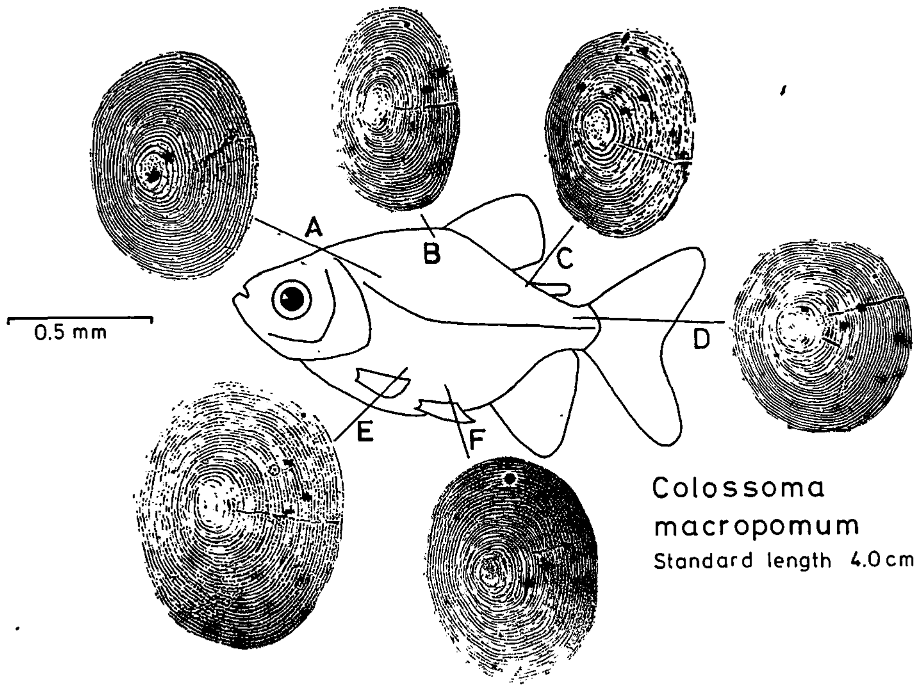

Figure 7:
Scale-size and -shape: *Colossoma macropomum*

This species has the most uniform scales of all fish investigated. The sclerites are arranged almost concentrically and very closely packed (6.6 - 8.6 mm x 10^{-3}), which is about half the distance found in the other species. Size-variation is limited, and both the sclerites and the nucleus are easily recognized. At first it is difficult to distinguish between scales from different regions. The distances between subsequent sclerites are greatest in the areas A, E, and F. Therefore these regions seem to be the most appropriated ones for age determination.

3.2. Number of sclerites and scale-radius

As seen above, no definite decision can be made with respect to the most suitable body area for sampling in the 6 species investigated. The size and the shape of the scales vary in all species, and the location of the most uniformly shaped scales is not the same. In order to define "standard scales" for each of the species, it is necessary to include an analysis of the sclerite numbers, and the related scale-radius in the different body areas. These results are summarized in fig. 8 and fig. 9.

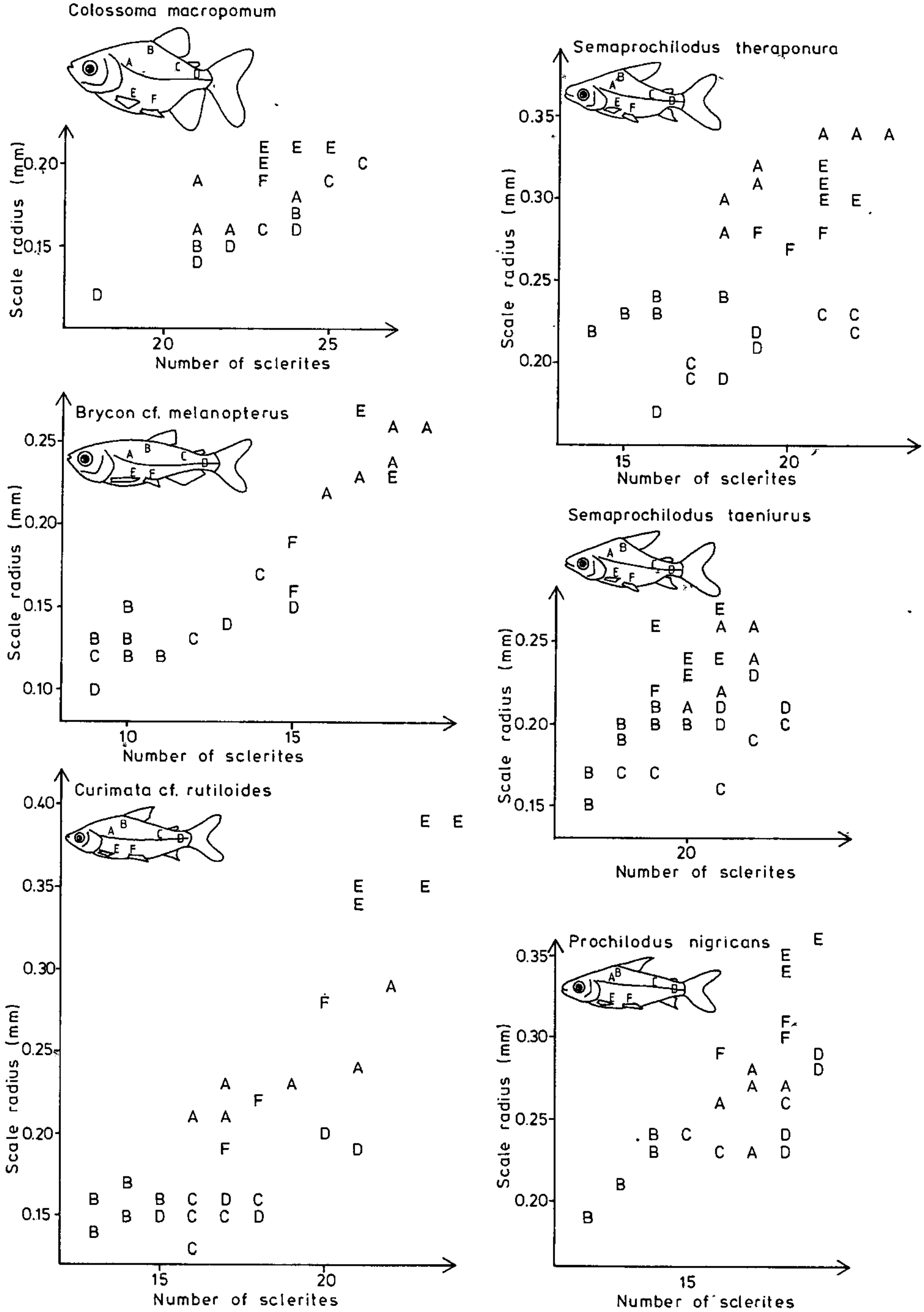

Figure 8:
Number of sclerites and scale-radius in the different body areas
Standard length: *C. macropomum*: 4.5 cm; *S. theraponura*: 4.0 cm; *B.* cf. *melanopterus*: 4.2 cm; *S. taenius*: 3.9 cm; *C.* cf. *rutiloides*: 3.8 cm; *P. nigricans*: 4.0 cm

Fig. 8 demonstrates the variation of sclerite numbers and scale radius in one specimen of each species. For this purpose 6 to 10 scales were taken from each body region, and then measured and counted. Only those scales are listed, in which the orad radius could be determined (first sclerite visible).

There is a general tendency in all species for high sclerite numbers to go along with a large scale radius, but there are some exceptions: *Semaprochilodus theraponura* has high sclerite numbers in region C, but the related scale radius is much smaller than in regions A and E, where similar numbers are found. Also, regions C and D of *Semaprochilodus taeniurus* carry more sclerites than the larger scales of region A and E.

This can be explained by the fact that scale formation begins, somewhat delayed, in the different body areas (FISHELSON 1966), and scale-shape and -size depend primarily on the region of the body rather than on the age of the scale. In all fish investigated this is reflected in the varying distances between sclerites on scales with identical sclerite numbers, but of different sizes. Provided furthermore that sclerite formation is rhythmic in fish in general, as this was shown for juvenile Matrinchã (WERDER 1983), the size and the shape of scales are of minor importance, and the most relevant parameter for selecting scales for age determination is the maximum number of sclerites.

In fig. 9 the highest sclerite numbers encountered in the different body areas of three fish of each species are listed. The orad radius of the related scale is given below.

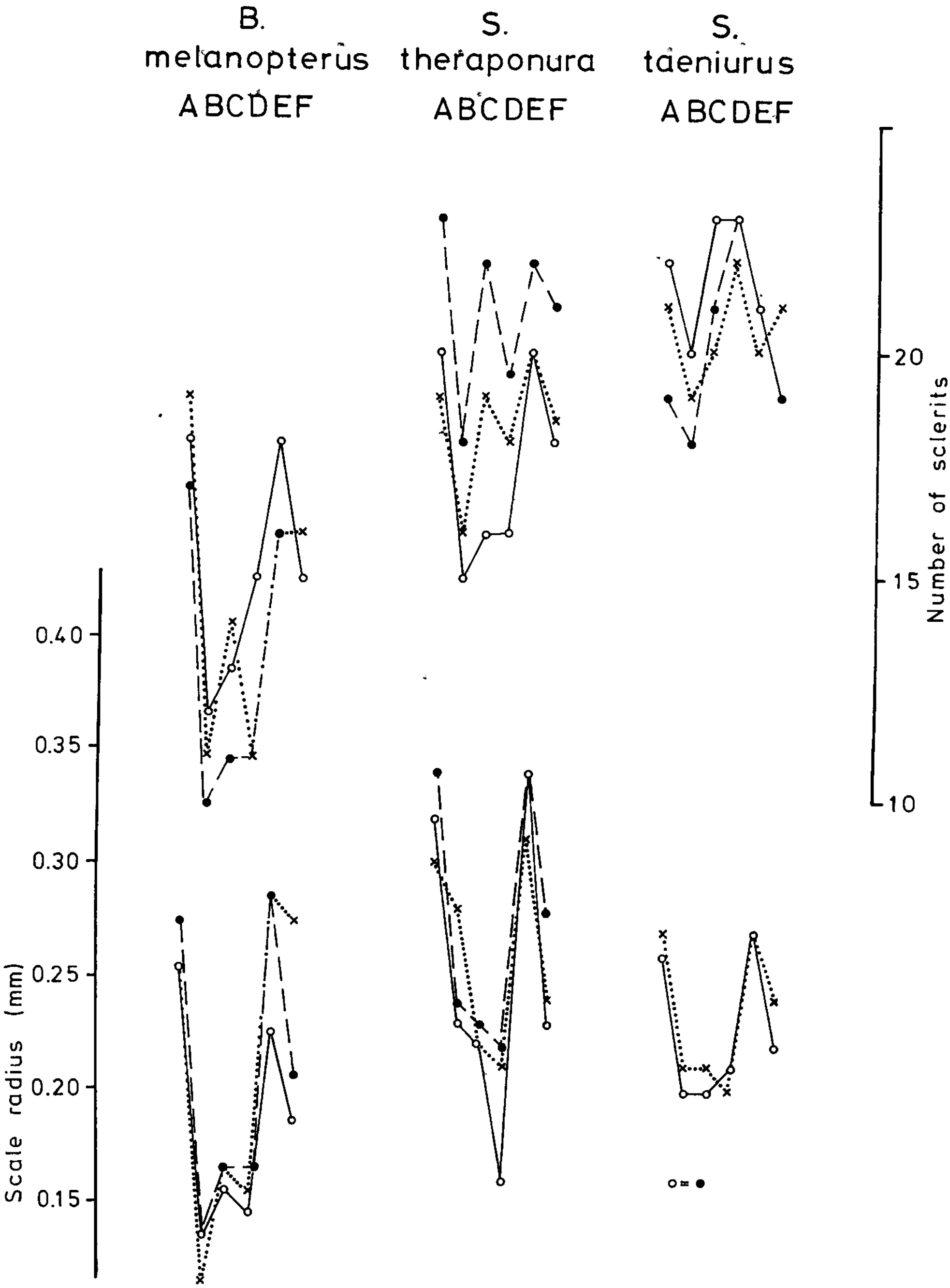

Figure 9:
Maximum sclerite number and orad radius of the related scales from six different areas of the body (3 specimens/species)

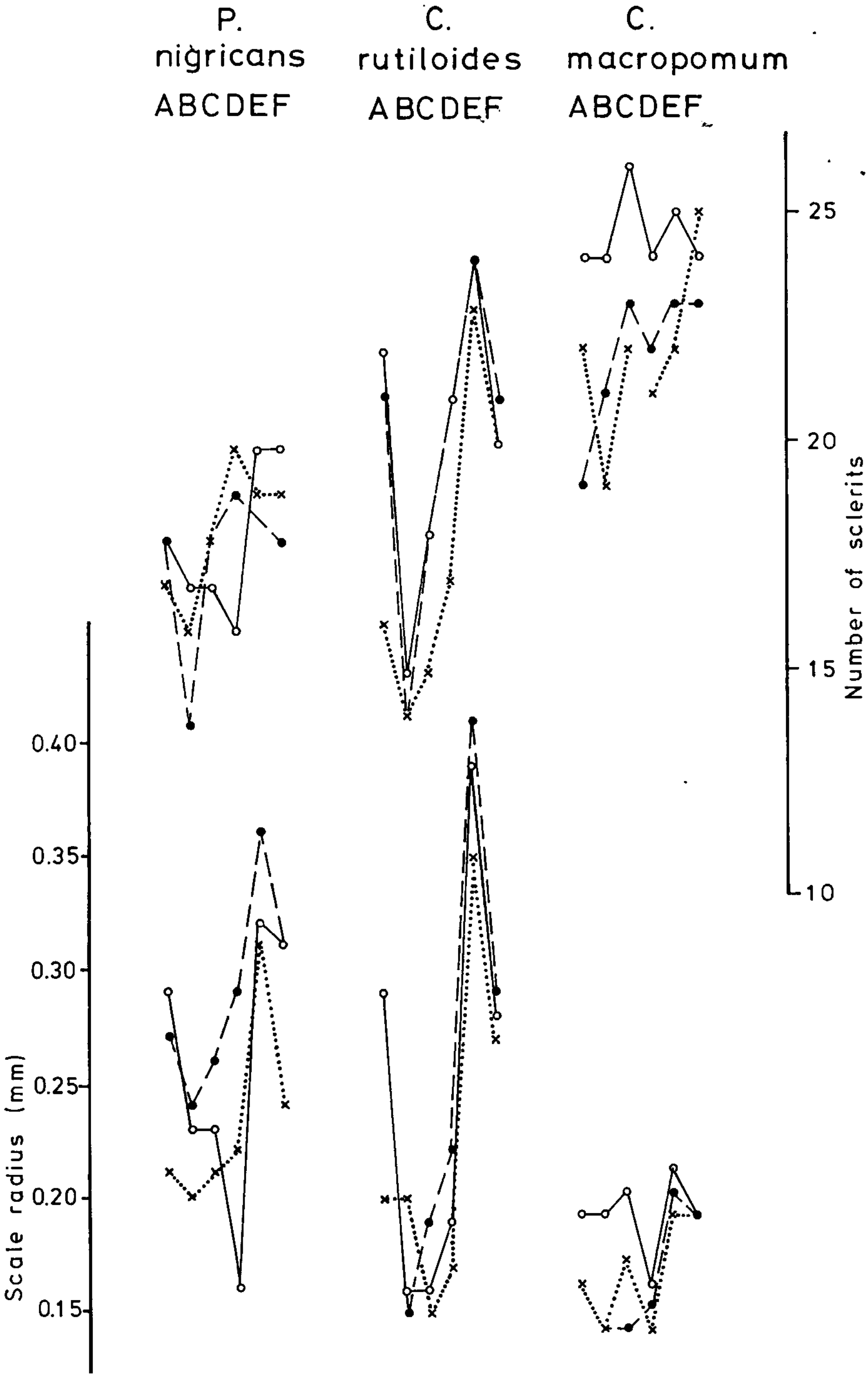

Figure 9:
Continuation

3.2.1. *Brycon* cf. *melanopterus*

The highest number of sclerites is found in region A in all 3 specimens. Only one specimen reaches the same maximum number also in region E. All other areas present smaller numbers. Although the scale radius is larger in regions E and F, the number of sclerites does not increase concomitantly. Instead, the distances between them become enlarged. This is most probably due to a "compensatory" growth of the scale in regard to shape and size of the related body area, rather than depending on the age of the fish.

As derived from the highest sclerite numbers in the investigated body areas, scale formation begins in region A somewhat earlier than in other body areas, and this is the best place for sclerite sampling.

3.2.2. *Semaprochilodus theraponura* (escama grossa)

S. theraponura generally possesses the highest number of sclerites in region A – with the exception of one fish, in which region E outnumbers A by one sclerite. Despite the high numbers of two specimens in region C, the radius is very small, resulting in the highest sclerite-density of all areas. It is also seen that the largest scales do not necessarily have the highest sclerite number.

The best region for taking scale samples is thus region A.

3.2.3. *Semaprochilodus taeniurus* (escama fina)

Different from two afore mentioned species, in *S. taeniurus* the highest sclerite numbers are found in the trunk region (D), and beneath the adipose fin (C), where scale formation obviously begins earlier than in other body areas.

The sclerite numbers are similar to those of *Semaprochilodus theraponura*, but the scales are much smaller. Both sclerite number and scale radius vary less, and the scales are somewhat more uniform with regard to size.

The best areas to take scales from are regions C or D.

3.2.4. *Prochilodus nigricans*

In this species scale formation begins in the area of the trunk region and belly, and proceeds to the head. Since the sclerite numbers of the oldest scales are quite similar, scales from all three regions D, E, and F are appropriate for scale sampling.

3.2.5. *Curimata* cf. *rutiloides*

More evident than *Prochilodus nigricans, Curimata* cf. *rutiloides* tends to have the highest sclerite numbers and the largest scales in region E. All other areas carry less sclerites, and in comparison to region A, the total number is 2 to 7 higher. This large discrepancy would not allow the application of any correcting factor for the latter one, and thus region E should be considered the most appropriate one for scale sampling.

3.2.6. *Colossoma macropomum*

The scales of *C. macropomum* are more uniform in shape and size than those of any of the other species investigated. The highest sclerite numbers are found in the anal region, beneath the adipose fin, and in the pectoral area, being most pronounced in region C, which outnumbers the others by 1 to 2 sclerites. The scales seem to develop almost simultanously in different body areas with the least variation of sclerite numbers and size in all three specimens. Still, the highest sclerite number of the whole sample was found in region C, which therefore appears to be the best for age determination.

3.2.7. Conclusion

Derived from fig. 8 and fig. 9, the following areas are most suitable for age determination:

Semaprochilodus theraponura	: region A
Brycon cf. *melanopterus*	: region A
Semaprochilodus taeniurus	: regions C, D
Prochilodus nigricans	: regions D, E, F
Curimata cf. *rutiloides*	: region E
Colossoma macropomum	: region C

3.3. Age determination

As shown by WERDER (1983), age determination in juvenile *Brycon* cf. *melanopterus* is based on a 2-day rhythm of sclerite formation, and the approximate spawning of the parent-population can be calculated by the formula

$$d = c - (n \cdot 2 + 14)$$

d = day of birth (spawning/egg fertilization)
c = number of days of a year at the day of capture
n = number of sclerites

where 14 stands for the assumed mean number of days which have passed from the day of fecundation until the formation of the first sclerites.

3.3.1. *Brycon* cf. *melanopterus*

The three fish investigated here are part of a larger sample, which was collected on February 21, 1980. The maximum numbers of sclerites are 17, 18, and 19 for each specimen, and derived from the above formula, their individual ages are 48, 50, and 52 days. The day of capture was the 52nd day of the year, and therefore these fish were most probably born in the period between Dec. 31, 1979, and Jan. 04, 1980.

In order to verify the likelihood of spawning events during this period it is necessary to have a look at the ecological conditions at the time concerned. Figure 10 informs about the level of the Rio Negro at the port of Manaus in Dec. '79 and Jan. '80. Also, the precipitation data of two stations are given.

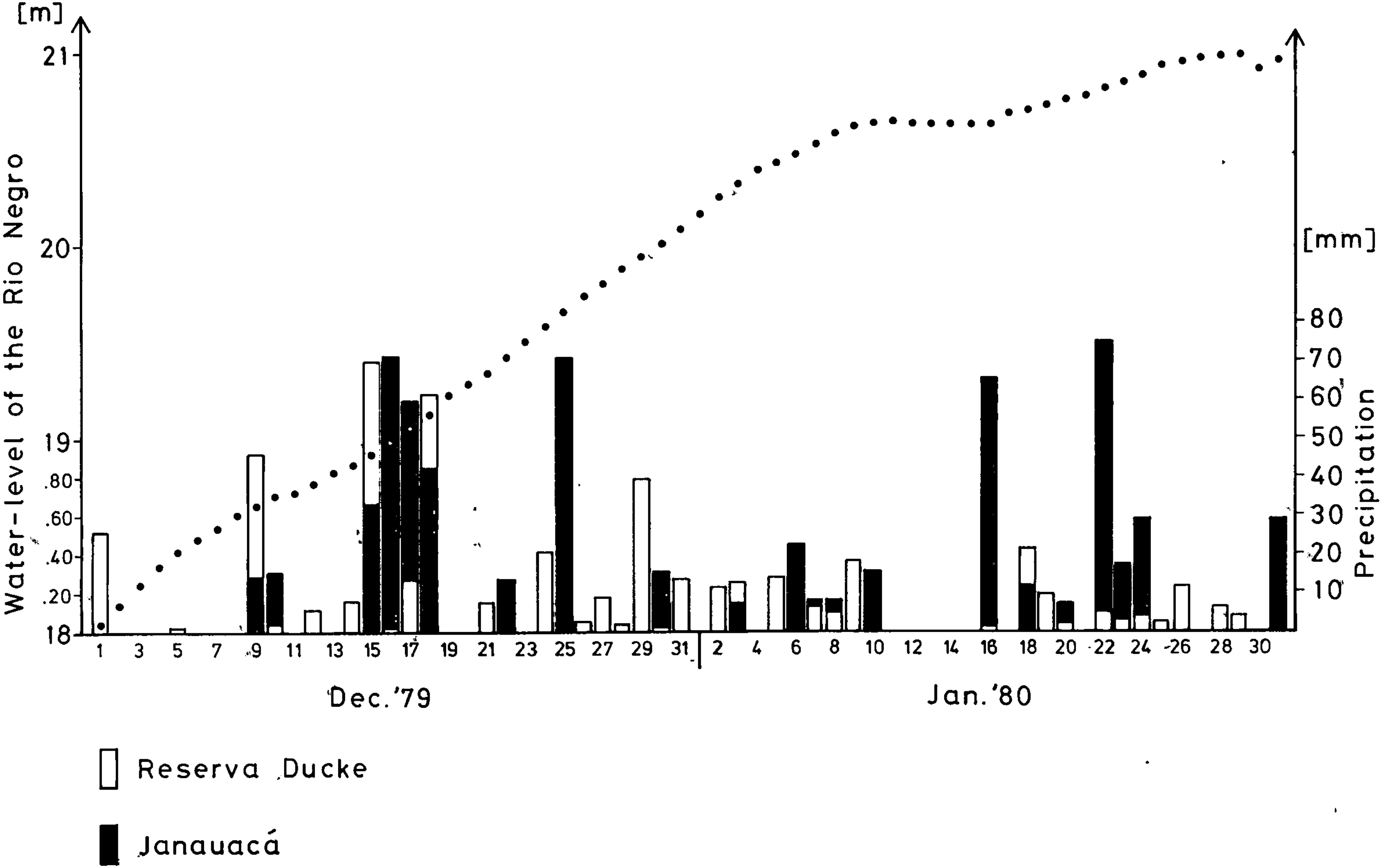

Figure 10:
Water level* of the Rio Negro and precipitation** in Dec. 1979 and Jan. 1980

* Source: Capitania dos Portos, Manaus
**Source: Maria de Nazari Jóes Ribeiro, INPA

The open bars stand for a station on the "terra firme", about 40 km north of the spawning grounds, while the closed bars reflect data collected about 30 km upstream the Rio Solimões. At the calculated dates the water level of the Rio Negro was very close to the threshold mark of about 20 m, at which the spawning season usually begins (WERDER 1983). Precipitation was recorded at both stations, and the river level showed rising tendency of up to 8 cm per day. Thus all favourable pre-conditions were given for spawning, and the calculated birthdays of the investigated fish must be considered highly probable.

3.3.2. Application of the sclerite method to other species.

3.3.2.1. *Semaprochilodus theraponura, Semaprochilodus taeniurus, Curimata* cf. *rutiloides, Prochilodus nigricans*

In order to apply the above equation for age determination to other species, too, two basic requirements must be fulfilled: sclerite formation must be rhythmic, and the approximate period of time between fecundation and the beginning of sclerite formation should be known.

In part 3.2. it was shown that independent of the shape or the size of the scales, the maximum number of sclerites of *Semaprochilodus theraponura* (20/23), *S. taeniurus* (23), and *Curimata* cf. *rutiloides* (24) were almost identical. Also, the total variation of the distances between sclerites (8.6 - 18.9 mm x 10^{-3}) are nearly within the same range as in *Brycon* cf. *melanopterus* (10.0 - 18.1 mm x 10^{-3}). Derived from this it can be deduced that the rhythms of sclerite formation were the same for all three species. Even more support for the existence of a 2-day rhythm is received from the smaller number of sclerites of *Prochilodus nigricans* (20), caught 8 days earlier, on May 14, 1980. If multiplied with the factor 2, the difference of 3 - 4 sclerites would make up exactly the time lying between the two sampling dates. It therefore seems justifiable to assume that all 4 species have identical rhythms of sclerite formation, being very similar to the one of *Brycon*.

All species, including *Brycon*, spawn under very similar ecological conditions. Most important are rise of the river level, accompanied by heavy precipitation (GOULDING 1980; WERDER 1982, 1983). Their eggs are pelagic or semipelagic, and hatching occurs as BREDER (1962) describes this in general for largely transparent eggs, "at what is evidently the earliest possible time" (BREDER 1962, p. 561). In *Prochilodus* sp. hatching takes place about one day after fertilization, and yolk absorption is normally finished after less than a week (FONTENELLE et al. 1946, pers. obs.). Conditions are similar in *Colossoma macropomum* (DA SILVA et al. 1977, pers. obs.), which will be referred to later. In their natural habitats the fry of most of the species mentioned above have been observed swimming up and feeding actively a few days after fertilization (JUNK 1975). In view of this rapid embryonic and larval development – which under the given ecological conditions increases the chances of survival (WELCOMME 1975) – it becomes evident that scale formation should begin at an early stage of development, too. WERDER (1983) used an estimate of 14 days for calculating the age of juvenile *Brycon* cf. *melanopterus*, which led to very trustworthy results. Taking into consideration that all scale features and also the ecological conditions for the species investigated here are nearly identical, no large objections should be made for the application of the same correcting factor as in *Brycon* (14 days) for the determination of the day of fecundation of the other 4 species.

Table 1 summarizes the calculated birthdays of the 4 species as derived from the above formula.

Table 1: Calculated ages and birthdays of *S. theraponura, S. taeniurus, P. nigricans*, and *C.* cf. *rutiloides*

Species	Sampling date	Sclerite Number	Age (d)	Calculated birthday
S. theraponura	22.05.'80	20/23	54/60	29.03.'80/23.03.'80
S. taeniurus	22.05.'80	23	60	23.03.'80
P. nigricans	14.05.'80	20	54	21.03.'80
C. cf. *rutiloides*	22.05.'80	24	62	21.03.'80

The calculated birthdays of 4 different species fall into the period between March 21 and 29, 1980. During the three weeks before the calculated birthdays the waterlevel of the Rio Negro fell constantly until the 17th of March. Also, very little rain was recorded at station I, and none at all near the assumed spawning grounds at station II. Such conditions are highly disfavourable for the onset of spawning (WERDER 1983). After 2 days of stagnation, the riverlevel began to rise again on the 20th of March, 6 to 10 cm per day. At this time very strong rainfalls occurred (more than 142 mm in three days at station II), furnishing excellent conditions for spawning (Fig. 11).

As the calculated birthdays show, the first fish to spawn were *C.* cf. *rutiloides* and *P. nigricans*, while the two *Semaprochilodus* species reproduced a couple of days later (one specimen of *S. theraponura* was born a week later). Despite possible differences in regard to the individual developmental stages of the investigated fish, this is quite likely. It is a well known fact that different species and different populations of the same species do not necessarily spawn on the same day, but rather subsequently, according to the order in which they arrive at the spawning grounds (GOULDING 1980). During our field studies we could personally observe spawning activities of different schools over a period of several days, and the local fishermen caught large quantities of mature fish on such occasions.

The results also show that the period between fecundation and the beginning of scale formation cannot be much longer than the estimated 14 days. Otherwise the calculated birthdays would fall into periods of absolutely unfavourable ecological conditions for spawning. It is furthermore worth reminding that none of the investigated fish possesse a number of sclerites higher than 24, which, if so, would also have meant that they were born before the changing of ecological conditions to the better. This is another support for the existence of a rhythm of sclerite formation in the four investigated species, which seems to be identical with the one of *Brycon* cf. *melanopterus*. These findings justify the application of the equation for age determination by sclerite numbers, which initially was established for *Brycon* only.

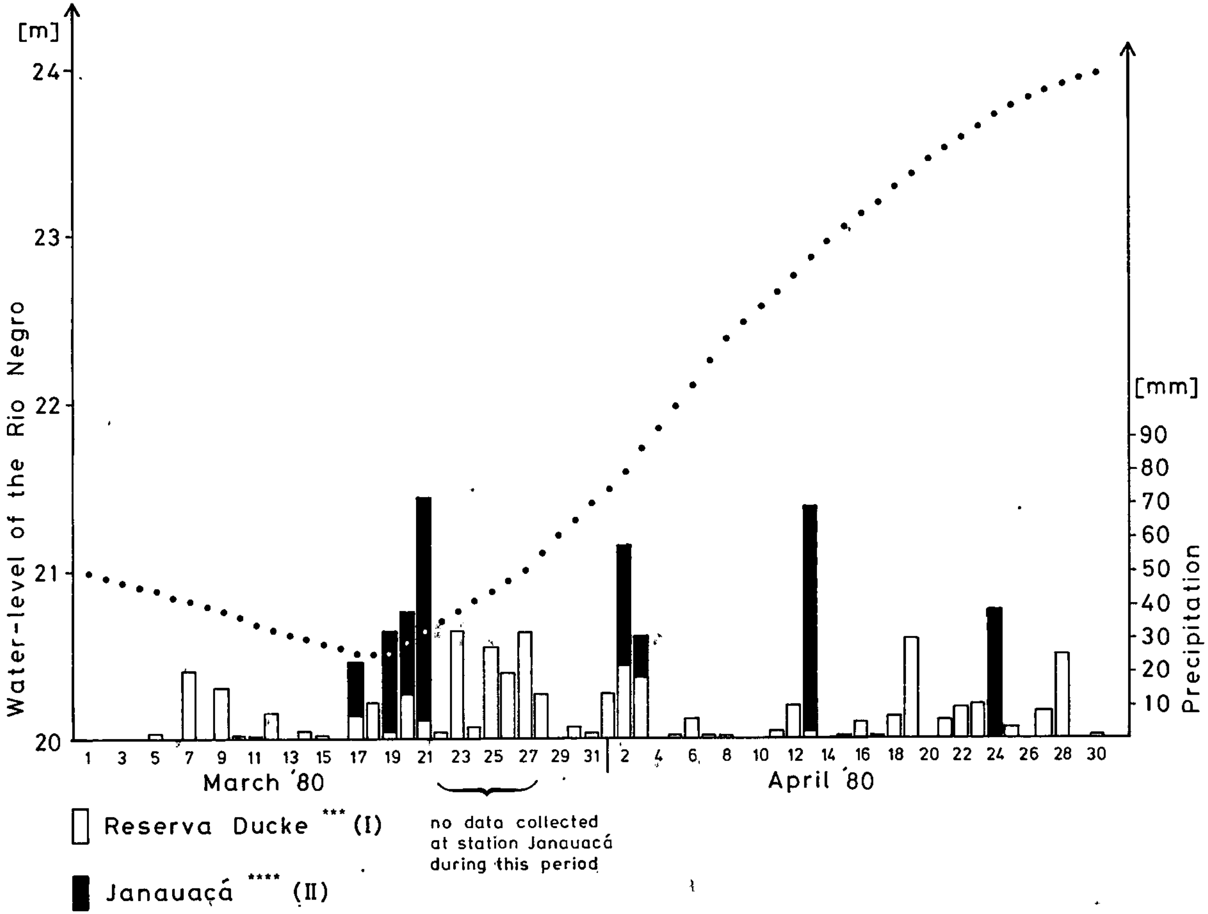

Figure 11:
Water level* of the Rio Negro and precipitation** in March and April 1980

*Source: Capitania dos Portos, Manaus

**Source: Maria de Nazari Jóes Ribeiro, INPA

***ca. 40 km north of spawning site on the "terra firme"

****ca. 30 km southwest of spawning site in the Rio Solimões

3.3.2.2. *Colossoma macropomum*

The fry of *Colossoma macropomum* were obtained from a hatchery (see: Materials and Methods), where the eggs had been fertilized artificially. The fish were about four weeks old when they were air mailed to our institute (DA SILVA, pers. comm.), where they died between the 7th and 12th day after. So their ages were 35 to 40 days when the scales were taken from the dead fish.

Colossoma's larval development takes about one week (DA SILVA et al. 1977), and assuming that scale formation begins another week later – as in the other species – only 21 to 26 days were available for the formation of sclerites. This perfectly corresponds with the number of sclerites encountered on the scales of the 3 investigated specimens (23, 25, and 26). Therefore, it must be concluded that sclerite formation in *Colossoma* does not follow the 2-day rhythm of the other species, but quite exactly a 1-day rhythm of its own.

Although the causative factors are not known, this explains the large discrepancies in regard to sclerite density as compared with the other species (see part 3.2., and fig. 8, 9).

Table 2: Medium distances between sclerites in 3 specimens of 6 species (calculated from the scales with the highest sclerite numbers in the 6 different body areas, and the related orad scale-radius)

	Medium distances between sclerites (mm x 10^{-3})			
Species / No.	1	2	3	medium
S. theraponura	14.1	14.2	13.0	13.8
S. taeniurus	10.8	11.2	11.4	11.2
B. cf. *melanopterus*	12.3	14.5	13.4	13.4
C. cf. *rutiloides*	12.0	12.6	13.0	12.5
P. nigricans	14.1	12.7	16.3	14.4
C. macropomum	7.7	7.5	7.6	7.6

The values given in table 2 represent the medium distances between sclerites of all 6 selected body areas, derived from the oldest scale of each of these regions. The results show, that in *C. macropomum* the distances are almost identical for all 3 specimens. They are between 32.1 % (*S. taeniurus*) and 47.2 % (*P. nigricans*) smaller than in the other species.

In other words, the sclerites are much thinner, and two of them require about the same space as the larger ones of the other species. Our present state of knowledge allows no causative explanations for this, but it seems that *C. macropomum*, instead of forming one big sclerite every other day, produces two delicate ones in the same period of time.

This daily rhythm of sclerite formation requires only a slight modification of the formula for age determination, which is then:

$$d = c - n + 14$$

4. Discussion

As the results of this work show, age determination by sclerite numbers can only be accomplished successfully after first defining the body region from which the scales should be taken, and this, for every individual species. HOFFBAUER (1898) and WALTER (1901) considered the constancy in the shape of scales as an important criterion for age determination, while PERLMUTTER & CLARKE (1949) mentioned the maximum number of sclerites as most relevant for the selection of the largest scales of a fish. Our results show that the latter assumption is not valid in general for the investigated species. Often the largest scales have less sclerites than smaller ones.

Many authors were aware of the variability of scales in different body areas, and some concluded that only scales from distinct body regions could furnish comparable and reliable results in regard to age determination (SEGERSTRÅLE 1933; GEYER 1939; EINSELE 1943). Unfortunately, other investigators (GODOY 1959; McLARNEY 1973) were not conscious of the fact that intraspecific size-variations of the scales of one species do not automatically account for other species in the same way and to the same extent. Some (EINSELE 1943; BLACKBURN 1951) have even chosen scales from body areas in which it is extremely difficult to distinguish between true yearmarks and otherwise disturbed sclerite patterns. CHUGUNOV (1925) and especially MONASTUIRSKY (1926) have both criticized the careless adoption of methods, and they vigorously demanded a careful analysis of species investigated for the first time before applying any "standard method" to them. The importance of such procedure becomes obvious when looking at the results of our investigation. The species examined present a large variability in size and shape of the scales in different parts of the body. The largest scales are generally found above and beneath the lateral line in the post cranial regions A and E. Scales of the lateral line itself were not considered, since the canal-system makes the counting of sclerites very difficult if not impossible. The smallest ones are found beneath the dorsal, near the adipose fin, or in the trunk region. While size variations of the scales are little in the disk-shaped *Colossoma macropomum*, the orad scale radius of *Curimata* cf. *rutiloides* and the other more elongated species may vary up to 300 %. From this can be concluded that, as a general rule, the shape and the size of the scales are primarily determined by their specific location on the body, and therefore the size of the scales or their shape should be considered as of minor importance for the purpose of age determination.

Earlier investigators (WINGE 1915; TAYLOR 1916; GRAHAM 1929) supposed the existence of rhythmic scale growth, which they deduced from nearly identical time-intervals between the formation of subsequent sclerites in different species from temperate climate zones. But data were scarce, and no attempt was made to develop a method for age determination. OTTAWAY (1978) was able to demonstrate a diurnal rhythm of Glycin (^{14}C)-incorporation in isolated scales of *Rutilus rutilus*, and only recently WERDER (1983) showed through pond-experiments that a 2-day rhythm of sclerite formation exists for juvenile *Brycon* cf. *melanopterus*. This rhythm is obviously not influenced by the size of the scales nor by the length of the fish, although inherent rhythms might be overlapped by exogenous factors (GRAHAM 1929). The results of the present investigation clearly show that the number of sclerites does not depend on the size of the scales, but rather on the body area from which the scales were taken. This fact does not contradict the rule of rhythmic sclerite formation at all, but is rather attributed to the delayed formation of scales in different parts of the body (SCHNAKENBECK 1955). FISHELSON (1966) showed that scale formation of *Tilapia* sp. begins two to four weeks after fecundation (*T. macrocephala*: 15 days, *T. nilotica*: 20 days, *T. tholloni*: 24 days). He observed that 17 days later the oldest scales possessed 8 - 9 sclerites, while the latest formed scales had only 1 sclerite. This strongly indicates the existence of a 2-day rhythm of formation, also for these species, but no attempt was made to verify this, and the author did not consider its relevance for age determination. In our investigation similar differences of sclerite numbers were found for all individual fish, allowing us to deduce that an average time of 1 - 3 weeks is needed until the body is completely covered with scales. It becomes obvious that the error in calculating the exact birthday of the fish would be within the same range if the scales were taken from the wrong body area. Assuming a constant rhythm of sclerite formation in all parts of the body, the latest formed scales can never reach numbers of sclerites equal to those of the oldest ones, and it is then evident that the best scales for age determination are those with the highest sclerite numbers. For species, in which the oldest scales are the smallest ones, it might be feasible to determine an average difference of sclerite numbers in comparison with larger and better "readable" scales. Provided a larger number of specimens than we used in our investigation, this would make possible the application of a correcting factor, which then would allow to calculate the age of a fish also from later formed scales.

The difference of 1 - 2 days regarding the formation of scales in subsequent body areas is similar to the one observed for *Tilapia* (FISHELSON 1966), and so are the overlapping-effects in between these areas. Furthermore it is shown that the first scales do not arise from the same body area in all species. Only *Semaprochilodus taeniurus* and *Prochilodus nigricans* confirm the general opinion (SCHNAKENBECK 1955) that the first scales are formed in the trunk region. *S. theraponura*, a very closely related species, differs substantially with regard to the sequence of scale formation as compared to those. This finding supports MONASTUIRSKY's (1926) demand for a careful investigation of new species, and now proves that standard scales must be defined for each species individually.

FISHELSON (1966) explains the interspecific differences regarding the onset of scale formation by different ecological necessities of the three *Tilapia* species. This does not account for most of the presently examined fish. Five of the six species spawn in the same areas under identical ecological conditions (JUNK 1975; GOULDING 1980), and sometimes even on the same day (WERDER 1983). This is also reflected in the calculated birthdays (see table 1). Larval development of the species concerned is very rapid (JUNK 1975), and the alevins live in the same nursary habitats where they often congregate in mixed schools. Although they probably differ somehow in regard to their growth rates, their general living conditions are quite the same, and from the present work it becomes clear that *S. theraponura, S. taeniurus, C.* cf. *rutiloides,* and *P. nigricans* all have the same 2-day rhythm of sclerite formation as *Brycon* cf. *melanopterus.* Also the estimated period of 14 days between fecundation and the beginning of sclerite formation seems to be the same for all. Assuming a period of much more than 2 weeks, the calculated spawnings would have coincided with absolutely disfavourable ecological conditions under which reproduction normally would not take place. It also cannot be much shorter than this, because larval development already requires about one week. Still, experimental studies are necessary to verify this, and to see whether the estimated time of 14 days between egg fertilization and the appearance of the first scales is valid for all of the investigated species, and maybe for others, too.

It is quite difficult to explain the different rhythm of sclerite formation in *Colossoma macropomum*, but it is worth mentioning that this species lives under somewhat different ecological condition than the others. It can reach total weights of up to 30 kg (GOULDING 1980), while the other species usually do not substantially exceed 2 and 5 kg respectively. HILDERS & BORTONE (1977) and DA SILVA et al. (1978) showed in pond experiments that *Colossoma* grows about two times faster in the first year than *Brycon* (WERDER 1981, 1982), and the same was observed in our investigation of the very young fish. However, the scales are relatively small, and two of the very delicate sclerites formed in a 1-day rhythm occupy the same space as one sclerite of the other species. Up to date little is known about the factors causing the different rhythms of sclerite formation, and basic studies are necessary to illuminate this question.

In comparison with PANNELLA's (1971) otolith method, the sclerite method is more feasible and requires less expenditure of time and equipment. It is also, by far, better applicable than CHOATE's (1964) method of tetracycline marking of bones. Provided that similar rhythms of sclerite formation exist for other age groups and other species than the investigated ones, this method would very much facilitate the age determination of tropical fish, and could serve as a good base for studies in population dynamics.

5. Summary

The results of the present investigation show that scale size, scale shape, and the number of sclerites vary substantially in different body areas of 6 different Amazonian fish species. Only the oldest scales are appropriate for age determination, also the part of the body in which they occur is not the same for all species. Since 5 of the species have identical 2-day rhythms of sclerite formation, age determination by the sclerite method after WERDER (1983) is possible. One of the species studied reveals a 1-day rhythm of sclerite formation, making necessary a slight modification of the formula.

6. Zusammenfassung

Die Untersuchungen an Jungfischen 6 verschiedener Amazonasarten dreier Familien zeigen, daß hinsichtlich der Schuppenform, der Schuppengröße und der Skleritenzahl eine für alle Arten zu beobachtende Variabilität unterschiedlicher Ausprägung vorliegt. Erst nach Bestimmung derjenigen Körperregion, in der die ältesten Schuppen anzutreffen sind, ermöglicht sich die Altersbestimmung anhand der Skleritenzahl nach der Methode von WERDER (1983). Bei 5 der untersuchten Arten erfolgt die Skleritenanlage in einem 2-Tage Rhythmus, während bei der 6. Art täglich ein Sklerit gebildet wird. Eine Anpassung der Bestimmungsformel an diese unterschiedliche Rhythmik erlaubt auch bei letzterer Art die Altersbestimmung an Schuppen.

7. Resumo

Foram investigados juvenis de 6 espécies icticas amazônicas em respeito à possibilidade de usar escamas para a determinação de idade. Os resultados mostram que 5 espécies possuem o mesmo ritmo de formação de escleritos (2 dias/esclerito) nas escamas. O ritmo de uma outra espécie é diferente (1 dia/esclerito). As melhores escamas para determinação de idade são as mais idosas, as quais se encontram em diferentes regiões do corpo de cada espécie. A determinação de idade é possivel para todas as espécies através do método de WERDER (1983).

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