CHELODINA PARKERI, A NEW SPECIES OF CHELID TURTLE FROM NEW GUINEA, WITH A DISCUSSION OF *CHELODINA SIEBENROCKI* WERNER, 1901

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ABSTRACT. *Chelodina parkeri*, a new species of chelid turtle from New Guinea, is described. Seventeen specimens of the new species are compared to a series of 27 specimens referable to *Chelodina siebenrocki* Werner, 1901, also from New Guinea. *C. parkeri* differs from all other *Chelodina* species in having a light, vermiculate color pattern on the dorsal surface of the head and the mandible. Various other shell and skull characters also differentiate it from other *Chelodina*. *C. parkeri* is endemic to southern New Guinea and is apparently restricted to large inland grass swamps surrounding Lakes Murray and Balimo and the Fly and Aramia Rivers. It is most closely related to *C. siebenrocki*. *C. siebenrocki* is found on the south coast of New Guinea and on certain islands in the Torres Strait. It is most closely related to *Chelodina rugosa* Ogilby, 1890 from northern Australia and may be synonymous with this species. However, the small amount of northern Australian material currently available makes it impossible to draw a conclusion concerning the relationship of these two animals.

INTRODUCTION

The chelid turtle genus *Chelodina* is restricted to Australia and New Guinea and is composed of seven living species divided into three species groups (Burbidge, 1967; Burbidge, et al., 1974; Goode, 1967). The status of two members of species group B—*Chelodina rugosa* Ogilby, 1890, from northeastern Australia (type locality: Cape York, Queensland) and *Chelodina siebenrocki* Werner, 1901 (type locality: German New Guinea)—has not been clear. The major problem has been the lack of a sufficiently large series for taxonomic studies. The only descriptions available of *C. rugosa* and *C. siebenrocki* are the original ones. These are based exclusively on external characters and are inadequate for comparative purposes. No osteological descriptions have been made, locality data from museum specimens have never been carefully checked and nothing has been published on the habitat of either species.

Over the past few years, Fred Parker of New Guinea has provided the Museum of Comparative Zoology at Harvard University (MCZ) with an excellent series of New Guinean chelid turtles, the largest ever collected. Twenty-one specimens in this series are referable to *C. siebenrocki*[3]. While studying the Parker series with the hope of clarifying the *C. siebenrocki-C. rugosa* problem, we found eight specimens of a previously undescribed *Chelodina* species.

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[3] The type specimen of *C. siebenrocki* was lost during World War II (G. Peters, personal communication). However, Werner's (1901) description of this turtle includes photographs of the carapace and plastron of the type (Fig. 1). On the basis of the very close resemblances of Parker's 21 specimens to the type photographs and original description of *C. siebenrocki*, we have concluded that Parker's animals represent *C. siebenrocki*.

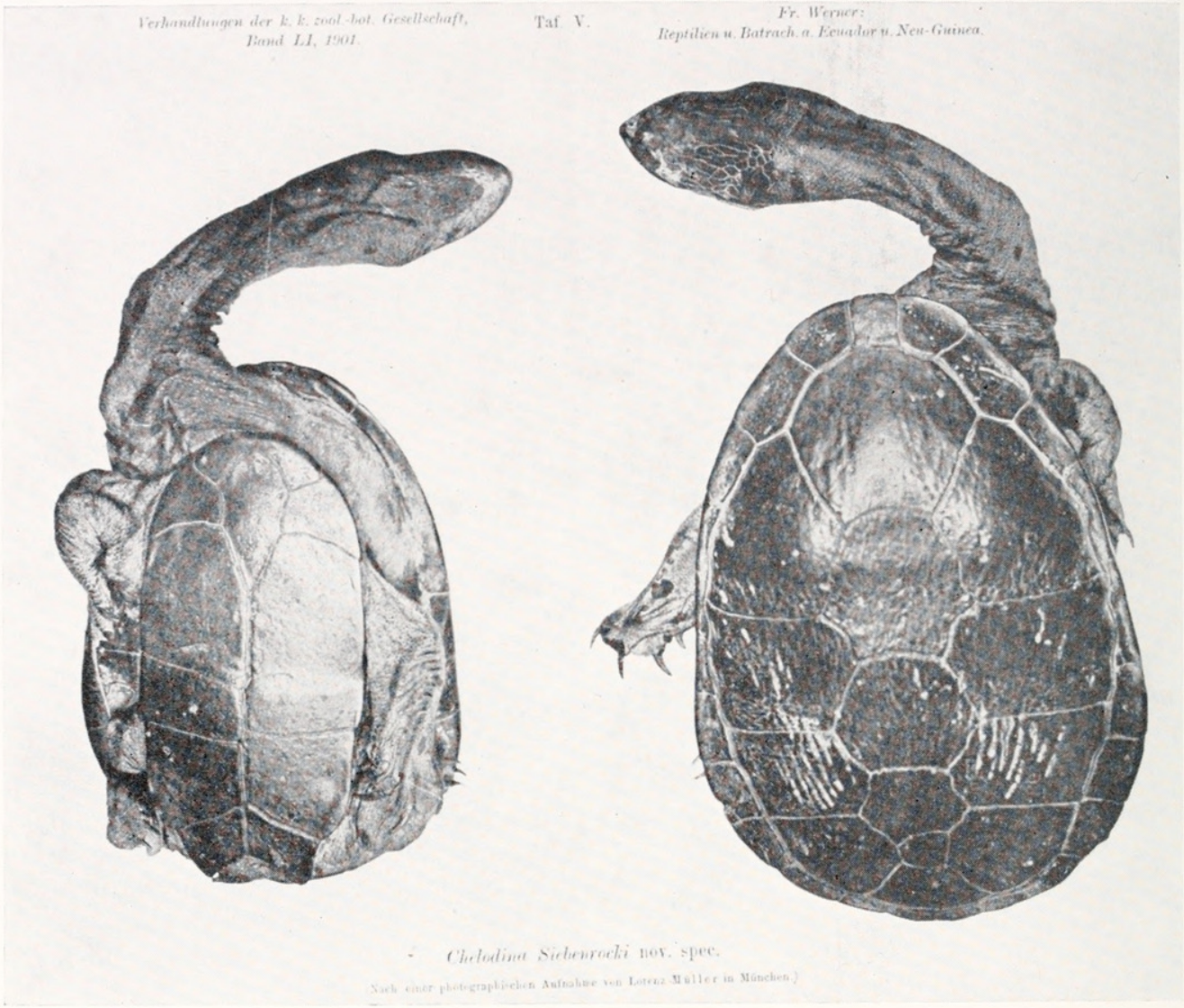

Figure 1. Ventral and dorsal views of the type specimen of *Chelodina siebenrocki* from Werner (1901).

In addition to the 21 Museum of Comparative Zoology specimens, we have examined six other turtles referable to *C. siebenrocki*. These include four collected by Parker and deposited in the Australian Museum in Sydney (AMS) and the American Museum of Natural History in New York (AMNH), and two collected by Müller in 1886 and deposited in the Staatliches Museum für Naturkunde in Stuttgart (SMNS)—bringing the total to 27. In addition to the eight specimens of the new species collected by Parker for the MCZ, we have examined six collected by Harold Cogger of the Australian Museum, and have data on three more collected by Parker and deposited in the Papua New Guinea Museum in Port Moresby (PNGM)—bringing the total for this species to 17.

MATERIAL STUDIED

A total of 27 specimens of *C. siebenrocki* were examined. All specimens, except for SMNS 3991-1 and SMNS 3991-2, were collected by Parker on mainland New Guinea and the offshore island of Daru. The two SMNS specimens were collected by Müller on Saibai Island. MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; AMS = Australian Museum, Sydney; AMNH = American Museum of Natural History, New York; SMNS = Staatliches Museum für Naturkunde, Stuttgart, West Germany.

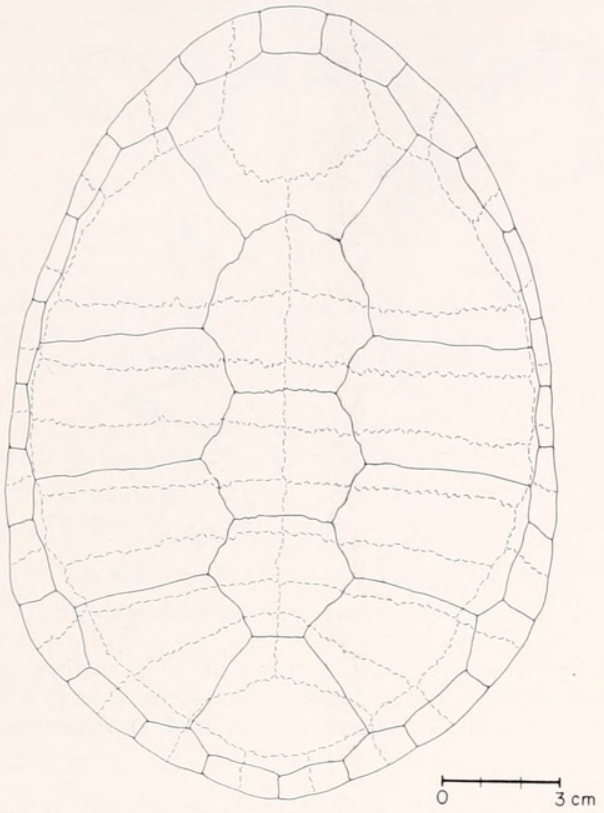

Figure 2. Dorsal view of the carapace of MCZ 134404, a 203 mm female specimen of *C. siebenrocki*. Solid lines indicate scute seams, dotted lines bone sutures.

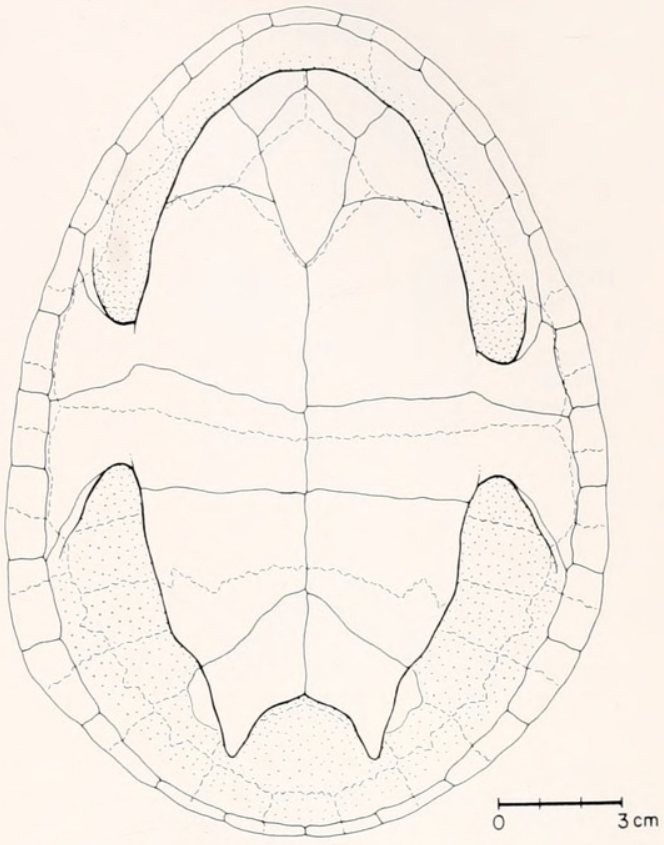

Figure 3. Ventral view of *C. siebenrocki* (MCZ 134404). Note the shape of the anterior plastral lobe and the extent of the anterior ventral marginals.

Balumuk: MCZ 134406, 139551; Boze: MCZ 134466; Daru: MCZ 119721; Dorogori: MCZ 118611; Katatai: MCZ 135397–8, 139541–2, 142496–7, AMNH 111645–6, AMS 40696–7; Mawatta: MCZ 141288; Saibai: SMNS 3991-1, 3991-2; Sigabaduru: MCZ 139547–9; Togo: MCZ 134403–5, 134467–8; Waidoro: MCZ 141694.

Chelodina siebenrocki Werner, 1901
Figures 1–12

Diagnosis. *Chelodina siebenrocki* is a medium-sized species with a roughly egg-shaped carapace, widening markedly posteriorly but without flaring margins (Fig. 2). The carapace has no keel, is weakly domed, and has a rugose surface and thin scutes. *Anterior ventral marginals*[4] form a very narrow rim between the anterior edge of the carapace and the attachment of skin from the dorsal surface of the neck, so that the ventral surface of the nuchal scute[5] is wider than it is long (Fig. 3). The intergular tends to be long and narrow (Fig. 3). The anal notch is deep and usually semicircular (Fig. 3). The plastron tapers anteriorly and is moderately elongate (not as narrow and long as in *Chelodina oblonga*, not as wide as in *Chelodina longicollis*, Fig. 3). The head is long, wide and relatively flat (flatter than in *C. longicollis*, not as flat as

[4] We have introduced a number of terms new to the chelonological literature, especially for certain skeletal features. These terms are indicated by italics, defined in Appendix I and illustrated in Figs. 3, 4, 5, 6, 8 and 16.

[5] Zangerl (1969) suggests *cervical scute* be used for what most previous authors have called nuchal scute. His reasoning is to avoid confusing the scute and the underlying bone, also called nuchal. Although we otherwise follow Zangerl's terminology, we do not agree with him here. Since there has been little confusion regarding the use of this term, we feel that the introduction of a new term is unnecessary, and simply differentiate between the two "nuchals" by context or add "scute" or "bone."

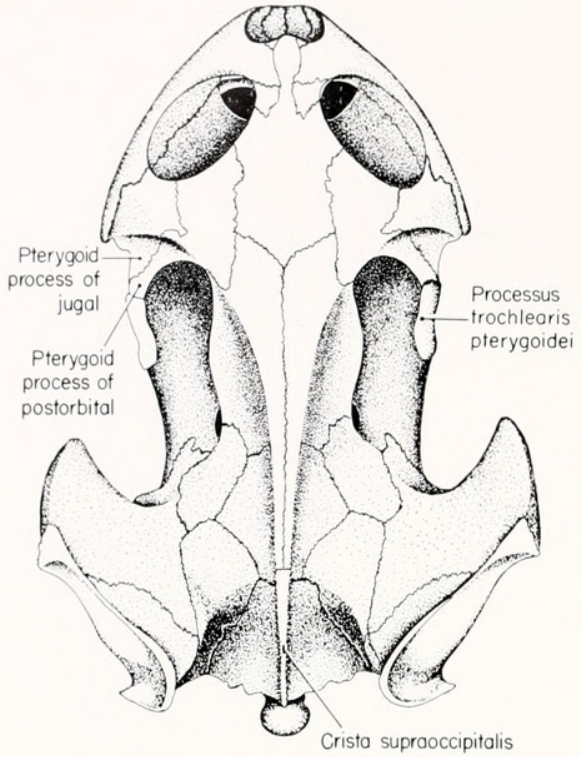

Figure 4. Dorsal view of the skull of *C. siebenrocki* (AMS 40696). The labelled terms include new terms introduced in this paper and defined in Appendix I.

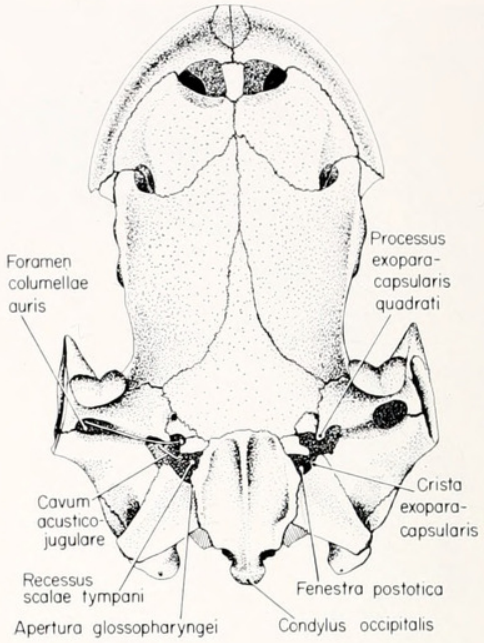

Figure 5. Ventral view of the skull of *C. siebenrocki* (AMS 40696). The labelled terms include new terms introduced in this paper and defined in Appendix I.

Chelodina expansa, Figs. 1, 9). The neck is long and thick (Figs. 1, 9). Coloration is uniform dark brown to black on all dorsal surfaces, uniform yellowish white to tan on all ventral surfaces. The carapace lacks neural bones (Fig. 2). The skull is similar to *C. oblonga*, but the vomer does not usually separate the palatines (Fig. 5). The *prefrontal spine* is relatively prominent (Fig. 6). The hyoid has a clearly defined *crista ventralis hyoideus* (Fig. 8).

EXTERNAL CHARACTERS

Head, neck and limbs. Head flat, broad and elongate, covered on dorsal surface with fine reticulate pattern of skin creases giving the impression of numerous, small, irregularly-shaped scales. Creases absent from tympanum, maxilla, mandible, nasal region and a triangular area along the midline posterior to the orbits (Figs. 1, 9). Chin barbels present, variable in number; often four or more.

Neck long and thick; approximately 75 per cent of length of carapace[6], dorsal surface covered by irregular, flattened tubercles (Figs. 1, 9).

Forelimbs with a single column of transverse, crest-shaped scales on dorsal surface, usually eight; but varying from six to 10. Similar scales on ventral surface of hindlimbs; usually arranged in two columns, with four to six in the medial column and eight to 12 in the lateral column; lateral column extends onto lateral edge of foot and to upper limb; scales rapidly diminish in size as they radiate out towards the foot and the thigh.

Carapace. Carapace roughly egg-shaped, moderately elongate (adult length averaging 1.38 times width; juveniles 1.31 and hatchlings 1.29), fairly flat (length averaging 2.72 times height), widening markedly posteriorly, and with a narrow, pointed anterior portion (Figs. 1, 2, 9). No flaring of marginals either laterally or posteriorly. Supra-anal ridging as in *C. longicollis* also absent. No carapacial keels or tuberculations. No central furrowing along midline of carapace. Weak central depression along

[6] For an explanation of all measurements used in this paper, see Appendix II.

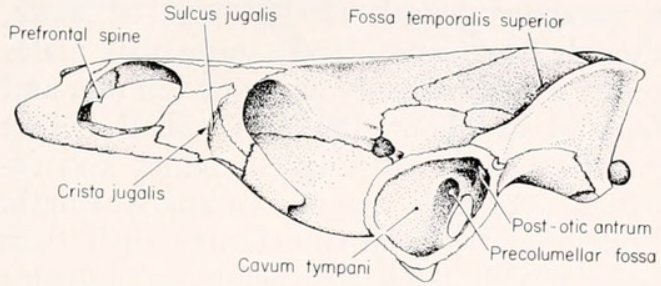

Figure 6. Lateral view of the skull of *C. siebenrocki* (AMS 40696). The labelled terms include new terms introduced in this paper and defined in Appendix I.

midline in very large females. Surface of carapace weakly rugose with reticulate pattern of numerous, very shallow furrows. Furrows on vertebrals oriented longitudinally along midline; furrows on pleurals not oriented in any particular way. Length of dorsal surface of nuchal scute usually greater than width, averaging 1.20 in length: width ratio. All 27 specimens examined had fully formed nuchal scutes. Width of ventral surface of nuchal scute greater than length, averaging 0.42 in length:width ratio (Fig. 3). Anterior ventral marginals form a narrow rim between edge of carapace and attachment of skin from dorsal surface of neck; carapace averages 33.4 times longer than width of second ventral marginal. Width of fifth vertebral greater than length, with the length:width ratio averaging 0.87. Shape of pleurals and first four vertebrals apparently not significant. Twelve marginals on each side of carapace; fifth marginal always in contact with first pleural; eleventh marginal usually in broad contact with fifth vertebral (Figs. 1, 2, 9).

Plastron. Plastron fairly elongate and narrow (Figs. 1, 3). Carapace width averaging 1.87 times plastron width; carapace length averaging 2.53 times plastron width; length of plastron itself averaging 1.89 times width. Plastron shorter than carapace, with carapace length averaging 1.34 times plastron length (Fig. 3). Anterior lobe generally much narrower than posterior lobe and tapering anteriorly to end in a blunt point (Fig. 3). Tapering less pronounced in large adults. Anal notch deep and semicircular, width averaging 2.25 times depth (Fig. 3). Intergular scute narrow and elongate, length averaging 1.96 times width (Figs. 1, 3). In approximately 15 per cent of specimens examined, the intergular completely separates the gulars and reaches all the way to the anterior plastral margin (as in the type specimen of *Chelodina intergularis* Fry, 1915, which has been synonymized with *C. siebenrocki* by Goode [1967]).

Figure 7. Medial and slightly ventral view of the right side of the mandible of *C. siebenrocki* (AMS 40696).

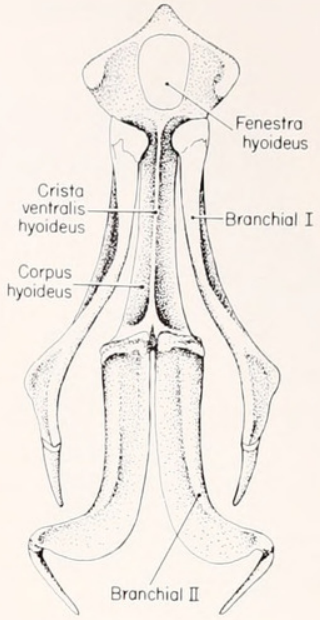

Figure 8. Ventral view of the hyoid of *C. siebenrocki* (MCZ 118611).

COLORATION

Head, neck and limbs. Color of head uniform dark gray to grayish brown dorsally, grayish white to yellowish ventrally. Neck color dark gray to grayish brown dorsally, dull yellowish white to light yellowish brown ventrally. Limbs and tail dark gray to grayish brown dorsally. Ventral surfaces of feet brown to grayish brown; ventral surfaces of limbs grayish white to

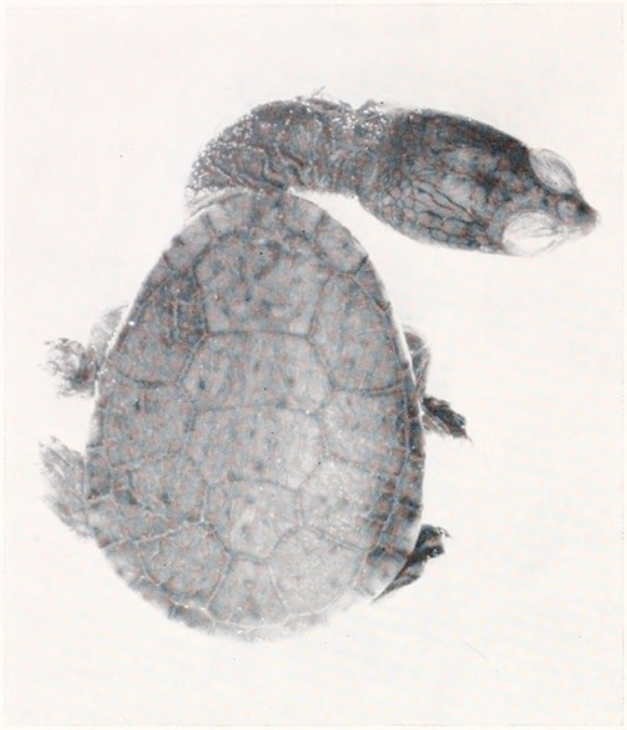

Figure 9. Dorsal view of MCZ 139551, a 37 mm hatchling of *C. siebenrocki.*

light yellowish brown. Soft skin in axillary and inguinal pockets and at base of tail white to light yellowish brown to very light brown.

Carapace. Coloration of dorsal surface of carapace uniform dark brown to black. Coloration of ventral surfaces same color as plastron. Dorsal surface of carapace in hatchlings with fine black spots scattered on dark ground color (Fig. 9).

Plastron. Coloration of plastron uniform light to dark cream or tan; sometimes sutures between scutes finely outlined in dark brown.

Size. Goode (1967) states that *C. siebenrocki* can reach at least 300 mm in carapace length, and Cogger (1972) gives 380 mm as a maximum. Males and females reach approximately the same size; the largest male examined by us was 263 mm, the largest female 273 mm.

Sexual dimorphism. Adult males are distinguished from adult females by tail size and shell height. Adult males have a tail which is considerably longer and thicker than that of females. In our specimens, this difference is apparent only in animals with a carapace length of 150 mm or more, though Bergmans (1966) states that males reach sexual maturity at about 125 mm and females at about 150 mm. Shell height can be used to distinguish males and females over 175 mm in carapace length. Males have a relatively flatter shell than females, with the length:height ratio greater than 2.60. In females, the ratio is less than 2.60. The flatter shell is not due to plastral concavity in male *C. siebenrocki.* No sexual dimorphism is noticeable in shape or depth of anal notch or width of head.

OSTEOLOGY

Skull. Skull moderately elongate, length averaging 1.54 times tympanic width and 1.92 times maxillary width; markedly flattened, with length averaging 6.03 times height, and maxillary width averaging 3.07 times height; narrowed anteriorly, with tympanic width averaging 1.28 times maxillary width. No parietosquamosal connection. Vomer connecting maxillae and palatines, but usually not separating palatines (exception: one of the 12 skulls examined has vomer extending beyond choanal border, separating palatines and reaching anterior edge of pterygoids). Basisphenoid somewhat elongate, length averaging 1.27 times width. Foramen columellae auris on the ventral surface of the skull fairly large and pyriform, with the wider portion laterally located. Processus trochlearis pterygoidei, when viewed from dorsal aspect, makes an approximately 30° angle with the *pterygoid processes of the jugal and postorbital* (Fig. 4). Lateral rim of cavum tympani nearly ovoid, widening slightly anteroventrally. Triturating surfaces of maxillae fairly narrow posterolaterally, contributing only about 13 per cent of skull width at maxillary-pterygoid border. The following features are of importance within cavum acustico-jugulare: recessus scalae tympani entirely open to a large, wide fenestra postotica; small, delicate *processus exoparacapsularis quadrati* barely covers the columella (Fig. 5); crista exoparacapsularis

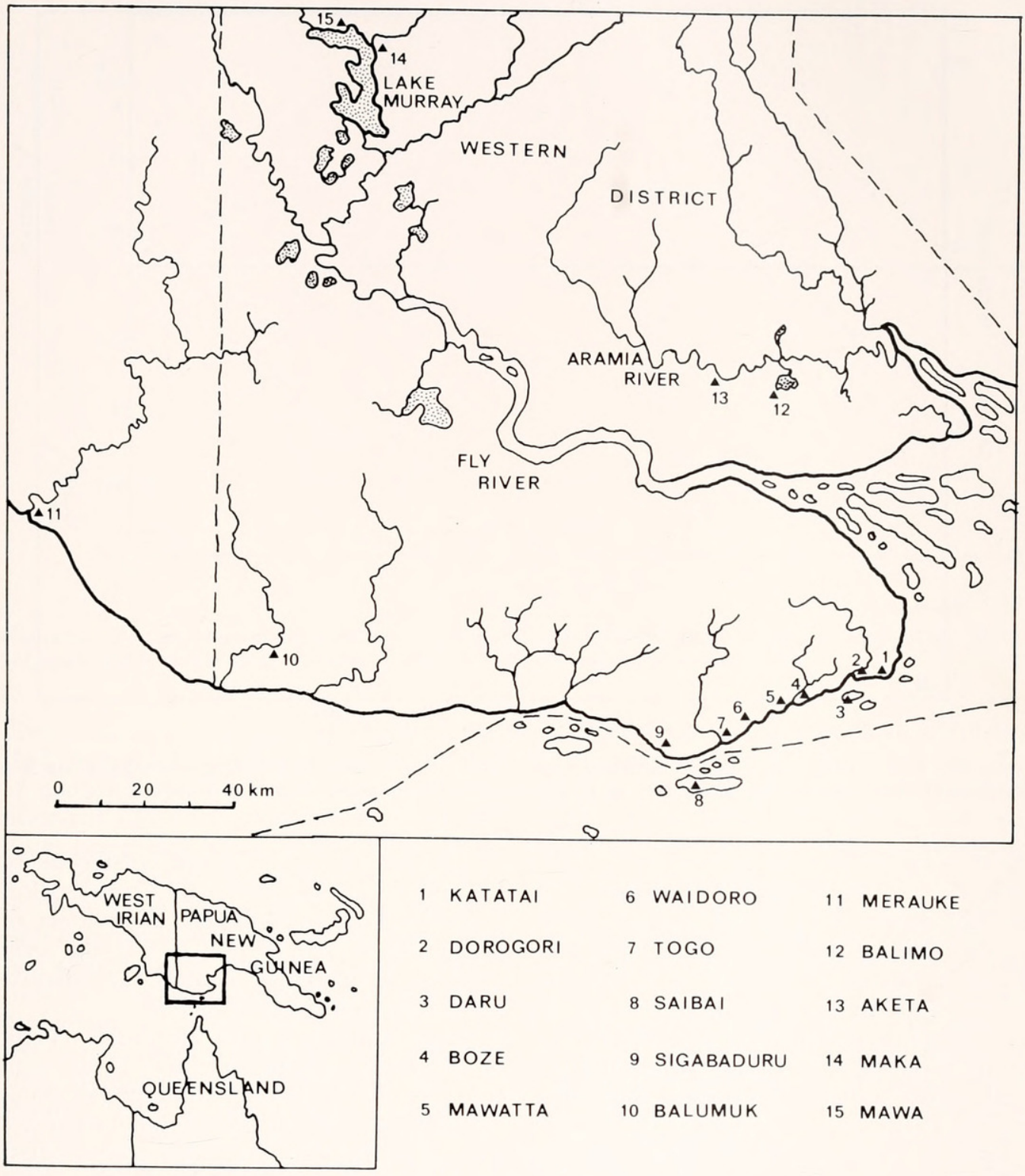

Figure 10. Map of southern New Guinea showing the localities where *C. siebenrocki* and *C. parkeri* have been collected. Localities 1–11 represent *C. siebenrocki*; localities 12–15 are *C. parkeri*.

present only as a weak ridge, dividing the deep medial cavum acustico-jugulare from an extremely shallow or absent lateral fossa; apertura glossopharyngei set close to edge of opisthotic, often present as an incisura in crista exoparacapsularis. Parietals extremely emarginate medially, creating a narrow dorsal surface for attachment of skin. Prefrontals with a well-developed, posteriorly directed spine (*prefrontal spine*—Fig. 6) on the interior anteromedial margin of the orbit. Precolumellar fossa in cavum tympani

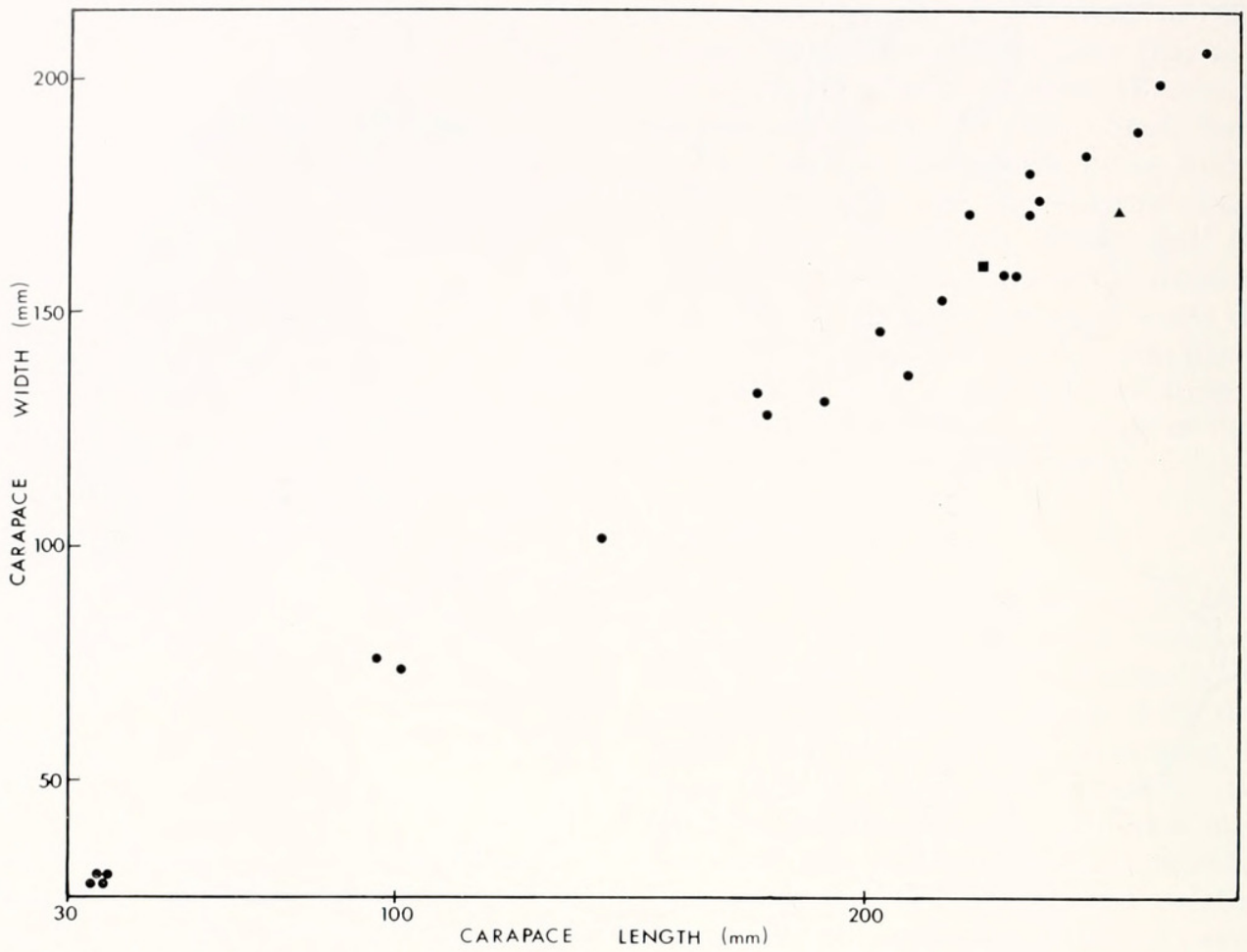

Figure 11. Plot of carapace length vs. carapace width. Solid circles = *C. siebenrocki* specimens discussed in this paper; solid square = type photograph of *C. siebenrocki*; solid triangle = type of *C. rugosa*.

tends to be shallow, ill defined and of the same size or smaller than lateral aspect of foramen columellae auris (Fig. 6). *Sulcus jugalis* (Fig. 6) well-defined; situated posterior to sharp, sometimes overhanging *crista jugalis* (Fig. 6). Columella slender throughout its length, with only slight flattening or flaring at its lateral end. Mandible weak, with a narrow, slanted triturating surface (Fig. 7).

Hyoid. Hyoid very elongate and massive (Fig. 8). Skull length averages 1.78 times length of corpus hyoideus, and carapace length averages 6.09 times length of corpus. Ventral surface of corpus with a well-defined crista ventralis hyoideus (Fig. 8).

Cervical column. Cervical column typical of pattern outlined for all Chelidae by Williams (1950). Data from three specimens indicates that C1 and C7 are amphicoelus, C2, C3 and C4 are opisthocoelus, C5 and C8 are biconvex and C6 procoelus. As pointed out by Williams, this pattern of N(2(,(3(,(4(,(5),)6),)7(,(8) is the only pattern of cervical central articulation known to occur in the Chelidae.

Shell. Carapace with 16 costals (eight on each side), 22 peripherals (11 on each side), nuchal, pygal and suprapygal. Neurals absent. Nuchal bone totally separates first peripherals and partially separates first costals. First peripherals contact first costals (Fig. 2).

Plastron with diamond-shaped entoplastron and paired epiplastra, hyoplastra, hypoplastra and xiphiplastra (Fig. 3).

HATCHLING CHARACTERISTICS

Hatchlings differ in a number of ways from adults and therefore merit separate

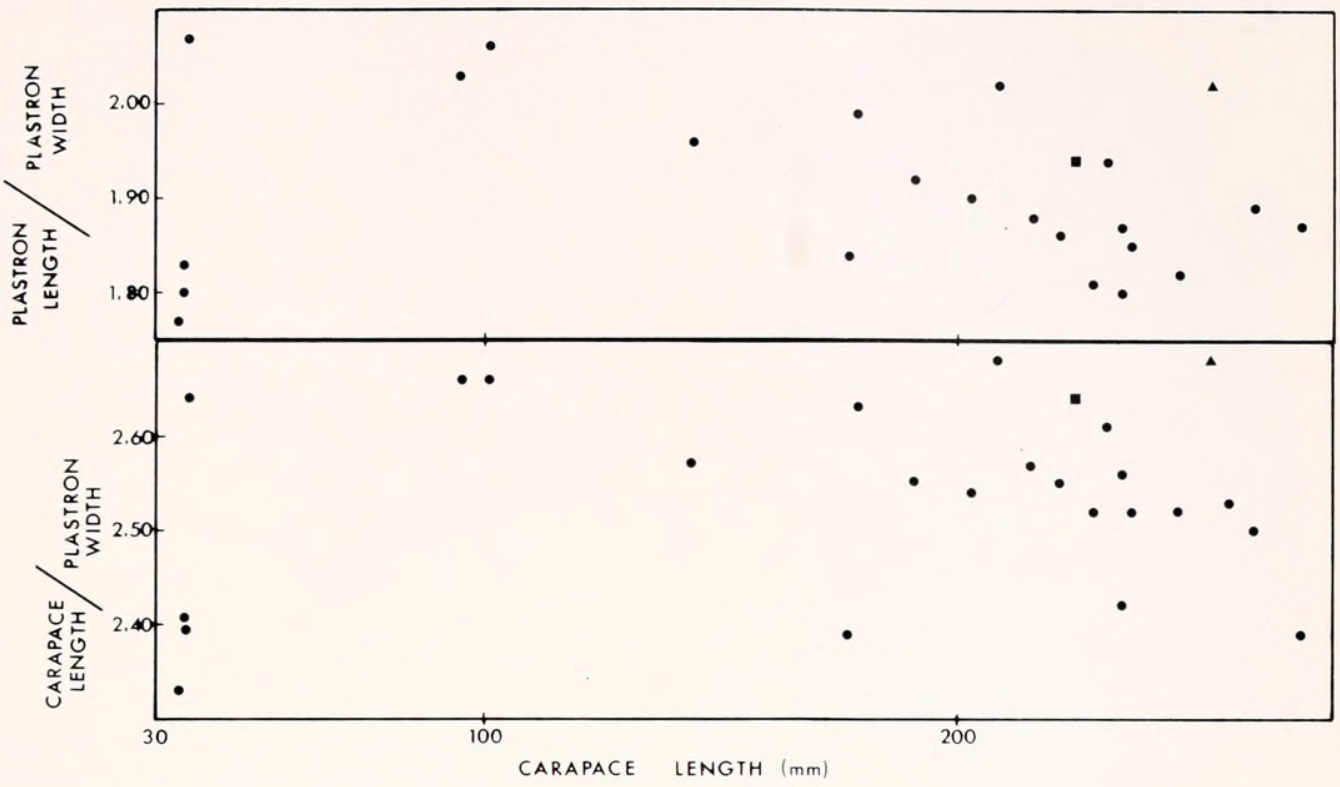

Figure 12. Bottom: Plot of carapace length vs. the ratio of carapace length to plastron width. Top: Plot of carapace length vs. the ratio of plastron length to plastron width. Symbols as in Fig. 11.

discussion here. In general shape of the shell, intergular, dorsal and ventral surfaces of nuchal scute, width of anterior ventral marginal rim and coloration of head and neck, hatchlings agree with adults. However, they differ in a number of other features. The coloration of the carapace differs slightly in hatchlings in that small black spots cover the dark brown surface (Fig. 9). This characteristic was first noted by Siebenrock (1905) in his description of five hatchlings of what he called *C. oblonga* from Saibai Island. The spots vary in number. Each marginal tends to have one, and the vertebrals and pleurals have from zero or one to 10–15 spots each. The width of the head and length of the neck are much greater in relation to carapace length in hatchlings than in adults. During growth, ratios of head length, head width and neck length to carapace length change allometrically and become proportionally much less. Allometric changes in carapace shape include a gradual elongation and decreased posterior widening. The hatchling carapace is also rugose, but longitudinal orientation of furrows occurs on entire surface. The juvenile carapace retains trace of hatchling scute on posteromedial section of each scute and has growth lines radiating out from trace of hatchling scute. The anal notch is deep as in adults, but is more an acute or right angle than a semicircle.

The hatchling skull differs in a number of features from the adult skull. Although length:width ratio is roughly the same as in adults, the maxillary width:height ratio is 1.96, compared to 2.18 in juveniles and 3.07 in adults, and the length:height ratio is 3.38 compared to 4.74 in juveniles and 6.03 in adults—indicating a much flatter skull in adults than in hatchlings. The squamosal extension covering the postotic antrum is shortened and the rim of the cavum tympani is less elongate, being totally circular in the smaller of the two hatchling skulls examined. The precolumellar fossa is poorly defined, but very large and deep and much larger than the foramen columellae auris. The crista supraoccipitalis is short

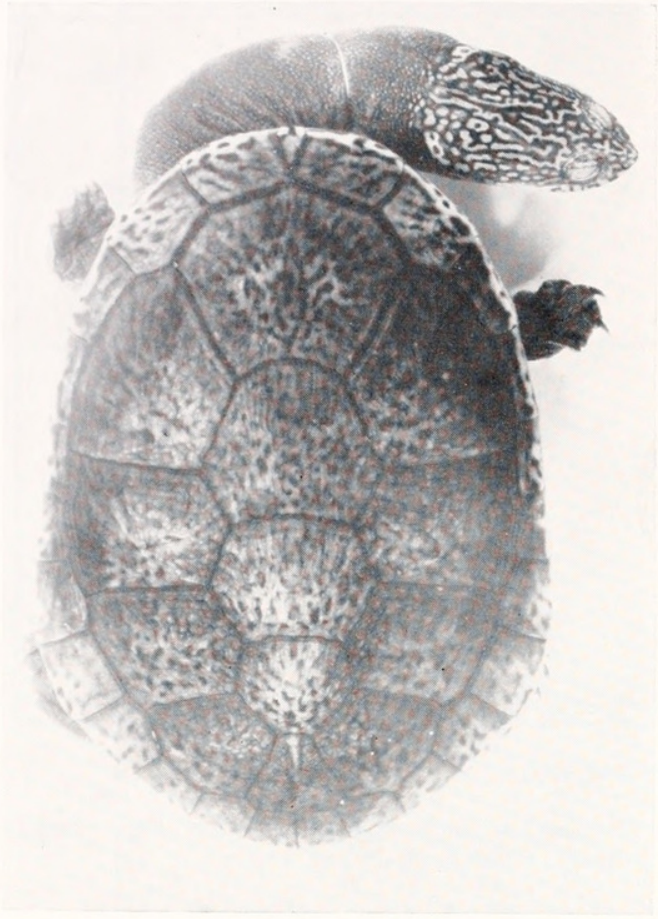

Figure 13. Dorsal view of MCZ 129897, a 136 mm specimen of *C. parkeri*. Note especially the vermiculate pattern on the head, the reticulate pattern on the carapace, the general shape of the carapace and the reduced triangular dorsal surface of the nuchal scute.

and flat, resulting in a very shallow fossa temporalis superior and a relatively enlarged parietal surface on top of the skull. The basisphenoid has its characteristic shape, as does the vomer, which as in most adults, does not separate the palatines. The prefrontal spine is present. The quadrate does not completely encircle the cavum tympani, leaving a notch in its ring at the site of the incisura columellae auris. The basioccipital is poorly developed but markedly biconcave. The hyoid has a rounded, not angulated, corpus, with no crista ventralis hyoideus. In general, the skull of hatchling *C. siebenrocki* is similar in degree of flattening to adults of group A species (Burbidge, et al., 1974), but becomes considerably flatter during the course of growth.

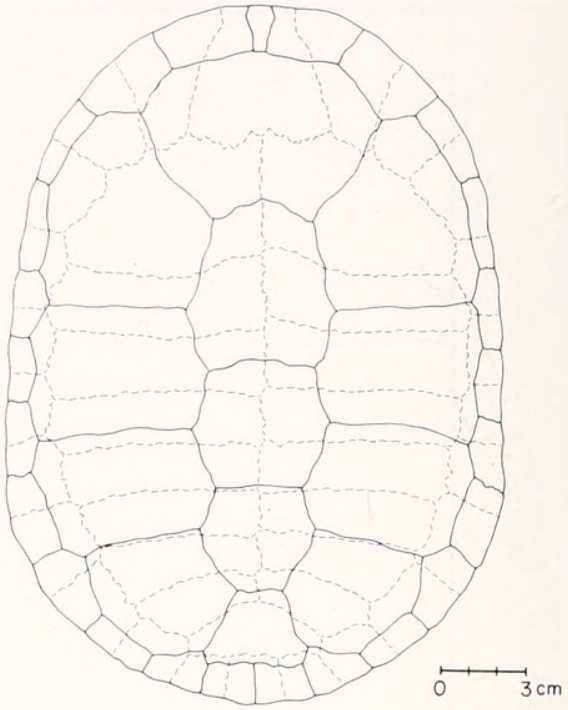

Figure 14. Dorsal view of the carapace of MCZ 134400, a 257 mm female specimen of *C. parkeri*. Solid lines indicate scute seams, dotted lines bone sutures.

DISTRIBUTION AND ECOLOGY

Distribution. *C. siebenrocki* is apparently restricted to the tidal portions of the small streams flowing to New Guinea's south coast, and to tidally-influenced coastal swamps and offshore islands such as Daru and Saibai (F. Parker, personal communication, 1973). Collecting localities which we have verified by examining specimens are restricted to the coastal areas of the low-lying marsh country to the south of the Fly River (Fig. 10). All collecting localities are in the Papua New Guinea Western District, with the exception of Saibai Island. There is also a reliable literature record for *C. siebenrocki* from Boeti, near Merauke in West Irian (Bergmans, 1963, 1966). We are not sure if *C. siebenrocki* occurs on the Cape York Peninsula of Australia. We follow Burbidge (1967) and Burbidge, et al. (1974) in considering *C. siebenrocki* distinct from *C. rugosa* of Cape York, but the relationship between these two species requires further investigation. Werner's type locality of German (now Northeast)

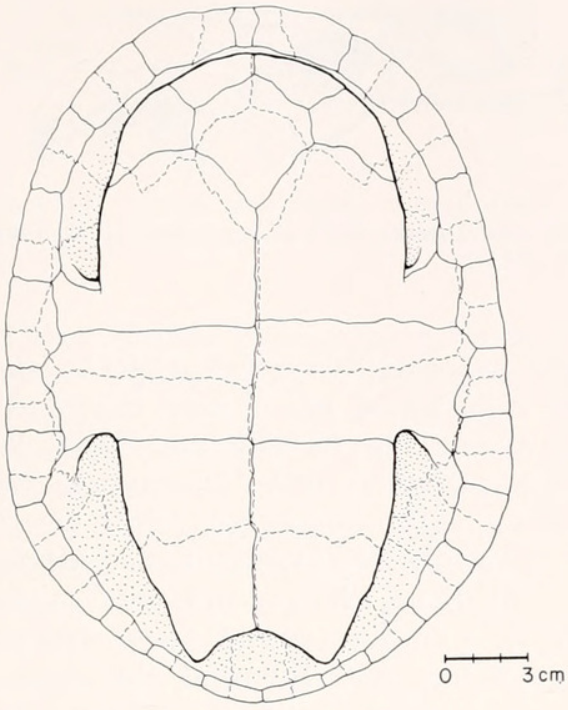

Figure 15. Ventral view of *C. parkeri* (MCZ 134400). Note especially the shape of the anterior plastral lobe and the extent of the anterior marginals.

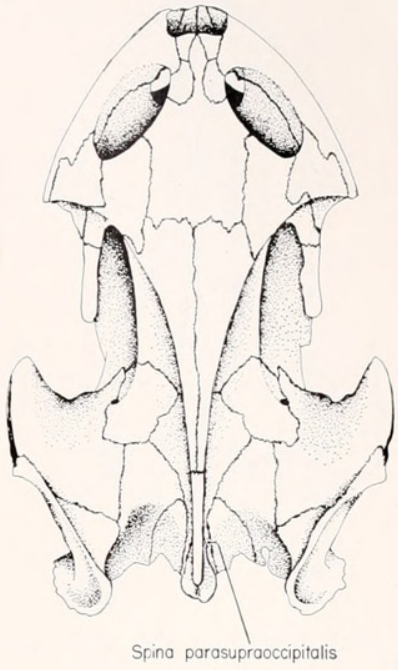

Figure 16. Dorsal view of the skull of *C. parkeri* (AMS 21434). Note the location of the spina parasupraoccipitalis.

New Guinea is probably incorrect, since no specimens of *Chelodina* are known from north of the Central Ranges (Brongersma, 1958, 1961; Cogger, 1972). The only chelid turtle which appears to inhabit Northeast New Guinea is *Elseya novaeguineae* (Brongersma, 1961; Cogger, 1972).

Ecology. Little is known of the habits of *C. siebenrocki.* It does not bask, but spends most of its time on and in deep, soft mud characteristic of the south coast (Parker, personal communication, 1974). It is usually caught by feeling around with bare feet in the mud. It is not an aggressive animal and will not bite even when handled. Local villagers in New Guinea do not eat it, although *Emydura subglobosa* and *Elseya novaeguineae* are readily eaten and sold at markets (Parker, personal communication, 1974). It is apparently carnivorous, using its long neck to strike for food (Bergmans, 1966).

C. siebenrocki appears to breed seasonally, laying eggs at the end of the wet season in May, which hatch at the start of the next wet season in November or December (Parker, personal communication, 1974). Copulation takes place in the water, with the male mounting the female from behind (Bergmans, 1966). The female leaves the water to lay her eggs in a nest which she digs in the available substratum. Bergmans (1966) figures a 95 mm deep nest dug by a captive female. It has an unusual shape, cylindrical in the upper half, but bulging out to one side at the base (Bergmans, 1966). Two egg clutches collected by Parker at Katatai had 17 and four eggs. The average size of the eggs in the larger clutch was 35.0 × 28.25 mm, and in the smaller clutch 36.1 × 28.9 mm. An attempt at artificial incubation yielded an 18 mm embryo after 187 days, and a 28 mm embryo after 272 days (Parker, personal communication, 1974). Although no fully developed hatchlings resulted from this attempt, a linear extrapolation to 35 mm results in an estimated incubation time of 330 days. This unusually long incubation period may result from the artificial conditions. However, at least one other *Chelodina*, *C. expansa*, has an incubation period that normally exceeds 324 days (Goode and Russell, 1968).

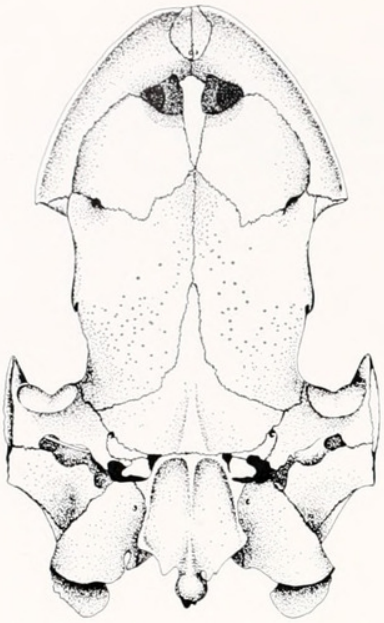

Figure 17. Ventral view of the skull of *C. parkeri* (AMS 21434).

Hatching under natural conditions appears to occur at a carapace length of about 35 mm. A recent hatchling caught by Parker at Sigabaduru on January 17 measured 36 mm, while another from Balumuk, caught on February 19, measured 37 mm.

C. siebenrocki apparently occurs sympatrically with *Chelodina novaeguineae, Emydura subglobosa* and *Elseya novaeguineae*, and possibly *Carettochelys insculpta* and *Pelochelys bibroni.*

DISCUSSION

Nomenclature. The major nomenclatorial problem involving *C. siebenrocki* has resulted from the belief that *Chelodina oblonga*, a distinct species endemic to southwestern Australia, extends as far north as northern Australia and islands south of New Guinea. Gray (1844) referred a specimen from Port Essington (Darwin) in the Northern Territory of Australia to *C. oblonga*, while Strauch (1890) and Schenkel (1901) added to the confusion by reporting *C. oblonga* from Prince of Wales Island and Thursday Island, both in the Torres Strait near the northern Australian coast. These three localities are all within the range of *C. rugosa.* Finally, Siebenrock

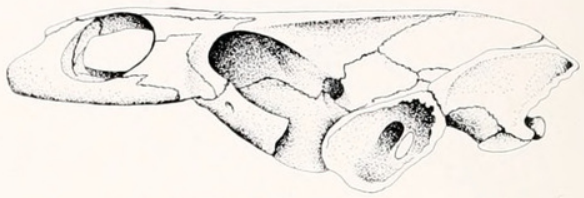

Figure 18. Lateral view of the skull of *C. parkeri* (AMS 21434).

(1905) referred five embryos of *C. siebenrocki* from Saibai Island near the coast of New Guinea to *C. oblonga.* Most later authors (Werner, 1909; Siebenrock, 1909; DeRooij, 1915; Loveridge, 1948; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961; Mehrtens, 1967) recognized *C. siebenrocki* as a distinct species from mainland New Guinea, but followed the error of earlier authors by citing *C. oblonga* from northern Australia and islands in the Torres Strait.

Siebenrock (1915) synonymized *C. siebenrocki* with *C. oblonga*, after already having synonymized *C. rugosa* with *C. oblonga* in 1909.

Goode (1967) considers *C. rugosa* of northern Australia and *C. siebenrocki* of New Guinea to be conspecific and refers to both as *C. siebenrocki*, although the name *C. rugosa* Ogilby, 1890 has priority over *C. siebenrocki* Werner, 1901.

Blackmore (1969) considers *C. siebenrocki* only subspecifically distinct from *C. oblonga.*

Burbidge (1967) and Burbidge, et al. (1974) are the first to assert that *C. oblonga* does not occur in northern Australia and on the Torres Strait Islands, but is endemic to southwestern Australia and clearly distinct from *C. siebenrocki* and *C. rugosa.*

Peters (1969) mentions *C. siebenrocki* from Cooktown on the Cape York Peninsula, but his specimens are probably referable to *C. rugosa.*

Cogger (1972) discusses *C. siebenrocki* from New Guinea. However, his description and the accompanying photograph are of the new species, *Chelodina parkeri*, and not of *C. siebenrocki.*

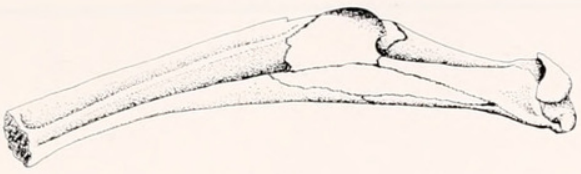

Figure 19. Medial and slightly dorsal view of the right side of the mandible of *C. parkeri* (AMS 21434).

Other authors mentioning *C. siebenrocki* include Ogilby (1905), Stejneger (1909), Loveridge (1934) and Pritchard (1967).

Relationships with C. rugosa and other species. The series of *C. siebenrocki* described in this paper shows little phenotypic variation. The greatest variation within the series is found in a single specimen (MCZ 134406), which has a vomer that separates the palatines and a very wide head. Large, wide heads occasionally occur in adult specimens of some other Australian chelids (Worrell, 1963), and may also in *C. siebenrocki*. The differences exhibited by MCZ 134406 are probably best explained in this way.

C. siebenrocki is most closely related to *C. rugosa*, with which it may be synonymous, although Burbidge (1967) and Burbidge, et al. (1974) believe that it is distinct. The relationship between these animals remains unclear. We have compared the New Guinean series discussed here with the type specimen of *C. rugosa* and with a series of seven specimens from the Cape York Peninsula of northern Australia that have been referred to *C. rugosa* on the basis of locality. The type specimen of *C. rugosa* is only a shell (carapace and plastron). Although it has a slightly narrower carapace and plastron (Figs. 11, 12), it agrees in most respects with the New Guinean series and the type photographs of *C. siebenrocki*. The seven Cape York specimens are quite variable compared to the New Guinean series, and the sample is too small to permit any conclusions concerning specific status to be drawn. For the present, we prefer to simply refer to all *C. rugosa*-like turtles (including *C. siebenrocki*) from northern Australia and New Guinea as the *C. rugosa* complex, and defer final judgment on the relationship between *C. rugosa* and *C. siebenrocki* until more adequate material from northern Australia becomes available.

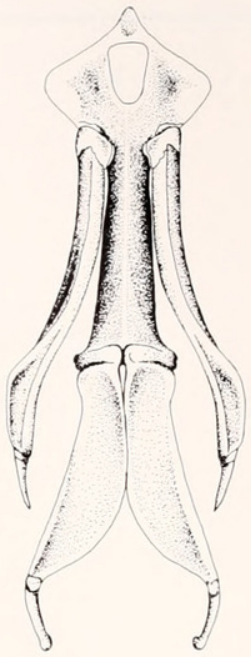

Figure 20. Ventral view of the hyoid of *C. parkeri* (AMS 21353).

C. siebenrocki is also closely related to the new species which we are describing. It is less closely related to *C. oblonga* of southwestern Australia and *C. expansa* of southeastern Australia. It is distinguished from *C. oblonga* by the absence of neurals (*C. oblonga* being the only *Chelodina* with neural bones [Burbidge, 1967; Burbidge, et al., 1974]), the shorter vomer which rarely extends posteriorly to separate the palatines, the presence of a prefrontal spine, and the less elongate shell. It is distinguished from *C. expansa* by the higher skull, the prefrontal spine, the narrower carapace, the narrower, tapering plastral lobe, the narrow rim of anterior ventral marginals, and the smaller maximum size (*C. expansa* reaches a length of 423 mm [Goode, 1967]).

Chelodina parkeri sp. nov.
Figures 10, 13–24

Holotype: AMS 21425, Mawa, Lake Murray, Western District, Papua New Guinea, collected November 7, 1963 by Harold Cogger.

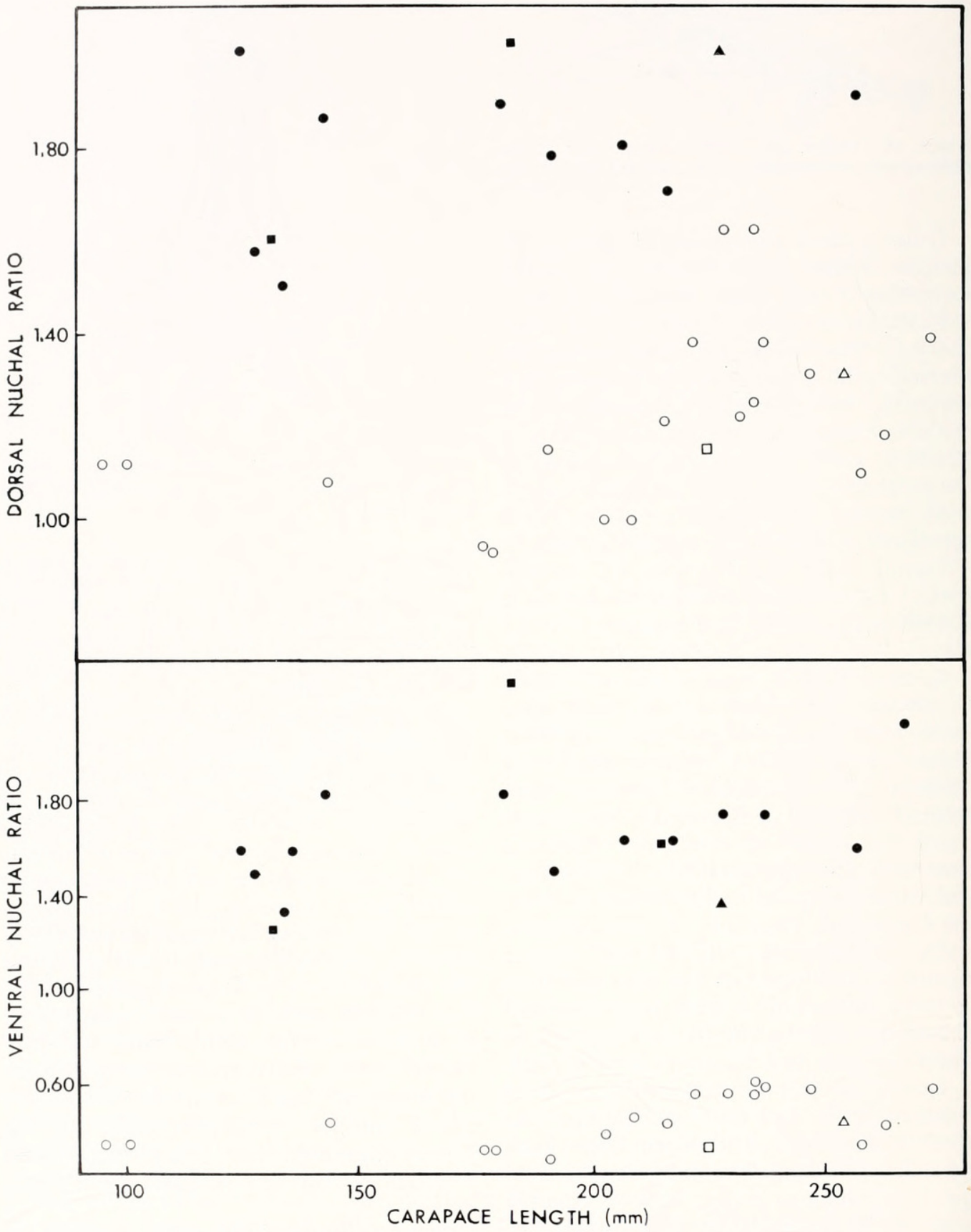

Figure 21. Bottom: Plot of carapace length vs. the ratio of length to width of the ventral surface of the nuchal scute. Top: Plot of carapace length vs. the ratio of length to width of the dorsal surface of the nuchal scute. (Specimens with triangular nuchals are not plotted.) Solid circles = paratypes of *C. parkeri*; solid triangle = holotype of *C. parkeri*; solid squares = specimens of *C. parkeri* from the Papua New Guinea Museum (measurements provided by Fred Parker); open circles = specimens of *C. siebenrocki* discussed in the first part of this paper; open square = type photograph of *C. siebenrocki*; open triangle = type specimen of *C. rugosa*.

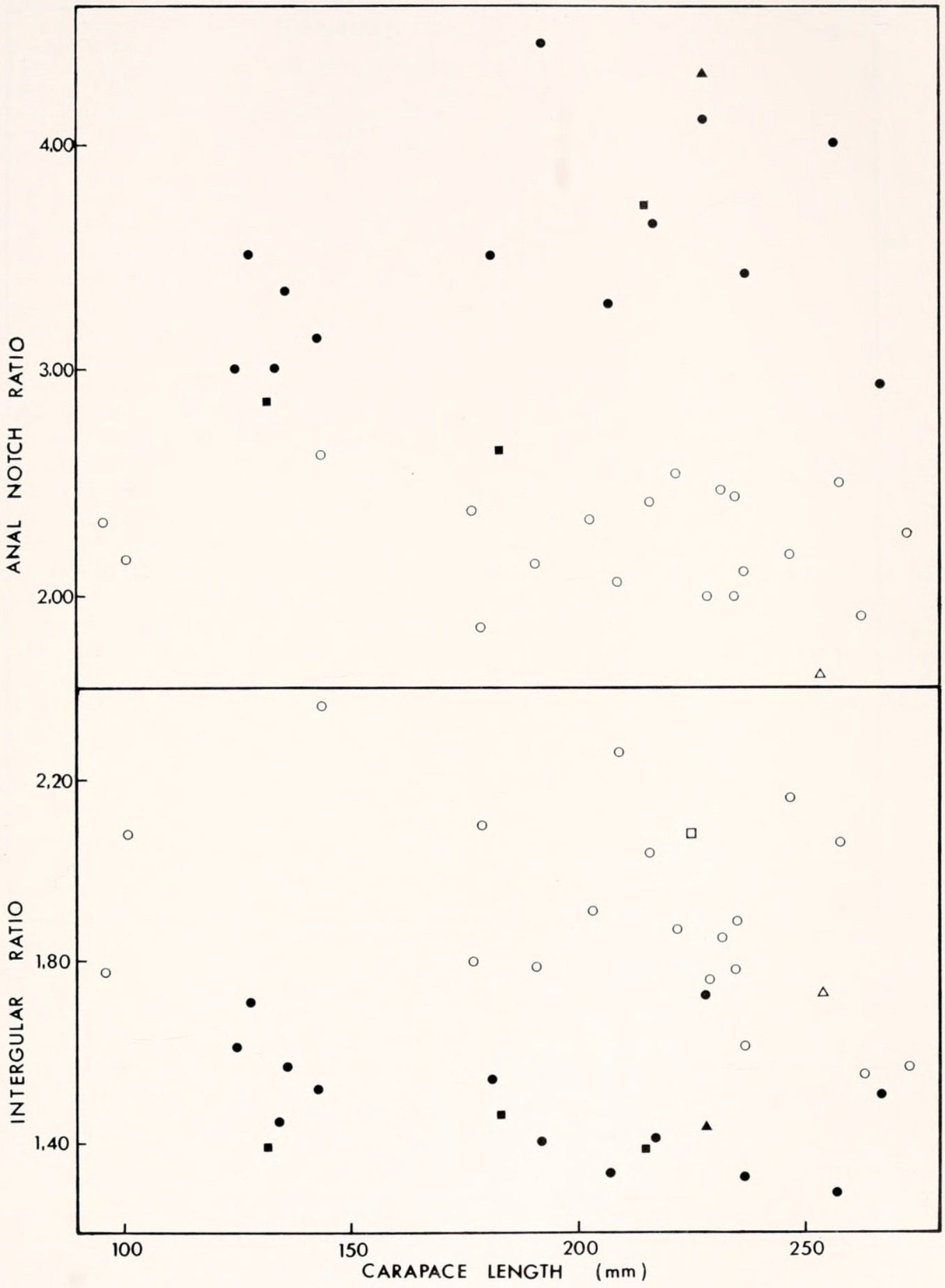

Figure 22. Bottom: Plot of carapace length vs. the ratio of length to width of the intergular scute. Top: Plot of carapace length vs. the ratio of width to depth of anal notch. Symbols as in Fig. 21.

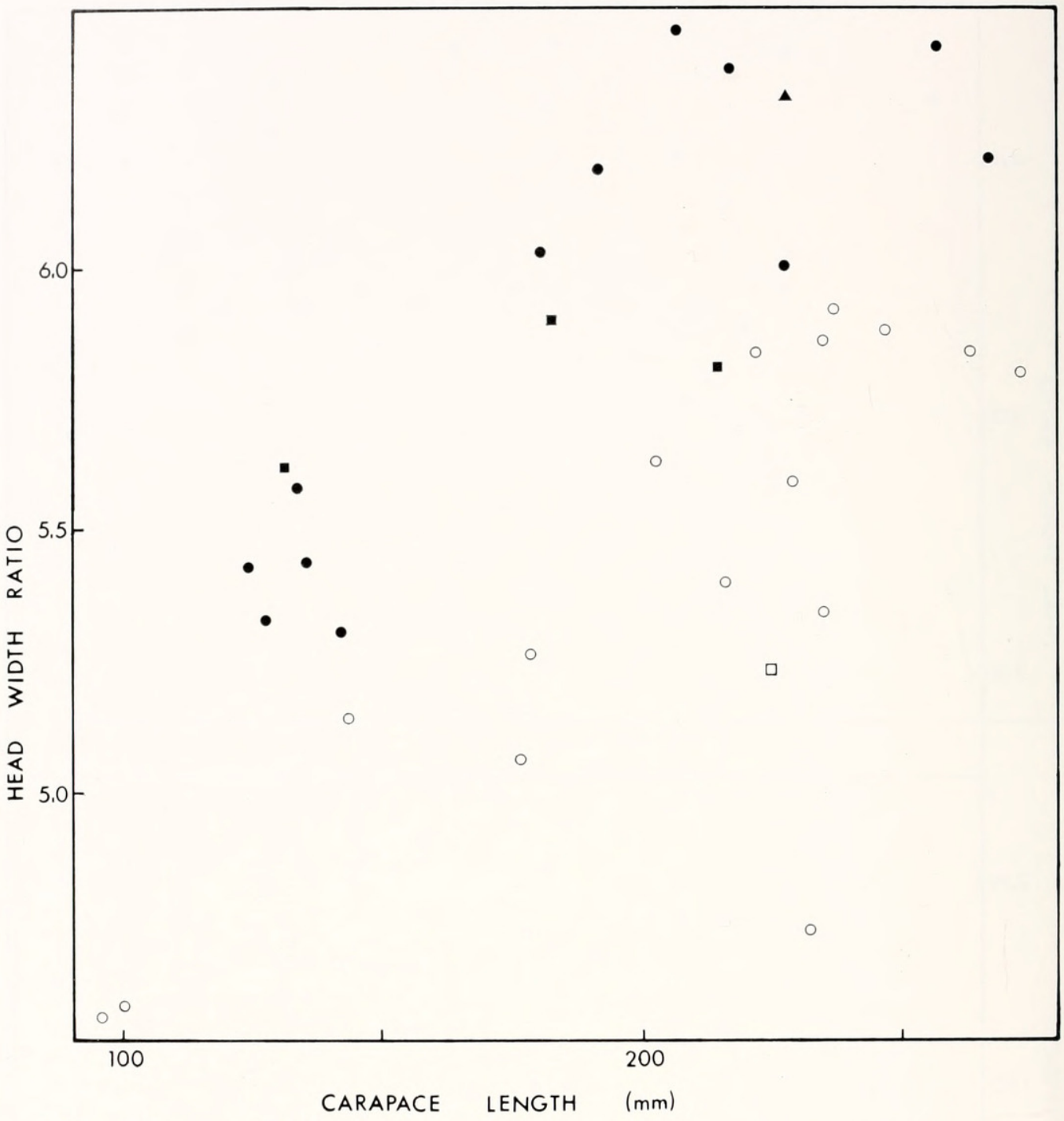

Figure 23. Plot of carapace length vs. the ratio of carapace length to head width. Symbols as in Fig. 21.

Paratypes: MCZ 119722, 119723, Balimo, Western District, Papua New Guinea, collected November 7, 1967 by Fred Parker; MCZ 129897, 134400, Maka, Lake Murray, Western District, Papua New Guinea, collected June 7, 1969 by Fred Parker; MCZ 134401, Maka, Lake Murray, collected July 23, 1969 by Fred Parker; MCZ 134402, Balimo, collected March 14, 1969 by Fred Parker; MCZ 134464, Maka, Lake Murray, collected November 6, 1969 by Fred Parker; MCZ 134465, Maka, Lake Murray, collected November 22, 1969 by Fred Parker; AMS 21159, Aketa, Aramia River, Western District, Papua New Guinea, collected October 31, 1963 by Harold Cogger; AMS 21423–4, Mawa, Lake Murray, collected November 7, 1963 by Harold Cogger; AMS 21353, 21434, Balimo, collected October 29, 1963 by Harold Cogger.

In addition to the type series, Parker (personal communication, 1974) has provided us with information on three specimens in the Papua New Guinea Museum (PNGM R1225, Balimo, collected March 14, 1969 by Fred Parker; PNGM R1601,

Maka, Lake Murray, collected November 6, 1969 by Fred Parker; PNGM 11635, Maka, Lake Murray, collected January, 1973).

We are pleased to name this new species in honor of Fred Parker and in recognition of his many superb collections which have contributed so much to our knowledge of New Guinean herpetology.

Diagnosis. Chelodina parkeri is a medium-sized species closely resembling *C. siebenrocki*, but distinguished by the color pattern on the head which is unique within the genus *Chelodina* (Fig. 13). The entire dorsal surface of the head and the mandible are extensively vermiculated with white, yellow or pale green lines and dots on a dark brown background, while a larger, brighter, more prominent blotch is present posteromedial to each tympanic membrane. This color pattern is retained in adult animals, although the pattern is faded in some specimens. The carapace is similar to *C. siebenrocki*, though it is not as egg-shaped and has more nearly parallel sides with a less expanded posterior margin and a wider anterior margin (Figs. 14, 15). Juveniles and subadults have vertebral tuberculations which disappear with age. Hatchlings of *C. parkeri* are unknown at the present time. The plastron is moderately elongate and tends to have a wide, truncate, anterior lobe (Fig. 15). The anterior ventral marginals form a wide margin between the edge of the carapace and the dorsal skin attachment, so that the ventral surface of the nuchal scute is longer than it is wide (Fig. 15). The intergular is not greatly elongate, and tends to be shorter and wider than in *C. siebenrocki* (Fig. 15). The anal notch is shallow and triangular (Fig. 15); the neck long and thick (Fig. 13). The head is long, wide and relatively flattened (Fig. 13). The coloration of the carapace differs from *C. siebenrocki*, being lighter brown, often with indistinct pale yellow reticulations mainly along anterior and posterior margins, but also at times covering the entire carapace (Fig. 13). The plastron is dull yellow and has no pattern. There are no neural bones in the carapace (Fig. 14).

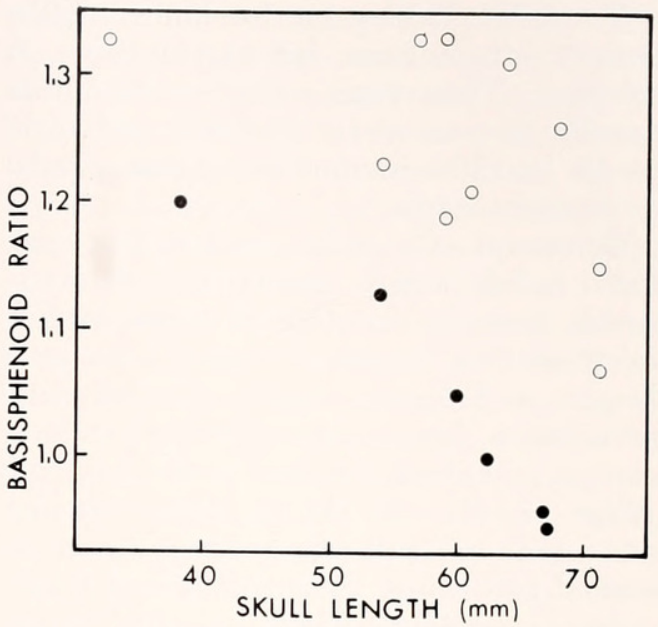

Figure 24. Plot of skull length vs. the ratio of length to width of the basisphenoid bone. Symbols as in Fig. 21.

The skull is similar to *C. siebenrocki*, but the vomer separates the palatines (Fig. 17); a prefrontal spine is absent (Fig. 18), and a *spina parasupraoccipitalis* is present to varying extent (Fig. 16). The hyoid does not have a sharp crista ventralis hyoideus, but instead a more obtusely-angulated corpus hyoideus (Fig. 20).

EXTERNAL CHARACTERS

Head, neck and limbs. Head elongate, flattened and wide, though narrower than in *C. siebenrocki* (Figs. 13, 23); covered on the dorsal surface with a fine, reticulate pattern of skin creases which give the impression of numerous, small, irregularly-shaped scales. Creases absent from tympanum, maxilla, mandible, nasal region and a triangular area along the midline posterior to the orbits. Variable number of chin barbels present, but usually only two and of smaller size than in *C. siebenrocki.*

Neck long and thick, averaging about 75 per cent of carapace length, and covered on dorsal surface with very small, pointed, well-defined tubercles set closely together (Fig. 13).

Transverse scales on forelimbs usually seven in one column, but varying from six to nine. Transverse scales on hindlimbs usually five to seven medially and eight to 11 laterally in double column similar to *C. siebenrocki*.

Carapace. Carapace moderately elongate (adult length averaging 1.43 times width, juveniles length 1.38 times width), fairly shallow, length averaging 2.59 times height, and having nearly parallel sides with only a slight expansion at the posterior margin, and a wide, truncate anterior margin (Figs. 13, 14). No flaring of the margins, no supra-anal ridging, no keels, and no central furrowing. Broad, flattened tuberculations on third, fourth and fifth vertebrals in larger juveniles and subadults up to a carapace length of about 150 mm, after which the tuberculations gradually disappear or are worn off, leaving the adult shell evenly domed. It is not known if hatchlings and small juveniles possess these tuberculations since no specimens under 125 mm have been collected. Surface of carapace smooth, with generally thinner scutes than *C. siebenrocki* and a similar but shallower pattern of rugosities. Juvenile scute pattern same as in *C. siebenrocki*, with hatchling shields retained, and a radiating pattern of growth ridges and rings. These hatchling scutes eventually peel off to reveal the rugose adult pattern. Dorsal surface of nuchal scute narrow and elongate, length averaging 1.80 times width when fully present. Approximately 30 per cent of specimens possess reduced triangular nuchals which do not totally separate the first marginals and do not contact the first vertebral. None of the specimens examined entirely lacked the nuchal. Length of ventral surface of nuchal scute greater than width, length averaging 1.66 times width and always fully present. Anterior ventral marginals form a wide margin between edge of carapace and dorsal skin attachment, with carapace length averaging only 15.5 times the width of the second ventral marginal (Fig. 15). Length of fifth vertebral greater than width, with the length:width ratio averaging 1.23. Shape of pleurals and first four vertebrals apparently not siginificant. Twelve marginals present; fifth marginal always in contact with first pleural; eleventh marginal usually in narrow contact or not in contact with fifth vertebral (Figs. 13, 14).

Plastron. Plastron fairly elongate and moderately narrow, with carapace width averaging 1.73 times plastron width, carapace length averaging 2.45 times plastron width, and plastron length itself averaging 1.90 times its width (Fig. 15). Plastron shorter than carapace, with carapace length averaging 1.28 times plastron length (Fig. 15). Anterior lobe generally as wide as or wider than posterior lobe, ending anteriorly in a broad, truncate manner (Fig. 15). Anal notch shallow and triangular, width averaging 3.46 times depth (Fig. 15). Intergular not markedly elongate, tending to be shorter and wider than in *C. siebenrocki*, length averaging 1.48 times width (Fig. 15). In none of the specimens examined does the intergular reach the anterior plastral margin.

COLORATION

Head, neck and limbs. *C. parkeri* is the only member of the genus *Chelodina* that has a light color pattern on its head. In juveniles, the reddish brown to brown ground color on the dorsal surface of the head and the mandible is covered with bright yellow vermiculations made up of irregular, though sharply outlined, lines and dots (Fig. 13), with a larger, whiter, more prominent blotch posteromedial to each tympanic membrane. Ground color of adult head grayer, with white, yellow or pale green vermiculations on dorsal surfaces and white vermiculations on mandible. Adult head markings similar to but sometimes less sharply demarcated than those of juveniles. Occasional specimens have a very faded head pattern, but the pattern is always present to some extent. Color of vermiculations fades to pale grayish white in preserved specimens. Adult eye

color brown, with a narrow but distinct ring of yellow rimming free edge of iris.

Dorsal surfaces of limbs and neck gray; ventral surfaces grayish white, sometimes with pinkish tint.

Carapace. Ground color of carapace brown to dark brown, though in general lighter than in *C. siebenrocki.* Pale yellow reticulations of irregular shape usually present as a thin band along anterior and posterior margins of carapace, but may vary in extent from totally absent to covering entire carapace. Intensity and extent of reticulations apparently not age-related. Ventral surfaces of carapace same color as plastron.

Plastron. Coloration of plastron uniform pale yellow.

Size. The largest specimen of *C. parkeri* measured was a 267 mm female. The largest male measured 217 mm. It is possible that this disparity indicates some sexual dimorphism in size, but it is more likely the result of absence of large males from the small sample analysed.

Sexual dimorphism. Sexual dimorphism is similar to that of *C. siebenrocki*, with mature males over 150 mm having larger tails and flatter shells than females. The flatter shell in males is not due to plastral concavity. A length:height ratio of greater than 2.60 characterizes a male, as in *C. siebenrocki.*

OSTEOLOGY

Skull. Skull moderately elongate, length averaging 1.63 times tympanic width and 2.00 times maxillary width; skull also markedly flattened, with length averaging 6.20 times height, and maxillary width averaging 3.14 times height; skull narrowed anteriorly, with tympanic width averaging 1.23 times maxillary width (Figs. 16, 17, 18). No parietosquamosal connection (Fig. 18). Vomer connecting maxillae and palatines, separating palatines along most of their length and usually reaching the anterior border of the pterygoids (Fig. 17). Basisphenoid as wide as long, with the length: width ratio averaging 1.02 (Fig. 17). Foramen columellae auris on the ventral skull surface fairly small and rectangular or slitlike (Fig. 17). Processus trochlearis pterygoidei, when viewed from dorsal aspect, continues as a straight extension of pterygoid processes of jugal and postorbital, not making an angle with them as in *C. siebenrocki* (Fig. 16). Lateral rim of cavum tympani elongate, flattened and pyriform, with the wider aspect located anteroventrally (Fig. 18). Triturating surfaces of maxillae fairly wide posterolaterally, contributing about 20 per cent of skull width at maxillary-pterygoid border (Fig. 17). The following features are of importance within cavum acustico-jugulare: recessus scalae tympani nearly completely roofed over by basioccipital and opisthotic and only narrowly open to a small fenestra postotica; substantial though delicate processus exoparacapsularis quadrati covers the columella; crista exoparacapsularis present as a sharp ridge, dividing cavum acustico-jugulare into two deep fossae, a medial one for the paracapsular sac and a lateral one for the vena capitis lateralis and columellar artery; apertura glossopharyngei fully penetrating opisthotic, never present as an incisura in crista exoparacapsularis (Fig. 17). Parietals considerably emarginate medially, though not quite as extensively as in *C. siebenrocki* (Fig. 16). Prefrontals lack the prefrontal spine which is characteristic of *C. siebenrocki*, but supraoccipital has a spinous process (spina parasupraoccipitalis, Fig. 16) extending posteriorly along dorsal surface of exoccipital in a specific sulcus. Spina parasupraoccipitalis varies considerably in length, being no more than an indistinct spur in some specimens, but reaching the posterior skull border and giving the impression of a split exoccipital in others. Precolumellar fossa tends to be deep, well-defined and of the same size or slightly larger than lateral aspect of foramen columellae auris (Fig. 18). Sulcus jugalis poorly developed and shallow, situated posterior to a weak crista jugalis (Fig. 18).

Columella less slender than in *C. siebenrocki* and greatly flattened and flared out at its lateral end. Mandible weak, with a wide, partly horizontal triturating surface (Fig. 19).

Hyoid. Hyoid elongate and massive, structurally very similar to *C. siebenrocki.* Skull length averages 1.65 times length of corpus hyoideus, and carapace length averages 6.25 times length of corpus. Long ventral surface of corpus without a sharp crista ventralis hyoideus, but rather a very weak ridge that creates an approximate right angle along the shaft of the corpus hyoideus (Fig. 20).

Cervical column. The pattern of central cervical articulation for three specimens examined for this character is N(2(,(3(,(4(,(5),)6),)7(,(8), which is identical to all Chelidae previously described (Williams, 1950).

Shell. Carapace with 16 costals (eight on each side), 22 peripherals (11 on each side), nuchal, pygal and suprapygal (Fig. 14). Neurals absent. Nuchal bone totally separates first peripherals, but does not separate first costals. First peripherals contact first costals.

Plastron with diamond-shaped entoplastron and paired epiplastra, hyoplastra, hypoplastra and xiphiplastra (Fig. 15).

DISTRIBUTION AND ECOLOGY

Distribution. C. parkeri is apparently endemic to New Guinea, being restricted to the large inland grass swamps surrounding Lakes Murray and Balimo and the Fly and Aramia Rivers (Parker, personal communication, 1973). Verified collection localities are restricted to the Western District's savanna regions north of the Fly River (Fig. 10).

Ecology. C. parkeri appears to inhabit the open edges of lakes and rivers, where a dense growth of grass and aquatic vegetation floats on the shallow water (Parker, personal communication, 1973; Cogger, personal communication, 1974). The lagoons where it is found are subject to periodic inundation and partial or complete drying during exceptionally dry seasons (Cogger, 1964; Parker, personal communication, 1973). Most specimens were collected in muddy streamside shallows by feeling around in the mud with bare feet, although some animals were also taken with nets in shallow water (Cogger, personal communication, 1974). In captivity, *C. parkeri* is apparently exclusively piscivorous (Sachsse, personal communication, 1974).

C. parkeri shares its habitat with large numbers of *Emydura subglobosa* (Cogger, personal communication, 1974), but is itself rather rare (Parker, personal communication, 1973). It apparently also occurs sympatrically with *Chelodina novaeguineae, Elseya novaeguineae, Carettochelys insculpta* and possibly *Pelochelys bibroni.* It is nowhere sympatric with the exclusively coastal *C. siebenrocki.*

DISCUSSION

Relationships with C. siebenrocki and other species. C. parkeri is a *Chelodina* group B turtle (Burbidge, et al., 1974). It is most closely related to *C. siebenrocki* and *C. rugosa* and less closely related to *C. expansa* and *C. oblonga.* The major distinguishing features of *C. parkeri* are the head color pattern and the shape of the ventral surface of the nuchal scute. *C. parkeri* is the only member of the genus *Chelodina* which has any kind of light color pattern on the dorsal surface of the head and this criterion is usually enough to differentiate it. However, in some specimens, the head color pattern is so faded that other criteria must also be used. The lack of neural bones and the wider carapace and plastron separate *C. parkeri* from *C. oblonga.* It is distinguished from *C. expansa* by its higher skull, narrower carapace and smaller maximum size. The elongate ventral surface of the nuchal scute is the most useful character (aside from head coloration) for separating *C. parkeri* from specimens of the *C. rugosa* complex (including *C. siebenrocki*). Members of the *C. rugosa*

complex invariably have a nuchal scute with a very wide ventral surface (Fig. 21). Correlated with this feature, the anterior ventral marginals form a wide rim in *C. parkeri* and a narrow rim in members of the *C. rugosa* complex.

There are several other differences between *C. parkeri* and the *C. rugosa* complex which are helpful but not necessarily by themselves sufficient to distinguish the species. The most important of these are the prefrontal spine, the vomer, the spina parasupraoccipitalis and the vertebral tuberculations. The prefrontal spine is always absent in *C. parkeri*, always present in *C. siebenrocki* and almost always present in *C. rugosa* (a single specimen from the Kimberly Plateau in Western Australia lacks this spine). The vomer separates the palatines and reaches the pterygoids in *C. parkeri*, but only rarely (one out of 12 skulls) does so in *C. siebenrocki*. The size of the vomer in *C. rugosa* is variable; some individuals have a *C. parkeri*-like vomer and others a shorter one of the *C. siebenrocki* type. The spina parasupraoccipitalis is always absent in members of the *C. rugosa* complex and always present in *C. parkeri*, though it varies greatly in size and is sometimes very small. Vertebral tuberculations are present in juvenile and subadult (and possibly also hatchling) *C. parkeri*, but never in *C. siebenrocki*.

Finally, there are a host of less important and more variable features which help distinguish *C. parkeri* from *C. siebenrocki*, but which must be used in combination with other more important characters. The dorsal surface of the nuchal scute is generally longer and narrower in *C. parkeri*, but there is some overlap with *C. siebenrocki* (Fig. 21). The anal notch is not as deep in *C. parkeri* (Fig. 22). The intergular is not as elongate in *C. parkeri* (Fig. 22). The fifth vertebral tends to be longer and narrower in *C. parkeri*. The sides of the carapace in *C. parkeri* are more nearly parallel and often have reticulations along the edge. The anterior plastral lobe in *C. parkeri* tends to be more truncate and wider. The head is narrower in relation to carapace length in *C. parkeri* (Fig. 23). The basisphenoid is wider and shorter in *C. parkeri* (Fig. 24). The foramen columellae auris is more rectangular than oval in *C. parkeri*. The processus trochlearis pterygoidei forms a straight, rather than angulated continuation of the pterygoid processes of the jugal and postorbital in *C. parkeri*. The rim of the cavum tympani is more elongate and pyriform in *C. parkeri*. The triturating surface of the maxillae is wider. The parietals are not as extensively medially emarginate in *C. parkeri*. The precolumellar fossa tends to be deeper and better defined in *C. parkeri*. The sulcus jugalis and crista jugalis are less developed in *C. parkeri*. The recessus scalae tympani is more roofed over and less open to the fenestra postotica. The processus exoparacapsularis quadrati is slightly larger in *C. parkeri*. The crista exoparacapsularis creates a deep lateral fossa rather than a shallow one. The apertura glossopharyngei is more completely enclosed by the opisthotic in *C. parkeri*. The hyoid lacks a crista ventralis hyoideus in *C. parkeri*. The columella in *C. parkeri* has a wider, more flared lateral end. The mandible has a more horizontal triturating surface in *C. parkeri*.

Additional comments. *C. parkeri* is apparently not only endemic to New Guinea, but is also restricted to inland areas on the southern part of the island. It does not occur in the coastal region of southern New Guinea and is thus isolated from access to the Torres Strait, an apparent "cross-over" route for fauna of northern Australia and southern New Guinea. All other New Guinean chelid turtles, and also the cryptodire *Carettochelys insculpta*, have ranges that include this coastal region. In addition, all these other species either also occur in the northern coastal areas of Australia (*Carettochelys insculpta, Chelodina novaeguineae*) or have closely related (and possibly conspecific) relatives in northern Australia (*Elseya novaeguineae-E. dentata, Emydura*

subglobosa-E. kreffti, C. siebenrocki-C. rugosa) (Cogger, 1970; Burbidge, et al., 1974). *C. parkeri* is thus the only New Guinean species that neither occurs in northern Australia nor has a very close relative there.

The only previous mention of specimens referable to *C. parkeri* is in Cogger (1972). He assigns a photograph of *C. parkeri* to *C. siebenrocki* and describes the vermiculated head and reticulate carapace patterns of *C. parkeri* as being characteristics of *C. siebenrocki.*

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APPENDIX I—GLOSSARY

The italicized terms defined here are new terms first used in this paper. Other terms are defined by the authors cited below.

Anterior ventral marginals—the ventral surface of the anteriormost marginal scutes (usually marginals 1–4 on each side and the ventral surface of the nuchal scute) that are situated anterior to the two axillae (Fig. 3).

Apertura glossopharyngei—McDowell, 1964

Branchial I—Siebenrock, 1898

Branchial II—Siebenrock, 1898

Cavum acustico-jugulare—Gaffney, 1972

Cavum tympani—Gaffney, 1972

Condylus occipitalis—Gaffney, 1972

Corpus hyoideus—Siebenrock, 1898

Crista exoparacapsularis—McDowell, 1964

Crista jugalis—the sharp bony vertical crest which runs along the posterior third of the jugal and part of the postorbital, and serves as the anterior wall for the soft tissue "Mundplatte" (Fig. 6).

Crista supraoccipitalis—Gaffney, 1972

Crista ventralis hyoideus—a bony crest running lengthwise along the midline of the ventral aspect of the corpus hyoideus, from just posterior to the fenestra hyoideus to just anterior to the articulation with branchial II (Fig. 8).

Fenestra hyoideus—Siebenrock, 1898

Fenestra postotica—Gaffney, 1972

Foramen columellae auris—Siebenrock, 1897

Fossa temporalis superior—Gaffney, 1972

Incisura columellae auris—Gaffney, 1972

Post-otic antrum—Williams, 1954

Precolumellar fossa—Williams, 1954

Prefrontal spine—a bony spur of the prefrontals on the interior anteromedial margin of the orbit, directed posteriorly and ventrally towards the choanae (Fig. 6).

Processus exoparacapsularis quadrati—a

delicate bony extension of the quadrate reaching posteromedially to partially roof over the anterolateral aspect of the cavum acustico-jugulare and the medial third of the columella (Fig. 5).

Processus trochlearis pterygoidei—Gaffney, 1972

Pterygoid process of jugal—the portion of the jugal, posterior to the crista jugalis, which serves as the anterior extension of the processus trochlearis pterygoidei and on which the soft tissue "Mundplatte" rests (Fig. 4).

Pterygoid process of postorbital—the portion of the postorbital, posterior to the crista jugalis, which serves as the anterior extension of processus trochlearis pterygoidei and on which the soft tissue "Mundplatte" rests (Fig. 4).

Recessus scalae tympani—Gaffney, 1972

Spina parasupraoccipitalis— a spinous process from the supraoccipital projecting posteriorly along the dorsal surface of the exoccipital, embedded in a specific sulcus and appearing to split the exoccipital roughly in half (Fig. 16).

Sulcus jugalis—a groove, immediately posterior to the crista jugalis, which extends from jugal to postorbital and on which the soft tissue "Mundplatte" rests (Fig. 6).

APPENDIX II—EXPLANATION OF MEASUREMENTS USED

Carapace length is measured in an axial, not curved, line along the midline of the carapace. Carapace width is maximum width measured perpendicular to the carapace midline. Carapace height is the maximum height measured in the carapace midline. Plastron length is measured along the midline and does not include the anal spurs. Plastron width is measured across the axillary notches, regardless of whether this is maximum width or not. Length of dorsal and ventral surfaces of nuchal scute, length of intergular and length of fifth vertebral are lengths measured along the midline; widths of these scutes are maximum widths measured perpendicular to the midline. Width of anterior ventral marginals is the distance between the edge of the carapace and the area of skin attachment, measured at the midpoint of the second marginal. Depth of the anal notch is the ratio of the distance between the tips of the anal spurs divided by the distance from the apex of the notch to the imaginary line connecting the tips of the two anal spurs. Width of head is measured across the tympanic membranes, in a line perpendicular to the midline of the skull. Length of neck is the distance from the tip of the snout to the anterior edge of the carapace, measured along the midline.

Skull length is measured along the midline, from the anterior surface of the premaxillae to the posterior surface of the condylus occipitalis. Tympanic width of skull is measured across the middle of the cavum tympani, in a line perpendicular to the midline of the skull. Maxillary width of skull is measured at the widest part of the maxillae, perpendicular to the midline of the skull. Skull height is the maximum height at the level of the posterior border of the maxillae. Length of basisphenoid is measured along the midline; width of basisphenoid is the maximum width measured perpendicular to the midline of the skull. Length of hyoid is only the length of the corpus hyoideus, measured from the posterior border of the fenestra hyoideus to the articulation with branchial II.