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Hydrodynamic Aspects of Shark Scales

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LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

ACKNOWLEDGEMENTS

INTRODUCTION

The energetics of fish locomotion depends on a balance between thrust and drag. The interest stimulated by "Gray's Paradox", that is the seeming lack of sufficient power to overcome many of the estimated values of drag, has resulted in the delineation of a number of potential drag reducing mechanisms (Webb, 1975). Of particular interest is a variety of structural mechanisms, such as scombroid scale corselets (Walters, 1962) and scale ctenii (Burdak, 1969; Bone, 1972), which increase surface roughness and thereby alter boundary layer characteristics. Elasmobranch placoid scales, or dermal denticles, may perform such a function. Bone and Howarth (1966) have suggested that this type of scale reduces drag by creating turbulence in the boundary layer, thereby preventing its separation. More recently, Walsh and Weinstein (1978) have shown that surfaces composed of longitudinally arranged v-shaped grooves can significantly reduce drag through a reduction in the turbulent bursting activity. Placoid scales from a number of galeoid shark species exhibit this type of surface morphology and may therefore represent a potential drag reduction mechanism.

Following its eruption through the epidermis, a typical scale consists of three parts (Applegate, 1967). An expanded, plate-like crown lies above the surface of the skin and is attached by a somewhat more narrow neck or pedicel to a rectangular or stellate base anchoring the scale into the integument. The crown normally exhibits a large medial ridge or keel which runs longitudinally along the midline and is flanked along either side by one or more lateral keels (Compagno, 1979). These

keels often extend the posterior margin of the crown into medial and lateral cusps. This general arrangement is found in many widely separated phylogenetic groups (White, 1937).

A comparison of various crown dimensions with that of the theoretical, grooved surface proposed by Walsh and Weinstein is difficult to obtain from the existing literature for a number of reasons. Although several authors have presented representative scales from various shark species (Bigelow and Schroeder, 1948; Castro, 1983; Radcliffe, 1916), it is often difficult to determine their actual shapes and dimensions from these drawings. In addition, a great deal of variation is found between scales from different locations on a single specimen, including not only their general shape (Applegate, 1967; Compagno, 1979; Daniel, 1928; Sayles and Hershkowitz, 1937) but also the angle of inclination of the crown to the body surface (Chernyshov and Zayets, 1970) as well. Finally, all living species of galeoids are characterized by a synchronomorial scale type (Compagno, 1973) whose size and shape often change dramatically through replacement (Garrick, 1960; Radcliffe, 1917; Raschi, et al., 1982; Reif, 1974). The aims of this study then, are to compare the surface structure of scale crowns from a variety of shark species with the above model as well as to examine what changes may occur to these scales during their replacement.

METHODS AND MATERIALS

A total of 129 skin samples from 15 species of sharks was examined (Table I). The majority of the fish were obtained from either sportfishing tournaments (Virginia Beach and Charleston Shark fishing clubs) or through the longline surveys conducted by the Virginia Institute of Marine Science (VIMS) during the summers of 1981 and 1982. Additional material was also collected from a variety of other sources including the R/V Columbus Iselin cruise CI-7803, Taute Bros. (Marathon, Fla.), Pflueger Marine Taxidermy and a number of individual sportfishermen. Collection data is presented in Appendix I. Latitudes and longitudes are not available for those specimens collected at fishing tournaments in Charleston, S.C.; for specimen #64 on loan from the Institut Fondamental d'Afrique Noire and for the two aquarium specimens, #82 and 83. Nomenclature follows Robins et al. (1980).

Skin patches, measuring 25-50 sq. cm, were removed from just below the anterior margin of the first dorsal fin. Subsamples were washed and placed in a concentrated solution of sodium hypochlorite to remove the scales while the remainder of the sample was frozen for future examination. Individual scales were washed in several rinses of distilled water and air dried. Approximately fifteen scales from each sample were then mounted on an aluminum SEM stub and coated with gold-palladium by vacuum evaporation.

Four sets of measurements were made on five separate scales from each stub (figure 1). Initially, the length and width of each crown was taken from directly above its surface (0-20 degree tilt). Secondly, the

3

Table I. Summary of the material collected for scale examination.

Species	Number of individuals examined	Size range (total length in cm)
Carcharhinus falciformis	5	103-268
Carcharhinus leucas	4	169-278
Carcharhinus limbatus	5	148-173
Carcharhinus obscurus	17	86-334
Carcharhinus plumbeus	30	59-216
Carcharhinus signatus	8	76-222
Galeocerdo cuvieri	12	156-404
Ginglymostoma cirratum	2	72-77
Isurus oxyrinchus	3	132-182
Mustelus canis	10	37-127
Odontaspis taurus	9	165-247
Prionace glauca	13	34-348
Rhizoprionodon terraenovae	7	40-106
Sphyrna lewini	3	54-225
Sphyrna mokarran	1	252
	129	

Fig. 1. Scale measurements used in this study. Abbreviations are as follows: "A", crown widths; "B", crown length; "C", primary inter-keel distance; "D", primary keel height; 1°, 2°, 3° are the primary, secondary, and tertiary keels. (Redrawn by J. Estep)
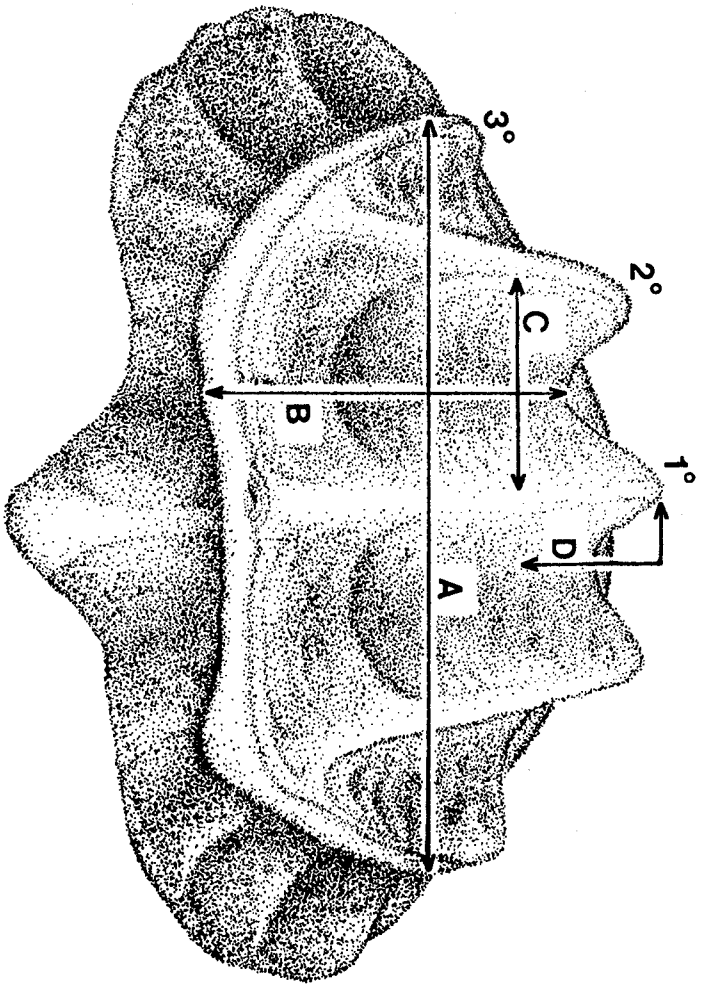
inter-keel distance, or spacing, was measured between the peaks of adjacent keels. These were taken from a posterior aspect with the crown surface tilted between 30 and 50 degrees. The bilaterally averaged pair of spacings between the medial, or primary keel, and the adjacent lateral, or secondary keels, is designated as the primary value. Similarly, that pair of distances between the secondary keels and their adjacent lateral, or tertiary keels, are considered the secondary values. Similar nomenclature is used for each subsequent pair. The mean was then calculated for all the averaged values for each of these pairs on a crown. Finally, the heights of the ridges were measured with the crown tilted so as to provide a view parallel with its surface (70-90 degrees tilt). Pairs of the secondary and tertiary keels were averaged and compared with the primary ridge. A mean value for all the keels on each crown was also calculated. All measurements were taken directly from the CRT screen to the nearest five microns, with specimens at magnifications between 180 and 200 X. The actual angle to which a scale was tilted depended on both the angle at which the crown sat on the scale base as well as on variations of the seating of the scale on the stub. In addition to the above measurements, the number of keels on each scale was counted and a photograph of one scale from each specimen taken for future reference. The regressions of all these measurements on body lengths for each species follows Snedecor and Cochran (1967) with significance set at the 99% level.

RESULTS

Scale Types

Three different morphological types of scales were distinguished in this study. The first (figure 3) is characterized by a relatively thin crown exhibiting a single, prominent primary keel and a variable number of lateral, often smaller, keels. The anterior margin is normally evenly rounded with the posterior either emarginate or smooth. This type is found on all specimens in the genus Carcharhinus as well as on Isurus oxyrinchus, Prionace glauca, Rhizoprionodon terraenovae, Sphyrna lewini and S. mokarran. The second morphological type (figure 19) exhibits a similarly thin crown with a medial pair of primary keels flanked by successive pairs of lateral keels. It has a typically blade-like, or lanceolate shape, with a broadly rounded anterior margin and a sharply pointed posterior margin. This type is found only on specimens of Mustelus canis in this study, but appears to be typical of all the species in the genus Mustelus (Bigelow and Schroeder, 1948), except for the South American M. dorsalis (Bigelow and Schroeder, 1940). The third type (figure 21) is characterized by a very thick crown and correspondingly heavy base. The scale necks are disproportionately thicker and tend to be somewhat reduced in height. The crown exhibits a very prominent primary keel with a somewhat smaller pair of secondary keels. The margins are evenly rounded with the absence of any noticeable cusps. This type of scale is found on Galeocerdo cuvieri, Odontaspis taurus and Ginglymostoma cirratum.

8

Microrelief

In addition to the normal ridges, approximately 50% of the scales examined in this study also exhibit additional microrelief. This microrelief is typically arranged in the form of hexagonal or octagonal pockets (figure 2), often becoming compressed along the scale margin. The surface area covered by microrelief, when present, varies from only the anterior margin to the entire dorsal surface of the scale (Table II). It is found in varying degrees on all specimens of C. falciformis, C. signatus, M. canis, P. glauca, R. terraenovae, S. lewini, S. mokarran; on only a few specimens of C. leucas, C. limbatus, C. obscurus, C. plumbeus; and is completely absent from all specimens of G. cuvieri, I. oxyrinchus, G. cirratum and O. taurus.

By dividing all of the scales into two artificial groups; one designated as completely covered, with microrelief covering between 75% and 100% of the crown surface (figure 2, 18) and the other designated as only partially covered, with microrelief covering from 25% to 50% (figure 5a, 19), it becomes apparent that the relative degree of microrelief development reflects the relative size of the specimen within each species (compare with Appendix I). In those species which contain specimens exhibiting both complete and partial covering, such as C. falciformis, C. obscurus, C. plumbeus, P. glauca and R. terraenovae, only the smallest individuals have completely covered scales while those from larger specimens tend to be only partially covered. Furthermore, several species examined, such as C. leucas, C. limbatus and M. canis, exhibited only partially covered scales in addition to those completely devoid of any microrelief; whereas none contained only specimens with

9

Fig. 2. Scanning electron micrographs of scales from _Prionace_ _glauca_ showing the presence of microrelief. (a) From a 34 cm TL male (specimen no. 106) at 190 X magnification, (b) From a 46 cm TL female (specimen no. 109) at 520 X magnification.
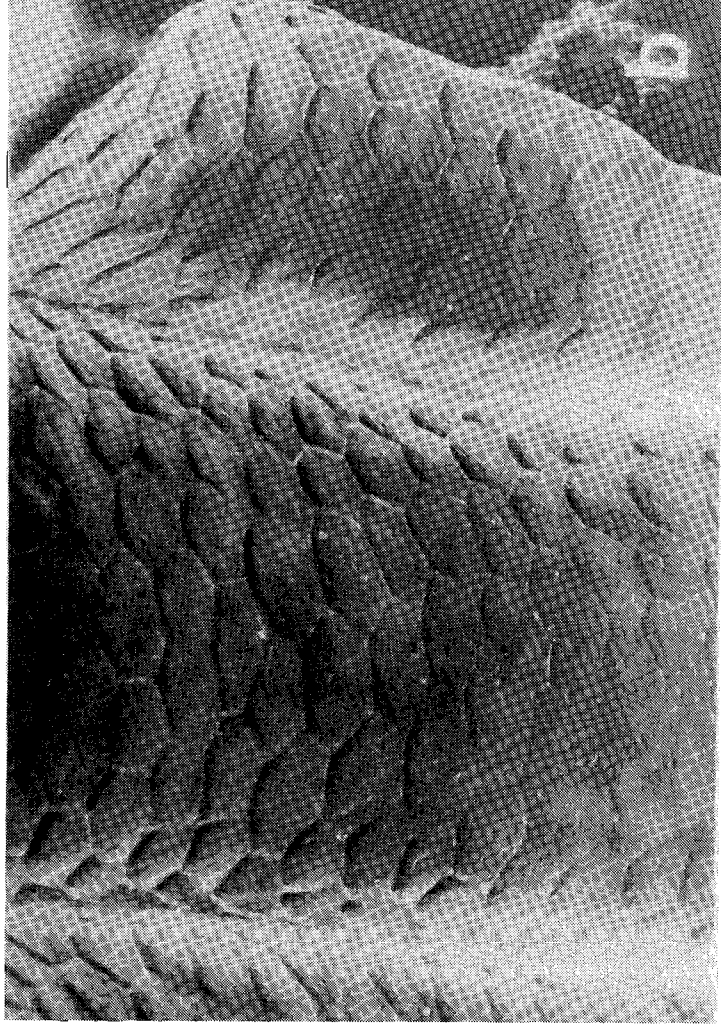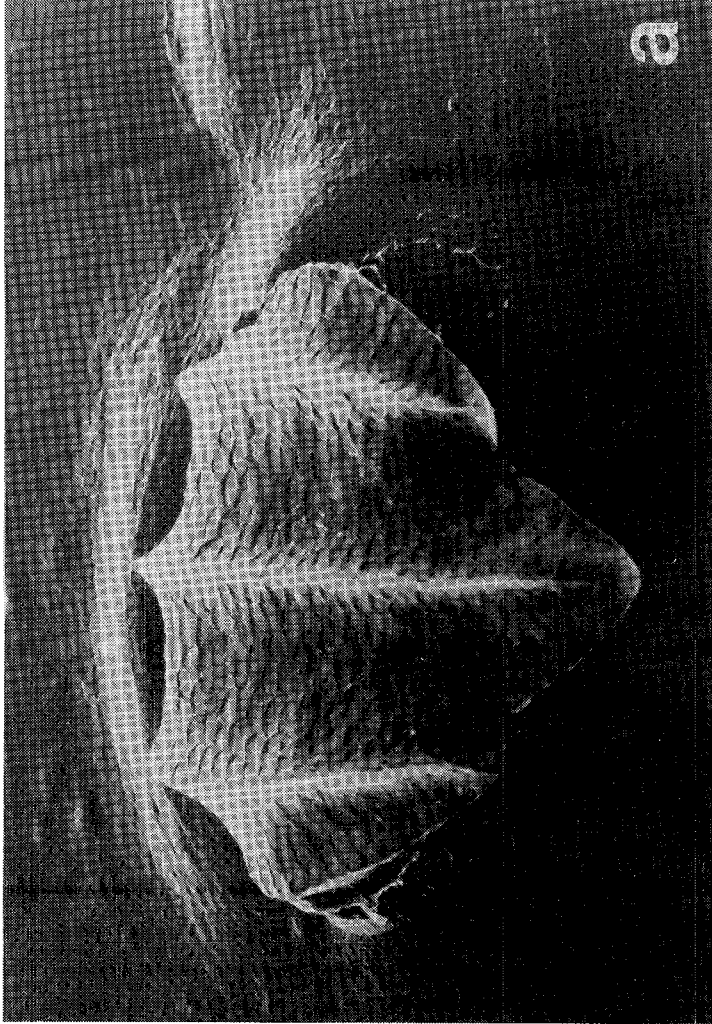
Table II. Occurrence of microrelief

	Specimen number	
	Complete	Partial
C. falciformis	1-3	4, 5
C. leucas		6
C. limbatus		13, 14
C. obscurus	15-17, 19	18, 20-23, 25-31
C. plumbeus	32-40	41
C. signatus	62-64, 67-69	65, 66
M. canis		87-96
P. glauca	106-115	116-118
R. terraenovae	119-121	122-125
S. lewini	126	127, 128
S. mokarran	129	

completely covered scales. Both pieces of evidence strongly suggest that microrelief is more prevalent on smaller scales from smaller specimens, decreasing in relative degree on larger replacement scales. The significance of microrelief will be further discussed in a subsequent report.

The dimensions of the scale crowns exhibit considerable intraspecific variation and will be used to characterize scales from each individual species.

Species Descriptions

C. plumbeus

The greatest number of scales were examined from this species and may therefore provide the most reliable picture of postpartum, ontogenetic scale development. Scales were removed from specimens at 5 cm intervals between total lengths of 59 to 216 cm. This accounts for 83% of the total size range of between 56 cm (Bigelow and Schroeder, 1948) and 249 cm (Garrick, 1982) previously recorded for this species. The scale crown is moderately thick with very prominent ridges. It is generally ovoid in shape, with broadly rounded margins and a relatively short pedicel (figure 3).

The width of the crown is greater than the length throughout the size range studied (figure 4). Widths increase ontogenetically with replacement at a rate of 3.02 microns/cm ($r = 0.93**$). This rate yields an estimated crown width of from 150 microns to 703 microns over the total size range. Actual measurements range from 170 microns (specimen # 37) to 785 microns (specimen # 61). Crown lengths also increase

Fig. 3. Scanning electron micrograph of the posterior margin of

scales from <u>Carcharhinus</u> <u>plumbeus</u>. (a) From a 88 cm TL female (specimen

no. 37), (b) From a 188 cm TL female (specimen no. 57).

15

Fig. 4. Scale morphometrics for C. plumbeus. Each data point represents the average of five measurements. Spacings and heights are average values for all the keels on each crown. Line equations are calculated from the total number of individual measurements. The equation describing the increase in the number of keels is based on only those specimens larger than 110 cm TL (specimen no. 42-61).

16

Carcharhinus plumbeus
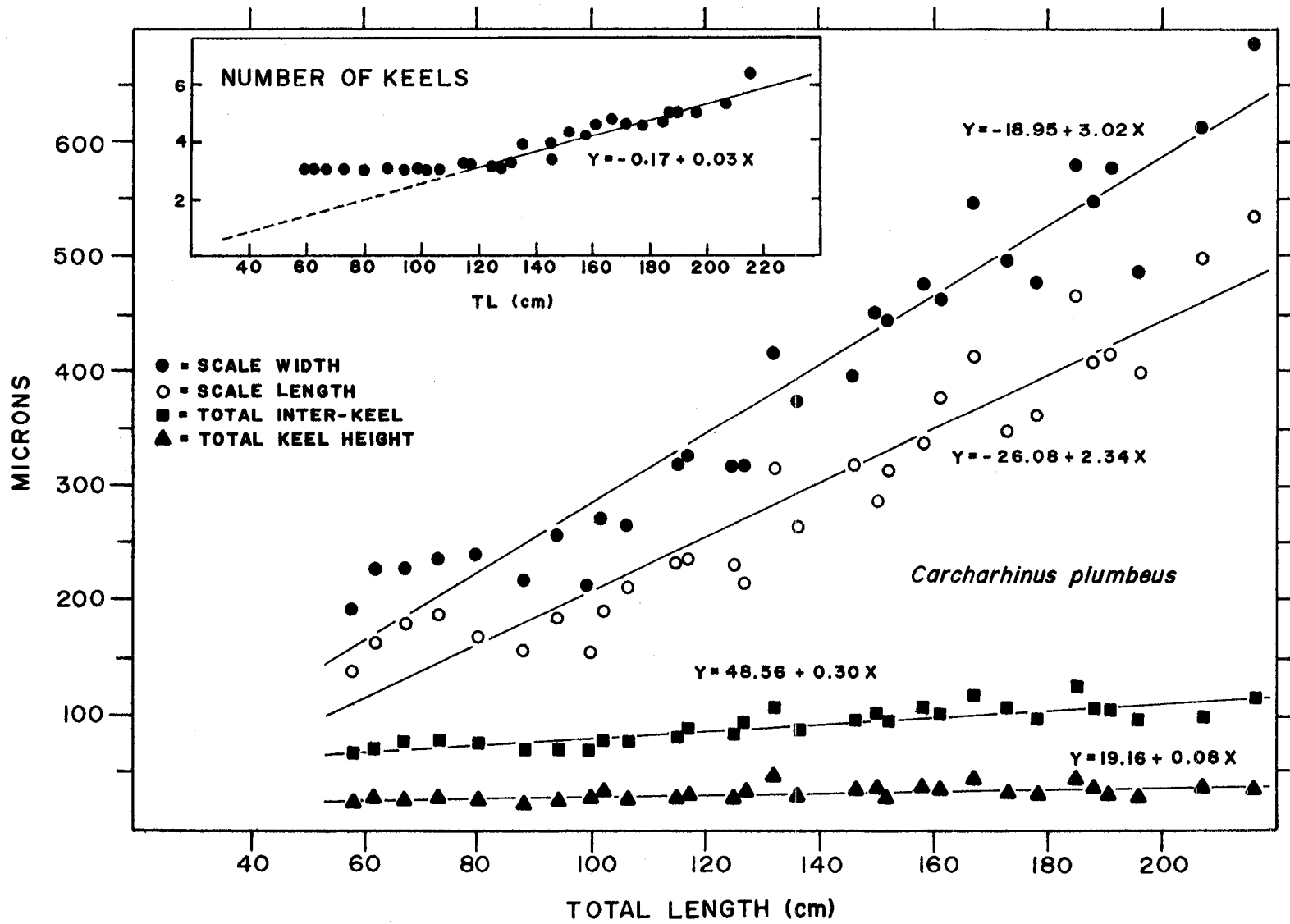
ontogenetically at a rate of 2.34 microns/cm (r = 0.91**), yielding a corresponding estimated range of from 105 microns to 533 microns over the total size range. Actual measurements range from 125 microns (specimen # 32, 37) to 625 microns (specimen # 61).

Smaller specimens of C. plumbeus exhibit scales with only three prominent ridges, whereas on fish longer than 120 to 140 cm TL, that number increases with the replacement scales at a rate of 0.03 keels/cm TL (t = 6.32**). The averaged, total inter-keel distance on a single crown ranges from 55 microns (specimen # 38) to 125 microns (specimen # 53, 56, 61). These spacing values also increase ontogenetically at a rate of 0.30 microns/cmTL (t = 16.62**). This rate yields estimated spacings of from 65 microns to 120 microns. The primary inter-keel distance varies from 55 microns (specimen # 38) to 150 microns (specimen # 61), while the average secondary inter-keel distances are between 75 microns to 183 microns. This corresponds to a decrease of between 6.1% and 31.0% (average = 18.6%) from the primary.

Keel heights tend to remain relatively constant, with an increase in the average height for all keels on a single crown of only 0.08 microns/cm TL (t = 7.74**). Total averaged heights range from 18 microns (specimen # 37, 41) to 52 microns (specimen # 46), while predicted values range from only 24 microns to 38 microns over the total size range. The primary keel is normally from 20 microns (specimen # 32, 34, 37, 38, 39, 41) to 70 microns (specimen # 53) high. The secondary keels exhibit an average reduction in height from that of the primary by 10.9% (ranging from an increase of 33% to a decrease of 40%), with the bilaterally averaged measurements ranging between 18 microns (specimen #

18

32, 41) and 55 microns (specimen # 53). Tertiary keels show a still greater reduction of 45.7% from the primary keel (ranging from 7% to 75%), with values ranging between 5 microns (specimen # 43) and 43 microns (specimen # 61)

C. obscurus

This species is larger than C. plumbeus, ranging from 69 cm (Bass, et al, 1973) to a maximum of 363 cm (Garrick, 1982). Scales were examined from over 84% of this range. By comparison, these scales are generally smaller. Their crowns appear much thinner and less heavily sculptured (figure 5). The anterior margin is broadly rounded while that of the posterior is always emarginate.

Scales are wider than long only on specimens smaller than approximately 190 cm (figure 6), ranging from 180 microns (specimen # 22) to 500 microns (specimen # 31). These values increase ontogenetically at a rate of 0.66 microns/cm TL ($r = 0.85^{**}$), resulting in a somewhat smaller estimated range of from 229 microns to 418 microns. Similarly, the length of the crown increases on replacement scales at a rate of 0.99 microns/cm TL ($r = 0.87^{**}$). Actual lengths measured between 170 microns (specimen # 22) and 560 microns (specimen # 31) as compared with the projected estimated values of from 188 microns to 472 microns.

The number of ridges range from 3 on smaller specimens to 7 on the larger. This number increases at a rate of 0.01 keels/cm TL which is not significantly different from 0 ($t = 2.21$). The average total inter-keel distance increases with body length at a rate of 0.05 microns/cm TL ($t =$

Fig. 5. Scanning electron micrograph of scales from <u>Carcharhinus</u> <u>obscurus</u> taken from the posterior, (a) From a 127 cm TL male (specimen no. 23), (b) From a 334 cm Tl female (specimen no. 31).
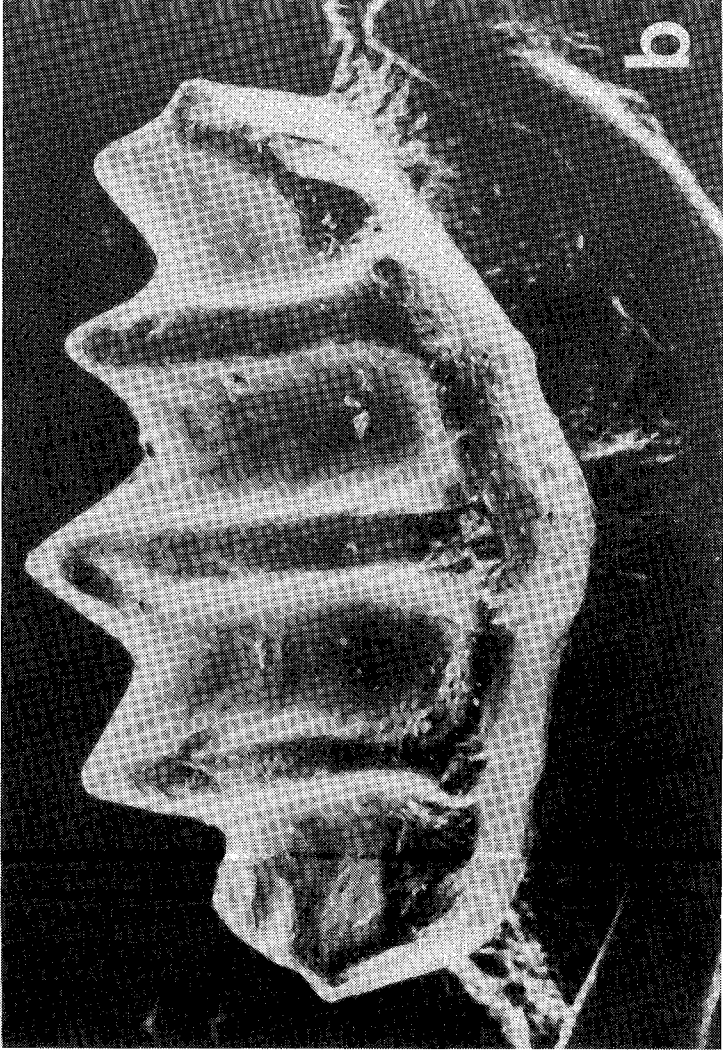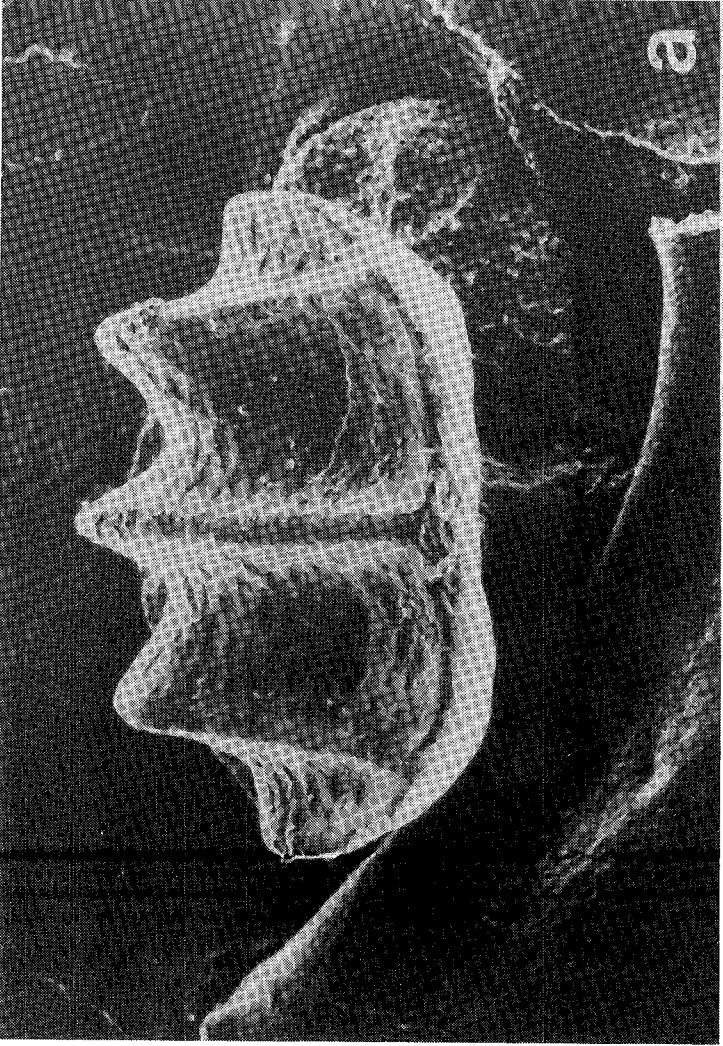
a

b

21

Fig. 6. Scale morphometrics for C. obscurus. Each data point

represents the average of five measurements. Spacings and heights are

average values for all the keels on each crown. Line equations are

calculated from the total number of individual measurements.

Y = 119.99 + 0.99 X

Y = 183.07 + 0.66 X

Y = 49.31 + 0.05 X

Y = 9.84 + 0.03 X

Carcharhinus obscurus

● = SCALE WIDTH
○ = SCALE LENGTH
■ = TOTAL INTER-KEEL
▲ = TOTAL KEEL HEIGHT

NUMBER OF KEELS

Y = 4.08 + 0.01 X

TL (cm)

MICRONS

TOTAL LENGTH (cm)

23

2.792*), with averaged values between 41 microns (specimen # 23) and 76 microns (specimen # 31). The estimated average distance over the total size range of this species is between 58 and 67 microns. Primary values range from 53 microns (specimen # 19, 23) to 95 microns (specimen # 31), while secondary distances exhibit a decrease from that of the primary by from 13% to 45% (average = 30%). Secondary spacings range from 30 microns (specimen # 23) to 78 microns (specimen # 31).

Keel heights are again the most constant parameter, increasing with body length at a rate of only 0.03 microns/cm TL (t = 3.71**). Average total measurements from a single crown are between 8 microns (specimen # 22) and 26 microns (specimen # 31). Estimated values over the recorded size range of this species are from 12 to 21 microns. The height of the primary keel ranges from 10 microns (specimen # 22) to 45 microns (specimen # 31), while the height of the secondary keels range only from 8 microns (specimen # 22) to 38 microns (specimen # 31), an average reduction of 32.6%. The bilaterally averaged heights of the tertiary keels show a further reduction to 58.1% of the primary, with values ranging between 5 microns (specimen # 15, 16, 17, 19, 21, 22, 23) and 20 microns (specimen # 31).

P. glauca

Scale crowns from this species range in shape from thin and blade-like on smaller specimens (figure 2a) to thicker and more angular on larger specimens (figure 7). Their general outline is continuous, with little indication of cusps along the posterior margin. Scales were sampled from 89% of the recorded total size range of from 53 cm to 383

Fig. 7. Scanning electron micrograph of the posterior margin of

scales from _Prionace glauca_, (a) From a 190 cm TL male (specimen no. 112),

(b) From a 248 cm TL male (specimen no. 116).
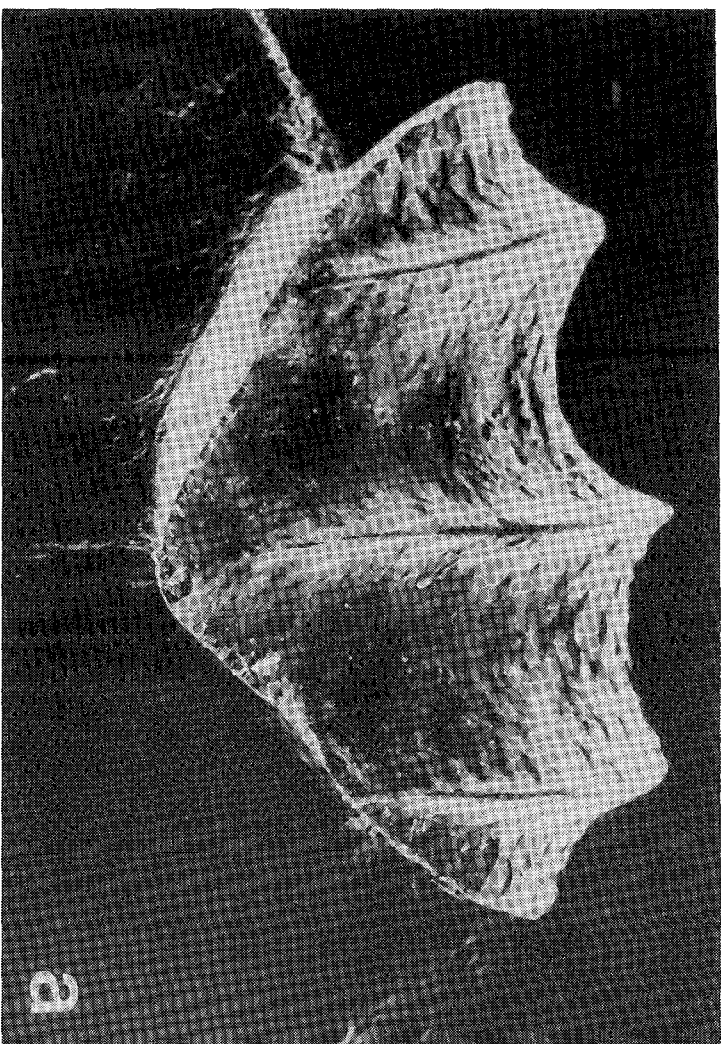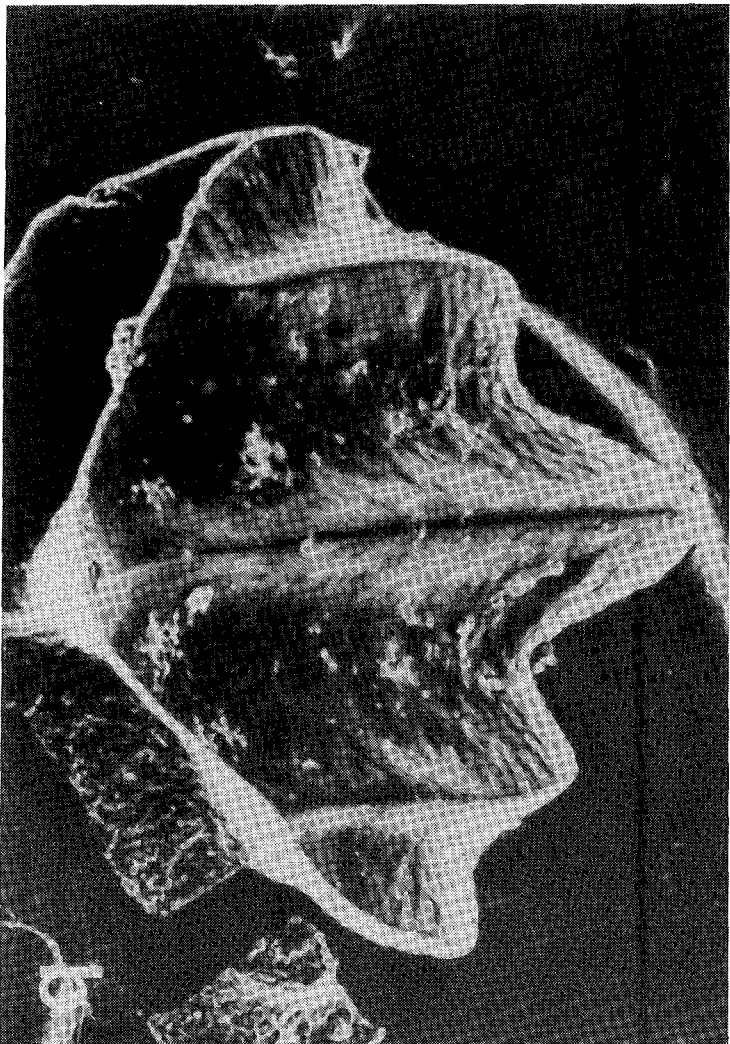
cm (Bigelow and Schroeder, 1948). These samples, however, include near-term embryos; excluding which, the postpartum individuals account for only 55% of this size range.

Scales are longer than wide only on specimens shorter than 180 to 200 cm (figure 8). Lengths range from 235 microns (specimen # 106) to 455 microns (specimen # 114); postpartum values increasing with body length at a rate of 0.54 microns/cm (r = .536**). This rate projects estimated values of from 226 microns to 404 microns over the total size range. However, with the inclusion of the scales from the embryos, lengths decrease with body length at a rate of 0.08 microns/cm TL, a slope, however, not significantly different from 0 (t = 1.13). Scale widths also increase ontogenetically at a rate of 0.82 microns/cm (r = .638**) for only postpartum individuals; with values ranging from 205 microns (specimen # 106, or 235 microns for the smallest postpartum individual of specimen # 116) to 560 microns (specimen # 118). These slopes yield estimated widths of from 271 microns (187 microns for just postpartum) to 400 microns (459 microns for just postpartum).

While some variation exists in the number of keels on each crown, they appear to remain at a nearly constant value of 3 keels/crown over the total size range. The average distance between the keels on a single crown ranged from 73 microns (specimen # 113) to 128 microns (specimen # 113, 117, 118), increasing on replacement scales at a rate of 0.06 microns/cm (t = 3.84**). Estimated values over the total size range are from 97 microns to 116 microns. The primary inter-keel distance ranges between 75 microns (specimen # 106) and 128 microns (specimen # 113, 117, 118); while secondary values were somewhat smaller, ranging from 53
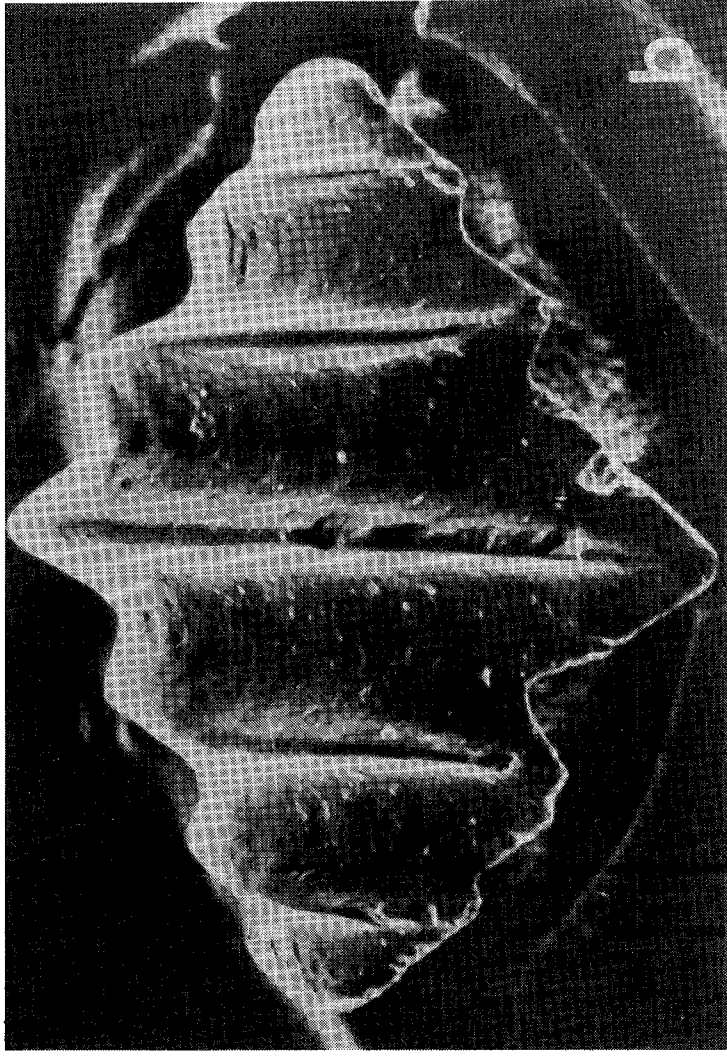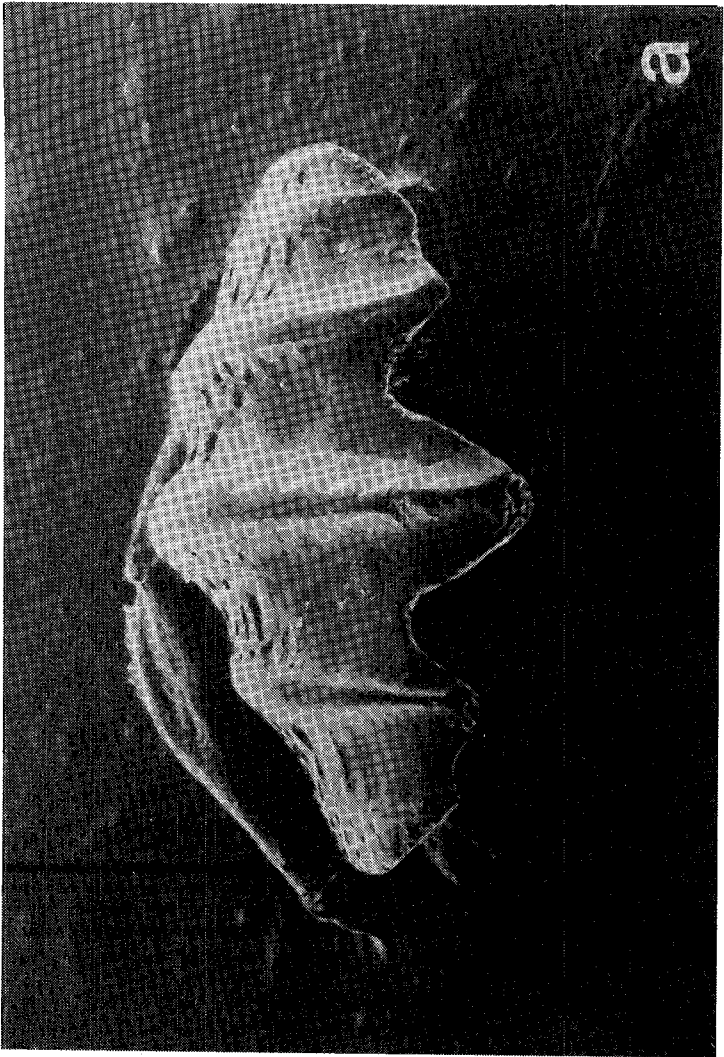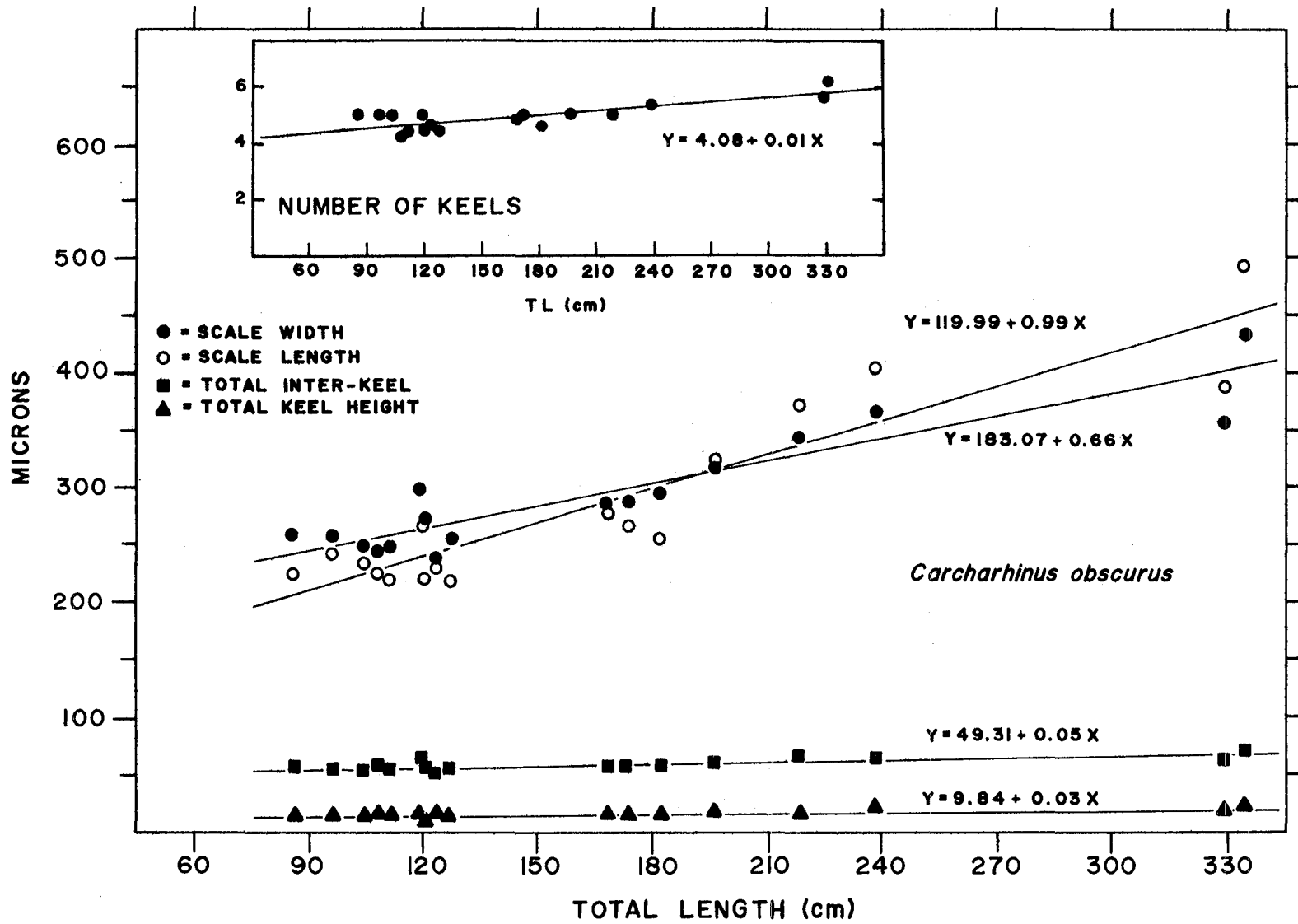
Fig. 8. Scale morphometrics for P. glauca. Each data point represents the average of five measurements. Spacings and heights are average values for all the keels on each crown. Line equations are calculated from the total number of individual measurements. Solid lines representing scale lengths and widths are based on only post-partum individuals; dotted lines (equations in parentheses) include measurements from the embryos.

Prionace glauca

Y = 144.81 + 0.82X

(Y = 250.69 + 0.39X)

Y = 197.67 + 0.54X

(Y = 350.59 − 0.08X)

Y = 93.35 + 0.06X

Y = 26.90 + 0.03X

O = SCALE LENGTH
● = SCALE WIDTH
■ = TOTAL INTER-KEEL
▲ = TOTAL KEEL HEIGHT

NUMBER OF KEELS

Y = 3.07 + 0.00X

TL (cm)

MICRONS

TOTAL LENGTH (cm)

microns (specimen # 113) to 73 microns (also specimen # 113). This amounts to a reduction from the primary value of from 34.1% to 43.2% (average = 38.9%). The average heights for all the keels on a single crown vary from 14 microns (specimen # 113) to 45 microns (specimen # 116), increasing ontogenetically at a rate of 0.03 microns/cm (t = 3.59**). This rate yields an estimated height of from 28 microns to 38 microns. The primary keels were the largest, measuring from 20 microns (specimen # 106) to 70 microns (specimen # 116) high. Bilaterally averaged heights for the secondary keels exhibited an average reduction of 20% from that of the primary keels (ranging from an increase of 21.4% to a decrease of 53.6%), with values between 15 microns (specimen # 113) and 43 microns (specimen # 108, 117). Tertiary keels exhibit a further reduction of from 81% to 85% (average = 83%), ranging in size from 5 microns (specimen # 113) to 10 microns (specimen # 111, 113).

C. signatus

Scales removed from this species (figure 9) exhibit relatively thin crowns with relatively low keels. They are typically semicircular in shape with a smooth anterior margin and a weakly emarginate posterior margin. Scales were removed from specimens over 91% of the recorded total size range of from 67 cm (Bigelow and Schroeder, 1948) to 227 cm (Raschi et al., 1982).

Scales are longer than wide (figure 10) on individuals up to between 100 cm and 120 cm long, above which they are wider than long. Widths of individual crowns range from 190 microns (specimen # 63) to 480 microns (specimen # 68), increasing with body length at a rate of 1.16

Fig. 9. Scanning electron micrograph of the posterior margin of scales

from <u>Carcharhinus signatus</u>, (a) From a 94 cm TL female (specimen no. 63),
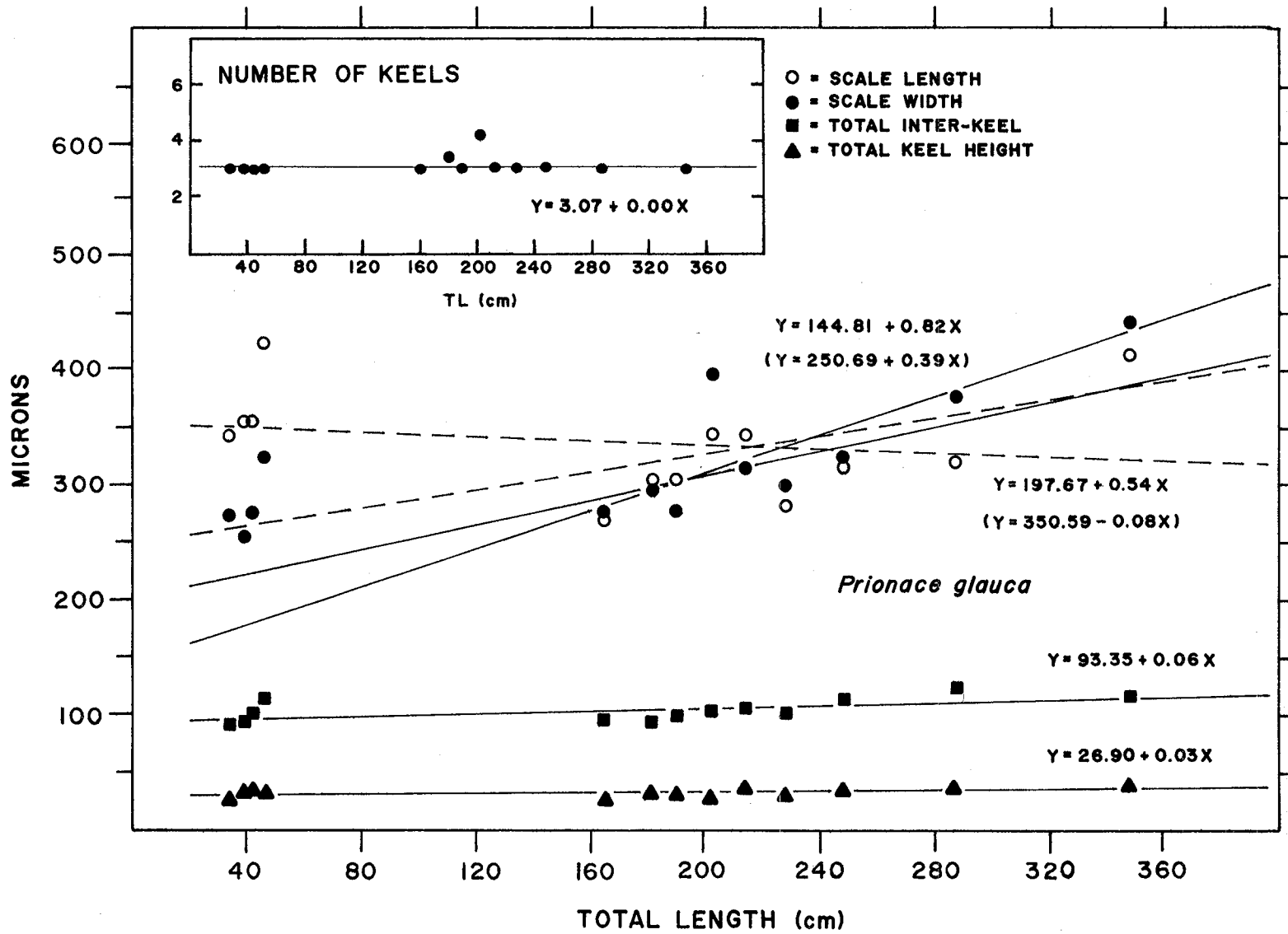
(b) From a 217 cm TL male (specimen no. 68).

Fig. 10. Scale morphometrics for C. signatus. Each data point represents the average of five measurements. The spacings and heights are average values for all the keels on each crown. Line equations are calculated from the total number of individual measurements.

Legend:
- O = SCALE LENGTH
- ● = SCALE WIDTH
- ■ = TOTAL INTER-KEEL
- ▲ = TOTAL KEEL HEIGHT

Inset plot (NUMBER OF KEELS vs TL (cm)): $Y = 0.82 + 0.03X$

$Y = 140.93 + 1.16X$

$Y = 205.87 + 0.57X$

Carcharhinus signatus

$Y = 86.08 - 0.09X$

$Y = 23.35 + 0.00X$

MICRONS

TOTAL LENGTH (cm)

34

microns/cm TL (r = 0.90**). This results in an estimated average value of between 218 and 404 microns over the recorded size range. Lengths of individual scales range from 200 microns (specimen # 63) to 390 microns (specimen # 66), increasing with body length at a rate of 0.57 microns/cm TL (r = 0.73**). This similarly results in an estimated average value of between 244 and 335 microns.

The number of keels on an individual scale crown varies from 3 on the smaller individuals to 7 on the larger, increasing with body length at a rate of 0.03 keels/cm TL (t = 13.768**). The average distance between all the keels on a particular crown varied from 58 microns (specimen # 66) to 93 microns (specimen # 62), decreasing with body length at a rate of 0.09 microns/cm TL (t = 6.04**). This yields an estimated average inter-keel distance of from 79 microns to 63 microns. The primary inter-keel distance ranges from 65 microns (specimen # 63) to 95 microns (specimen # 69), while the secondary spacing decreases from the primary by between 6.7% and 37.1% (average of 19.6), ranging from 55 microns (specimen # 64) to 73 microns (specimen # 69).The values of the tertiary inter-keel distances also decreases from those of the primary by from 34.5% to 59.4% (average = 45.8%), ranging from 33 microns (specimen # 68) to 53 microns (specimen # 66, 69). Average keel heights on a single crown remains a constant 23 microns throughout the range of body lengths, with actual measurements ranging only from 19 microns (specimen # 68) to 30 microns (specimen # 65). The primary keel is larger than the lateral keels, ranging in height from 25 microns (specimen # 62, 63, 67) to 45 microns (specimen # 69). The bilaterally averaged heights of the secondary keels decreases from the primary keel heights by from 0% to

35.7% (average = 16.8%), ranging from 18 microns (specimen # 62, 66) to 40 microns (specimen # 69). Similarly, the bilaterally averaged height of the tertiary keels decreases from the primary by from 25% to 61.1 % (average = 42.7%), ranging from 10 microns (specimen # 63) to 28 microns (specimen # 69).

R. terraenovae

Scales were examined from specimens covering 72% of the previously published size range of from 28 cm (Bigelow and Schroeder, 1948) to 120 cm (Castro, 1982). Crowns are relatively thin, with keels somewhat less pronounced than in the previous species (figure 11). The general outline of the posterior margin is very angular, with noticeable cusps present on scales of smaller specimens.

Crown lengths are greater than widths only on specimens smaller than from 95 cm to 105 cm TL (figure 12). Crowns range from 170 microns (specimen # 119) to 355 microns (specimen # 124) wide, increasing ontogenetically at a rate of 2.28 microns/cm TL (r = 0.86**). This rate projects estimated values of between 133 microns to 310 microns over the published size range. Similarly, scales lengths range from 225 microns (specimen # 119) to 350 microns (specimen # 123, 124), again increasing ontogenetically at a rate of 1.13 microns/cm TL (r = 0.66**) and resulting in estimated lengths of from 220 microns and 308 microns over the recorded total lengths.

Scale have from 3 to 5 ridges which increase on replacement scales at a rate of 0.03 keels/cm TL (t = 7.184**). Average spacings between all the keels on a single crown range from 50 microns (specimen # 120)

36

Fig. 11. Scanning electron micrograph of the posterior margin of scales from _Rhizoprionodon terraenovae_, (a) From a 40 cm TL male (specimen no. 119), (b) From a 101 cm TL female (specimen no. 124).
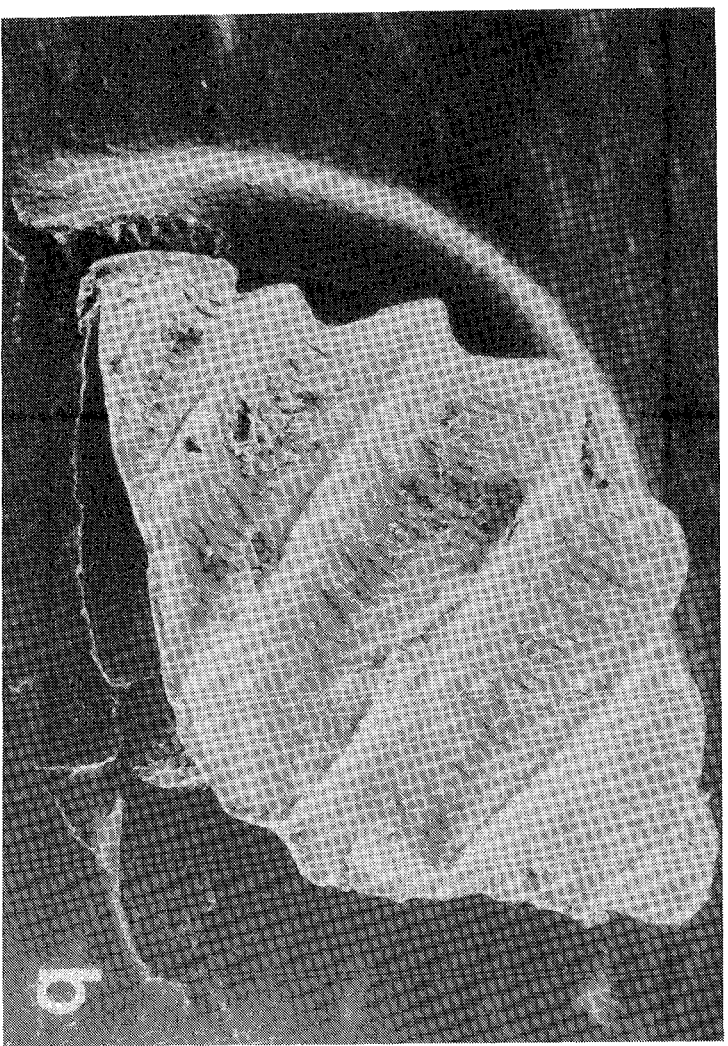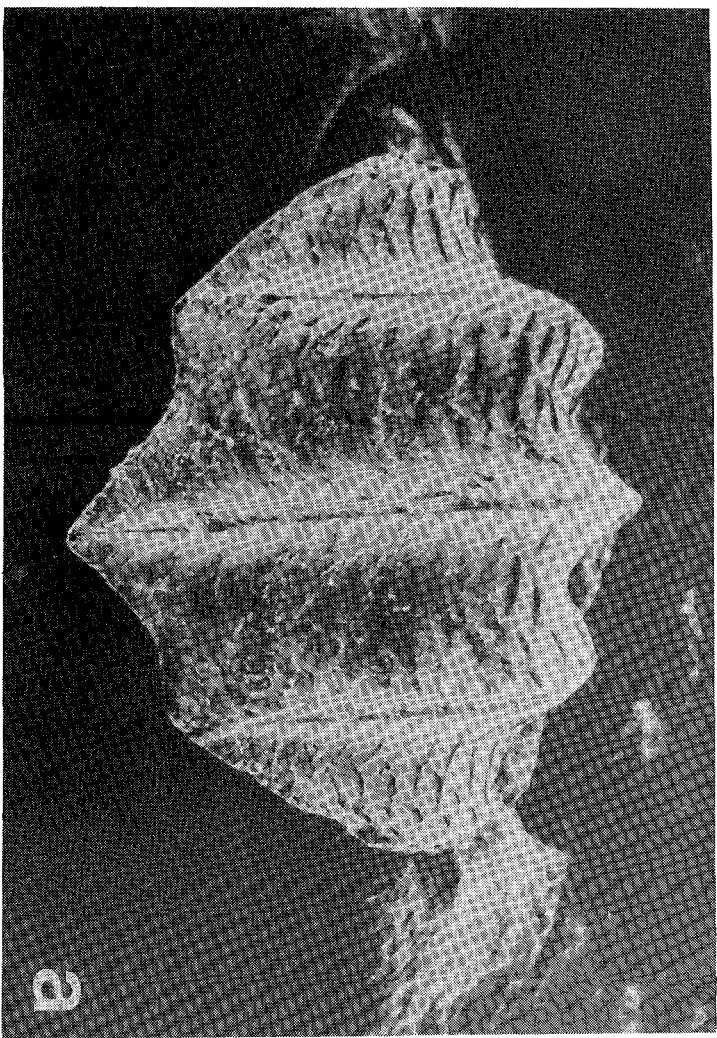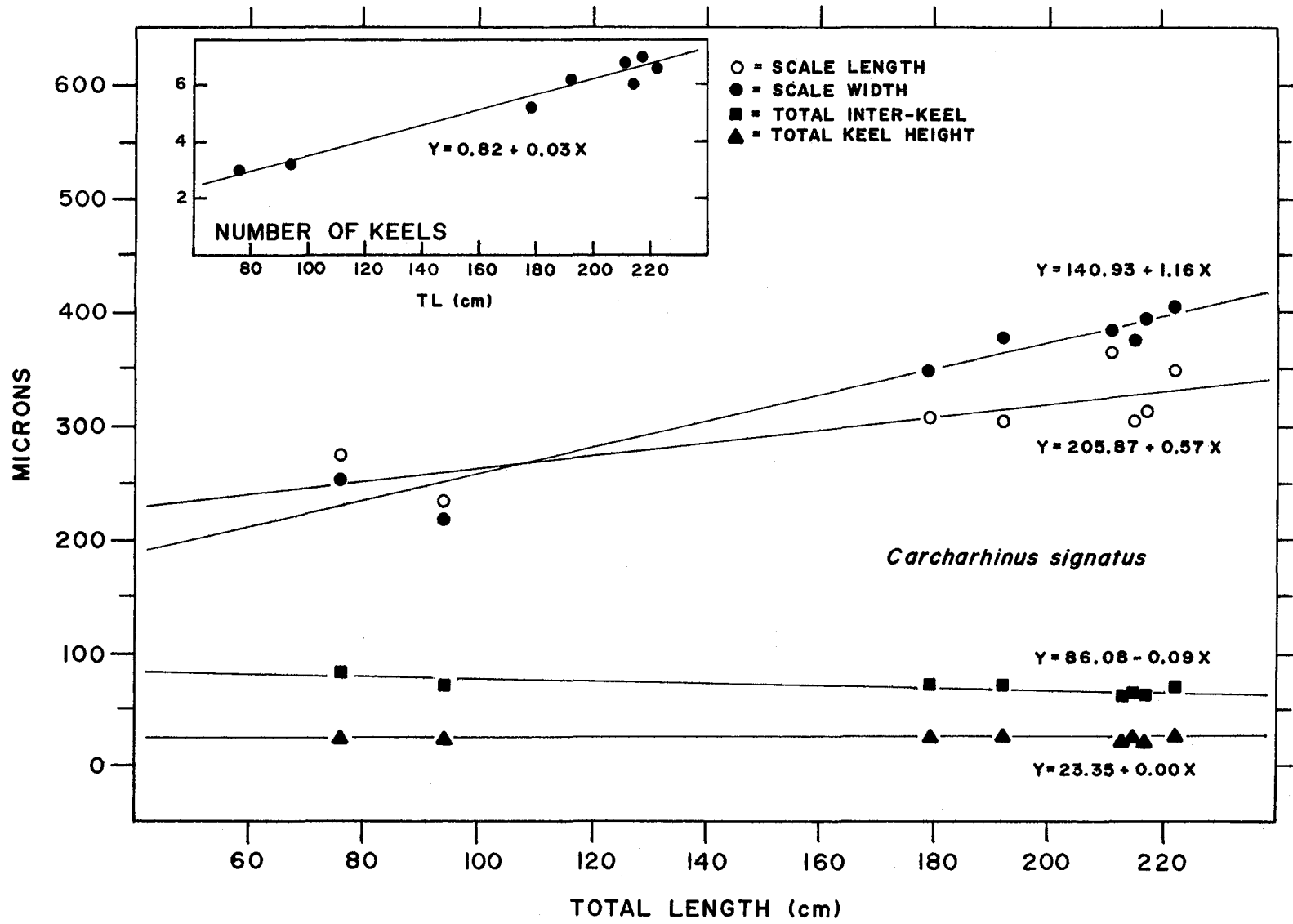
Fig. 12. Scale morphometrics for R. terraenovae. Each data point represents the average of five measurements. The spacings and heights are average values for all of the keels on each crown. Line equations are calculated from the total number of individual measurements.
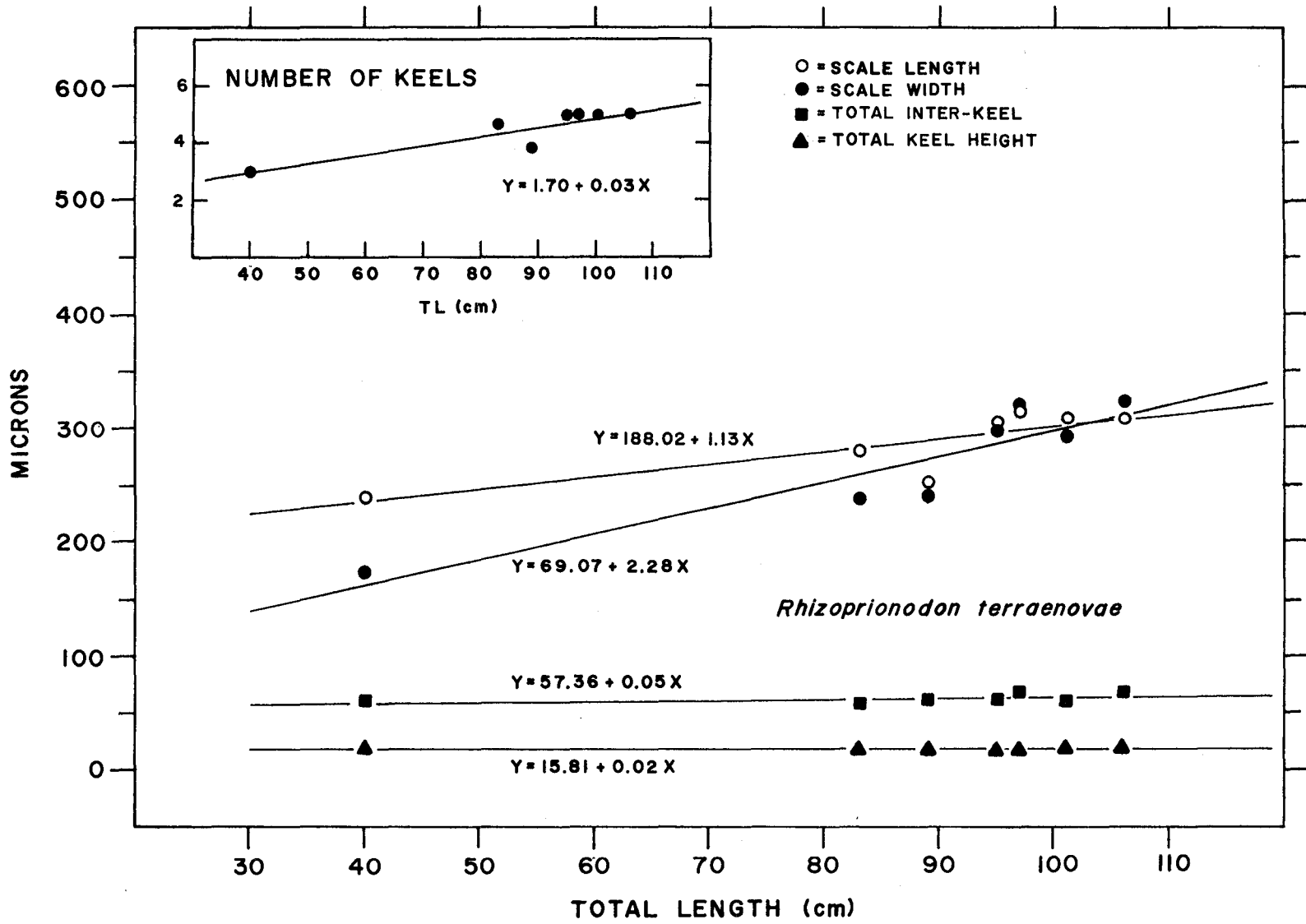
to 70 microns (specimen # 122, 123, 125), remaining a constant 57 microns throughout increasing body length (t = 1.17). The primary inter-keel distance is from 58 microns (specimen # 120, 124) to 80 microns (specimen # 122), while secondary spacings range from 43 microns (specimen # 120) to 63 microns (specimen # 123). This amounts to a decrease from that of the primary of between 14.3% and 32.1% (average = 22.4%). The average heights for all the keels on a single crown vary from 14 microns (specimen # 120, 122, 123) to 23 microns (specimen # 125), and increase on replacement scales at a rate of only 0.02 microns/cm TL, with a slope not significantly different from 0 (t = 0.920). This yields an average height of 16 microns throughout this species' size range. The primary keels are between 15 microns (specimen # 122, 123) and 35 microns (specimen # 125) high, while bilaterally averaged secondary keels range from 13 microns (specimen # 119) to 25 microns (specimen # 124, 125) high. This amounts to an average reduction from the primary keel of 17.5% (ranging from an increase of 16.7% to a decrease of 40.0%). Similarly, bilaterally averaged tertiary keels are from 5 microns (specimen # 120) to 18 microns (specimen # 124) high, amounting in a reduction from the primary keel heights of from 25% to 80% (average = 47.7%).

C. falciformis

Scales were examined on specimens from only slightly more than 64% of the recorded size range of from 73 cm (Poll, 1951) to 330 cm (Castro, 1981; the length of 350 cm listed by Blache, et al. (1970) appears to be a typographical error). These scales are relatively small on even the

41

largest individuals, with weakly sculptured crowns (figure 13). They exhibit a generally subcircular outline with broadly rounded margins.

Scales are wider than long (figure 14) on specimens larger than from 90 cm to 110 cm TL. Widths range from 150 microns (specimen # 3) to 330 microns (specimen # 5), increasing on the replacement scales at a rate of 0.77 microns/cm TL (r = 0.915**). This amounts to an average estimated scale width of between 163 microns and 342 microns. Scale lengths range from 160 microns (specimen # 3) to 290 microns (specimen # 5), and increase ontogenetically at a rate of 0.50 microns/cm TL (r = 0.881**), with a projected range of from 170 microns to 286 microns over the size range of this species.

The average number of keels on each crown ranges from 4 to 7, increasing in number on replacement scales at a rate of 0.01 keels/cm TL (t = 8.091**). The average distance between the ridges on each crown is 45 microns, ranging from 40 microns (specimen # 3, 4) to 57 microns (specimen # 3) and increasing with body length at a rate of 0.01 microns/cm TL, although this slope is not significantly different from 0 (t = 1.10). Primary spacings range from 45 microns (specimen # 3, 4) to 65 microns (specimen # 3), while secondary spacings range from only 30 microns (specimen # 3) to 50 microns (specimen # 5), amounting to a decrease from 9% to 39% (average = 24%). The tertiary spacings range from 30 microns (specimen # 4) to 43 microns (specimen # 5), corresponding to a further reduction of between 23% and 41% (average of 32%) from the primary. The averaged heights of the keels on a single crown varied from 9 microns (specimen # 1, 3) to 19 microns (specimen # 5), increasing on replacement scales at a rate of 0.03 microns/cm TL

Fig. 13. Scanning electron micrograph of the posterior margin of

scales from _Carcharhinus_ _falciformis_, (a) From a 103 cm TL male (specimen

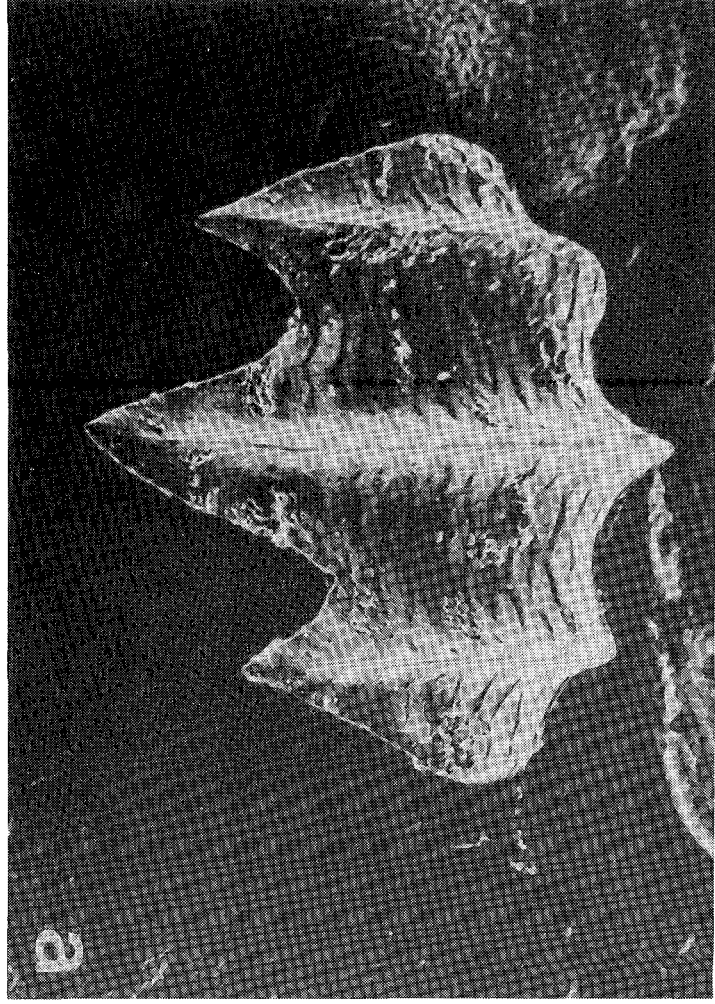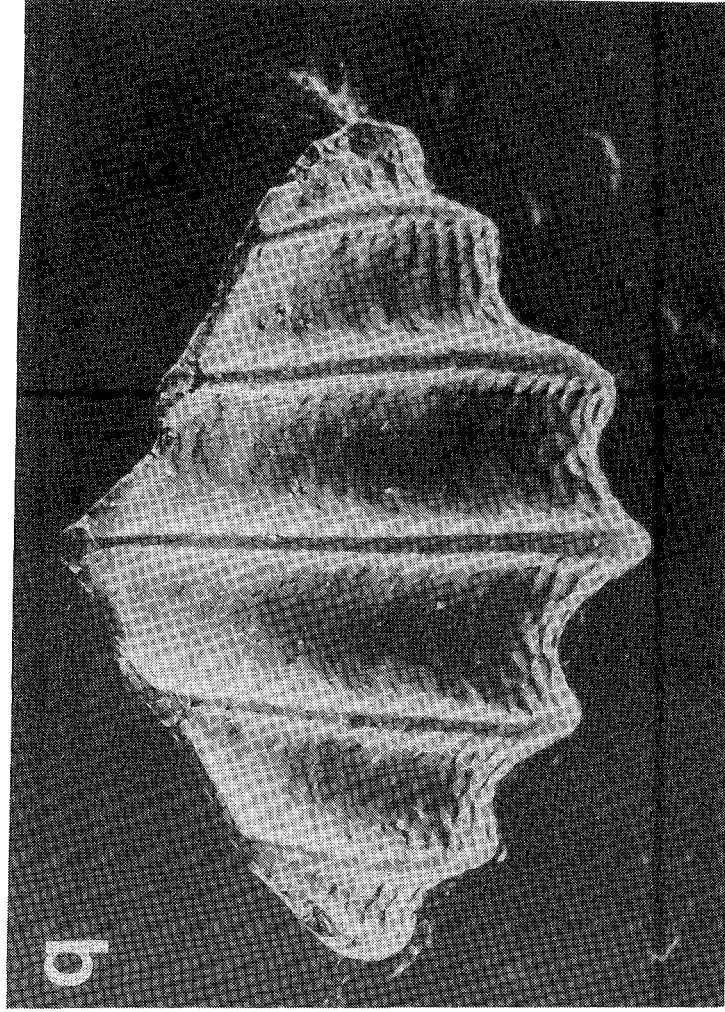no. 1), (b) From a 268 cm TL female (specimen no. 5).
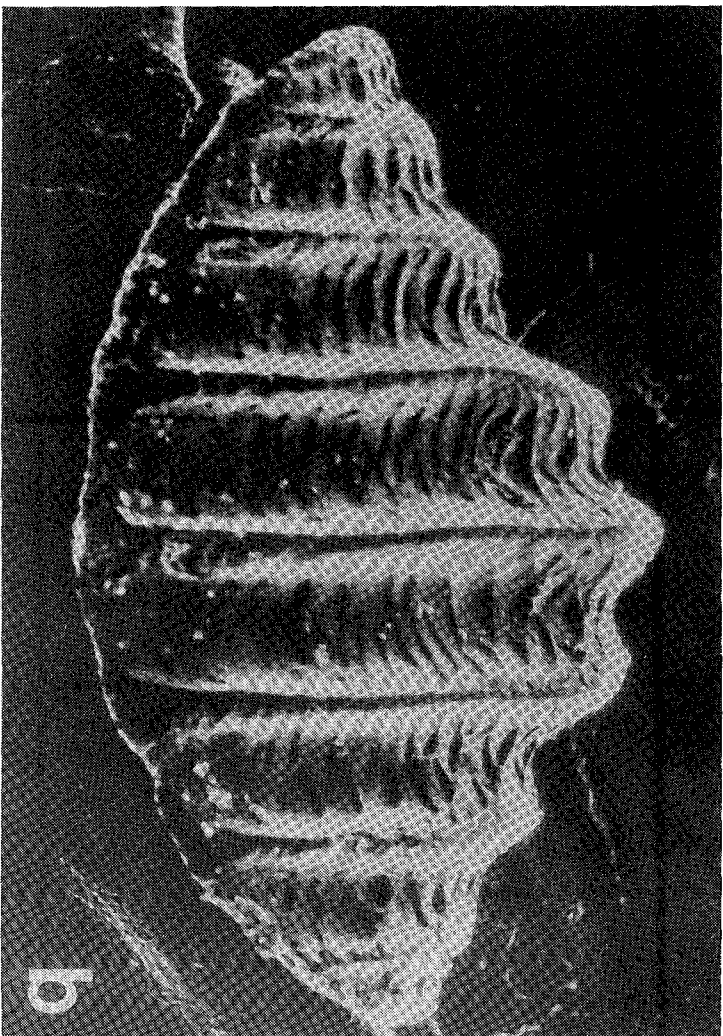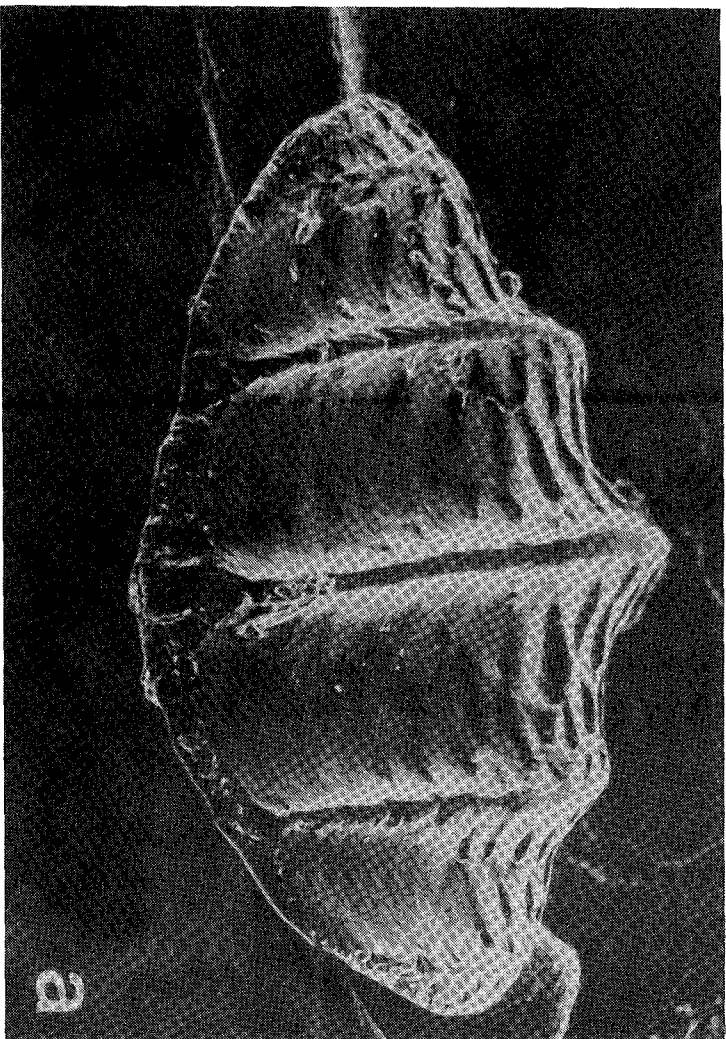
Fig. 14. Scale morphometrics for C. falciformis. Each data point represents the average of five measurements. The spacings and heights are average values for all of the keels on each crown. The line equations are calculated from the total number of individual measurements.
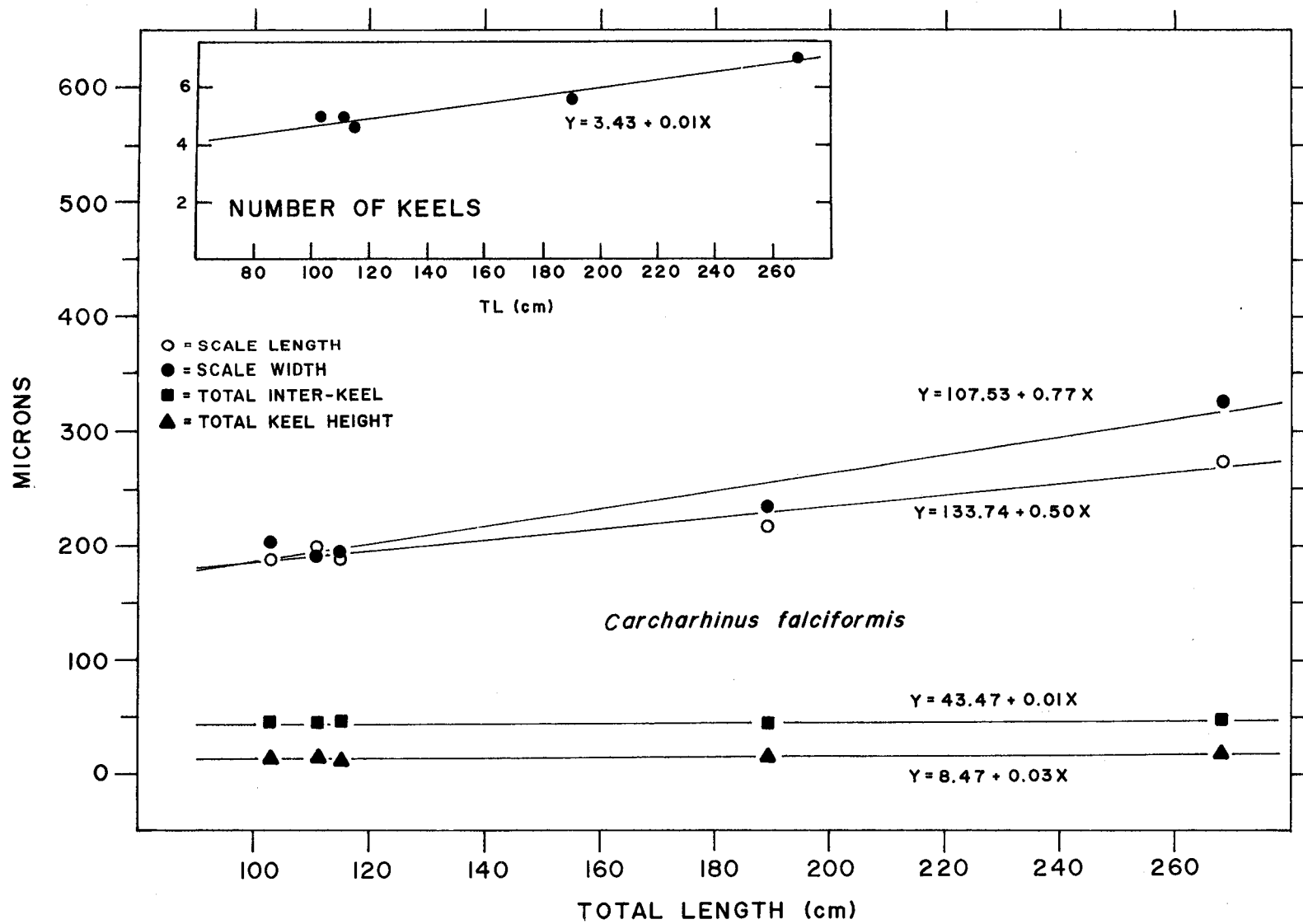
(+ = 5.302**). This results in an estimated total average height over the total size range from of 11 microns to 18 microns. The heights of the primary keels range from 15 microns (specimen # 1, 2, 3, 4) to 30 microns (specimen # 5). The bilaterally averaged heights of the secondary keels range from 10 microns (specimen # 1, 3) to 25 microns (specimen # 5), amounting in an average reduction from the primary values of 21% (ranging from 0% to 50%). The bilaterally averaged heights of the tertiary keels range from 5 microns (specimen # 1, 3) to 18 microns (specimen # 5), amounting in a further average reduction in height from the primary keels of 51% (ranging from 25% to 75%).

Additional Species

In addition to those previously mentioned, scales from the following five species would also appear to belong to this first morphological type, although either too few specimens were available, or were examined from too narrow of a size range, to allow for a proper statistical consideration. Scale morphometrics from these species are presented in Table III.

Scales from C. leucas (figure 15) were examined from specimens ranging between 169 cm and 278 cm TL, representing the middle of their total size range of from 61 cm (Bass, et al., 1973) to 366 cm (Bigelow and Schroeder, 1948). These scales are relatively large, ranging between 405 microns (specimen # 6) and 955 microns (specimen # 9) wide and from 360 microns (specimen # 6) to 780 microns (specimen # 9) high. The average width for the five scales examined from each specimen were between 467 microns and 896 microns while the average length was between

47

Table III. Scale morphometrics for the additional species as listed in the text. Measurements, in microns, listed are an average and range for five individual scales for each specimen. Ranges are rounded to nearest whole number.

Species	Specimen #	Scale Length	Scale Width	# of Keels	Inter-keel Spacing				Keel Height			
					Total	1°	2°	3°	Total	1°	2°	3°
Carcharhinus leucas	6	435	467	3.6	116.8	122.5	96.3		54.2	62.0	58.0	22.5
		360-475	405-520	3-5	110-123	110-133	95-98		48-60	55-65	53-63	20-25
	7	534	589	5.0	143.0	107.5			52.6	77.0	62.0	31.0
		435-615	485-695		138-153	103-113			48-63	75-85	58-70	25-45
	8	580	680	5.2	126	149	107	85	48.7	75	54	33
		530-675	600-750	5-6	119-134	138-158	100-113		47-54	70-80	53-58	28-38
	9	738	896	6.6	134.1	161	127.5	106.9	49.7	74	59	45
		670-675	845-955	5-7	131-141	118-180	115-163	98-123	45-54	70-80	45-68	43-50
Carcharhinus limbatus	10	344	396	6.8	56.8	68.5	54.5	46.5	13.7	22.0	18.5	11.5
		320-375	370-430	6-7	53-60	63-73	50-60	43-50	11-15	15-25	15-20	10-15
	11	266	346	5.8	53.3	61.5	49.5	40	13.1	19	15.5	10.5
		255-310	325-370	5-7	51-55	60-65	48-50	38-43	11-14	15-20	13-20	10-13
	12	263	311	5.4	51.7	56.5	50	37.5	13.9	20.0	16.5	10.0
		245-275	275-330	5-7	48-54	55-58	48-53		11-18	15-25	13-23	8-13
	13	254	321	5.2	51.2	58.0	46.5	30	13.3	20.0	14.5	9.5
		230-270	310-335	5-6	50-53	55-63	45-50		12-15		13-18	8-10
	14	266	347	5.4	53.8	62.5	45.5	35	13.9	22.0	15.5	9.0
		220-305	305-370	5-6	51-58	58-65	38-50		13-15	20-25	13-18	8-10
Ginglymostoma cirratum	82	599	566	3.0	196.5				39.3	49.0	36.5	
		480-675	305-690		153-220				37-42	45-55	30-43	
	83	539	531	3.0	174.5				25.7	28.0	24.5	
		455-615	380-660		115-218				18-30	20-40	18-28	
Isurus oxyrinchus	84	160	137	2.6	41.3				8.3	9.0	7.0	
		140-195	120-150	1-3	38-43				5-10	5-10	8-10	
	85	168	141	2.8	44.0				7.5	11.0	5.5	
		155-180	125-160	2-3	40-53				7-10	10-15	5-8	
	86	183	143	3.0	43.5				7.3	10.0	6.0	
		135-210	110-160		38-48				7-10		5-10	
Sphyrna lewini	126	173	137	3.0	38.0				8.3	10	7.5	
		155-185	130-140		35-43				7-10		5-10	
	127	291	290	6.6	39.8	44.0	39.5	35.5	11.4	18.0	14.5	10
		270-300	260-320	6-7	38-42	43-45	35-40	33-40	11-13	15-20	13-15	
	128	319	297	6.0	44.2	47.0	43.0	36.7	11.8	17.0	13.5	10
		295-335	280-330	5-7	38-50	40-53	38-48	35-40	10-14	15-20	13-15	
Sphyrna mokorran	129	353	308	5.0	61.5	73.0	50.0		18.4	32.0	19.0	11.0
		315-395	270-345		56-65	68-78	45-53		17-20	30-35	18-23	10-13

Fig. 15. Scanning electron micrographs of the posterior margin of

scales from <u>Carcharhinus</u> <u>leucas</u>, (a) From a 169 cm TL female (specimen

no. 6), (b) From a 278 cm TL female (specimen no. 9).
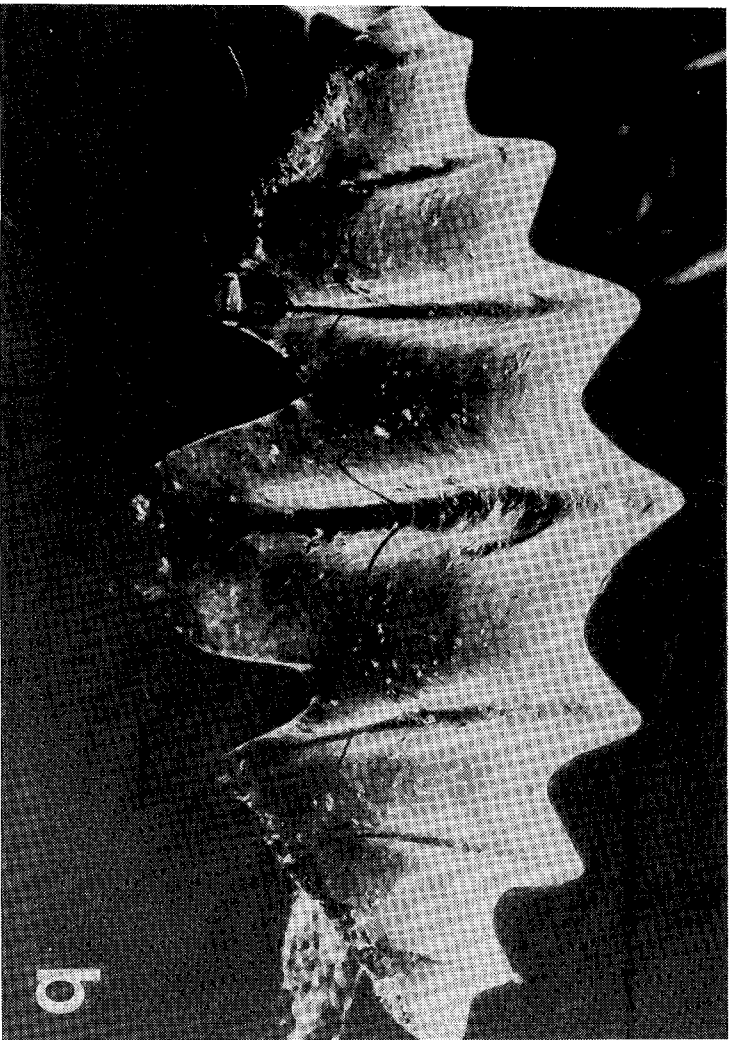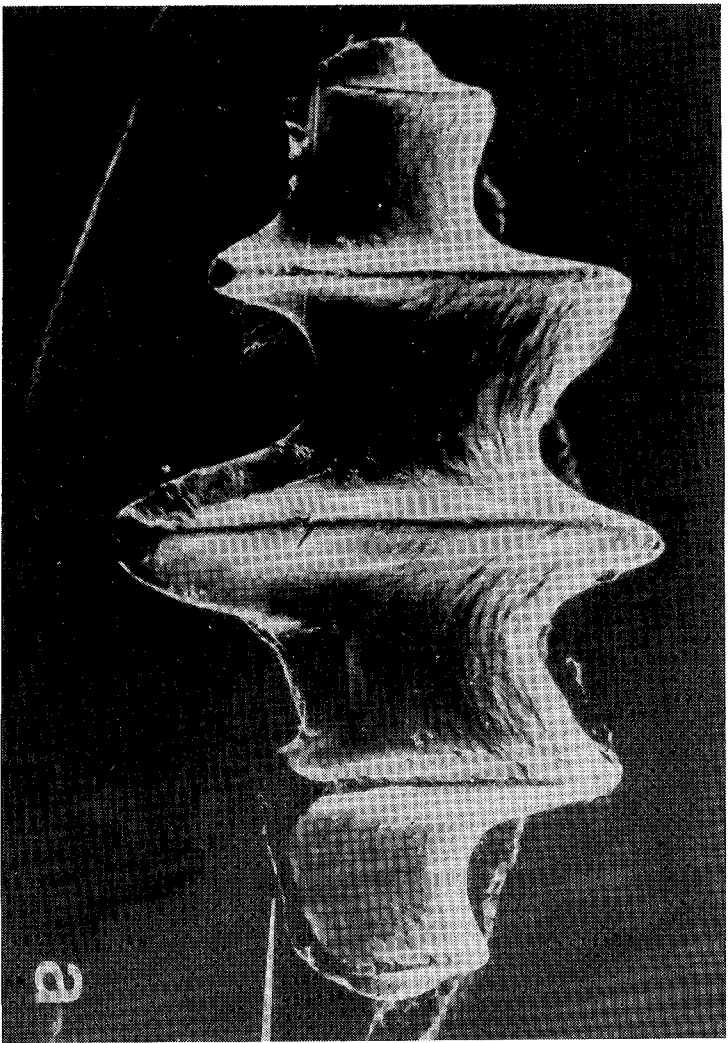
435 microns and 738 microns. Both lengths and widths would appear to increase with body length. Crowns are strongly sculptured, with between 3 and 7 keels and a posterior margin exhibiting 3 strongly, angular cusps. The number of keels appears to also increase ontogenetically, with average values for five scales ranging from 3.6 (specimen # 6) to 6.6 (specimen # 9). Average keel heights range from 49 microns (specimen # 8) to 54 microns (specimen # 6), with primary keels being largest while secondary and tertiary keels are somewhat reduced. The average spacing between all the keels on a crown range from 117 microns (specimen # 6) to 143 microns (specimen # 7), with primary values being the largest and the tertiary the smallest. Both heights and spacings appear to remain nearly constant over the animal's size range.

The average size and shape of the scales from C. limbatus (figure 16) are strikingly different from those just described from C. leucas. The crown is very small, ranging between 220 microns (specimen # 14) and 375 microns (specimen # 10) long and between 275 microns (specimen # 12) and 430 microns (specimen # 10) wide. The average crown width for each specimen is between 311 microns (specimen # 12) and 396 microns (specimen # 10), while the average length is between 254 microns (specimen # 13) and 344 microns (specimen # 10). Neither scale lengths nor widths show indications of ontogenetic variation. Crowns are only weakly sculptured, with keels being broadly rounded and varying in number from 5 to 7. Average values are between 5.2 (specimen # 13) and 6.8 (specimen # 10). Again, there is no indication of an increase in the number of keels on replacement scales. The average distance between these keels on a single crown range from 48 microns (specimen # 12) to

Fig. 16. Scanning electron micrograph of a scale from a: (a) 173 cm TL male specimen of <u>Carcharhinus</u> <u>limbatus</u> (specimen no. 14), taken from directly above, (b) 77 cm TL male specimen of <u>Ginglymostoma</u> <u>cirratum</u> (specimen no. 83), apical view.

53
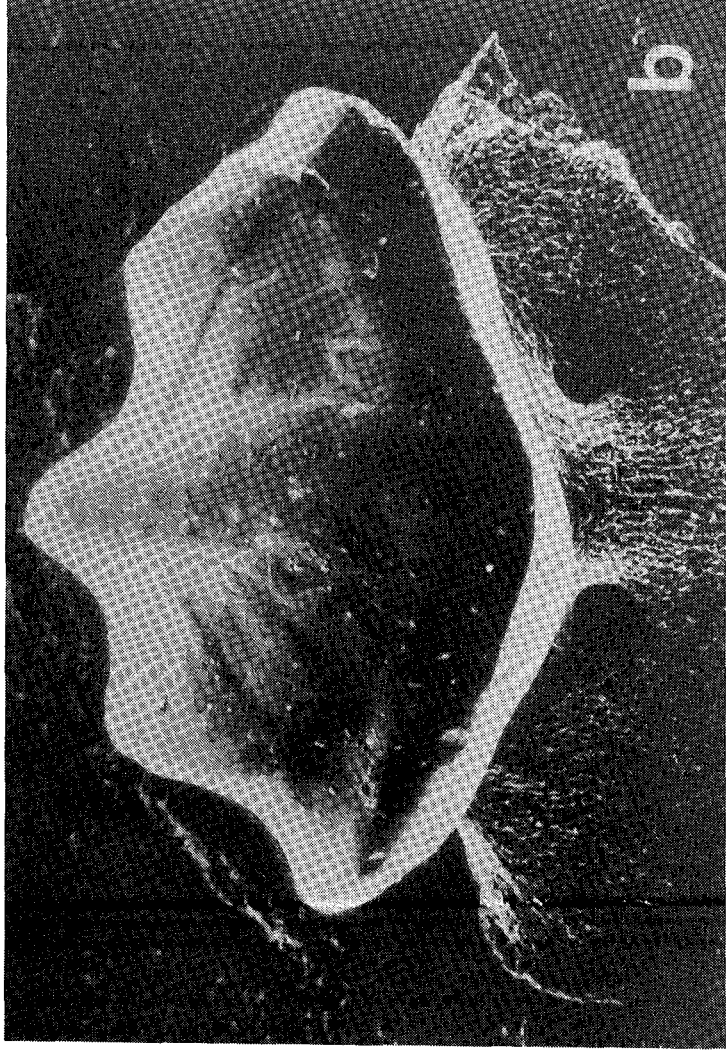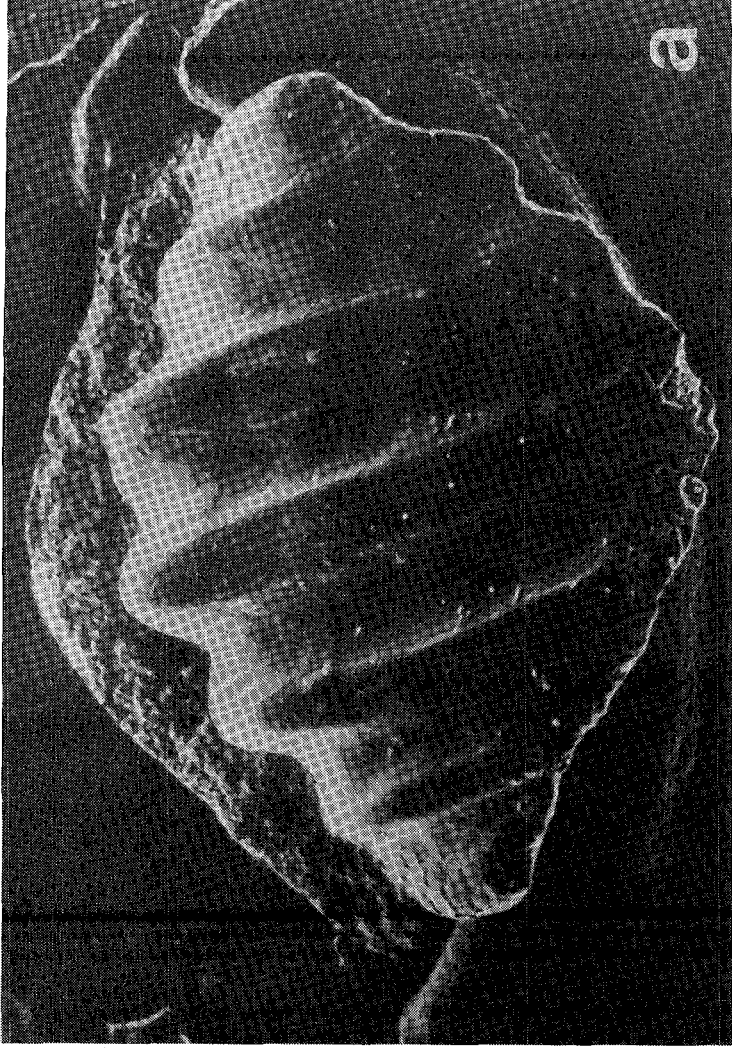
60 microns (specimen # 10), with mean values for the five scales from each specimen between 51 microns (specimen # 13) and 57 microns (specimen # 10). Average keel heights from individual crowns range between 11 microns (specimen # 10, 11, 12) and 18 microns (specimen # 12), ranging between 13 microns (specimen # 11, 13) and 14 microns (specimen # 10, 12, 14) for five scales from each specimen. The heights and spacings of these keels decreased from the primary values, while total values appear to remain nearly constant. Unfortunately however, this material was obtained from an extremely narrow range of from 148 cm to 173 cm and therefore represents a very small portion of the overall range of from 52 cm (Branstetter, 1982) to 255 cm (Castro, 1983).

Isurus oxyrinchus (figure 17b) exhibits the proportionately smallest scales observed in this study. Samples were obtained from specimens up to nearly 50% of the maximum total length for this species of 337 cm (Applegate, 1966). The crowns on these scales are only weakly sculptured and often appear to be slightly concave. Average lengths range between 160 microns (specimen # 84) and 183 microns (specimen # 86) and average widths between 137 microns (specimen # 84) and 143 microns (specimen # 86). Both lengths and widths appear to generally increase ontogenetically. The keels, which range only between 1 and 3 on individual scales and average from 2.6 (specimen # 84) to 3.0 (specimen # 86) on the five scales from each specimen, also increase ontogenetically. The average spacing between these keels are between 38 microns (specimen # 84, 86) and 53 microns (specimen # 85) on a single crown and average from 41 microns (specimen # 84) to 44 microns (specimen # 85) for the five scales. Keel heights are extremely small,

54

Fig. 17. Scanning electron micrograph of the posterior margin of

scales from a: (a) 252 cm TL male specimen of Sphyrna mokarran

(specimen no. 129), (b) 132 cm TL male specimen of Isurus oxyrinchus

(specimen no. 84).
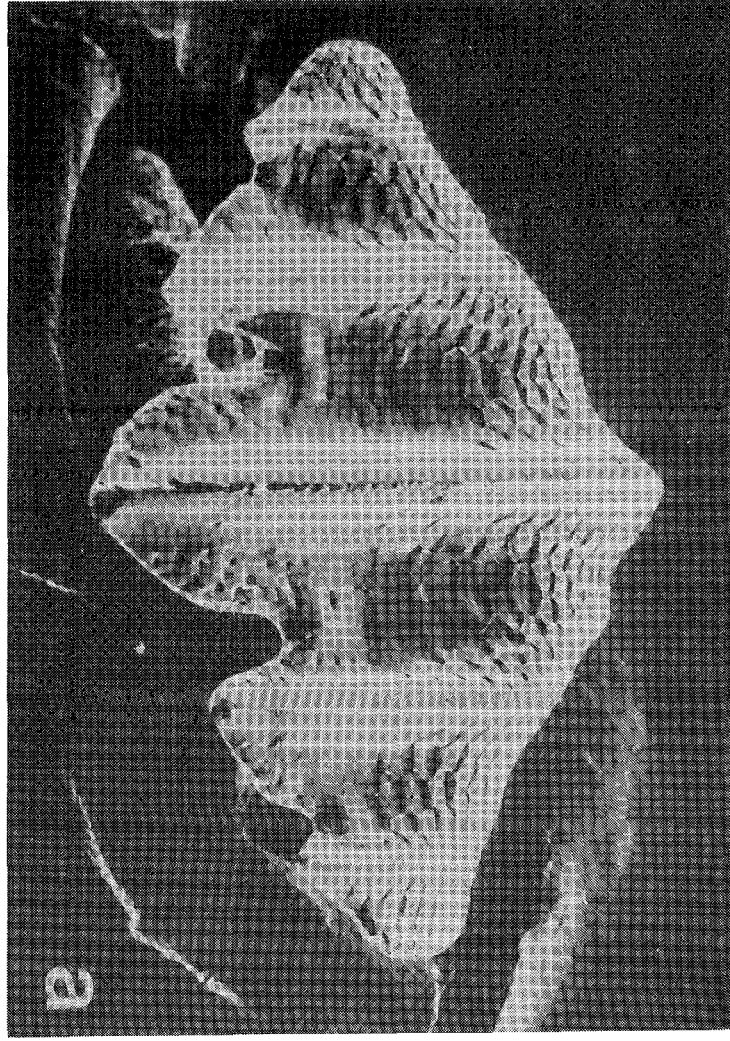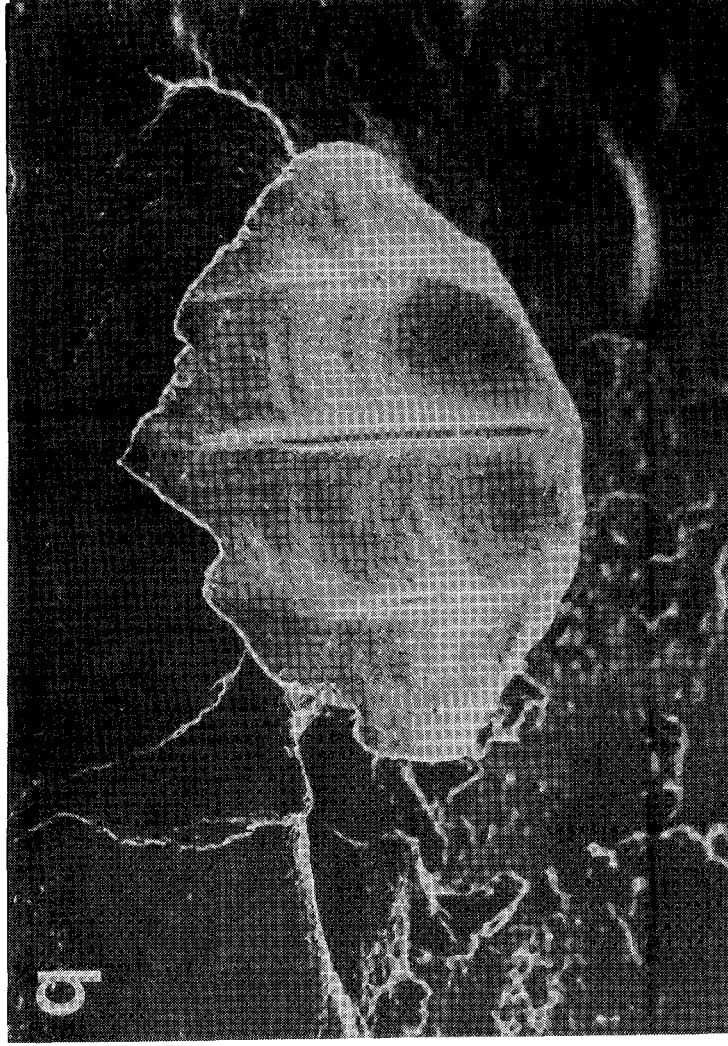
with total values ranging only between 5 microns (specimen # 84) and 10 microns (specimen # 84, 85, 86), averaging from 7 microns (specimen # 86) to 8 microns (specimen # 84) for five scales. Spacing values appear to remain constant with body length while the heights of the keels appear to actually decrease.

The scales that were examined from Sphyrna lewini (figure 18) were removed from one specimen only slightly larger than those recorded by Bass et al. (1975) as freshly pupped and from two additional specimens of approximately 1/2 the recorded maximum size of 400 cm TL (Bass, et al., 1975). Scale crowns exhibit a nearly circular outline, with extremely weak cusps along the posterior margin. Crown lengths average between 173 microns and 319 microns, ranging from 155 microns (specimen # 126) to 335 microns (specimen # 128) while widths average between 137 microns and 297 microns, ranging from 130 microns (specimen # 126) to 330 microns (specimen # 128). Both dimensions suggest a noticeable ontogenetic increase. Keels number from 3 to 7 on each crown, averaging between 3.0 (specimen # 126) and 6.6 (specimen # 127) for the five scales from each specimen. Keel spacings appear to increase slightly on replacement scales, ranging from 35 microns (specimen # 126) to 50 microns (specimen # 128), averaging between only 38 microns (specimen # 126) and 44 microns (specimen # 128) for each specimen. Spacing values decrease from the primary through the secondary to the tertiary. Heights also appear to increase slightly ontogenetically, ranging from seven microns (specimen # 126) to 14 microns (specimen # 128) and averaging only between 8 microns and 12 microns. These values also decrease from the primary keels through the tertiary keels.

Fig. 18. Scanning electron micrograph of the posterior margin of scales from <u>Sphyrna lewini</u>, (a) From a 54 cm TL female (specimen no. 126), (b) From a 225 cm TL male (specimen no. 128).

a

b

59
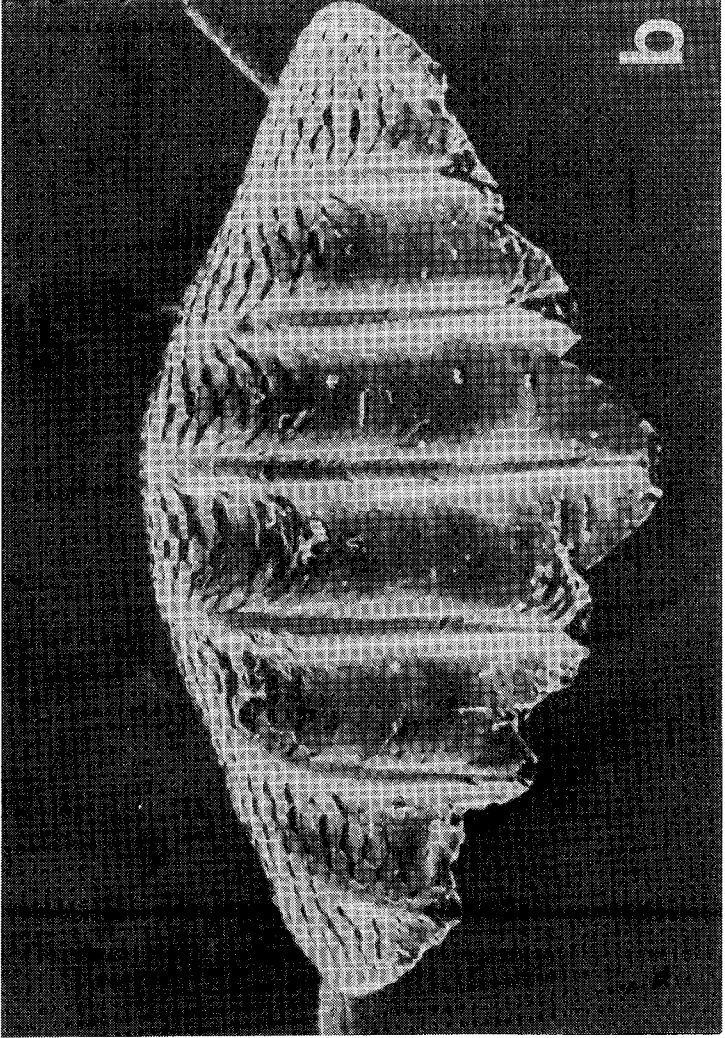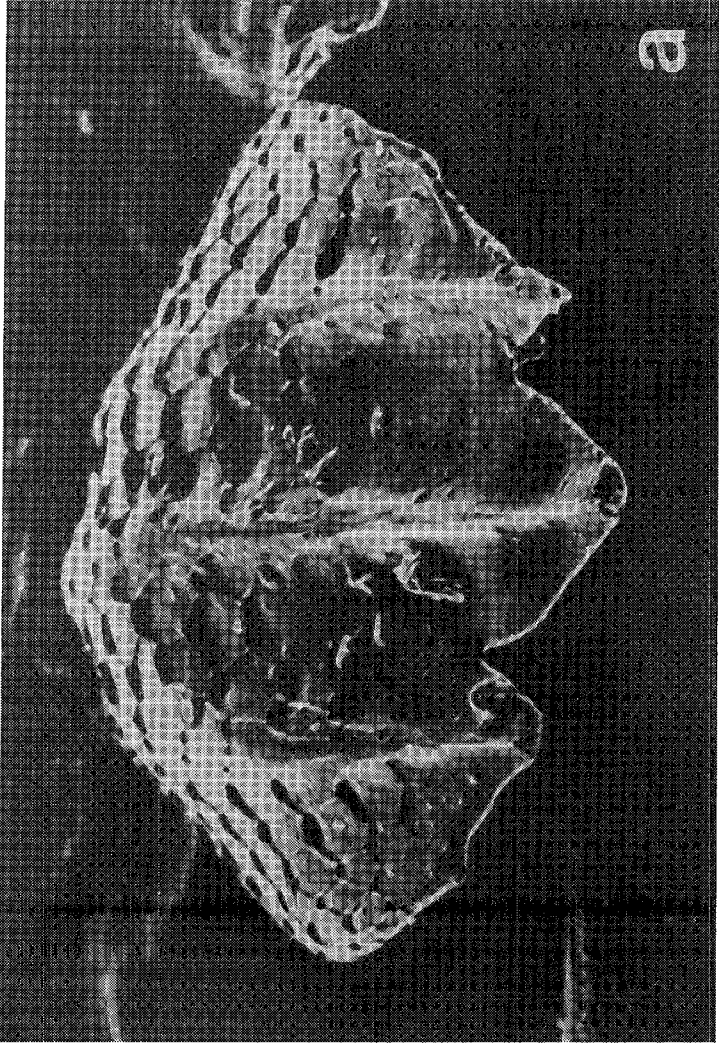
Finally, only one specimen of <u>Sphyrna mokarran</u> was available for examination (figure 17a), being slightly less than 1/2 of the recorded total length of 550 cm (Bass, et al., 1975). Both the overall scale shape and crown dimensions appear very similar to that of <u>S</u>. <u>lewini</u>. Scale lengths average 353 microns and widths average 308 microns. The number of keels are constant at 5.0, while keel heights, 18 microns, and spacings, 62 microns, are slightly larger than those of <u>S</u>. <u>lewini</u>. Both heights and spacings decrease laterally on the crown.

<u>Mustelus</u> <u>canis</u>

The scales from this species are sufficiently different from those previously described to warrant the establishment of a second morphological group, primarily due to the absence of a single central keel. This necessitates slight adjustments in the evaluation of keel morphometrics to account for two primary keels with only a single primary spacing on each scale (figure 19). Furthermore, the overall outline of the scale crown is quite different, being generally lanceolate, exhibiting a very acute posterior angle. Unfortunately however, the material examined here is from only 76% of the previously recorded total size range of from 34 cm to 152 cm (Bigelow and Schroeder, 1948).

Crown widths (figure 20) range from 155 microns (specimen # 88) to 405 microns (specimen # 94), increasing ontogenetically at a rate of 2.30 microns/cm TL (r = 0.90**). This yields an estimated width of between 139 microns and 411 microns over the published total size range. Similarly, lengths also increase with body lengths at a rate of 2.06

Fig. 19. Scanning electron micrograph of the dorsal surface of scales from <u>Mustelus</u> <u>canis</u>, (a) From a 37 cm TL male (specimen no. 87), (b) From a 127 cm TL female (specimen no. 96).

Fig. 20. Scale morphometrics for M. canis. Each data point represents the average of five measurements. The spacings and heights are average values for all the keels on each crown. Line equations are calculated from the total number of individual measurements.
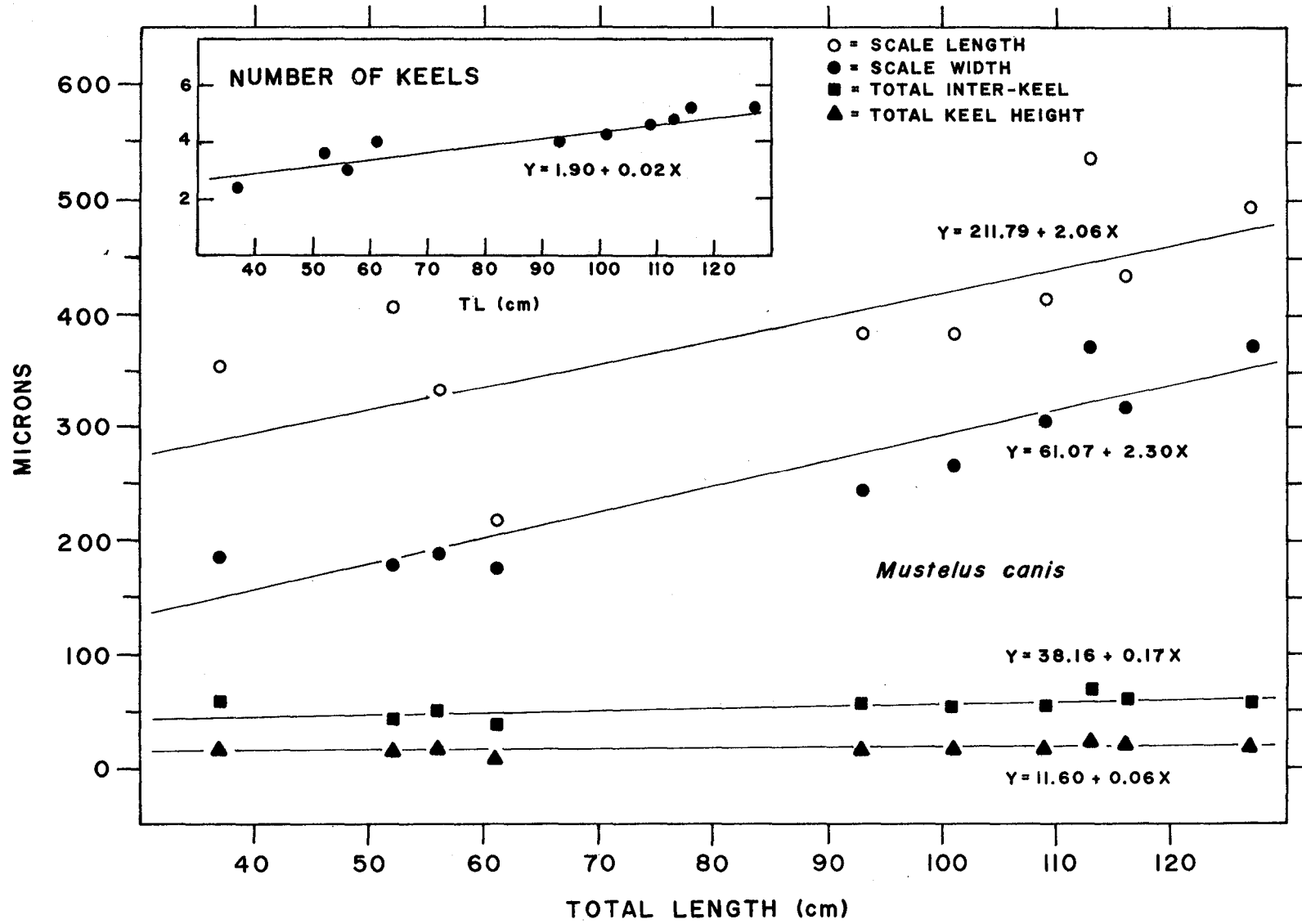
microns/cm TL (r = 0.67*), ranging between 195 microns (specimen # 90) and 585 microns (specimen # 94). This results in estimated lengths between 282 microns and 525 microns over the size range.

Two to 6 keels are present on each crown, the number of keels increasing on replacement scales at a rate of 0.02 keels/cm TL (t = 3.07*). The average spacing between these keels ranges from 35 microns (specimen # 90) to 73 microns (specimen # 94) on an individual crown, increasing ontogenetically at a statistically non-significant rate of 0.17 microns/cm TL (t = 1.768). Estimated spacing therefore remains a constant 38 microns over the total size range. The primary inter-keel distance varies between 35 microns (specimen # 90) and 80 microns (specimen # 94), while the secondary spacings exhibit a decrease from the primary of from 0% to 42% (average of 17.8%), ranging from 30 microns (specimen # 90) to 75 microns (specimen # 94). Similarly, the tertiary spacings exhibit a decrease of from 8% to 39% (average of 24.6%) from the primary value, ranging between 40 microns (specimen # 95) and 60 microns (specimen # 95). Average total keel heights on a crown range between 8 microns (specimen # 90) and 26 microns (specimen # 95), increasing ontogenetically at a rate of 0.06 microns/cm TL, a slope not significantly different from 0 (t = 1.146), and resulting in a constant value of 12 microns throughout the animal's size range. The bilaterally averaged heights of the two primary keels are from 10 microns (specimen # 87, 90) to 35 microns (specimen # 94). The averaged heights of the secondary keels exhibit an average reduction of 35.6% (ranging from an increase of 13% to a decrease of 71%) from the primaries, with values between 5 microns (specimen # 88, 89, 90) and 23

65

microns (specimen # 94, 96) while the tertiary keels exhibit a further reduction from the primary of 61% (ranging from 43% to 82%) with values between 5 microns (specimen # 92, 93, 94) and 10 microns (specimen # 93, 94, 95, 96).

Galeocerdo cuvieri

These next three species possess scales which belong to the third morphological type. Typical of this type, scales from Galeocerdo (figure 21) are much thicker and heavier, with relatively larger ridges. The general outline of the crown is rhomboidal, the margins lacking noticeable cusps. Scales from the largest specimen appeared morphologically different from those of the smaller specimens, with the crown becoming wider and secondary ridges becoming relatively larger. Unfortunately, scales examined in this study were removed from fish representing only 36% of the published size range of from 46 cm (Bigelow and Schroeder, 1948) to 740 cm (Fourmanoir in Bass et al., 1975).

Morphometrics for these scales are presented in figure 22. Scales are longer than wide on specimens shorter than between 330 cm and 370 cm TL. Crown lengths range from 190 microns (specimen # 70) to 810 microns (specimen # 81), increasing with body length at a rate of 1.73 microns/cm TL (r = 0.728**). This amounts to lengths between 116 microns and 1316 microns over the total published size range. Scale widths also increase with body length, at a rate of 2.36 microns/cm TL (r = 0.869**), ranging in size from 120 microns (specimen # 70) to 945 microns (specimen # 81). This rate corresponds to an estimated scale width of up to 1567 microns for the largest recorded size of this

Fig. 21. Scanning electron micrograph of the posterior margin of scales from Galeocerdo cuvieri, (a) From a 213 cm TL male (specimen no. 73), (b) From a 404 cm TL female (specimen no. 81).
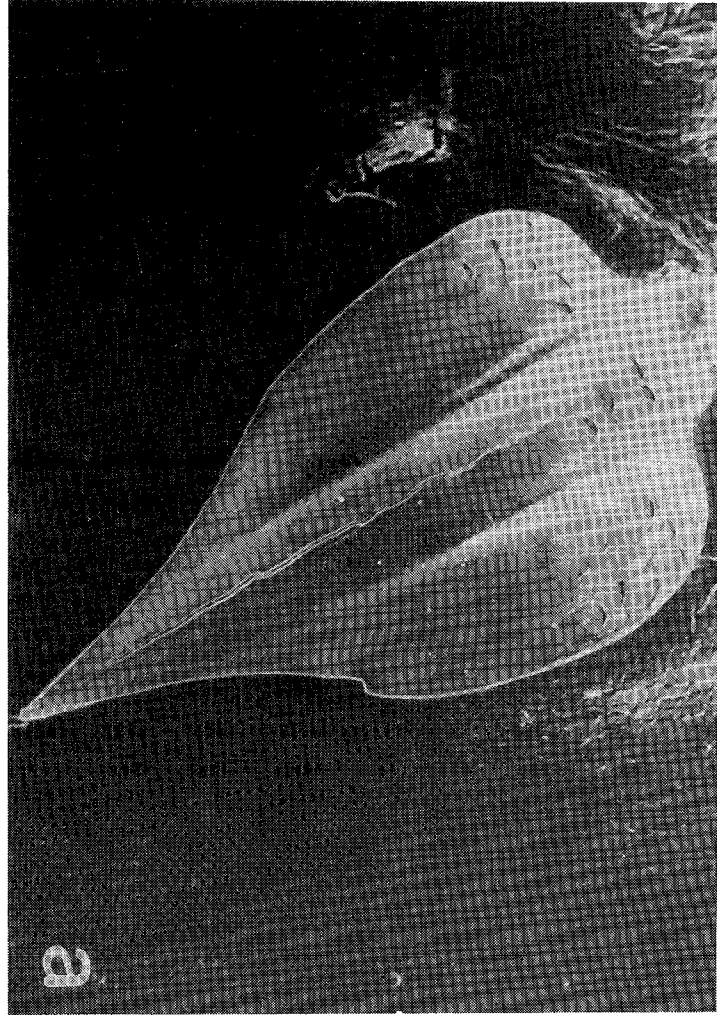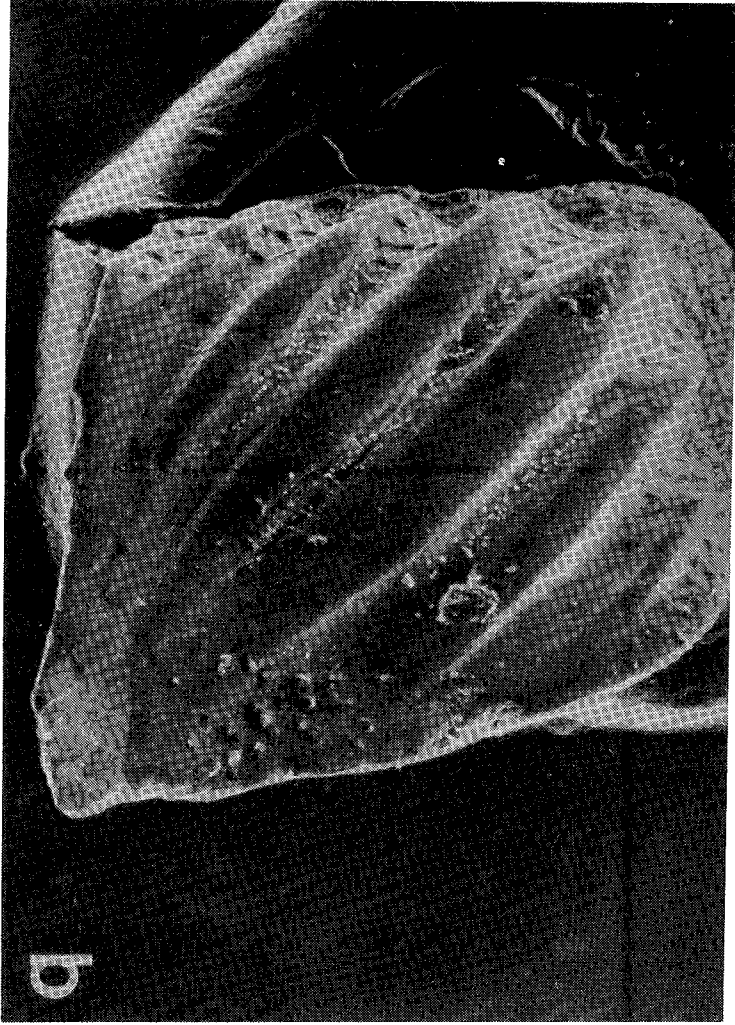
Fig. 22. Scale morphometrics for G. cuvieri. Each data point repre-

sents the average of five measurements. The spacings and heights are

average values for all the keels on each crown. Line equations are cal-

culated from the total number of individual measurements.
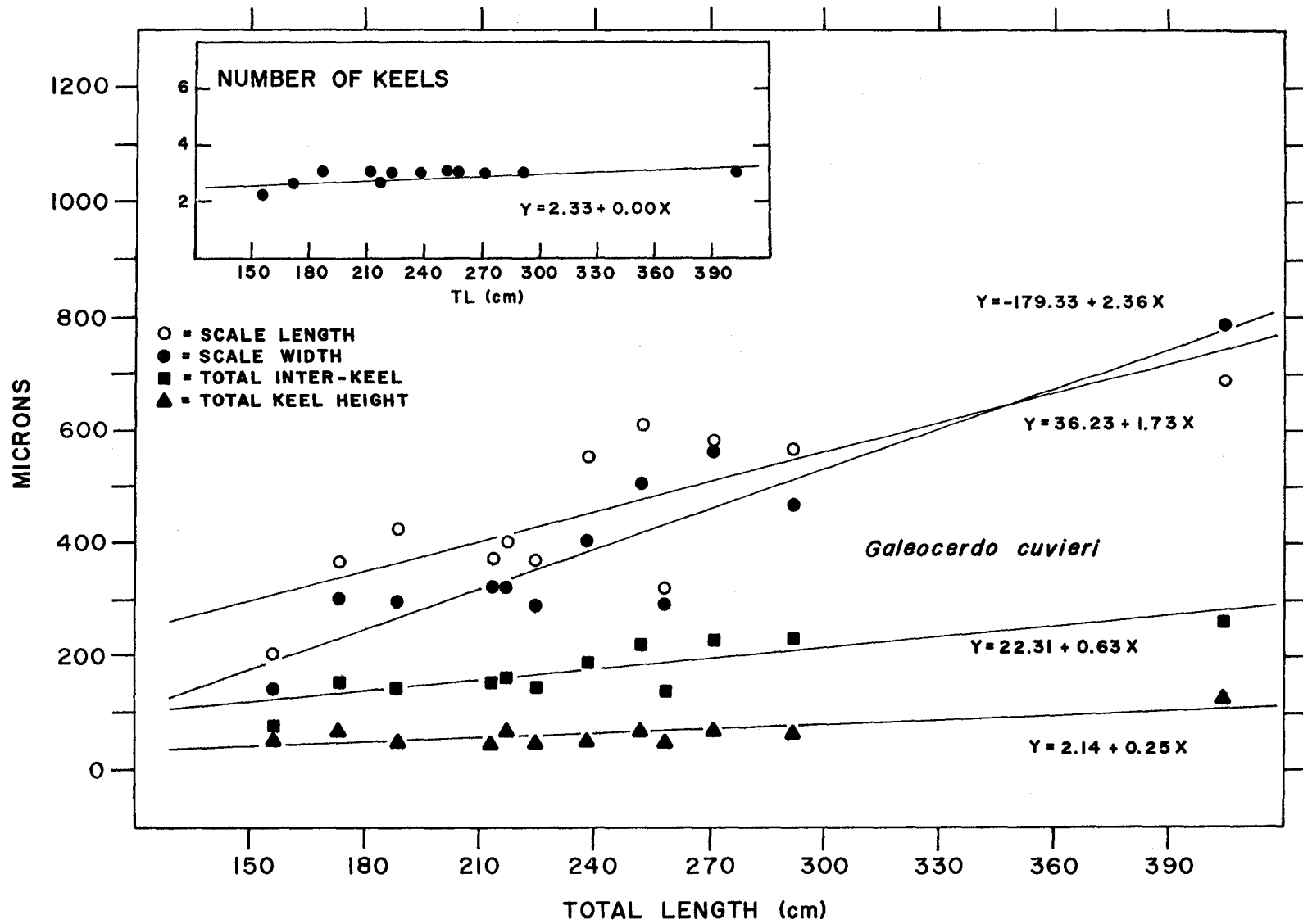
species.

Scale crowns exhibit from 1 to 3 ridges, with values slowly increasing at a rate of 0.02 keels/cm TL (t = 4.818**). Averaged total (and primary) keel spacings on a single crown increase on replacement scales at a rate of 0.63 microns/cm TL (t = 9.405**), ranging from 63 microns (specimen # 70) to 275 microns (specimen # 81). Estimated values range between 51 microns and 489 microns over the published size range. Similarly, the averaged total keel heights on an individual crown increase ontogenetically at a rate of 0.25 microns/cm TL (t = 6.349**), ranging from 35 microns (specimen # 70) to 153 microns (specimen # 81). This yields estimated values of between 14 microns and 187 microns over the published size range. Primary keel heights range from 75 microns (specimen # 73) to 190 microns (specimen # 81) while the bilaterally averaged secondary keels range from 5 microns (specimen # 70) to 135 microns (specimen # 81). This amounts to an average reduction in height from the primary keel of from 28.9% to 94.7% (average of 77.9%). Of particular interest is the striking change in general shape in larger specimens (as in specimen # 81) to one with proportionately much larger and prominent ridges.

Odontaspis taurus

Scales from this species (figure 23) are similar in many aspects to those of G. cuvieri. They are generally very large and heavy, with proportionately larger bases. Keels also tend to be very large and are generally limited to three in number, with the primary being disproportionately larger and the secondary ridges confluent with the

71

Fig. 23. Scanning electron micrograph of scales from <u>Odontaspis</u>
<u>taurus</u>, (a) Dorsal view of a scale from a 210 cm TL female (specimen no.
100), (b) Apical view from a scale from a 235 cm TL male (specimen no. 104).
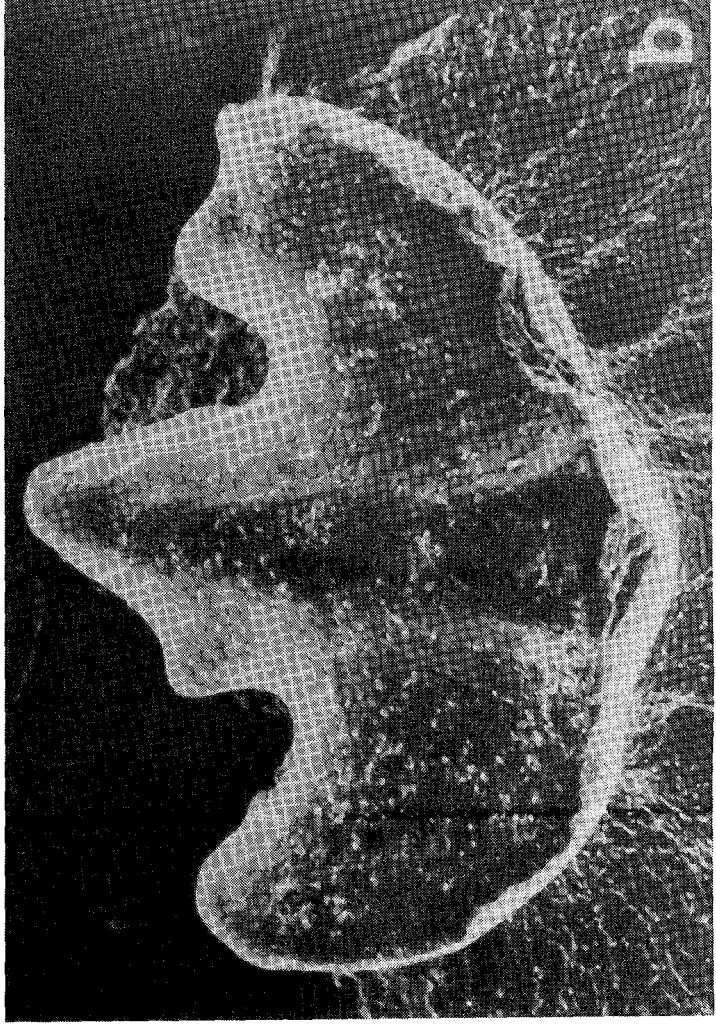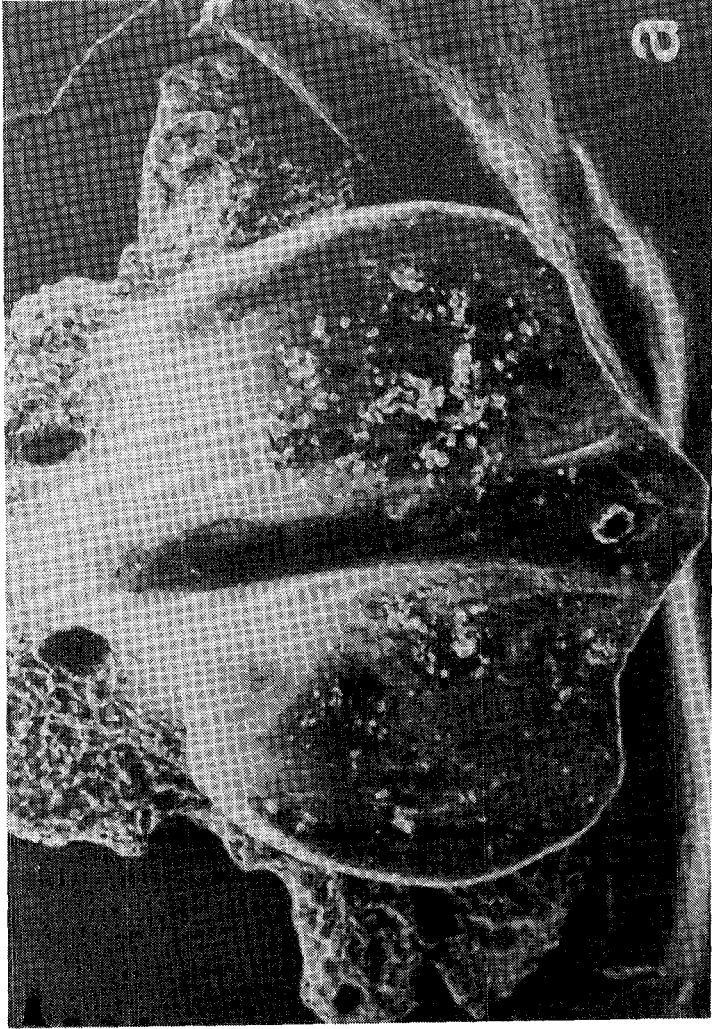
lateral margins of the crowns. Skin samples were removed from a very narrow portion (37.6%) of this species' published size range of between 100 cm (Castro, 1982) and 318 cm (Bigelow and Schroeder, 1948).

Scale crowns are generally wider than long (figure 24) on fish smaller than between 210 cm and 220 cm TL. Individual crown widths range from 340 microns (specimen # 97) to 565 microns (specimen # 99), increasing with body length at a rate of 0.84 microns/cm TL (r = 0.38**). This rate results in estimated values between 358 microns and 541 microns over the published size range. Crown lengths range between 265 microns (specimen # 97) and 615 microns (specimen # 103), increasing ontogenetically at a rate of 2.72 microns/cm TL (r = 0.69**). Estimated lengths vary from 146 microns to 739 microns over the published size range.

Crowns exhibit from 1 to 3 ridges, increasing ontogenetically at a rate of 0.02 keels/cm TL (t = 3.279**). These keels are located an average distance of from 130 microns (specimen # 97) to 225 microns (specimen # 104) apart. These spacings increase on replacement scales at a rate of 0.59 microns/cm TL (t = 3.709**), a rate which yields an estimated value of between 106 microns and 235 microns over the published size range. Average keel heights for all the keels on a single crown also increase with body length at a rate of 0.53 microns/cm TL (t = 2.755**), ranging from 32 microns (specimen # 98) to 160 microns (specimen # 99). Similarly, this rate yields a wide range of estimated values of from 15 microns to 130 microns over the published size range for this species. Primary keel heights vary between 50 microns (specimen # 100) and 160 microns (specimen # 99). Secondary keels are between 29%
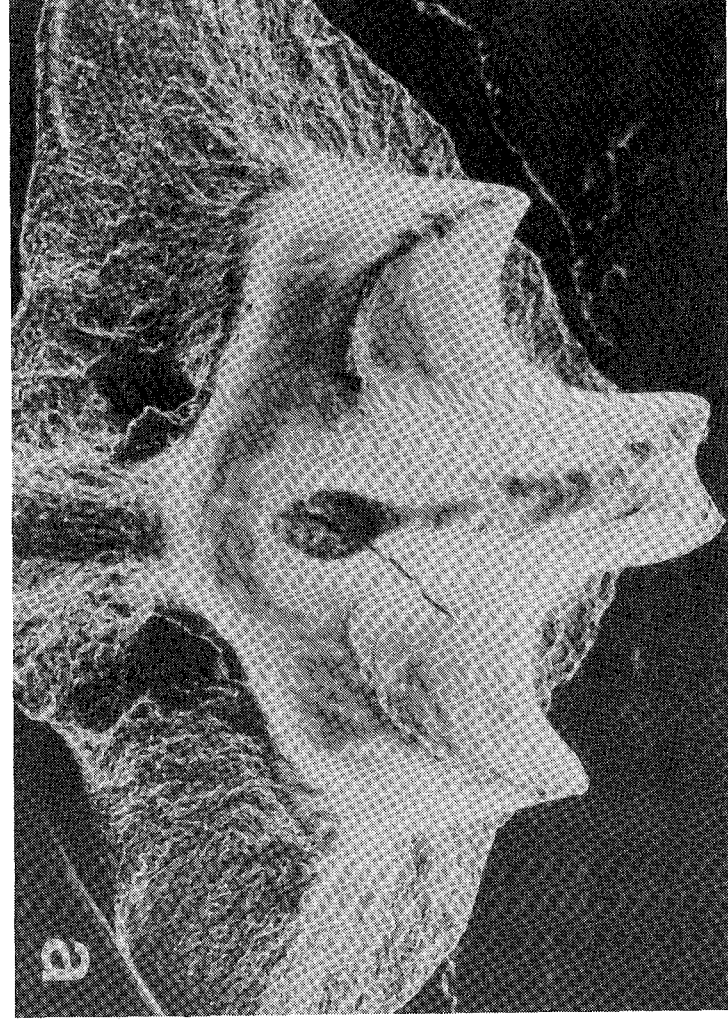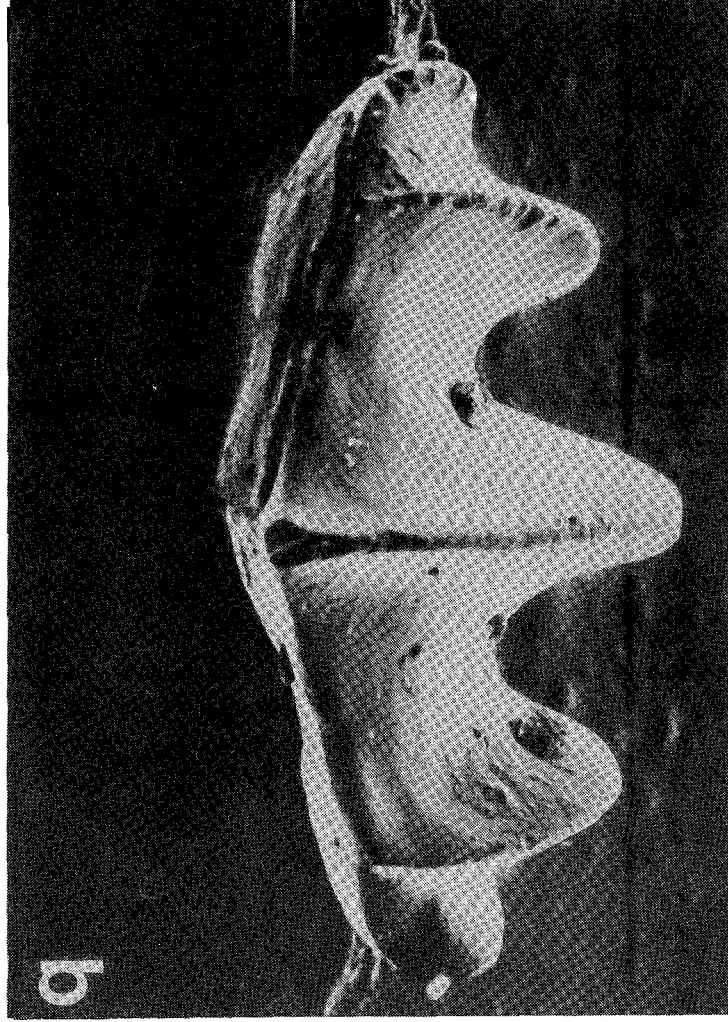
74

Fig. 24. Scale morphometrics for O. taurus. Each data point represents the average of five measurements. The spacings and heights are average values for all of the keels on each crown. Line equations are calculated from the total number of individual measurements. Symbols are the same as in other graphs.
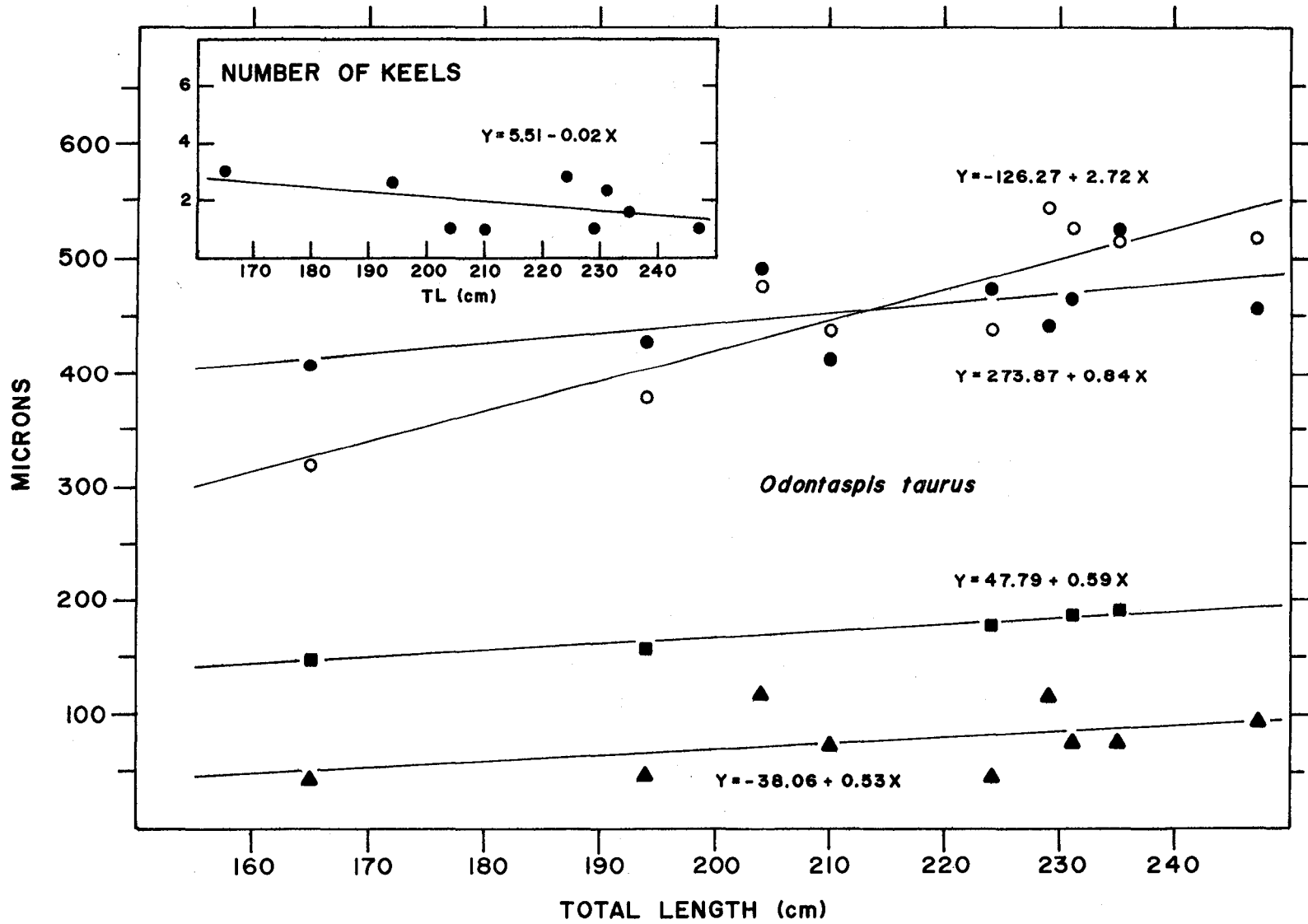
and 91% shorter (average of 56.9%) than the primaries, with values between 8 microns (specimen # 98) and 68 microns (specimen # 103).

Finally, the two specimens of Ginglymostma cirratum which were available for study possessed scales which exhibited many characteristics similar to those of both G. cuvieri and O. taurus. These scales (figure 16b) were generally broadly rounded and free of conspicuous cusps. Individual crown lengths range from 455 microns (specimen # 83) to 675 microns (specimen # 82), with average values for the five scales from each specimen between 539 microns (specimen # 83) and 599 microns (specimen # 82). Similarly, crown widths range between 380 microns (specimen # 83) and 690 microns (specimen # 82) with the range of values for each specimen between 531 microns (specimen # 82) and 566 microns (specimen # 82). While distinct keels are for the most part absent, there are distinguishable ridges or longitudinal elevations. Distances between these ridges range from 115 microns (specimen # 83) to 220 microns (specimen # 82), with average values for each specimen between 175 microns and 197 microns. Similarly, ridge heights range from 18 microns (specimen # 83) to 42 microns (specimen # 82), with total averaged values between 26 microns and 39 microns. These values however, are from specimens only 70 to 80 cm long, which amounts to less than 1/4 of the total length of 425 cm of the adult (Castro, 1982), and may therefore only be considered as an indication of the typical scale morphology from the juveniles of this species.

DISCUSSION

Previous studies of the squamation on pelagic galeoids by Reif and Dinkelacker (1982) provide scale keel spacing values for eleven species which closely agree with the average values obtained in this study. Individual measurements for $\underline{C}$. $\underline{obscurus}$, $\underline{I}$. $\underline{oxyrinchus}$, $\underline{P}$. $\underline{glauca}$ and $\underline{S}$. $\underline{lewini}$ fall within the range obtained in this study, while those of $\underline{C}$. $\underline{falciformis}$ are only slightly larger than those obtained here.

A comparison of crown morphometrics projected over the total size range for each species shows considerable intraspecific similarity (figure 25). In the majority of species, crown lengths range from approximately 100 microns on juveniles to nearly 500 microns on the largest adults, while crown widths exhibit a somewhat narrower range of from 125 microns on juveniles to a maximum of 425 microns on adults. Crowns of similar size were observed on smaller species, such as $\underline{Rhizoprionodon}$ $\underline{terraenovae}$, as well as the much larger species, such as $\underline{Carcharhinus}$ $\underline{obscurus}$. Even the greatly elongated crowns of the scales from $\underline{Mustelus}$ $\underline{canis}$ exhibit comparable widths and only slightly greater lengths. In contrast however, a few species possess scales with noticeably larger crowns. $\underline{Carcharhinus}$ $\underline{plumbeus}$, for example, possesses crowns with maximum widths up to 703 microns and lengths up to 533 microns. Moreover, much larger dimensions are found on both $\underline{Odontaspis}$ $\underline{taurus}$ and $\underline{Galeocerdo}$ $\underline{cuvieri}$. The largest individuals of this last species, for example, would appear to possess scales whose crowns are somewhat longer than 1300 microns and wider than 1500 microns. A few of the additional species, such as

78

Fig. 25. Lengths and widths of scale crowns as estimated from growth equations. Only those species are included for which sufficient data was available for such calculations.

LENGTH   WIDTH

	G. cuvieri
	O. taurus
	C. plumbeus
	M. canis
	C. obscurus
	P. glauca
	C. signatus
	C. falciformis
	R. terraenovae

1400   1000   600   200   200   600   1000   1400   1800

MICRONS
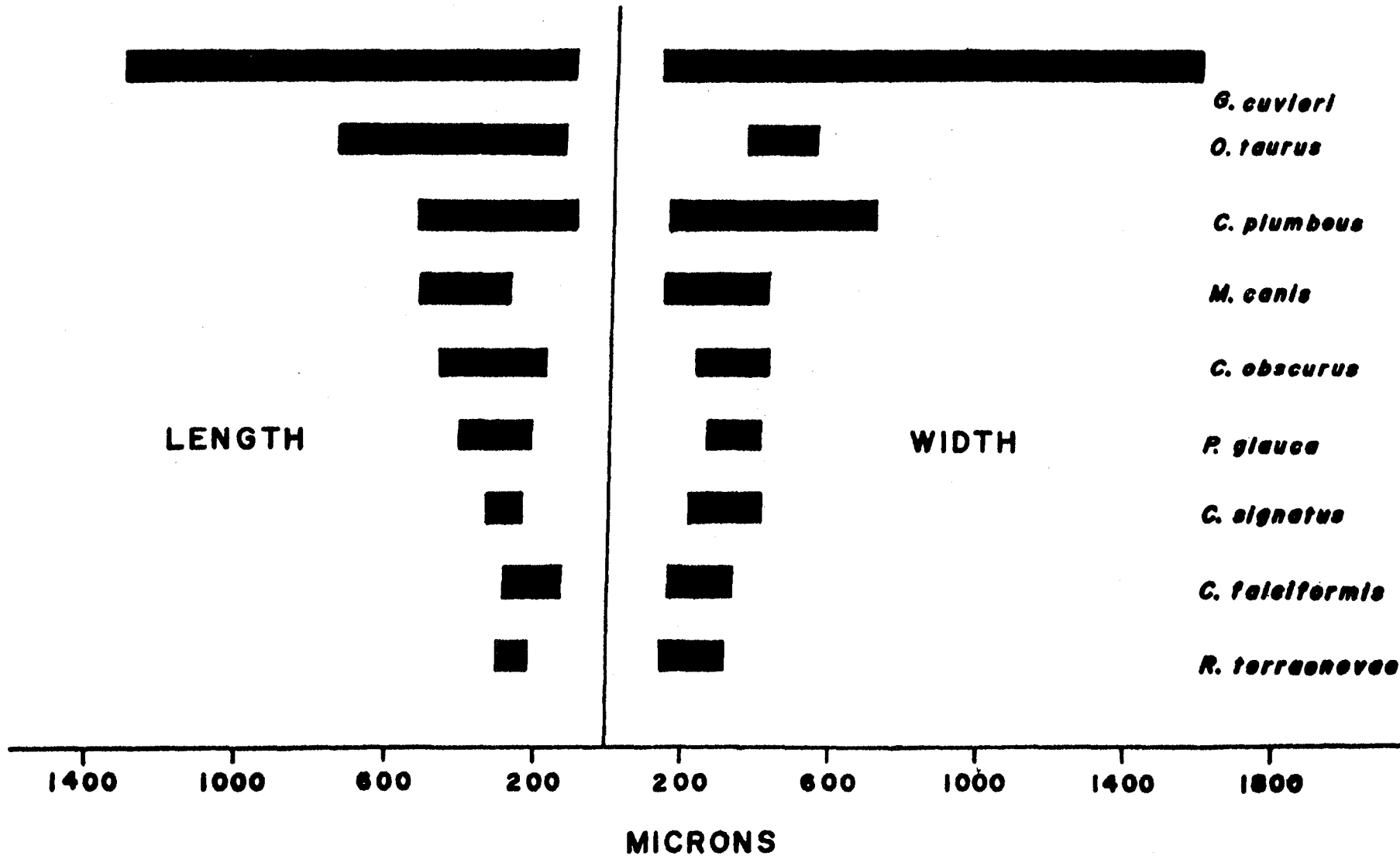
<u>Carcharhinus</u> <u>leucas</u> and <u>Ginglymostoma</u> <u>cirratum</u>, also appear to possess scales with significantly larger crowns.

The overall keel dimensions also exhibit a great deal of interspecific similarity (figure 26). The average maximum distance between adjacent keels on a crown normally lies between 50 microns and 100 microns in most species. However, <u>C. plumbeus</u>, <u>P. glauca</u> and probably <u>C. leucas</u>, possess scales with slightly larger spacings while those from <u>O. taurus</u>, <u>G. cuvieri</u>, and probably <u>G. cirratum</u>, exhibit much larger values. For example, the maximum spacing is more than 200 microns on scales from <u>O. taurus</u> and nearly 500 microns on <u>G. cuvieri</u>. The average keel heights remain less than 50 microns in the majority of species, with estimated maximum heights even as low as 10 microns in <u>Isurus oxyrinchus</u> and <u>Sphyrna lewini</u>. Again however, <u>O. taurus</u>, <u>G. cuvieri</u> and probably <u>C. leucas</u>, possess crowns whose keels are significantly higher, up to four times so in <u>Galeocerdo</u>.

The rates at which crown lengths and widths increase however, show a great deal of interspecific variation (Table IV). Lengths of successive replacement scales increase at rates between 0.50 microns/cm body length (<u>C. falciformis</u>) and 2.34 microns/cm (<u>C. plumbeus</u>) or 2.72 microns/cm (<u>O. taurus</u>); or may not increase at all, as in the case of <u>Prionace glauca</u>. Similarly, the rates at which the crown widths increase on replacement scales are also variable. Widths may increase as slowly as 0.39 microns/cm (<u>P. glauca</u>) and 0.66 microns/cm (<u>C. obscurus</u>) or as rapidly as 3.02 microns/cm (<u>C. plumbeus</u>).

Scales on the majority of galeoid species perform either a protective or hydrodynamic function (Reif, 1982). In either case, most,

Fig. 26. Heights and spacings of keels on the scale crowns as esti-
mated from growth equations. Only those species are included for which
sufficient data was available for such calculations.
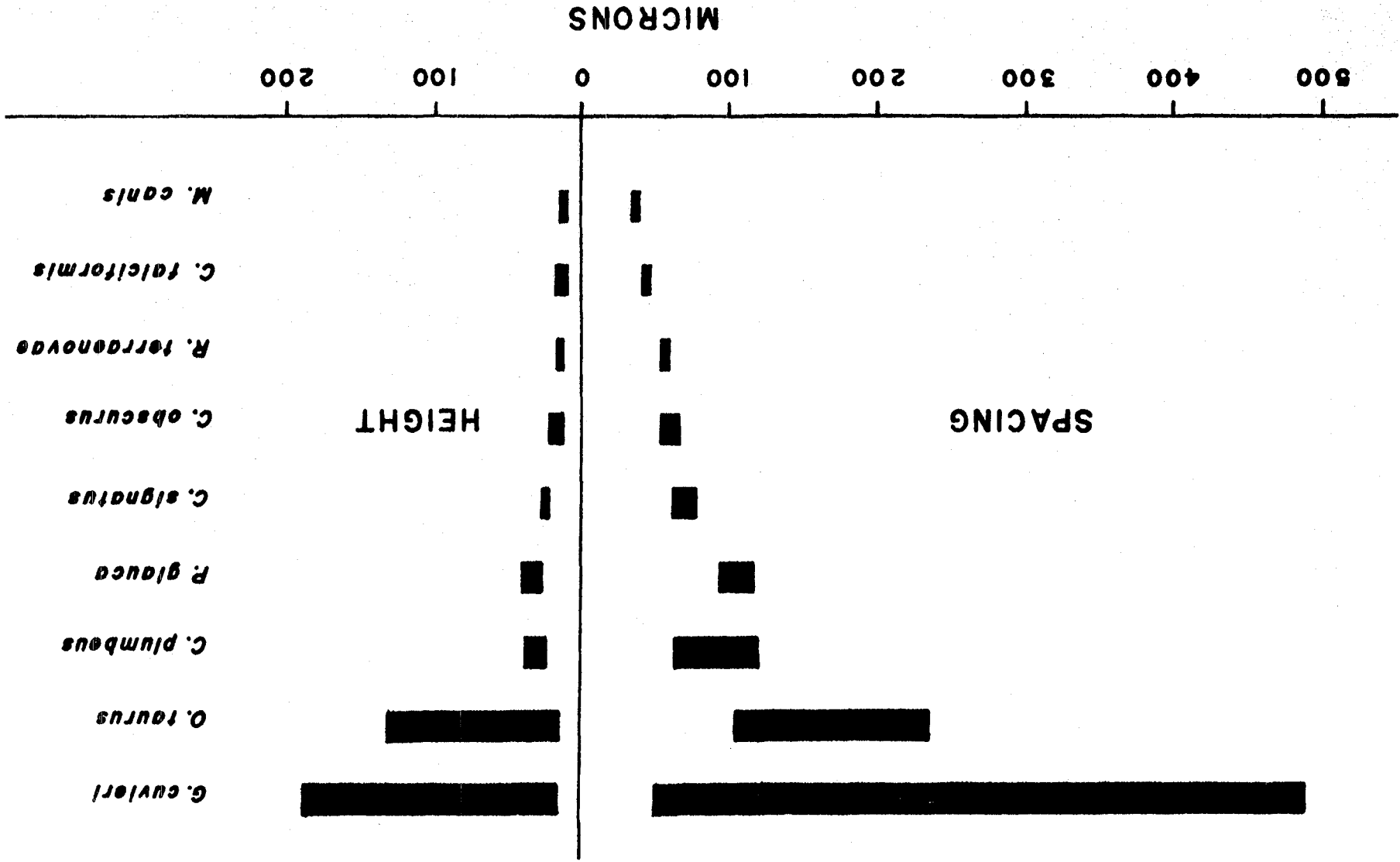
MICRONS

200　100　0　100　200　300　400　500

HEIGHT　　　SPACING

M. canis

C. falciformis

R. terranovae

C. obscurus

C. signatus

P. glauca

C. plumbeus

O. taurus

G. cuvieri

Table IV. Summary of slopes of the growth characteristics from scales of the nine species for which adequate numbers of specimens are available. Species are arranged in order of increasing rates of keel spacings.

Species	Length	Width	Spacing	Height
C. signatus	0.57	1.16	-0.09	0.00
R. terraenovae	1.13	2.28	0.00	0.00
M. canis	2.06	2.30	0.00	0.00
C. falciformis	0.50	0.77	0.00	0.03
C. obscurus	0.99	0.66	0.05	0.03
P. glauca	0.00	0.39	0.06	0.03
C. plumbeus	2.34	3.02	0.30	0.08
O. taurus	2.72	0.84	0.59	0.53
G. cuvieri	1.73	2.36	0.63	0.25

if not all, of the external surface of the fish's body must be covered despite an increasing surface area which results from continuous body growth. This requires that the ratio of the area of the skin covered by scales with the total area of skin remains constant throughout the individual's ontogeny (Reif, 1980). The amount of area covered by scale crowns results from a combination of an increase in the number of scales with the increase in the size of the individual crown. The wide variety of scale growth rates observed in this study reflects the interaction between these two processes.

A sharp dichotomy exists in growth rates of the keel morphometrics. The majority of species exhibit extremely slow rates of increase for keel spacings, ranging from an actual decrease in the inter-keel distance of C. signatus to the very slow rate of from 0.05 to 0.06 microns/cm in C. obscurus and P. glauca. Several species, including R. terraenovae, C. falciformis and M. canis, exhibit no increase at all. Similarly, the keels remain either at a constant height, as in C. signatus, R. terraenovae and M. canis, or increase only very slightly, as in C. falciformis, C. obscurus and P. glauca. In a second group of species however, inter-keel distances increase very rapidly; at rates up to 0.60 microns/cm, on scales from both O. taurus and G. cuvieri. Moreover, the heights of these keels increase on replacement scales at rates between 0.25 microns/cm on O. taurus and 0.53 microns/cm on G. cuvieri. Only C. plumbeus occupies an intermediate position between these two groups, with keel spacings increasing at a rate of 0.30 microns/cm and heights at a rate of 0.08 microns/cm.

In summary, these scales appear divided into two morphometrically

distinct groups. The majority of species exhibit scales whose crowns increase in size at a wide variety of rates to a maximum width of approximately 425 microns and a length of 500 microns. Ridges on these crowns remain a nearly constant 50 microns high throughout each species' size range and are normally located 100 microns apart. Such crowns are largely characteristic of both the first and second morphological types described earlier in this report. A second group of species, however, possess a much thicker, heavier scale. Crowns on these scales grow very rapidly, reaching maximum widths and lengths nearly twice that of the first group. The keels on these scales are set further apart, from 235 microns (O. taurus) to 490 microns (G. cuvieri), and are much higher, from 160 microns (O. taurus) to 187 microns (G. cuvieri). Both heights and spacings increase rapidly on replacement scales. These species largely comprise the third morphological group. Only a few species exhibit intermediate values for keel spacings (G. cirratum, C. plumbeus, C. leucas and P. glauca), keel height (C. leucas) or general growth rates (C. plumbeus).

In order to compare these measurements with a hypothetical model for drag reduction, it is first necessary to consider swimming speeds for each species. The little information presently available can be divided roughly into two categories. Burst speeds, such as those which might be used in capturing highly mobile prey or in escaping predators, have been estimated at 522 cm/sec for C. leucas and at 244 cm/sec for the lemon shark, Negaprion brevirostris (Gero, 1952). Values as large as 1000 cm/sec have been recorded for Carcharhinus (Prionace) glauca (Nikolsky, 1978). Secondly, a limited number of measurements are available for

86

voluntary, or sustained, speeds. Beamish (1978) estimated sustained speeds of between 18 and 202 cm/sec for C. leucas based on Thorson's (1971) tagging studies while Heard and Ripley (1951) have reported similar speeds of 43 cm/sec for the soupfin shark (Galeorhinus zyopterus); both being based on longer-term migrational studies. Specific shorter-term observations of cruising speeds have been reported for C. leucas of 56 to 83 cm/sec and for C. plumbeus of 60 to 67 cm/sec (Weihs, et al., 1981) from an aquarium study.

Due to the very limited number of actual measurements, it is necessary to rely only on estimates for the majority of other species. Weihs (1977) proposed the use of the following equation to predict voluntary swimming speeds:

$$U = 0.503 \, L^{0.43}$$

where U is the voluntary swimming speed and L is the body length. This equation closely approximates those values previously reported for both C. plumbeus and C. leucas. Similarly, Wardle (1975) proposed the following equation to predict maximum burst speeds:

$$U = AL/2T$$

where A is the stride length, based on Bainbridge's (1958) estimate of forward motion of from 60% to 80% of both length (L), (60% was used in the present study) and T is muscle contraction time (estimated to be about 0.08 S for fish of about 2 m in length, using Wardle's 1975 curves). While this equation has only been verified with teleost

data, it appears to provide a sufficient estimate for elasmobranchs. Therefore for example, estimated swimming speeds for a specimen of C. leucas between 1.5 and 2.0 meters long should lie between voluntary swimming speeds of 53 cm/sec to 60 cm/sec and burst swimming speeds of 900 cm/sec to 1200 cm/sec, values close to those previously reported from the literature.

It is now possible to evaluate the keel morphometrics exhibited by each species in terms of potential drag reduction. The actual measurements, expressed in metric terms, can be expressed in terms of law of the Wall coordinates through the following two equations (Walsh and Weinstein, 1978):

$$h^+ = hu/v \ (C_f/2)^{1/2}; \ s^+ = su/v \ (C_f/2)^{1/2}$$

where h^+ and s^+ are heights and spacing in terms of law of the Wall coordinates, h and s are heights and spacing in cm, u is the free stream velocity (here expressed in swimming speeds), v is the kinematic viscosity of sea water and C_f is skin friction. This later term can be calculated from the following equation:

$$C_f = .074 \ R^{-1/5}$$

where R is the Reynold's number: $R = Lu/v$; L, u, and v having been defined above. The major limitation on these equations lies in the paucity of information on specific swimming speeds.

Throughout their ontogeny, all of the species examined in this study (with the possible exception of the very largest specimens of G. cuvieri) possess scales with ridge spacings less than the proposed optimal value of 16 (in law of the Wall coordinates) at voluntary swimming speeds (figure 27). Moreover, a number of these species maintain keel spacings which approximate the optimal value projected for burst swimming speeds. This is particularly true in C. falciformis, C. limbatus, C. obscurus, C. signatus, Isurus oxyrinchus, Sphyrna lewini, and S. mokarran. In contrast, the ridge spacings on the scales from Galeocerdo cuvieri, Odontaspis taurus and Ginglymostoma cirratus rapidly increase ontogenetically to values well above this optimal level.

Similar trends are also observed in a comparison of actual keel heights to the corresponding theoretical optimal values (figure 28). At voluntary swimming speeds, all of the species which were examined here maintain scales whose keels are noticably smaller than the proposed optimal value of 8 (again expressed in terms of the law of the Wall coordinates). Moreover, keel heights closely approach the optimal values predicted for burst swimming speeds in all of these species, except G. cuvieri, G. cirratum and O. taurus.

Lastly, additional insight into the hydrodynamic significance of scale relief is available through interspecific comparisons of the relative closeness of keel morphometrics to these theoretical optimal levels. Whereas both C. falciformis and C. signatus maintain keel dimensions suprisingly close to those predicted for burst values, quite

89

Figure 27. Scale ridge spacing compared to predicted optimal dimensions for sustained (A - A´) and burst (B - B´) swimming speeds as a function of fish length . Species are as follows: (1) _Galeocerdo_ _cuvieri_, (2) _Odontaspis_ _taurus_, (3) _Carcharhinus_ _plumbeus_, (4) _Prionace_ _glauca_, (5) _Carcharhinus_ _obscurus_, (6) _Carcharhinus_ _signatus_, (7) _Carcharhinus_ _falciformis_.
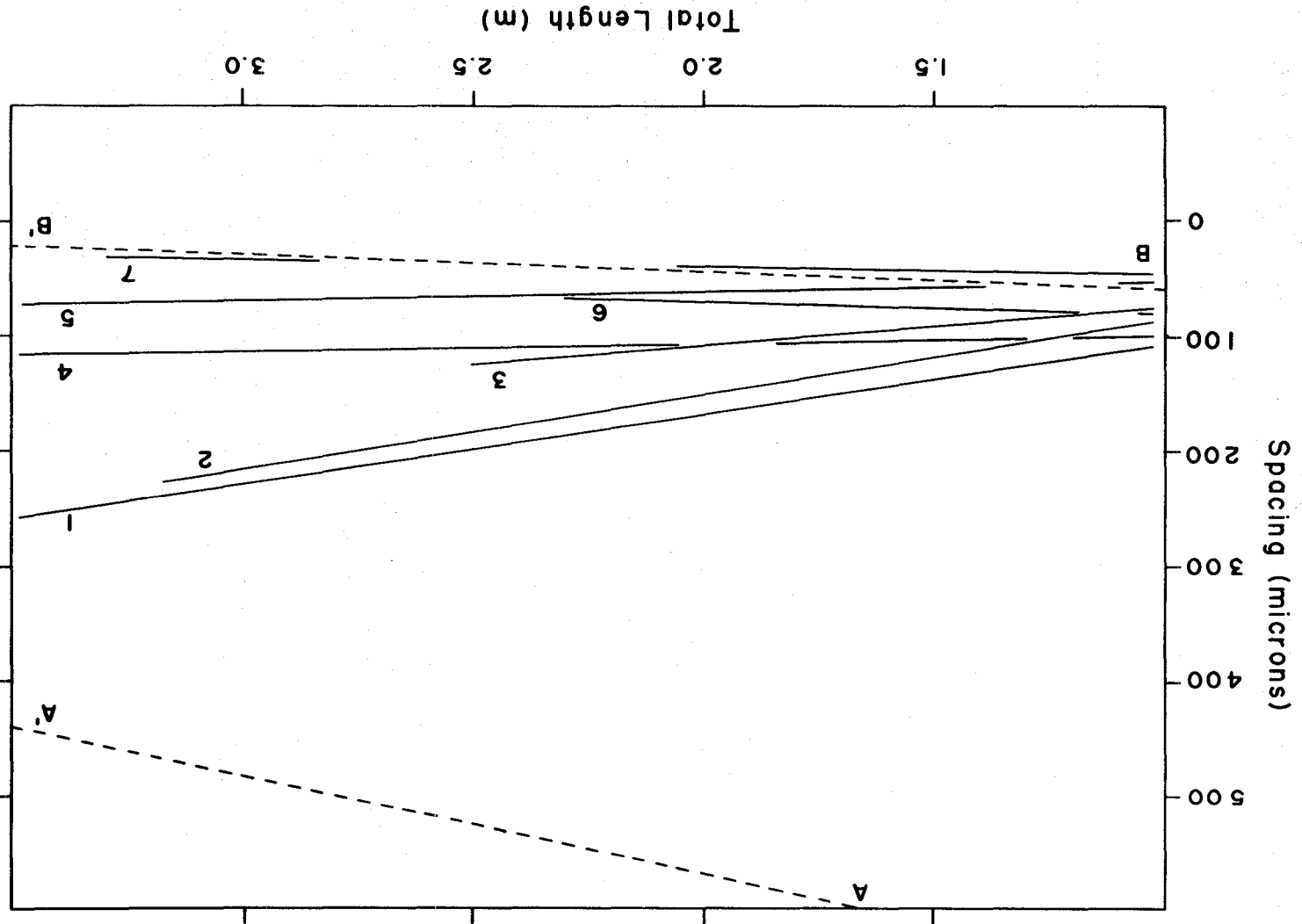
the opposite is observed on G. cuvieri and O. taurus. Scale morphometrics for C. obscurus, C. plumbeus and P. glauca appear intermediate between these two extremes. The explanation for this deviation in scale topography from optimal conditions predicted for burst swimming speeds may be partially found through interspecific comparisons of swimming speeds.

In conclusion, the keel morphometrics of species examined in this study exhibit a wide range of values with respect to proposed optimal drag reduction values. While the majority of the species, including C. falciformis, C. signatus, C. limbatus, I. oxyrinchus, S. lewini and S. mokarran, possess scales whose keel heights and spacings approach the optimal values predicted for burst swimming speeds, at least two other species, O. taurus and G. cuvieri, appear not to follow this trend and exhibit keel heights and spacings well above such levels over the majority of their size range. Such differences may reflect the balance between thicker, narrower scales adaptive for protection functions and the thinner, more specifically sculptured scales adaptive for drag reduction.

The presence of either scale type should, in part, reflect the overall speeds of each species. While this assumption is again hampered by the absence of actual measurements, generalizations can be inferred from natural history information such as that found in works by Bigelow and Schroeder (1948), Castro (1982), Clark and von Schmidtt (1965) and others. Of those species which possess scales with keel morphometrics suggesting optimal drag reduction capabilities, there is ample evidence

Figure 28. Scale ridge height compared to predicted optimal dimensions for

sustained (A - A') and burst (B - B') swimming speeds as a function of

fish length. Species are as follows: (1) <u>Galeocerdo cuvieri</u>, (2)

<u>Odontaspis taurus</u>, (3) <u>Carcharhinus plumbeus</u>, (4) <u>Prionace glauca</u>, (5)

<u>Carcharhinus obscurus</u>, (6) <u>Carcharhinus signatus</u>, (7) <u>Carcharhinus</u>
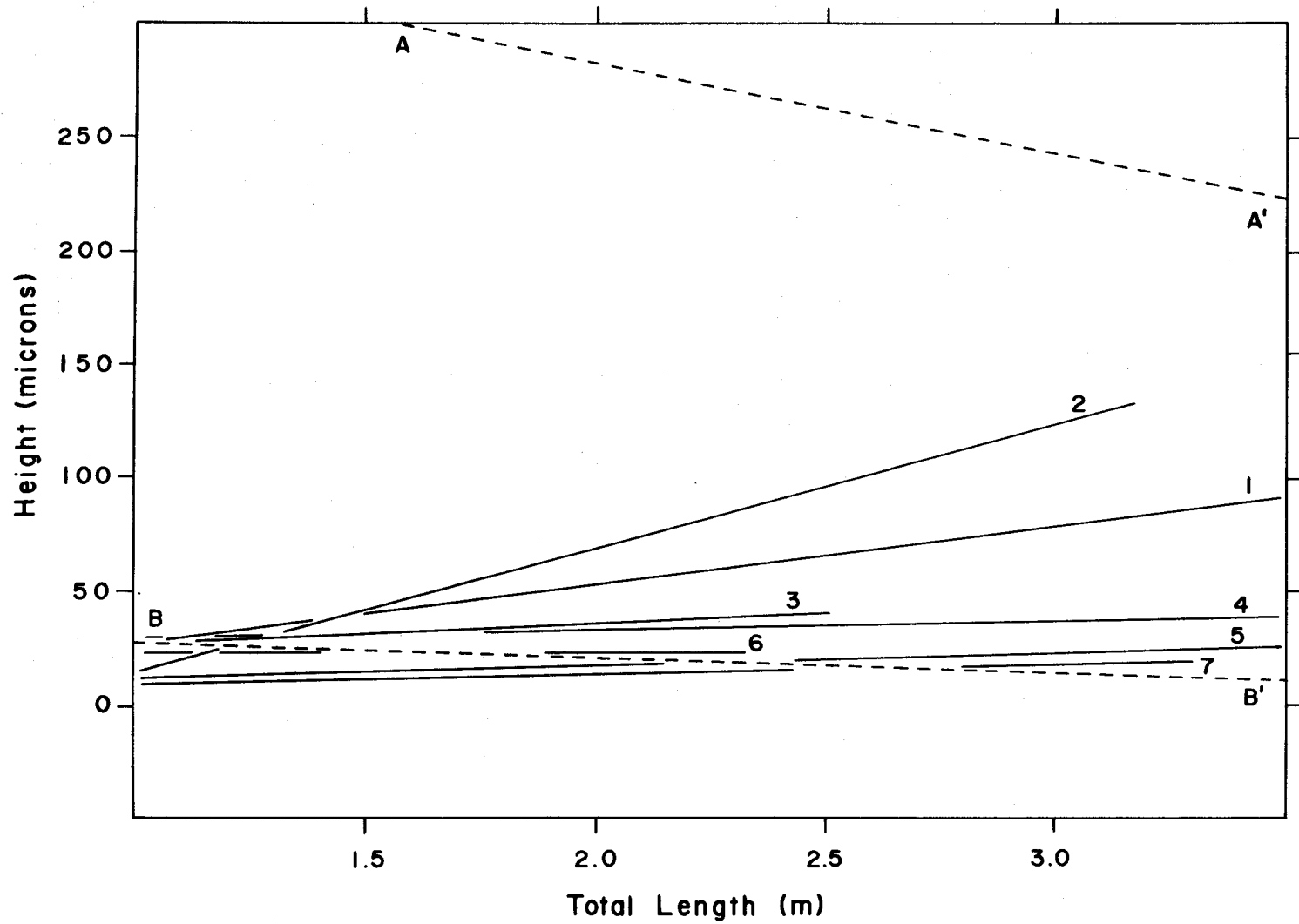
<u>falciformis</u>.

to indicate generally high swimming speeds. Carcharhinus signatus, C. falciformis and I. oxyrinchus are epipelagic (Castro, 1983; Raschi et al., 1982; and Strasburg, 1958) and exhibit a variety of structural adaptations which are necessary for the increased speed required by a predator in such an environment, including a conical or pointed snout, variously reduced fins and, in the last species, a lunate tail with lateral keels on the caudal peduncle. Furthermore, the prey consummed by these sharks, including squid and small tuna (Thunnus) for C. falciformis (Bane, 1966), squid and a variety of teleosts including exocoetids for C. signatus (Raschi, et al., 1982) and swordfish, tuna and other sharks for I. oxyrinchus (Randall, 1963), are fast, active swimmers whose capture would require higher swimming speeds. In addition, both I. oxyrinchus and C. limbatus, exhibit jumping behavior (Garrick and Schultz, 1963; Springer, 1963). Finally, the two species of hammerheads examined, S. lewini and S. mokarran, possess scales with morphologies matching those leading to the proposed optimal drag reduction. This is particularly interesting in light of the occasional argument presented that the lateral expansion of the sphyrnid head functions as a hydroplaning device for what many consider to be a particularly fast and agile group of sharks (see arguments in Budker, 1971).

In contrast, both G. cuvieri and O. taurus probably are more sluggish. Odontaspis taurus normally is found in very shallow, coastal waters. Whereas its stomach contents include a wide variety of both teleost and elasmobranch fish, it also feeds on a variety of benthic invertebrates and carrion (unpublished VIMS longline data). This species

95

tends to be very heavy bodied, with relatively large fins. Furthermore, O. taurus has been observed swallowing air and remaining motionless near the bottom (Bass and Ballard, 1972). Galeocerdo cuvieri must also be considered a sluggish species, often swimming somewhat indifferently (Randall, 1963), although it may become quite active when stimulated by hunger (Castro, 1982). Overall swimming speeds may be less than estimated however, as suggested by Dodrill and Gilmore's (1978) observation that the bird fraction in this species' diet actually consists of dead or moribund individuals. Galeocerdo cuvieri occurs in both oceanic and shallower coastal waters. While stomach contents certainly include a wide variety of more active teleosts, elasmobranchs and even cetaceans, a significant fraction of its diet includes garbage and carrion (Gudger, 1948, 1949), as well as slower benthic invertebrates and sea turtles. Like the previous species, it also is relatively heavy-bodied.

Additional examples of this trend can be found in those species with intermediate scale characteristics. The more heavily sculptured scales of C. leucas, for example, reflect both its relatively sluggish behavior (Randall, 1963) as well as its shallower, benthic distribution, this species often entering shallow estuaries and rivers. Carcharhinus plumbeus is also generally slower swimming, as suggested by the large numbers of crustacea and mollusks in its diet, and its normal habitat of shallow, coastal waters. In contrast, it sibling species, C. obscurus, which is semipelagic and seems to include a larger proportion of active teleosts in its diet, appears to be a more active species and exhibits much less heavily sculptured scales. Finally, P. glauca appears to be

96

something of an exception. This species is truly pelagic (Strasburg, 1958) and physically is very streamlined, with long pectoral fins, a long, pointed snout and a relatively thin body, all suggesting that this species is a very active swimmer. Furthermore, it frequently feeds on cephalopods (Clarke and Stevens, 1974) and faster teleosts (see for example Tricas, 1979). Therefore, it might be expected that ridges on the scales should be somewhat lower and more closely spaced than they actually are on the larger individuals.

The values reported here for both keel heights and spacings are average values. Each scale then, has a range of values for the keel morphometrics which might function over a wider range of speeds. Furthermore, the reduction in the heights and spacings from the primary values through more lateral values (Table V) might function in a compensatory role for those species with significant rates of increase in keel morphometrics. Comparing Tables IV and V, those species whose scales exhibit the most rapid growth rates, such as C. falciformis, C. obscurus and P. glauca, also exhibit the greatest reduction in lateral heights and spacings when compared with the primary values. This will allow therefore, for some portion of the scale to exhibit more appropriate values even while the overall dimensions increase rapidly.

In conclusion, it appears that the majority of the species examined in this study, with the exceptions of O.taurus and G. cuvieri, possess scales with dimensions which should promote significant drag reduction at estimated burst speeds. Different scale morphologies in the last two species may be associated with adaptations other than hydrodynamics, such as protection. The remaining species (C. leucas, C. obscurus, C.

97

Table V.   Reduction in the secondary and tertiary keel spacing and
heights (expressed in percentages) as compared with primary values. These
values are rounded to the nearest whole percentage and represent the average
and range (in parentheses).

Species	Keel Spacing		Keel Height	
	2°	3°	2°	3°
C. plumbeus	19 (6-31)	–	11 (+33-40)	46 (7-75)
C. signatus	20 (7-37)	46 (35-59)	17 (0-36)	43 (25-61)
R. terraenovae	22 (14-32)	–	18 (17-40)	48 (25-80)
C. falciformis	24 (9-39)	32 (23-41)	21 (0-50)	51 (25-75)
C. obscurus	30 (13-45)	–	33	58
P. glauca	39 (34-43)	–	20 (21-54)	83 (81-85)
M. canis	18 (0-42)	25 (8-39)	36 (13-71)	61 (43-82)
O. taurus	–	–	57 (29-91)	–
G. cuvieri	–	–	78 (29-95)	–

plumbeus, G. cirratum and P. glauca) vary in the agreement of observed scale dimensions to predicted optimal values. This variability probably reflects the differences in overall swimming speeds suggested by behavioral differences.

FUTURE STUDIES

While the data presented here strongly suggests that placoid scales are capable of providing significant drag reduction for a number of shark species, several additional lines of research could greatly enhance this picture. The most troublesome point in evaluating these scale morphologies arose from the paucity of reliable swimming speed values. While this was circumvented to some extent through inferences from natural history information, an understanding of overall swimming speed budgets, measured for extended periods of time, would be invaluable. Such work is now possible using radio telemetry in the field (for example, see Sciarrotta and Nelson, 1977) and would certainly be feasible for most of the species included in this report. "Flowmeter" types of equipment could potentially provide actual speeds, avoiding many of the problems inherent in long term tagging studies.

Secondly, an examination of additional species characterized by extremes in swimming speeds should be highly recommended. While the material for an evaluation of a more complete series of scales from I. oxyrinchus and C. limbatus has recently become available, the inclusion of additional "fast" species, in particular many of the lamnids would be particularly interesting. Similarly, more scales from additional sedentary species, such as the orectolobids, would provide information on non-drag related scales.

Finally, a reevaluation of the fossil record, in light of scale hydrodynamics may be particularly fruitful (Schaeffer, 1967). While a large amount of information is currently available regarding the overall

shape of individual scales from fossil species, the adequate
measurements required for hydrodynamic comparisons are still lacking.
Many of these scales, such as those found on members of the genus
Orodus, appear appropriately shaped and arranged (Zangerl, 1968) despite
their cyclomorial nature and may provide a suitable starting point.

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106

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Appendix I.   Collection data for the material examined

Species	Specimen number	Total length (cm)	Sex	Latitude	Longitude
Carcharhinus falciformis	1	103	M	Not available	
	2	111	M	37°03'	74°37'
	3	115	F	37°03'	74°37'
	4	189	F	37°03'	74°37'
	5	268	F	Not available	
Carcharhinus leucas	6	169	F	37°17'	75°46'
	7	201	M	37°17'	75°46'
	8	215	M	Not available	
	9	278	F	Not available	
Carcharhinus limbatus	10	148	M	37°17'	75°46'
	11	150	M	37°17'	75°46'
	12	157	M	36°54'	75°59'
	13	167	M	36°55'	75°42'
	14	173	M	37°17'	75°46'
Carcharhinus obscurus	15	86*	F	36°54'	75°59'
	16	96	F	36°55'	75°42'
	17	104	F	36°54'	75°59'
	18	108	F	37°00'	75°21'
	19	111	F	37°05'	75°55'
	20	119	F	36°55'	75°42'
	21	120	M	36°55'	75°42'
	22	123	F	36°54'	75°59'
	23	127	M	36°54'	75°59'
	24	168	M	37°00'	75°21'
	25	173	F	36°55'	75°42'
	26	182	F	37°00'	75°21'
	27	196	M	36°55'	73°42'
	28	218	F	37°00'	75°21'
	27	238	F	Not available	
	30	329	F	36°54'	75°59'
	31	334	F	36°54'	75°59'
Carcharhinus plumbeus	32	59	M	37°17'	75°46'
	33	62	F	37°17'	75°46'
	34	67	M	36°56'	76°01'
	35	73	M	37°05'	76°08'
	36	80	F	37°17'	75°46'
	37	88	F	37°05'	75°55'
	38	94	M	36°54'	75°59'
	39	99	M	37°05'	76°08'
	40	102	M	36°54'	75°59'
	41	106	M	37°05'	76°08'
	42	115	F	37°05'	76°08'
	43	117	F	37°05'	75°55'
	44	125	F	37°05'	75°55'
	45	127	F	36°54'	75°59'

Species	Specimen number	Total length (cm)	Sex	Latitude	Longitude
Carcharhinus plumbeus (continued)	46	132	F	37°00'	75°21'
	47	136	F	37°05'	76°08'
	48	145	M	36°54'	75°59'
	49	146	F	36°55'	75°42'
	50	152	F	37°00'	75°21'
	51	158	F	36°55'	75°42'
	52	161	F	37°00'	75°21'
	53	167	M	37°00'	75°21'
	54	173	F	36°55'	75°42'
	55	178	F	37°00'	75°21'
	56	185	F	37°00'	75°21'
	57	188	F	36°55'	75°42'
	58	191	F	37°00'	75°21'
	59	196	F	36°55'	75°42'
	60	207	F	37°00'	75°21'
	61	216	F	37°05'	76°08'
Carcharhinus signatus	62	76	M	Not available	
	63	94	F	Not available	
	64	179	F	Abidjan "Reine Pokon"	
	65	192	M	38°54'	73°25'
	66	211	M	Not available	
	67	215	M	Not available	
	68	217	M	Not available	
	69	222	M	38°54'	73°25'
Galeocerdo cuvieri	70	156	M	37°03'	74°37'
	71	173	F	37°07'	75°41'
	72	188	F	36°55'	75°42'
	73	213	M	37°00'	75°21'
	74	217	M	37°03'	74°37'
	75	223	F	36°55'	75°42'
	76	238	M	37°03'	74°37'
	77	252	F	Not available	
	78	258	F	36°54'	75°59'
	79	271	F	37°00'	75°21'
	80	292	F	36°55'	75°42'
	81	404	F	36°54'	75°59'
Ginglymostoma cirratum	82	72	F	Aquarium specimen	
	83	77	M	Aquarium specimen	
Isurus oxyrinchus	84	132	M	37°03'	74°37'
	85	163	F	Not available	
	86	182	F	37°03'	74°37'
Mustelus canis	87	37	M	37°07'	75°41'
	88	52	M	36°54'	75°59'
	89	56	M	Not available	
	90	61	F	37°17'	75°46'
	91	93	M	37°00'	75°21'
	92	101	M	37°00'	75°21'
	93	109	F	37°07'	75°41'
	94	113	F	37°07'	75°41'
	95	116	F	36°55'	75°42'
	96	127	F	37°07'	75°41'

Species	Specimen number	Total length (cm)	Sex	latitude	Longitude
<u>Odontaspis</u> <u>taurus</u>	97	165	F	$37^{\circ}17'$	$75^{\circ}46'$
	98	194	M	$37^{\circ}17'$	$75^{\circ}46'$
	99	204	F	$37^{\circ}17'$	$75^{\circ}46'$
	100	210	F	$37^{\circ}05'$	$76^{\circ}08'$
	101	224	M	$37^{\circ}05'$	$76^{\circ}08'$
	102	229	M	$37^{\circ}05'$	$76^{\circ}08'$
	103	231	F	$37^{\circ}17'$	$75^{\circ}46'$
	104	235	M	$37^{\circ}00'$	$75^{\circ}21'$
	105	247	M	$37^{\circ}00'$	$75^{\circ}21'$
<u>Prionace</u> <u>galuca</u>	106	34*	M	Bermuda	
	107	39*	F	Bermuda	
	108	42*	F	Bermuda	
	109	46*	F	Bermuda	
	110	165	M	$37^{\circ}03'$	$74^{\circ}37'$
	111	181	M	$37^{\circ}03'$	$74^{\circ}37'$
	112	190	M	$37^{\circ}03'$	$74^{\circ}37'$
	113	202	F	$37^{\circ}03'$	$74^{\circ}37'$
	114	214	M	$37^{\circ}03'$	$74^{\circ}37'$
	115	228	F	$37^{\circ}03'$	$74^{\circ}37'$
	116	248	M	$37^{\circ}03'$	$74^{\circ}37'$
	117	287	F	$37^{\circ}03'$	$74^{\circ}37'$
	118	348	F	$37^{\circ}03'$	$74^{\circ}37'$
<u>Rhizoprionodon</u> <u>terraenovae</u>	119	40	M	Not available	
	120	83	M	Not available	
	121	98	F	$37^{\circ}00'$	$75^{\circ}21'$
	122	95	F	$37^{\circ}05'$	$75^{\circ}55'$
	123	97	F	$37^{\circ}05'$	$75^{\circ}55'$
	124	101	F	$37^{\circ}05'$	$75^{\circ}55'$
	125	106	F	$36^{\circ}55'$	$75^{\circ}42'$
<u>Sphyrna</u> <u>lewini</u>	126	54	F	Not available	
	127	221	M	Not available	
	128	225	M	$37^{\circ}00'$	$75^{\circ}21'$
<u>Sphyrna</u> <u>mokarran</u>	129	252	M	Not available	

*embryo

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15. Supplementary Notes

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16. Abstract

   Ridge morphometrics on placoid scales from 12 galeoid shark species were
   examined in order to evaluate their potential value for frictional drag
   reduction. The geometry of the shark scales is similar to longitudinal
   grooved surfaces (riblets) that have been previously shown to give 8 percent
   skin-friction reduction for turbulent boundary layers. The present study of
   the shark scales was undertaken to determine if the physical dimensions of the
   ridges on the shark scales are of the right magnitude to be used by the sharks
   for drag reduction based on the previous riblet work. The results indicate
   that the ridge heights and spacings are normally maintained between the
   predicted optimal values proposed for voluntary and burst swimming speeds
   throughout the individual's ontogeny. Moreover, the species which might be
   considered to be the "faster" possess smaller and more closely spaced ridges
   that based on the riblet work would suggest a greater frictional drag
   reduction value at the high swimming speeds, as compared to their more
   sluggish counterparts.

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