A TAXONOMIC REVISION OF THE GENUS

SYNODONTIS (PISCES, MOCHOKIDAE)

IN SOUTHERN AFRICA

Dissertation

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ABSTRACT

The alpha taxonomy of the southern African Synodontis is reviewed, based on the analysis of 48 characters. The previously descriptive characters of barbel branching and humeral process shape are compared by various quantitative methods. The variation in colour pattern is recorded with the aid of detailed line drawings. The definitions of head length, head width and humeral process length are altered slightly from their traditional descriptions to ensure greater consistency and precision in measurement. New characters include the size of the caudal fork, the number, shape and arrangement of the premaxillary teeth, and two measurements between the cranium and pectoral girdle. Both uni- and bivariate methods are used to record and compare the intraspecific variation of each character. Principal components analysis of 19 morphometric characters is used to assess the degree of similarity of nine allopatric populations of S.zambezensis.

Ten species are recognized from the study area, two of which are described as new: S.nebulosus Peters 1852, S.zambezensis Peters 1852, S.nigromaculatus Boulenger 1905, S.njassae Keilhack 1908, S.woosnami Boulenger 1911, S.macrostigma Boulenger 1911, S.leopardinus Pellegrin 1914, S.thamalakanensis Fowler 1935, S.macrostoma sp.n. and S.vanderwaali sp.n. A key to their identification is provided.

Characters are discussed in terms of their contribution to the identification of the southern African species and, where possible, suggestions made concerning the value of these characters to the taxonomy of the genus as a whole. The rejection of certain characters previously used in Synodontis keys is discussed and alternatives proposed. The state of southern African Synodontis taxonomy is assessed and recommendations for future research are given.

CHAPTER 1

INTRODUCTION

The Synodontis are medium to small African catfishes characterized by a heavily-armoured head, large triangular humeral process and prominent, sharply-serrated fin spines. The earliest known record of these fishes comes from wall pictures in the Tomb of Ti near Saqqara, Egypt, painted during the 4th dynasty, circa. 2400 BC (von den Driesch, 1983). The genus Synodontis was officially introduced into the taxonomic literature at the very beginnings of zoological nomenclature with the description of S.clarias in the 10th edition of Linnaeus's (1758) 'Systema Naturae'. By 1916, Boulenger confirmed the existence of 50 Synodontis species from specimens housed in the British Museum. The most recent revision by Poll (1971) records 108 species, establishing it as one of the largest genera within the Ostariophysi. The present study concerns only the southern African Synodontis, in which ten species are recognized.

The earliest revision of the genus Synodontis was by Vaillant (1895, 1896). In terms of its contribution to our understanding of Synodontis taxonomy, the characters analyzed by Vaillant (op.cit.) merely involved the documentation of features previously considered diagnostic among the nominal taxa, derived mostly from the comparison of published descriptions. For the next half century the general format and content of Synodontis descriptions changed little from that adopted by Vaillant (1896).

Barnard (1948) questioned the validity of characters traditionally used in the identification of southern African Synodontis, noting that certain supposedly diagnostic features often showed a large degree of variation that was not previously recorded. In particular, Barnard (1948) demonstrated the increased number of moveable mandibular teeth with age and the presence of nodules on the anterior margin of the maxillary barbels in S.zambezensis as a character only expressed in juveniles. The humeral process shape and the length of the maxillary barbels he considered useful diagnostic features, despite their individual variation. Barnard (1948) also noted that most descriptions did not include sufficient information to distinguish between juveniles. Jubb (1967) attributed the inadequacies of these descriptions to the fact that most of the southern African Synodontis were described from single specimens and, in addition, to the lack of knowledge of the variation of their diagnostic features, particularly colour pattern. This problem was further complicated by the fact that five of the eight nominal species described from the Zambezi system were assigned names which referred to their colour pattern, namely, S.nigromaculatus Boulenger 1905, S.melanostictus Boulenger 1906, S.leopardinus Pellegrin 1914, S.macrostigma Boulenger 1911 and S.nebulosus Peters 1852.

The two most recent revisions of the southern African Synodontis by Farquharson (1969) and Poll (1971) were carried out independently, as the results of the former were never published. Although Farquharson (1969) confined his work to the southern African species, his revision represents the first attempt to evaluate, in any detail, characters traditionally used in Synodontis taxonomy. Unfortunately, Farquharson (1969) lumped the data of each species and, although certain characters were evaluated in terms of their contribution to individual variation, no attempt was made to show geographic or sexual variation. In addition, Farquharson's (1969) synonymies were incomplete, as he failed to consider two of the nominal species described from this area and personally examined only two holotypes, relying solely on published redescriptions of the other type specimens for comparison. Poll (1971), on the other hand, examined all but two of these types but rarely included more than four other specimens in each description. As seven of the twelve nominal species were described from single specimens, Poll's (1971) decisions were thus made with little knowledge of the variation in each species. The major discrepancies between these two revisions concern the taxonomic status of S.macrostigma and S.thamalakanensis Fowler 1935. Poll (1971) regards S.macrostigma as a valid species and S.thamalakanensis as a junior synonym of S.woosnami Boulenger 1911, while Farquharson (1969) regards S.macrostigma as a junior synonym of S.woosnami and S.thamalakanensis as a junior synonym of S.leopardinus. In addition, Farquharson (1969) included the description of a new species, "S.kafuensis", but this account was never published. Neither of these revisions resulted in the easier diagnosis of the southern African species, as the content of their keys differed little from those of previous authors. Although Farquharson (1969) adopts the general format of a dichotomous key, only four couplets of one character each are used to distinguish between the nine taxa he recognized, the remaining four species diagnosed by their supposedly non-overlapping geographic ranges.

Historically, Synodontis keys have consistently used four main characters, namely, barbel morphology, humeral process shape, colour pattern and moveable mandibular tooth number. Recent large collections of Synodontis from the Okavango Delta have shown that these characters are highly variable, an aspect not reflected in present keys, making the identification of certain specimens impossible. To add to this problem, the first three characters were compared by general description without the support of explanatory illustrations. Such descriptions have proven inadequate in their ability to demonstrate the often subtle differences between the many taxa of this speciose group. The need for a further revision based on a thorough character analysis was thus clearly evident.

In the present study, certain features of the three descriptive characters mentioned above are expressed quantitatively, so allowing for more accurate description and more meaningful comparison through standard statistical means. In addition, the variation in colour pattern is recorded with reference to a number of detailed illustrations. Many of the traditional characters evaluated by Farquharson (1969) are reexamined. A number of new characters are considered for the first time and include the number, size, shape and arrangement of premaxillary teeth, the size of the caudal fin fork and two measurements between the cranium and pectoral girdle.

The major objectives of the present study may thus be summarized as follows:

1. To review the alpha (descriptive) taxonomy of the southern African Synodontis based on an analysis of the intra- and interspecific variation of traditional and new characters.

2. To provide detailed diagnoses and descriptions of the species recognized.

3. To draw up a key to their identification.

Table 2.1 Chronological synopsis of Synodontis taxa described from southern Africa, including those described from adjacent river systems whose ranges extend into southern Africa. The division into two groups is based on morphological similarities explained on p.41.

Species	Locality
GROUP I	
S.zambezensis Peters 1852	Tete, Lower Zambezi River
S.zambezensis rukwaensis Hilgendorf & Pappenheim 1903	Lake Rukwa
S.nigromaculatus Boulenger 1905	Lake Banguelu
S.melanostictus Boulenger 1906	Lake Tanganyika
S.njassae Keilhack 1908	Lake Malawi
S.colyeri Boulenger 1923	Mansa River, Zambia
GROUP II	
S.nebulosus Peters 1852	Tete, Lower Zambezi River
S.woosnami Boulenger 1911	Okavango R., Lake Ngami District
S.macrostigma Boulenger 1911	Okavango R., Lake Ngami District
S.leopardinus Pellegrin 1914	Lealui, Upper Zambezi River
S.jallae Gilchrist & Thompson 1917	Sesheke, Upper Zambezi River
S.thamalakanensis Fowler 1935	Thamalakane River, Okavango Delta
"S.kafuensis" Farquharson 1969 (unpubl.)	Upper Kafue River

CHAPTER 2

TAXONOMIC HISTORY

Eight nominal Synodontis species have been described from southern Africa. A further four nominal species and one subspecies, described from outside the study area, are considered in this revision in that their distributions extend into southern Africa; four were described from the Zambian-Zaire system and one from Lake Tanganyika (Table 2.1). Also included with this list is "S.kafuensis" described by Farquharson (1969) in an unpublished MSc. thesis entitled 'Systematic studies on the genus Synodontis (Pisces, Mochokidae) in South Africa'. As no part of this work has ever been published in a recognized journal and less than five copies of this thesis are known to exist, in terms of Article 8(a), 9.9 and 9.11 of the International Code of Zoological Nomenclature (1985), the description of "S.kafuensis" does not meet the criteria of publication and thus remains undescribed. In addition, any reference to synonymies or decisions of taxonomic implication taken by Farquharson (1969) and quoted in this thesis must be seen in this context, as no taxonomic publication, to my knowledge, has ever referred to this work.

The taxonomic history of the thirteen taxa considered in this revision are divisible into two groups (Table 2.1). The characteristics of each group are based on morphological similarities explained in chapter 4 (p.41 & Table 4.2).

The first species to be described from the study area was S.zambezensis Peters

1852, from a collection of seven specimens from the Lower Zambezi River near Tete. Besides a fin formula, the only diagnosis given in the description is their vague similarity to S.arabi Cuvier & Valenciennes 1840. This situation was rectified in 1868 when Peters redescribed the S.zambezensis syntypes designating the largest male specimen as the lectotype, which he illustrated together with one of the smaller female paralectotypes. Pfeffer (1889) was the first to extend this species' range to a river system north of the Zambezi with a record from the Webi Shebeli River in East Africa (Somali Republic). Further northern extensions of its range were recorded by Günther (1894) from Lake Malawi, Boulenger (1911a) from the Tana, Ruvu and Pangani Rivers in East Africa, Hilgendorf & Pappenheim (1903) from Lake Rukwa, David & Poll (1937) from the Central Zaire basin, and Ricardo (1939) from Lake Banguelu.

In 1908 Keilhack described S.njassae from nine specimens taken at 77m depth near Langenburg in Lake Njassa (Nyasa, later to be known as Lake Malawi). Previous records of Synodontis from this lake by Günther (1894) and Boulenger (1898) were all referred to S.zambezensis. Keilhack (1908) considered this species to be closely related to the following species: S.multimaculatus Boulenger 1898 described from Lake Tanganyika; S.multimaculatus Boulenger 1902 described from the Ubangi River, a tributary of the Zaire; S.nigromaculatus Boulenger 1906 described from Lake Banguelu, and S.zambezensis. He distinguished S.zambezensis on its markings which are either unspotted or finely spotted in comparison with S.njassae which has irregularly distributed spots, slightly larger than the diameter of the eye. S.multimaculatus was distinguished by a more prominent keel on the humeral process, shorter head, shorter dorsal spine and shorter side branches of the outer mandibular barbels; S.multipunctatus by smaller spots and fewer mandibular teeth; and S.nigromaculatus by stronger serrations on the outer edge of the pectoral spine.

Boulenger (1898, 1911a) was the first to contest the validity of S.njassae and allocated all Lake Malawi specimens to S.zambezensis considering S.njassae a junior synonym, but gave no reasons for this decision. In support of this synonymy, Worthington (1933b) identified all 27 Lake Malawi specimens held in the British Museum as S.zambezensis but regarded them as approaching S.melanostictus Boulenger 1906 in having larger serrations on the outer margin of the pectoral spine. Boulenger's (1911a) decision was contested by Jackson (1959) who re-established the validity of S.njassae on the basis of a broader and more rounded head, substantiated by a significantly larger interorbital distance and confirmed the difference in colour pattern between S.njassae and S.zambezensis originally described by Keilhack (1908). Poll (1971) provided further evidence in support of S.njassae as a Lake Malawi endemic, distinct from S.zambezensis, on the basis of a shorter humeral process, shorter snout length, shorter dorsal spine and longer maxillary barbels.

The distribution of S.zambezensis is presently recognized from the study area only. All previous records of this species from river sytems north of the Zambezi were undoubtedly a result of its confusing colour pattern which includes both a spotted and an unspotted form. Jubb (1967), Farquharson (1969) and Poll (1971) all confirm the distribution of S.zambezensis from the Middle and Lower Zambezi southwards, to all east-flowing rivers up to the Pongolo River. The misspelling of this name as 'S.zambesensis' was introduced into the literature by Günther (1864). This error was unfortunately overlooked by Boulenger (1911a) and consequently adopted by many after him, including Worthington (1933a), Barnard (1948), Jubb (1954) and Poll (1971).

The only subspecies of Synodontis recorded from southern Africa, S.zambezensis rukwaensis, was described by Hilgendorf & Pappenheim (1903) from nine specimens from Lake Rukwa. In this description, their comparison with the type series of S.zambezensis was based solely on the descriptions published by

Peters (1852,1868) and Boulenger (1901). Hilgendorf & Pappenheim (1903) distinguished this subspecies from Lower Zambezi S.zambezensis in having shorter dorsal and pectoral spines, larger head (to total length), larger snout (to head length), smaller eye diameter and fewer inner pectoral spine serrations. The description of S.zambezensis rukwaensis appears to have been overlooked by all including Ricardo (1939) who recorded S.zambezensis from Lake Rukwa, until it was referred to by Poll (1971) who regarded it as a junior synonym of S.zambezensis, although he did not examine the types and gave no reasons for his decision.

In 1905 Boulenger described S.nigromaculatus from a single specimen collected from Lake Banguelu, distinguishing it from S.zambezensis in having stronger serrations on the outer margin of the pectoral spine. A year later Boulenger (1906) described S.melanostictus from a single specimen from Lake Tanganyika which he again distinguished from S.zambezensis on very similar characteristics. Besides the small discrepancy in the development of villosities on the sides of the body, the only difference between the descriptions of S.nigromaculatus and S.melanostictus was in their colour pattern. Boulenger (1906) noted that some of the spots on the posterior part of the body of S.nigromaculatus were confluent forming vermicular lines, in comparison with S.melanostictus which were all separate. Extensions of the range of S.melanostictus were recorded by Gilchrist & Thompson (1913) from Lake Ngami and the Upper Zambezi River near Lealui, Poll (1933) from Lake Mweru, Fowler (1935) from the Chobe River and Pellegrin (1936) from the Cunene River. Pellegrin (1936) also recorded S.nigromaculatus from the Cubango River, Angola. Characters used by Boulenger (1906) to distinguish S.melanostictus from S.nigromaculatus were exposed by Ricardo-Bertram (1943) as being misleading. The presence or absence of villosities, for example, were found to be dependent on the state of preservation, and the distribution of spots, the length of the dorsal spine and width of the humeral process all showed a large degree of variability. As no notable difference existed between these two nominal species, Ricardo-Bertram (1943) united them under the older name, S.nigromaculatus. This synonymy was accepted by Jackson (1961a) and Jubb (1961), the latter recognizing specimens as far south as the Limpopo River, a record that was later amended by the reidentification of the Limpopo specimens as S.zambezensis (Jubb, 1963a). In the description of S.colyeri, taken from a single specimen from the Mansa (Mansya) River near Lake Banguelu, Boulenger (1923) noted the close resemblance of this species to both S.zambezensis and S.nigromaculatus. After examining the types of all three species, Poll (1971) concluded that S.colyeri was a synonym of S.nigromaculatus.

The first species to be described from Group II was S.nebulosus Peters 1852 from a single specimen taken from the Lower Zambezi River near Tete. In 1868, Peters published a more comprehensive redescription which included an illustration of the holotype. Pfeffer(1889) identified S.nebulosus from the Ruvu River in East Africa, and a redescription by Vaillant (1896) included 6 specimens from the Chire (Shire) River. Barnard(1948) considered S.nebulosus a juvenile or an aberrant form of S.zambezensis, as the shape of the humeral process was unlike that of any other southern African species. After examining the types, Jubb (recorded in Jackson, 1961a) confirmed the validity of S.nebulosus, a decision accepted in the revisions of both Farquharson (1969) and Poll (1971).

S.woosnami and S.macrostigma were both described by Boulenger (1911a) from single specimens and from the same locality in the Okavango River, Lake Ngami district. Gilchrist & Thompson (1913) reported a single juvenile specimen of S.macrostigma from the Kafue River, noting a number of differences to the holotype including a proportionately larger eye, larger and fewer spots, fewer mandibular teeth and a shorter dorsal spine. The existence of S.macrostigma in the Kafue River was later confirmed by Boulenger (1914), and further extensions to the range were recorded by Pellegrin (1936) from the Cubango River in Angola and Jubb (1954) from the Upper and Middle Zambezi Rivers. New distributional records of S.woosnami were noted by Pellegrin (1936) from the Cubango River, by Jubb (1952) from the Limpopo River and by Jubb (1954) from the Upper Zambezi River.

S.leopardinus Pellegrin 1914 was described from a single specimen from the Upper Zambezi River near Lealui. In the diagnosis, reference is made to the very close resemblance of this species' colour pattern to S.woosnami, from which it was distinguished by its longer snout, shorter body depth, shorter maxillary barbels and longer dorsal spine. S.jallae Gilchrist & Thompson 1917 was described from a single specimen near Sesheke, the authors mistakenly referring the locality to Southern instead of Northern Rhodesia. In the description, this species compared closely to S.melanostictus but differed from the latter by its fewer mandibular teeth, tubercular mandibular barbels, broader and differently-shaped humeral process and smaller spots on the anterior of the body.

The most recently described species of Synodontis from southern Africa is S.thamalakanensis Fowler 1935, taken from two specimens from the Thamalakane River at the base of the Okavango Delta. Fowler (1935) noted his previous confusion of this species with S.woosnami, from which it differed primarily in colour pattern, having smaller spots which extend to the ventral regions of the head, trunk and tail. In reference to this colour pattern Jubb (1961) noted that the pattern and size of the spots were very variable in a large collection of S.woosnami from the Zambezi River above the Victoria Falls. Included in this variation were intermediate forms represented by the types of S.macrostigma and S.leopardinus, which were considered junior synonyms. Jackson (1961a) disagreed with Jubb (1961) on the criteria on which this decision was made, in the light of a collection of 69 S.macrostigma from the Kafue River with markings similar to the type and differing very little from one another. Jubb(1967) therefore re-established S.macrostigma as a valid species, emphasizing the large geographic variation between Kafue, Cunene and Okavango populations, in particular, noting differences in colour pattern, length of the maxillary barbels and the type of branching on the mandibular barbels.

Jubb(1967) was unable to recognize S.woosnami as the combination of thin filamentous barbels, particularly the mandibular barbels, and a broad obtusely-pointed humeral process, did not exist in any of the large number of Zambezi River specimens he examined. Farquharson (1969) considered the holotype of S.woosnami as aberrant in the form of its barbels and included S.macrostigma as a synonym on the basis of a similar movable mandibular tooth count, outer mandibular barbel length and predorsal length. Similar to Jubb (1967), Poll (1971) was also unable to identify other specimens of S.woosnami but, on examination of the holotypes of S.woosnami and S.macrostigma, concluded that they were sufficiently different to warrant separate status. The particular characteristics of S.macrostigma in its distinction from S.woosnami as noted by Poll (1971), were the presence of a basal membrane, papillae on the outer edge of the maxillary barbels, a wider head, a taller humeral process and larger overall dimensions of the eye.

Barnard (1948) placed S.thamalakanensis in synonymy with S.jallae on the basis of a similar-shaped humeral process, a nodular outer margin to the maxillary barbels and a similar colour pattern. Jubb (1967) synonymized both S.jallae and S.thamalakanensis with S.leopardinus because they shared a number of characteristics including a tall dorsal fin, relatively few mandibular teeth and a similar colour pattern. These synonymies were accepted by Farquharson (1969) and in part by Poll (1971) who considered S.thamalakanensis rather as a

Table 2.2 Chronological synopsis of the three most recent revisions of the southern African Synodontis

Jubb(1967)	Farquharson(1969)	Poll(1971)
S.nebulosus Peters 1852	S.nebulosus Peters 1852	S.nebulosus Peters 1852
S.zambezensis Peters 1852	S.zambezensis Peters 1852	S.zambesensis[sic] Peters 1852 syn: S.zambezensis rukwaensis Hilgendorf & Pappenheim 1903
S.nigromaculatus Boulenger 1905 syn: S.melanostictus Boulenger 1906	S.nigromaculatus Boulenger 1905	S.nigromaculatus Boulenger 1905 syn: S.melanostictus Boulenger 1906 syn: S.colyeri Boulenger 1923
	S.njassae Keilhack 1908	S.njassae Keilhack 1908
S.woosnami Boulenger 1911	S.woosnami Boulenger 1911 syn: S.macrostigma Boulenger 1911	S.woosnami Boulenger 1911 syn: S.thamalakanensis Fowler 1935
S.macrostigma Boulenger 1911		S.macrostigma Boulenger 1911
S.leopardinus Pellegrin 1914 syn: S.jallae Gilchrist & Thompson 1917 syn: S.thamalakanensis Fowler 1935	S.leopardinus Pellegrin 1914 syn: S.jallae Gilchrist & Thompson 1917 syn: S.thamalakanensis Fowler 1935	S.leopardinus Pellegrin 1914 syn: S.jallae Gilchrist & Thompson 1917
Synodontis sp.	S.kafuensis sp.n.	

synonym of S.woosnami. Poll's (1971) decision was based on the original description alone, as he did not examine either of the two type specimens of S.thamalakanensis.

Jubb (1967) mentioned an undescribed species from the Upper Zambezi River without describing or naming it. This species Jubb (1961) originally confused with S.woosnami but later recognized its greater resemblance to S.leopardinus, from which it differed by having a higher mandibular tooth count and a larger premaxillary tooth pad (Jubb, 1967). On examining these specimens Farquharson (1969) reallocated them to S.woosnami, showing that the above-mentioned differences were accommodated by the variation of these characters.

A chronological synopsis of the two most recent revisions to include the southern African Synodontis and those species listed in Jubb (1967) is given in Table 2.2. The geographic limits set by Jubb (1967) and Farquharson (1969) were different, the former excluding Lake Malawi from the Zambezi drainage and therefore did not consider S.njassae.

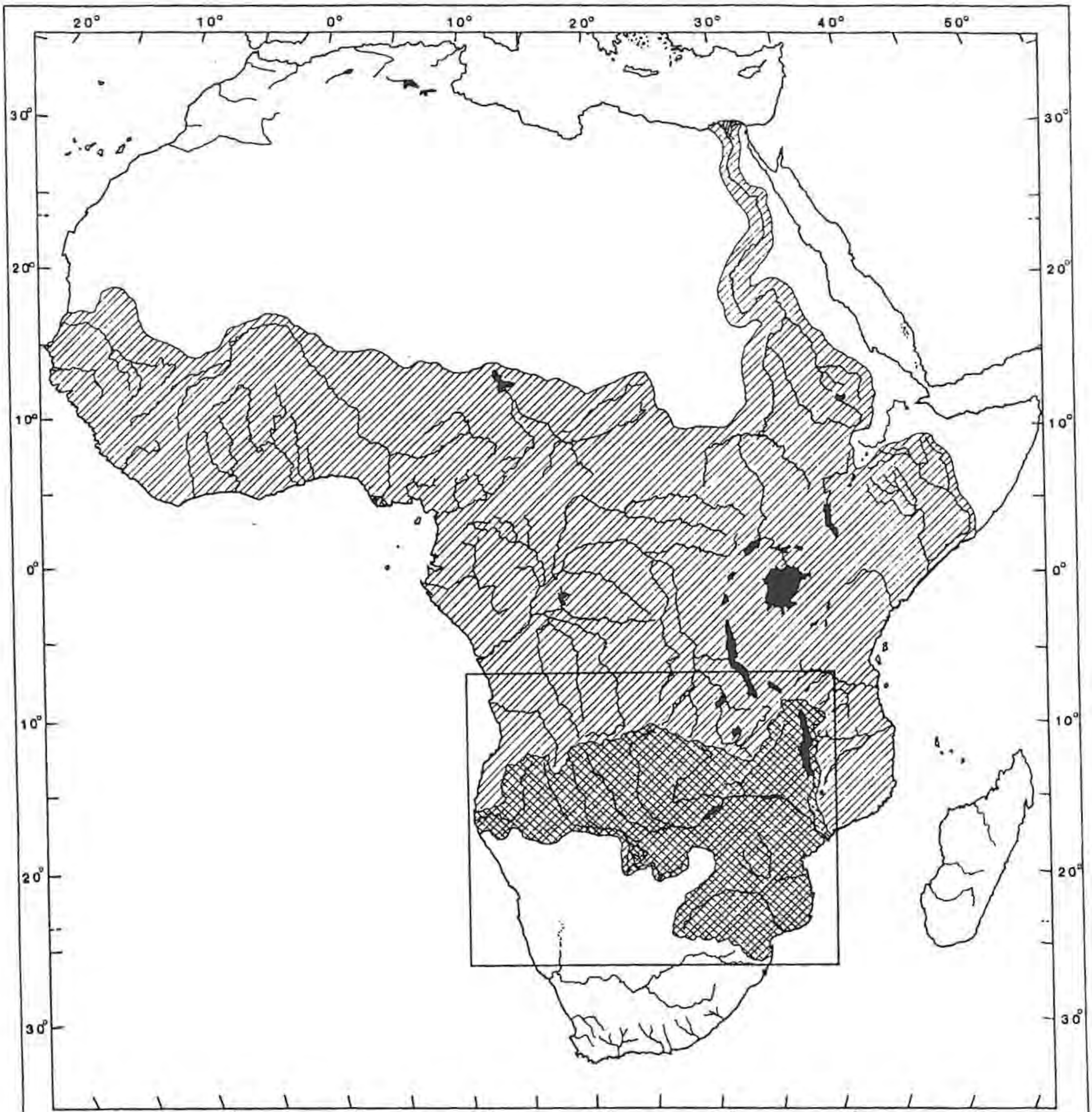

Figure 3.1 Generalized distribution of the genus Synodontis (hatched) showing limits of study area (cross-hatched) (adapted after Poll, 1971). Inner rectangle refers to Figure 3.2.

CHAPTER 3

STUDY AREA

The genus Synodontis is endemic to Africa where its species have been recorded from 52 distinct basins within the tropics and subtropics (Poll, 1971). The southern limit of this almost pan-African distribution is the Pongolo River in South Africa (Figure 3.1). Synodontis are also characterized by a high degree of specific endemism with 73 of the presently recognised 108 species known from single drainage basins (Poll,1971). The extent of the distribution of the remaining 35 species, however, is very variable.

Considerable disagreement exists in the ichthyological literature as to the geographic limits of "southern" Africa (see Penrith, 1982). Based on a comparison of the geographic distribution of freshwater fishes, Roberts (1975) recognized ten ichthyofaunal provinces throughout the African continent. The geographic limits of this study coincide with the southern-most province occupied by tropical species, namely, the Zambezi province (Figure 3.1). This area includes the entire hydrographic basins of the Cunene, Okavango and Zambezi and the east-flowing rivers southwards to the Pongolo River. Zoogeographically, the Zambezi, Sabi and Lundi river systems are further divided by natural barriers to fish movement. In total, 17 basins are recognized from the study area (Figure 3.2).

The largest of these basins, the Zambezi, was formed from several ancient water

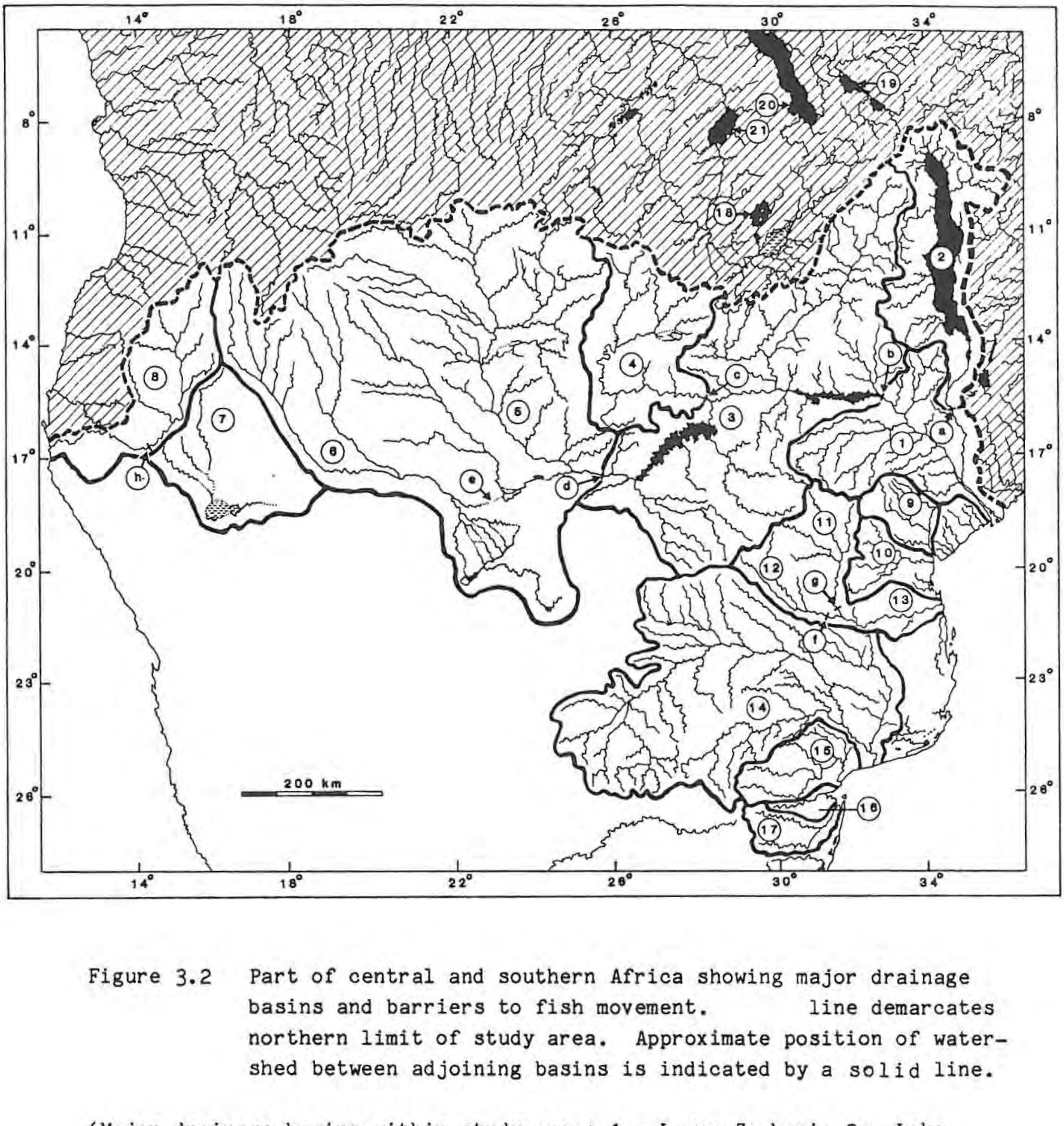

Figure 3.2 Part of central and southern Africa showing major drainage basins and barriers to fish movement. line demarcates northern limit of study area. Approximate position of watershed between adjoining basins is indicated by a solid line.

(Major drainage basins within study area: 1 = Lower Zambezi; 2 = Lake Malawi; 3 = Middle Zambezi; 4 = Kafue; 5 = Upper Zambezi; 6 = Okavango; 7 = Cuvelai; 8 = Cunene; 9 = Pungwe; 10 = Buzi; 11 = Upper Lundi; 12 = Upper Sabi; 13 = Save,Lower Sabi/Lundi; 14 = Limpopo; 15 = Incomati; 16 = Umbeluzi; 17 = Pongolo. Natural barriers: a = Kapachira Falls; b = Kebrabassa Rapids; c = Chasunta and Avumba Falls in Kafue Gorge; d = Victoria Falls; e = Selinda Spillway; f = Selawandoma Falls; g = Chivirira Falls; h = Ruacana Falls. Lakes mentioned in the text, north of the study area: 18 = Lake Banguelu; 19 = Lake Rukwa; 20 = Lake Tanganyika; 21 = Lake Mweru) courses, and in the past has experienced river capture, watershed migration, continental warping and confluence across floodplains, each event contributing to the fauna of the system (Davies, 1986). At present, four natural barriers are known to restrict the movement of fishes: the Kebrabassa Rapids, the Victoria Falls, the Chasunta Falls and the Kapachira Falls.

The Lower Zambezi system extends from the mouth to below the Kebrabassa Rapids and includes the Shire River to below the Kapachira Falls. The Kebrabassa Rapids have proven to be a barrier to only three species of Lower Zambezi freshwater fishes, namely, *Labeo rubropunctatus*, *Oreochromis placidus* and a *Barbus* species (Bell-Cross, 1972). In contrast, the 3 m high Kapachira Falls situated at the southern limit of the Murchison Cataracts, have been shown to be both a total barrier to the upstream movement of the Lower Zambezi fishes, as well as an ecological barrier to the downstream movement of the Upper Shire fishes (Tweddle, Lewis & Willoughby, 1979; Tweddle & Willoughby, 1979). The barrier to downstream movement has two components: the torrential nature of the river for 10 km above the falls, which constitutes an environment unsuitable for the majority of Lake Malawi species, and niche saturation coupled with high predation pressure by the Lower Zambezi species below the falls.

The Middle Zambezi extends upstream from the Kebrabassa Rapids to below the Victoria Falls. Its main tributaries are the Matetsi, Gwaai, Sanyati and Hunyani Rivers in the south, and the Kafue and Luangwa Rivers in the north. The Chasunta and Avumba Falls in the Lower Kafue Gorge restrict the movement of Middle Zambezi species to the Upper (plateau) Kafue, as shown by a sufficiently distinct fauna (Bell-Cross, 1965), and thus warrant separate analysis in this study.

The upper course of the Zambezi drains a huge shallow alluvial basin some 1440 km in length, with extensive rapid sections between Nangweshi and Katima Mulilo, and intermittently for 72 km above the Victoria Falls. The only waterfall in the main river which constitutes a barrier to fish movement is the Gonye Falls with a dry season height of 21 m (Bell-Cross, 1972). During the rainy season, however, the water level above and below the falls tends to even out, and no discontinuities to fish movement are known to occur (Bell-Cross, 1972). The major tributaries are the Chobe, Lungwevungu and Kabompo Rivers. The Chobe River is connected to the Kwando River in Angola via the Linyanti Swamps.

The Okavango (Cubango) River rises in the Bie plateau in central Angola and flows in a south-westerly direction for 1600 km to lose itself in an extensive delta-shaped swamp some 10 000 km^2 in area in the north east of Botswana. Though no permanent connection links the Okavango and Upper Zambezi systems, there is confluence in times of excessively high flood levels via the Makwanga or Selinda spillway (Wellington, 1955). Zoogeographically, these two systems are usually treated as one. Recent evidence has shown that up to 96% of the Okavango fish fauna are represented in the Upper Zambezi system (Skelton et al., 1985). Due to their tenuous links, however, and the possible ecological barrier of 200 kms of marshlands and shallow lakes between the fast-flowing rapid sections of their mainstream, specimens from each system were treated separately.

The Save/Sabi/Lundi drainage basin is divided into three by the Chivirira Falls on the Lundi River and the Selawandoma Falls on the Sabi River. These falls have proven an impassable barrier to the upstream migration of fishes for a considerable period in the history of these rivers (Jubb, 1967), and no <u>Synodontis</u> species have ever been recorded from above these falls (Bell-Cross, 1976).

Jubb (1967) noted that the distribution of certain fishes in the Limpopo system was not homogeneous, as Barbus polylepis and Labeo ruddi were not represented in the Nuanetsi, Umzingwane and Tuli tributaries. Due to the absence of any major (natural) physical barrier, however, all specimens examined from this system are considered together in the analysis.

The upstream migration of a number of species in the Buzi River is restricted by several waterfalls in its headwaters (Bell-Cross, 1973). The distribution of Synodontis in this and the remaining east-flowing rivers, namely, the Pungwe, Incomati, Umbeluzi and Pongolo, is restricted to their lower sections where no barriers to fish movement are known to exist (Bell-Cross, 1967,1973).

The only west-flowing river from the study area is the Cunene, which rises in the Huambo district of west-central Angola. The flow is disrupted twice along its 1200 km course, by the Epupa and Ruacana falls. The latter is situated on the rim of the continental plateau and extends over 120m, constituting a formidable barrier to the upstream movement of fish (Roberts, 1975). The lack of Synodontis specimens from below the falls in any of the collections in southern African museums, however, precludes comparison between the upper and lower fauna. The Cuvelai drainage is represented by a single specimen from the Olushandja Dam in northern Ovamboland. No Synodontis species, however, have previously been recorded from this system, and it is suspected that their translocation to this system was facilitated by the recent construction of irrigation canals linking the western drainage of the Cuvelai with the Cunene River, a few kilometres above the Ruacana Falls (van der Waal, in press.). This specimen has thus been included with the sample from the Cunene.

The geographic variation of taxonomic characters used in this study was analyzed by comparing populations of (usually) 30 or more individuals from each of the basins mentioned above.

CHAPTER 4

MATERIALS AND METHODS

CHARACTERS

Both quantitative and descriptive characters are used in this study. Quantitative characters include linear measurements, their proportions, and meristic features. Measurements were taken using needle-point dial calipers and recorded to the nearest 0,05 mm. Counts and measurements were consistently made on the left side of the body except where damaged. Soft body measurements of badly contorted specimens were excluded.

Morphometric characters

Linear measurements (Table 4.1, Figure 4.1) were taken as in Hubbs & Lagler (1947) with the following modifications or clarifications:

1. All measurements from the anterior end of the head are taken from the anterior point of the symphysis of the premaxillae.

2. Head length (HL) is taken from the anterior end of the head to the posterior margin of the post-temporal bone. This measurement was favoured rather than that described by Hubbs & Lagler (1947), as the relatively thick skin covering the operculum in *Synodontis* makes it difficult to locate the posterior margin.

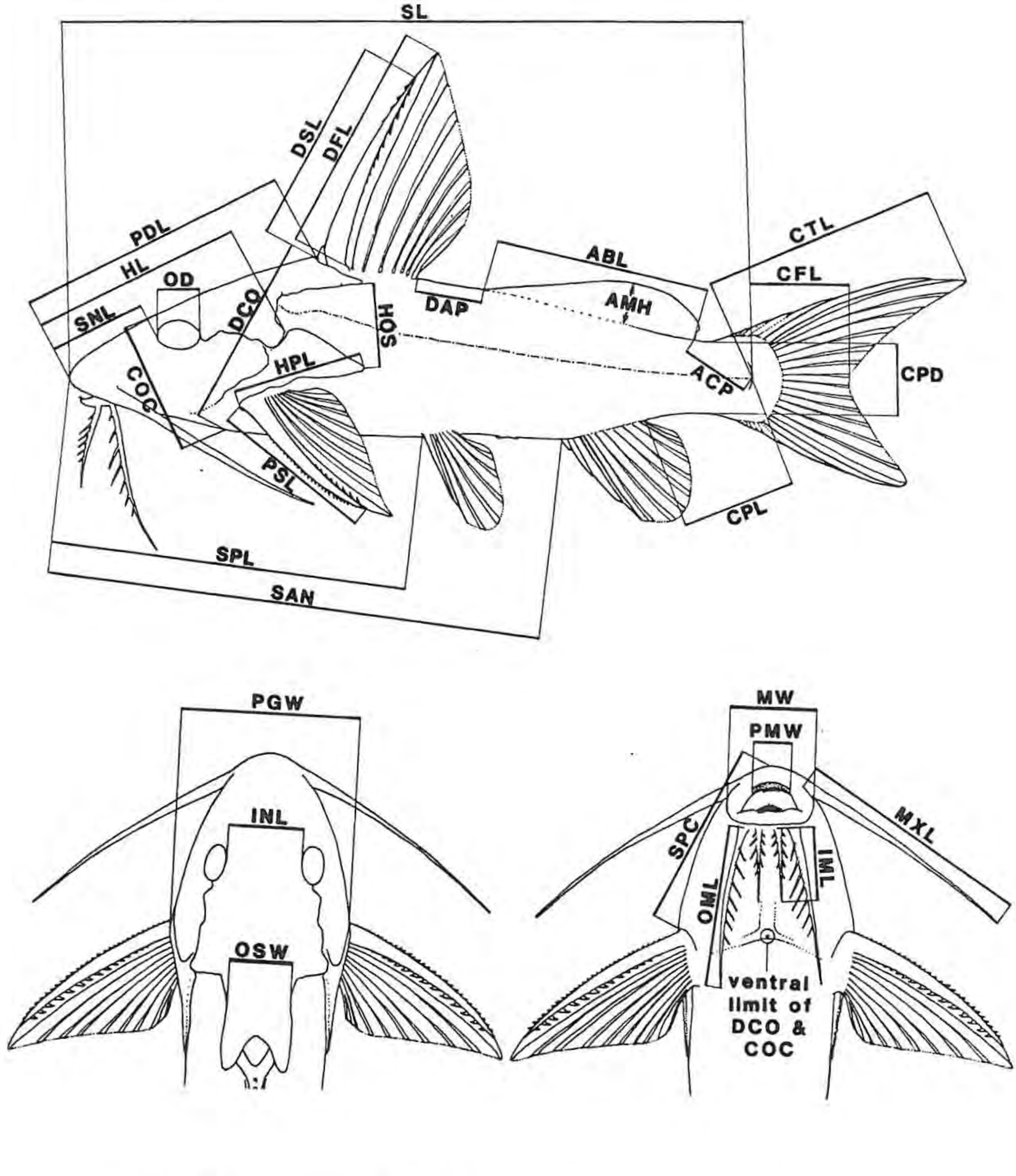

Figure 4.1 Linear measurements taken in this study. Abbreviations explained in Table 4.1.

Table 4.1 Morphometric characters examined in this study. Abbreviations used in Figure 4.1.

1	Standard length	SL
2	Predorsal length	PDL
3	Head Length	HL
4	Snout length	SNL
5	Interorbital length	INL
6	Dorsal to coracoid	DCO
7	Coracoid to cranium	COC
8	Snout to pectoral	SPC
9	Pectoral girdle width	PGW
10	Occipito-nuchal shield width	OSW
11	Humeral process length	HPL
12	Humeral process to occipito-nuchal shield	HOS
13	Orbit diameter	OD
14	Pectoral spine length	PSL
15	Dorsal spine length	DSL
16	Dorsal fin length	DFL
17	Caudal fork length	CFL
18	Caudal total length	CTL
19	Maxillary barbel length	MXL
20	Outer mandibular barbel length	OML
21	Inner mandibular barbel length	IML
22	Snout to pelvic	SPL
23	Snout to anal	SAN
24	Caudal peduncle length	CPL
25	Caudal peduncle depth	CPD
22	Dorsal to adipose	DAP
23	Adipose basal length	ABL
21	Adipose maximum height	AMH
22	Adipose to caudal peduncle	ACP
30	Mouth width	MW
31	Premaxillae width	PMW

3. Predorsal length (PDL) is the median distance from the anterior end of the head to the base of the first dorsal spine.

4. Dorsal spine length (DSL) and pectoral spine length (PSL) are both measured with their appropriate spines in the fully erect position.

5. Caudal fork length (CFL) is measured from the end of the mid-caudal hypurals, as determined by caudal flexure, to the posterior tip of the shortest mid-caudal ray.

6. Caudal total length (CTL) is measured from the end of the mid-caudal hypurals, as determined by caudal flexure, to the posterior tip of the longest caudal ray.

7. Pectoral girdle width (PGW) is the maximum width of the pectoral girdle. This measurement corresponds to Farquharson's (1969) "head width" and differs from Poll's (1971) measurement of the same name in that it was not taken from the base of the pectoral spines.

8. Dorsal to coracoid (DCO) is the distance from the base of the first dorsal spine to the midpoint on the postero-ventral margin of the coracoid bone.

9. Coracoid to cranium (COC) is the minimum distance measured in the medial plane from the dorsal surface of the cranium to the postero-ventral margin of the coracoid bone.

10. Humeral process length (HPL) is measured from the anterior margin of the base of the (erect) pectoral spine to the posterior tip of the humeral process.

11. Humeral process to occipito-nuchal shield (HOS) is the minimum distance from the posterior tip of the humeral process to the ventral margin of the occipito-nuchal shield.

12. Occipito-nuchal shield width (OSW) is the minimum distance, anterior to the base of the dorsal spine.

13. Adipose to caudal peduncle (ACP) is taken from the posterior base of the adipose fin to the end of the mid-caudal hypurals, as determined by caudal flexure.

14. Dorsal to adipose (DAP) is measured from the base of the last dorsal ray to the anterior base of the adipose fin. Difficulty in allocating the posterior limit to this measurement, which also affects the measurement of adipose basal length (ABL), is discussed in chapter 5 (p. 211).

Measurements are expressed as % standard length (SL) with the following exceptions: snout length (SNL) is expressed as % PDL; interorbital length (INL), dorsal to coracoid (DCO), coracoid to cranium (COC), snout to pectoral (SPC), pectoral girdle width (PGW), occipito-nuchal shield width (OSW), humeral process length (HPL), humeral process to occipito-nuchal shield (HOS), orbit diameter (OD), dorsal spine length (DSL), pectoral spine length (PSL), dorsal fin length (DFL), maxillary barbel length (MXL), outer mandibular barbel length (OML) and inner mandibular barbel length (IML) are expressed as % head length (HL); premaxillae width and mouth width are expressed as % pectoral girdle width (PGW); caudal fork length (CFL) is expressed as % CTL; adipose maximum height is expressed as % ABL.

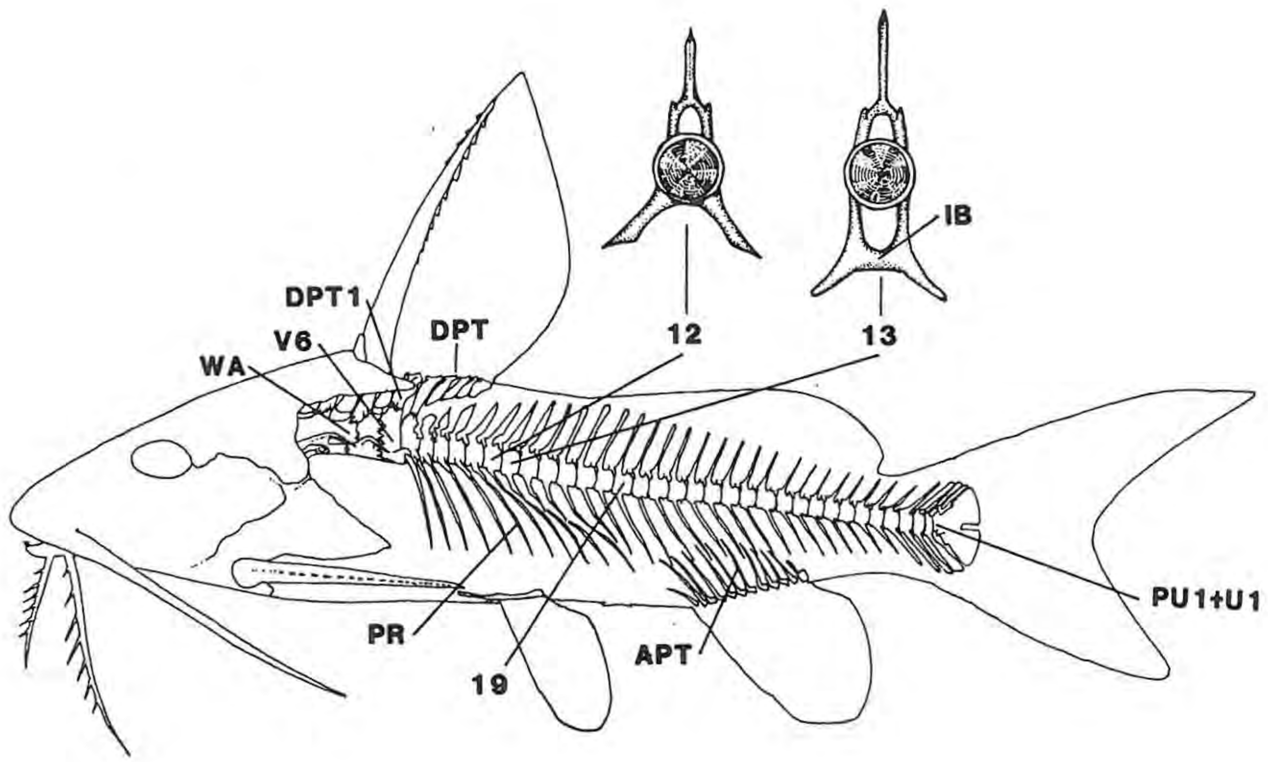

Figure 4.2 Diagram showing counts taken from the axial skeleton (APT = anal pterygiophores; DPT = dorsal pterygiophores; DPT1 = fused, first dorsal pterygiophore; IB = interparapophyseal bridge; PU1+U1 = compound ural centrum; PR = pleural ribs; V6 = 6th vertebra, last axial element of the Weberian apparatus; WA = Weberian apparatus; 12 = last precaudal vertebra; 13 = first caudal vertebra; 19 = last preanal vertebra).

Meristic characters

Skeletal meristics

Postcranial skeletal meristics (Figure 4.2) were taken from radiographs and include the following counts:

1. Total vertebral count. Includes the Weberian apparatus as six elements (Taverne & Aloulou-Triki, 1974) and the ural centrum as one (PU1 + U1; Lundberg & Baskin, 1969).

2. Precaudal vertebrae. All anterior vertebrae not possessing a closed haemal arch, including the Weberian apparatus as six elements.

3. Caudal vertebrae. All vertebrae posterior to, and including, the first centrum with a closed haemal arch. The bony interparapophyseal bridge is detectable as a distinct bright exposure point on radiographs (Skelton, 1980).

4. Preanal vertebrae. Vertebral count, up to and including that vertebra anterior to the spine of the second anal pterygiophore (the first anal pterygiophore is a half to a third the length of the second pterygiophore and does not intercollate with the vertebral haemal spines --- hence the use of the latter).

5. Anal pterygiophores.

6. Pleural ribs.

The single S.zambezensis specimen from the Pungwe River is not included in the data as its radiograph was illegible due to excessive decalcification.

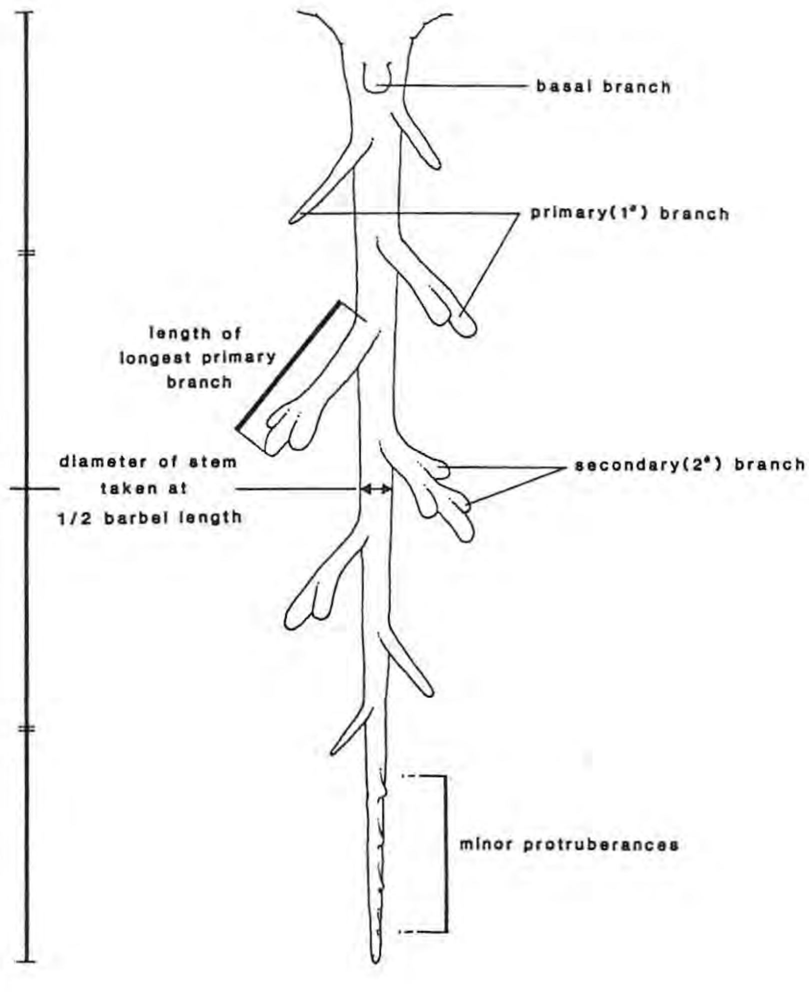

Figure 4.3 Diagram of a generalized mandibular barbel to show linear measurements and nature of barbel branching recorded in this study.

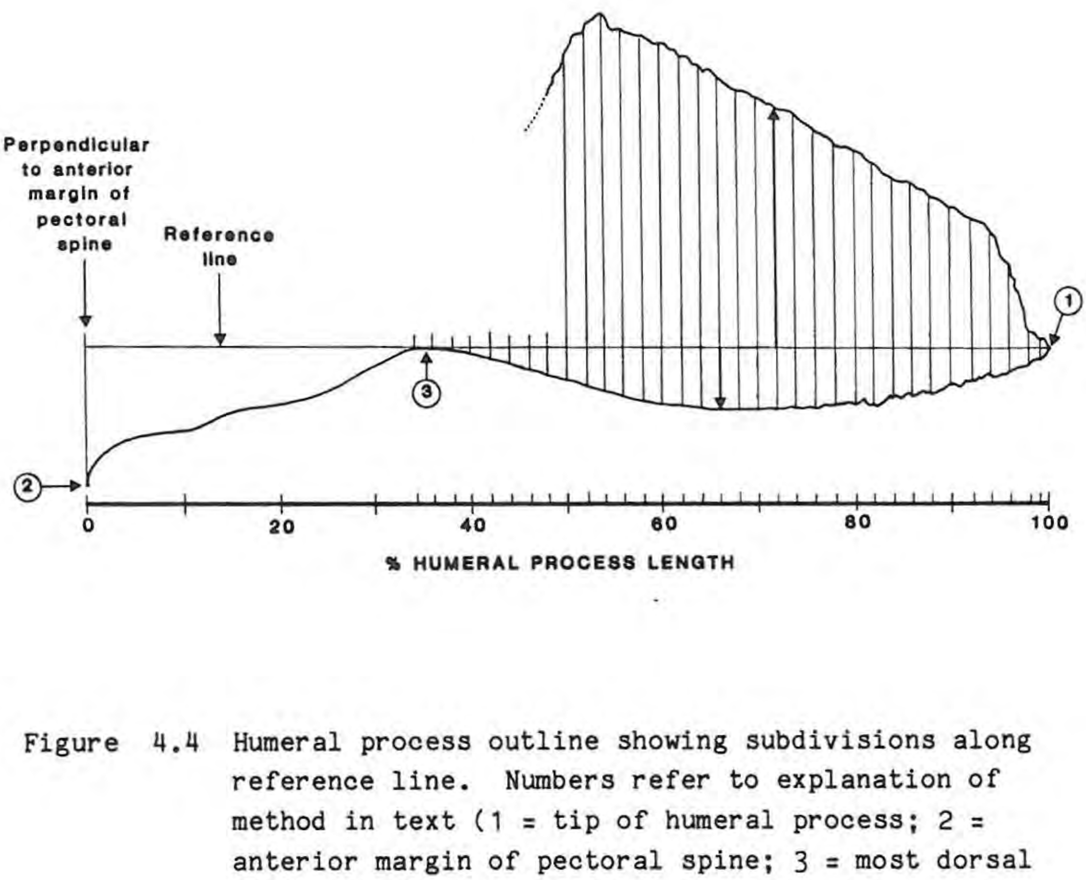

Figure 4.4 Humeral process outline showing subdivisions along reference line. Numbers refer to explanation of method in text (1 = tip of humeral process; 2 = anterior margin of pectoral spine; 3 = most dorsal point of the recess between 1 and 2).

Barbel branching

A barbel branch as opposed to a minor protuberance is defined by having a height greater than its basal diameter (Figure 4.3). The number of primary and secondary branches were recorded on both the inner and outer mandibular barbels. The length of the longest primary branch is expressed as a ratio of the diameter of the barbel stem taken at half barbel length.

The maximum width of the maxillary barbel basal membrane is expressed as a proportion of the width of the barbel stem immediately adjacent to this measurement.

Fin rays

The analysis of this character involves only soft rays, as the spinous rays of the dorsal and pectoral fins are standardized at one in each. The caudal fin ray count includes only the principal rays, i.e. branched caudal rays plus one dorsal and one ventral unbranched ray. The number of anterior unbranched anal rays was determined from radiographs as the small size of the first two rays made counting difficult, even with dissection. The last anal fin ray is considered to be branched in all cases, as the few specimens for which this ray was unbranched still retain a noticeable division on the posterior half, though not separated by a membrane. The pelvic fin in Synodontis is standardized at one anterior unbranched and six branched rays in all species (Poll, 1971).

Humeral process shape

The outline of the left humeral process, including the anterior margin of the (fully) erect pectoral spine, was drawn using a stereoscopic microscope fitted with a drawing tube to give an image of between 120 and 160 mm (Figure 4). From this outline three readily identifiable landmarks were recognized, (1) the tip

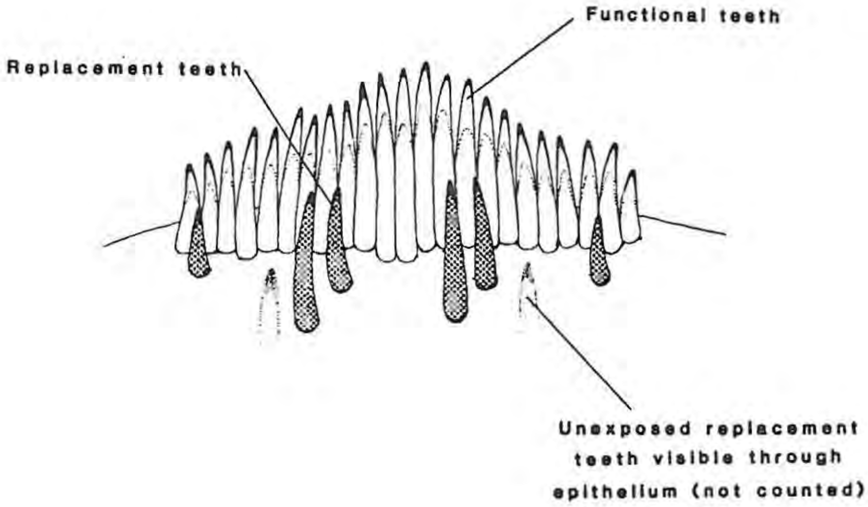

Figure 4.5 Diagram of generalized moveable mandibular teeth in anterior view to show relative position of functional and replacement teeth.

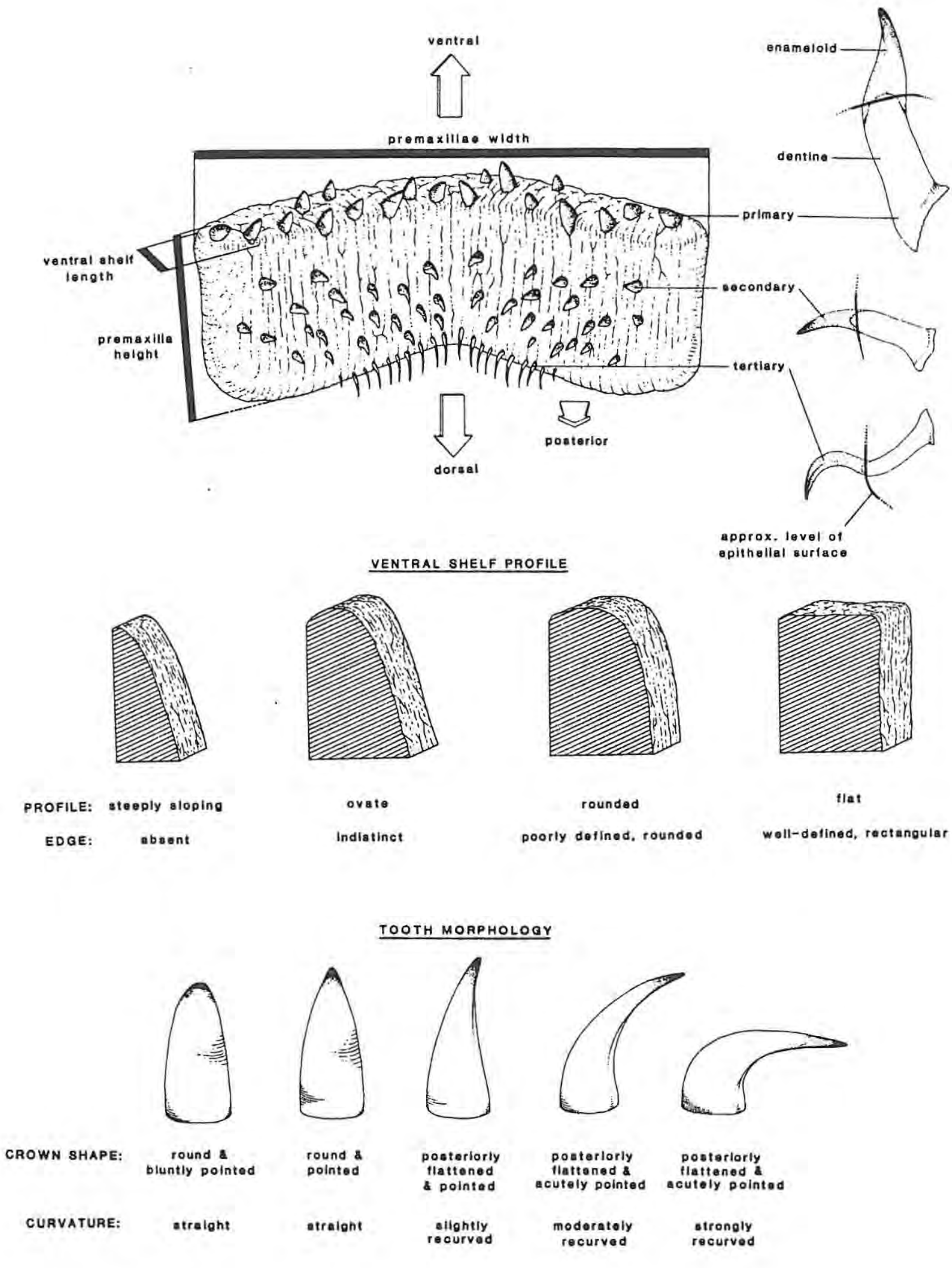

Figure 4.6 Diagram of generalized premaxillae in ventro-posterior view to illustrate size, shape and position of the primary, secondary and tertiary teeth. Terms used to describe ventral shelf profile and tooth morphology are also illustrated.

of the humeral process, (2) the anterior margin of the pectoral spine, and (3) the most dorsal point of the recess between these two points. A reference line was then drawn along the horizontal from the tip of the process through the dorsal point on the recess to the vertical intercept with the anterior margin of the pectoral spine. Measurements were then taken along the perpendicular, from the reference line to the outline at intervals of ten percent of the humeral process length. Analysis involved the calculation of the mean, standard deviation, standard error and range for each 10% interval. The last interval was divided by half to record the "nipple" at the posterior end of the humeral process of certain species. A generalized shape of the humeral process of each species was constructed by joining the mean values of each 10% interval.

Dentition

Cross-sections at various levels through the dentary bone in adult S.nigromaculatus specimens reveal all ontogenetic stages of the movable mandibular teeth, so confirming their continuous replacement. Scanning electron examination of the bases of functional (mature) teeth show a wedge-shaped band of basal collagen with the dentine extending to the attachment bone anteriorly. This derived Type 3 (hinged) tooth form (Fink, 1981, Figure 1i) confers a high degree of movement to these teeth. In all the southern African species replacement teeth at various stages of development are situated in front of a (usually) neat transverse row of functional teeth (Figure 4.5). The number of functional teeth and a combined (total) tooth count were recorded, the former referred to by Farquharson (1969) as "rank" teeth.

To my knowledge, the premaxillary teeth have never been referred to in Synodontis taxonomy other than to record the width of the tooth band exposed ventrally. In this study, the premaxillary teeth were studied in situ and described on the basis of their pattern, size, shape and position on the

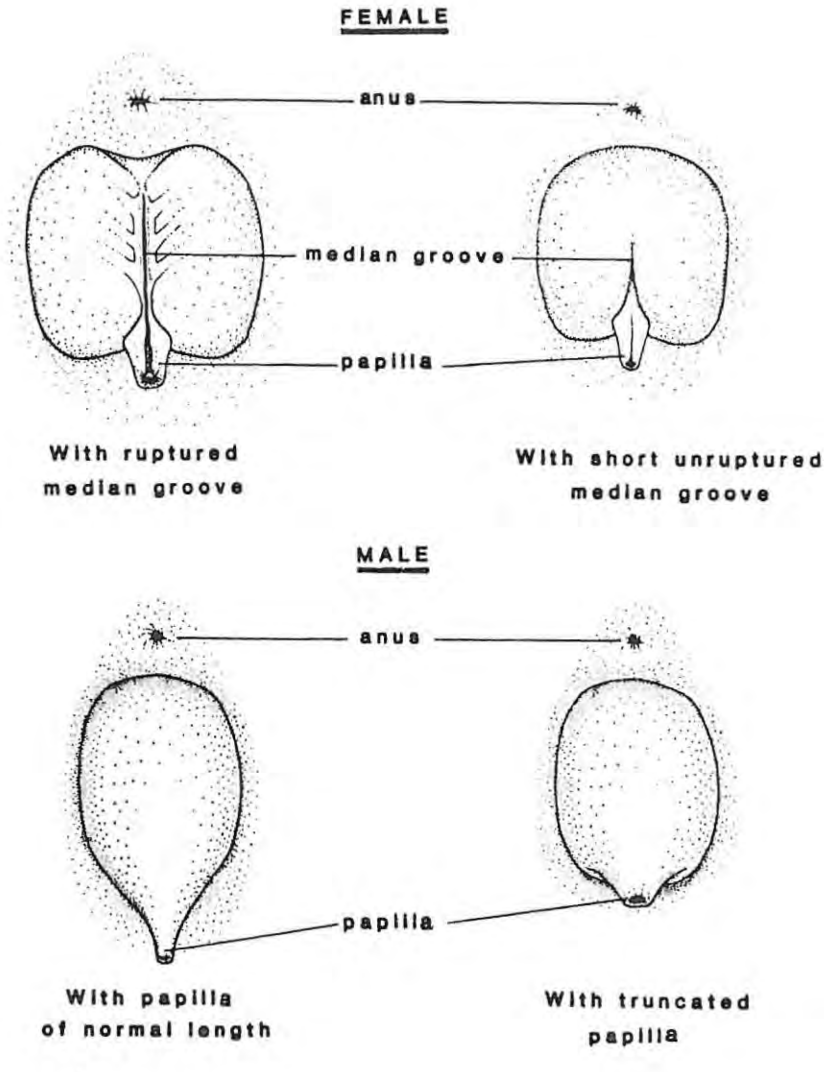

Figure 4.7 General diagrammatic ventral view of the external genitalia of mature Synodontis to show the extremes of form between the sexes.

premaxillae (Figure 4.6). Three types of teeth are recognized. The most ventrally situated or primary teeth are characterized by their large size, straight or posteriorly-curved cylindrical necks and position on or slightly below the ventral shelf. The secondary teeth are smaller with straight or dorsally-curved cylindrical necks and position on the posterior face of the premaxillae, between the primaries and tertiaries. The tertiary teeth are laterally-flattened, S-shaped, with a strongly recurved crown and usually held in one row on the postero-dorsal margin of the premaxillae.

Terms used to describe tooth morphology and ventral shelf profile are illustrated in Figure 4.6.

Sex

The external genitalia of mature male Synodontis is a muscular, ovoid protuberance elongated posteriorly into a conical-shaped papilla (Figure 4.7), the opening of which is slightly enlarged in the breeding season (Willoughby, 1974). The female genitalia is broader at the base with the ventral surface folded medially to form a groove, with a noticeably shorter papilla than males of the same size. The length of the median groove increases with age and, in females greater than 150 mm SL, the skin of the groove is often ruptured to form an opening extending the full length of the genitalia.

In this study it was found that, with few exceptions, sexing on the basis of the shape of their external genitalia was possible down to 70 mm SL in all species. Dissection to confirm sex was, however, required in a few specimens, where the papilla in males was very reduced in size or where the median groove was absent in females.

Colour pattern

In the descriptions a distinction is made between colouration and markings (cf. Barel et al.,1977). Markings refer to the dense concentration of (usually) melanophores on the body, head and fins to form dark brown or black spots and bars, which may be confluent forming elongated lines of variable length and form. The type and distribution of the remaining chromatophores are collectively referred to as the colouration.

The variation in colour pattern was determined from both live and preserved material. The colour pattern of live specimens was recorded on Ektachrome 64 (colour transparency) film using the methods described by Emery & Winterbottom (1980). Due to the obstruction of the large pectoral spines in Synodontis it was not possible to hold specimens up against the front pane of a photographic aquarium with an inclined glass plate, as recommended by the above method. To overcome this problem the glass plate was replaced by an opaque perspex sheet with a hole in the centre. Specimens were held in position by placing the right (erect) pectoral spine through the hole and securing it by means of a "bulldog" clip on the opposite side. This method effectively eliminated problems related to orientation, centering and movement of live specimens.

Post-mortem change in markings was assessed in each specimen photographed in the field by comparing them after three or more months in preservative. All specimens were fixed in 4% formalin for 5-6 weeks followed by preservation in 50% iso-propyl alcohol.

In the illustration of colour patterns, only those markings within circles on the body, dorsal fin and cheek are drawn in full. Markings elsewhere on the body and fins are drawn in outline only.

METHODS OF ANALYSIS

Statistical analysis

All statistical analyses were carried out on a CDC 4500L computer using the Statistical Package for Social Sciences (SPSS) (Nie et al.,1975).

Three principal methods are available to the taxonomist to compare differences in shape among groups: ratios, regressions and factor or component analysis (Humphries et al.,1981). This study has made use of all three methods.

Initial analysis of morphometric data involved the calculation of the arithmetic mean, standard deviation and standard error of their proportions, usually expressed as a percentage. I acknowledge the cautions of many workers on the use of ratios as they have been traditionally presented in systematic studies (see Humphries et al.,1981 for a review). In this respect, I follow Corruccini(1977) in his belief that "...ratios, properly used and understood, do enhance (the) understanding of data, despite theoretical objection." In support of the use of ratios in this study, I present the following:

1. Measurements and their proportions were used primarily to aid in identification of species in conjunction with descriptions. Only consistent differences, defined by their statistically significant distinctness over a similar length range, are presented in a species' diagnosis.

2. In defense of the criticism in the use of "ad hoc combinations of spatially unrelated measures" (Humphries et al.,1981), the denominator and numerator, where possible, are restricted to similar features of the body. For example, all measurements of the cranium were expressed

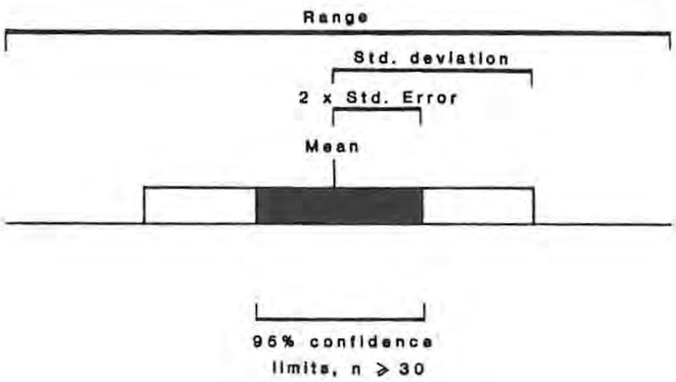

Figure 4.8 Method used to illustrate the variation of each sample in Dice-Leraas diagrams (adapted after Hubbs & Hubbs, 1953).

as a proportion of another cranial measurement, namely, head length.

3. The use of morphometric ratios has previously proven effective in discriminating between closely related species of southern African Synodontis (e.g. Jackson, 1959).

4. No morphometric ratio is considered in isolation. While the increased diagnostic value of certain characters may be emphasized, a combination of many morphometric, meristic and descriptive characters is used in the identification of each species.

Descriptive statistics of morphometric ratios were computed using SPSS subprogram 'CONDESCRIPTIVE'. Results were compared graphically in Dice-Leraas diagrams (Hubbs & Hubbs, 1953) explained in Figure 4.8. Student's t-test was used to test the degree of similarity between populations using subprogram 'T-TEST'.

Bivariate analysis of morphometrics was carried out using SPSS subprogram 'SCATTERGRAM', which involved the plotting of scattergrams and the calculation of regressions and correlation coefficients. This procedure also allowed the early detection of typographical errors in data files or in the actual measurement or sexing of specimens, identified by outlying points in the scattergrams.

Principal component analysis was used where data sets of three or more variables were compared. This multivariate technique was specifically designed to analyze sets of correlated variables (Humphries et al.,1981) but also allows for the analysis of structural relationships among individuals (Wiley, 1981). This method was chosen rather than discriminant function analysis, as the latter requires a priori grouping of individuals. In

Table 4.2 Characteristics of the two major groups of southern African *Synodontis* based on barbel morphology and humeral process shape (adapted after Jubb, 1967).

CHARACTER	GROUP I	GROUP II
Maxillary barbels	Long and slender.	Usually nodular along the outer edge.
	Usually appreciably longer than the length of the head.	Equal to or shorter than the length of the head.
Mandibular barbels	Long, slender, filamentous branches	Short, thick papillose or tubercular branches.
Humeral process	Longer than broad	As broad as they are long.
	Triangular and pointed with a straight or slightly concave upper margin.	Obtusely pointed, with a convex upper margin.

contrast, principal component analysis does not presume multiple groups and thus allows for their discovery (Humphries et al.,1981). Individual scores were computed using SPSS subprogram 'FACTOR', with 'VARIMAX' rotation of the axes.

Sequence of analysis and presentation of taxonomic groups

The southern African Synodontis are divisibile into two groups on the basis of barbel morphology and shape of their humeral process, a dichotomy originally identified by Jubb(1967)(Table 4.2). The one exception to this classification is S.woosnami, which has barbels similar to Group I and a humeral process shape similar to Group II. On the basis of a number of other features, however, this species has been shown to have a greater affinity with members of Group II.

Results are presented in a consistent order with species in Group I preceeding Group II, both in chronological order. To facilitate the comparison of data, particularly in Dice-Leraas diagrams and tables of meristic characters, new species introduced in this study are positioned below the species they most closely resemble. For example, S.macrostoma sp.n. is distinguished from S.macrostigma, and S.vanderwaali sp.n. from S.leopardinus. The order of presentation is thus S.zambezensis, S.nigromaculatus, S.njassae, S.nebulosus, S.woosnami, S.macrostigma, S.macrostoma sp.n., S.leopardinus, S.vanderwaali sp.n. and S.thamalakanensis. To further facilitate their comparison, where the results of Group I and Group II are presented together in tables their data are separated by a dashed line. The letters 'ND' appearing in diagrams and tables refers to the lack of data for that sample.

Where the availability of specimens would allow, each sample was chosen from as wide a size range as possible and equally represented by each (20 mm SL) size group (Table 4.3), to allow each character to be studied throughout its

Table 4.3 Frequency distribution of size of specimens used in the morphometric analysis.

Species	Drainage	n	Standard length (mm)										
			<30	30-50	50-70	70-90	90-110	110-130	130-150	150-170	170-190	190-210	>210
S.zambezensis	M.Zambezi	14				3	3	2	2	2	1		1
	L.Zambezi	18				4	3	5	2	3	1		1
	Pungwe	1				1							
	Buzi	2						2					
	Save	12				1	1	5	2	1	1	1	
	Limpopo	41					1	3	8	9	6	4	
	Incomati	5				2	1			1	1		
	Umbeluzi	2				2							
	Pongolo	30				1	3	6	7	7	5	1	
S.nigromaculatus	Okavango	60	1	2	10	9	3	4	4	6	12	8	2
	U.Zambezi	17					5	1	3	1	4	3	
S.njassae	L.Malawi	34			1	6	7	6	12	2			
S.nebulosus	M.Zambezi	13			1	1	9	2					
	L.Zambezi	1						1					
S.woosnami	Okavango	54		2	19	14	2	6	4	3	3	1	
	U.Zambezi	1							1				
	Cunene	11		1	4		1	3	1	1			
S.macrostigma	Okavango	61		1	9	15	15	9	10	2			
	U.Zambezi	21				1	2	12	5				
	Cunene	15			11	4							
S.macrostoma sp.n.	U.Zambezi	21		4	9	7	1						
	Cunene	2			2								
S.leopardinus	Okavango	44	2	4	6	11	2	8	2	4	7	2	
	U.Zambezi	22		1		7	7		4	3			
S.vanderwaali sp.n.	Okavango	36			7	15	7	4	2	1			
	U.Zambezi	4					4						
	Cunene	8					1		4	1			
S.thamalakanensis	Okavango	42		3	11	7	2	7	3	7	2		
	U.Zambezi	1							1				

development. Where this was not possible, and particularly where the morphometrics of two species are compared with only a small overlap in size range, for example between S.macrostoma sp.n. and S.macrostigma, bivariate analysis is used to assess the extent to which this bias affects the results.

"S.kafuensis" is excluded from all results as its type series was found to be polyspecific. A comparison of these 13 type specimens and an evaluation of the criteria on which this species was founded is presented separately in Chapter 5.

Material examined

A list of all material examined in this study is given in Appendix 1, including a brief description of the locality of each sample. Abbreviations for museums are as follows: AMG - Albany Museum, Grahamstown; ANSP - Academy of Natural Sciences, Philadelphia; BMNH - British Museum (Natural History), London; MNHN - Museum National d'Histoire Naturelle, Paris; NMZB - National Museum of Zimbabwe, Bulawayo; RUSI - JLB Smith Institute of Ichthyology, Grahamstown; SAM - South African Museum, Cape Town; SMWN - State Museum, Windhoek; TMP - Transvaal Museum, Pretoria; ZMH - Zoologisches Institut und Museum, Universitat Hamburg, Hamburg.

At least some of the types of all 11 nominal species considered in this study were examined. Only the types of S.zambezensis rukwaensis were not located. Four (out of eight) paralectotypes of S.njassae and the holotype of S.thamalakanensis were not examined.

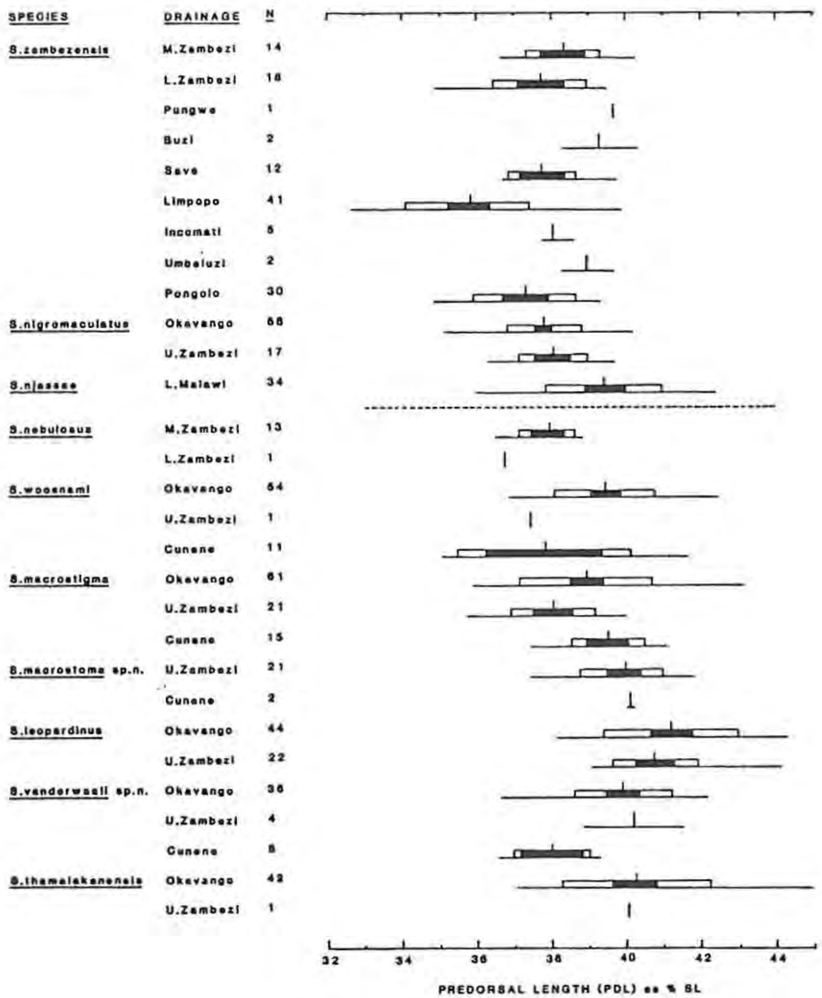

Figure 5.1 Predorsal length (PDL) expressed as a percentage of standard length. Data given in Appendix Table 2.1.

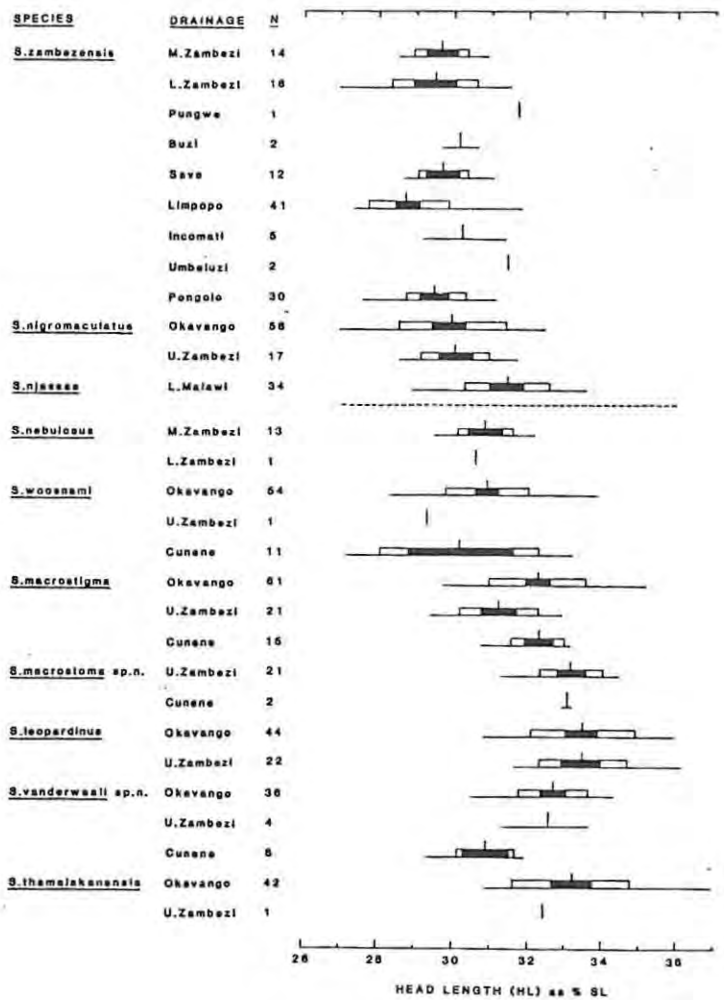

Figure 5.2 Head length (HL) expressed as a percentage of standard length. Data given in Appendix Table 2.2.

Chapter 5

RESULTS

MORPHOMETRICS

1. Predorsal length (Figure 5.1)

The intraspecific variation of this character is largest in S.zambezensis. Except for the Limpopo population of this species, the remaining eight populations show only a slight decrease in mean value with increasing latitude. The two most extreme values in S.zambezensis between the Limpopo and Middle Zambezi populations, however, are markedly dissimilar and, although their ranges are largely overlapping, their mean values are significantly different, even at 0,1% probability ($t = 5{,}48$, $df = 53$, $p > 0{,}001$). Although certain trends are discernible among the remaining species, their largely overlapping ranges prevent the use of this character as a diagnostic feature of importance. Among the southern African Synodontis, differentiation in predorsal length is possible only between S.leopardinus and S.nebulosus, two species that differ markedly in several other respects.

2. Head length (Figure 5.2)

The general pattern in distribution of mean values is very similar to that shown in the results of the previous character but differs from it in an overall reduction of both inter- and intraspecific variation. The difference between the two most widely separated means in S.zambezensis, for example, is

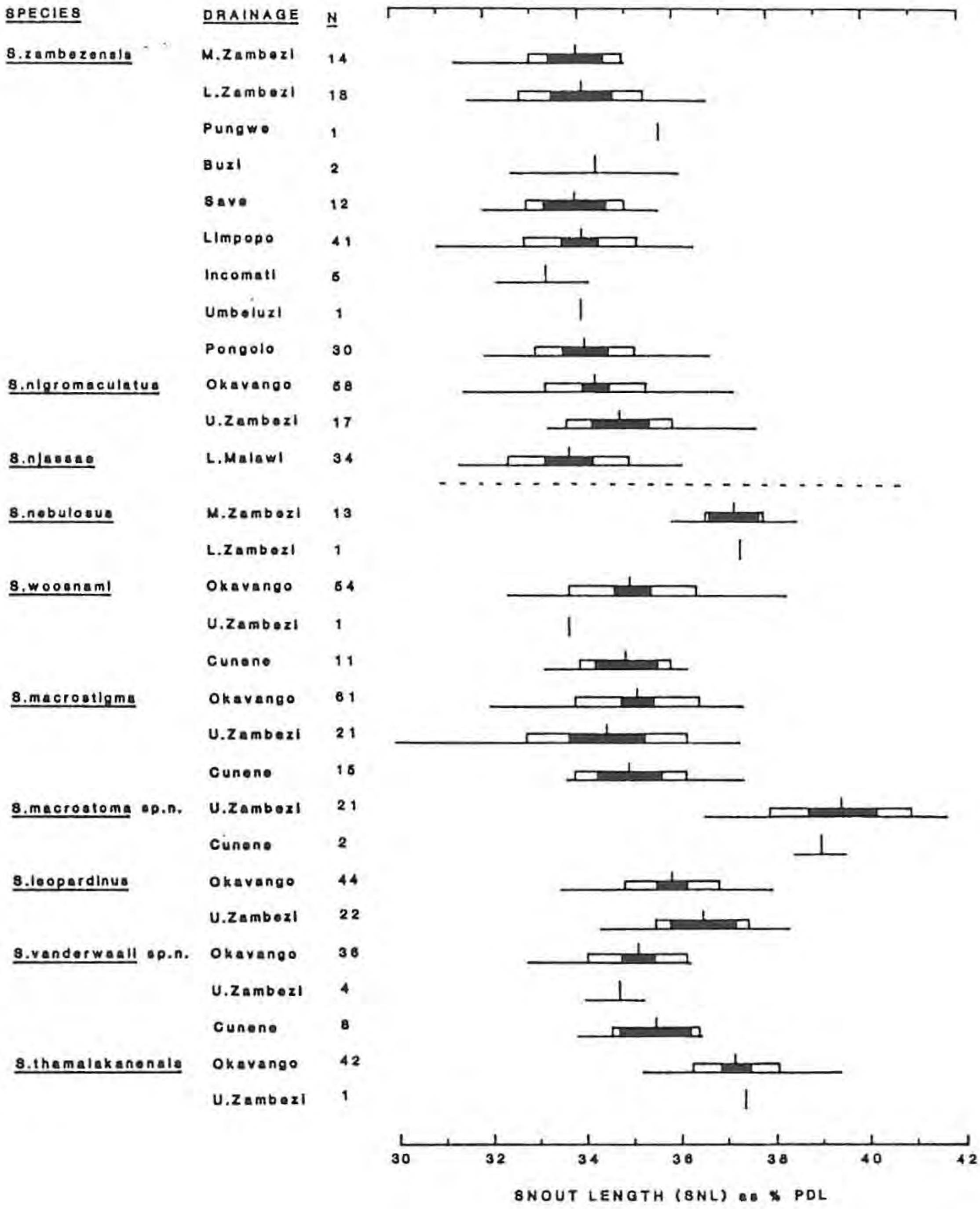

Figure 5.3 Snout length (SNL) expressed as a percentage of predorsal length. Data given in Appendix Table 2.3.

only 0,93%, in comparison to an average of their combined standard deviations of 0,86%.

The larger mean value of S.njassae among the species of Group I is particularly relevant in its comparison to S.zambezensis in the adjacent drainage basin of the Lower Zambezi, where it is significantly different at 0,01% probability ($t = 5,77$, $df = 47$, $p > 0,001$). The large overlap in range between these two species, however, reduces the diagnostic value accordingly.

Both predorsal length and head length record distances between fused elements of the cranium, that allow a high level of precision in measurement, but the largely overlapping ranges of these characters precludes their diagnostic use among the southern African Synodontis. Certain trends, however, are discernible, e.g. the shorter head and predorsal lengths of S.zambezensis and S.nigromaculatus and the longer values of the same for S.macrostoma sp.n. and S.leopardinus.

3. Snout length (Figure 5.3)

In comparison with the previous two characters this measurement shows the least intraspecific variation. The mean values for each of the nine samples of S.zambezensis, for example, differ by only 0,19% in comparison with a total range in this species of 5,74%.

No significant difference exists between the species of Group I. Among the species of Group II, S.nebulosus, S.macrostoma sp.n., and to a lesser extent also S.thamalakanensis, show consistently higher values than the other five species. Due to the close resemblance between specimens of S.macrostoma sp.n. and S.macrostigma, particularly in juveniles, their dissimilarity in this character is of particular importance. Although the difference between the mean value of S.macrostoma sp.n. (39,46%) and a combined value for all three

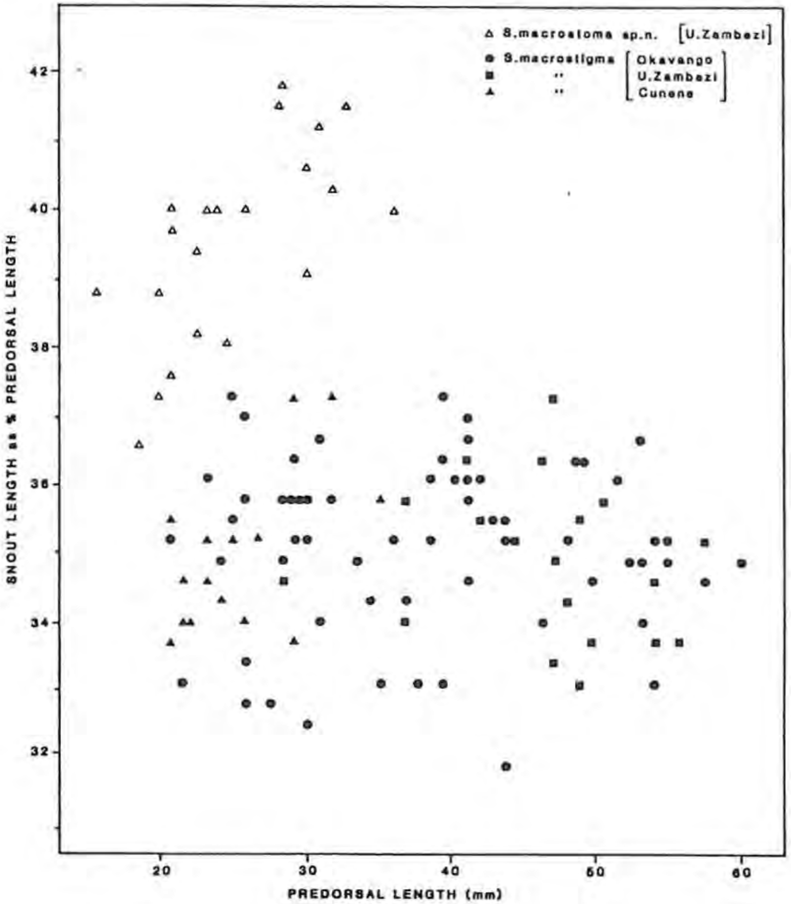

Figure 5.5 Comparison of the regressions of S.macrostoma sp.n. and S.macrostigma in the relationship of snout length to predorsal length.

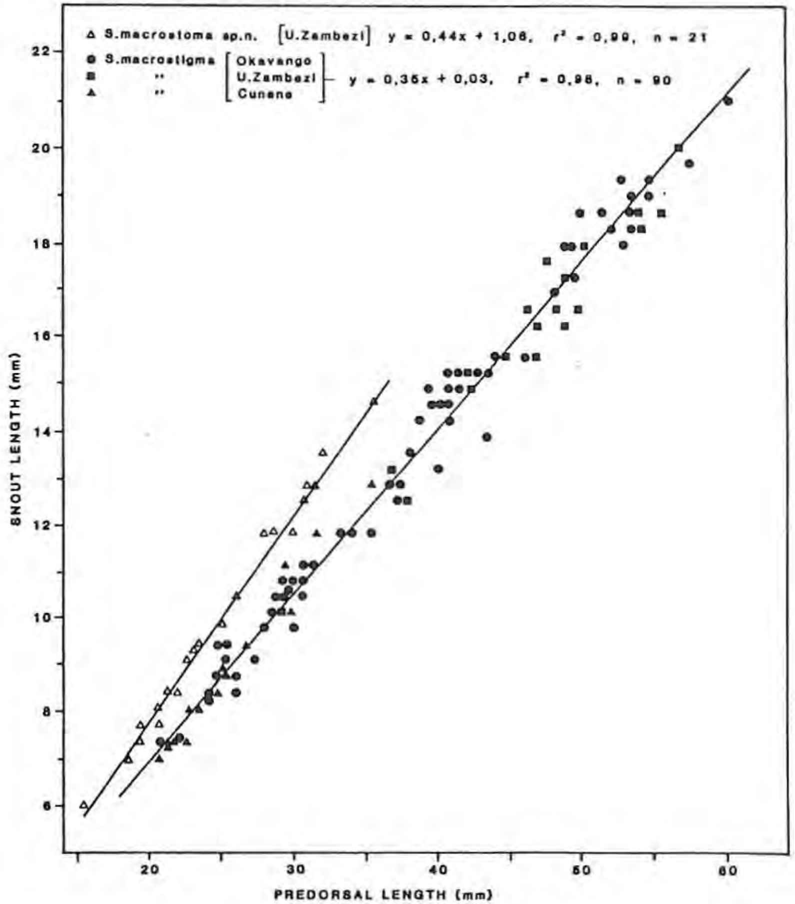

Figure 5.4 Scattergram of the percentage of snout length to predorsal length with predorsal length for selected populations of S.macrostoma sp.n. and S.macrostigma.

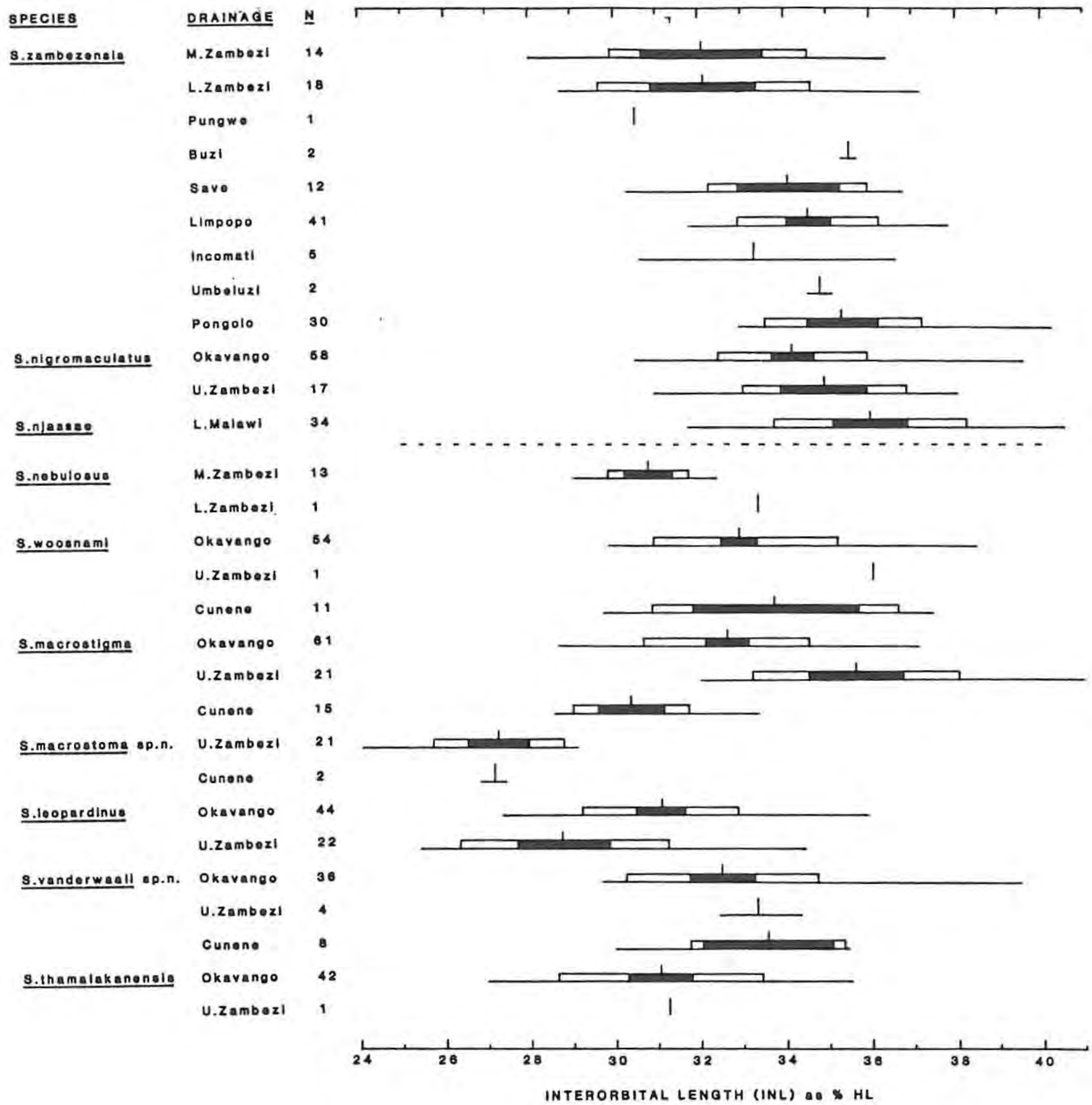

Figure 5.6 Interorbital length (INL) expressed as a percentage of head length. Data given in Appendix Table 2.4.

populations of S.macrostigma (34,98%) is strongly significant (t = 12,77, df = 80, p > 0,001), the value of this potentially important diagnostic feature is somewhat reduced by the small (0,44%) overlap in ranges. The bivariate analysis of this data reveals the source of this variation in greater detail (Figure 5.4). A distinctly positive allometric trend is evident in S.macrostoma sp.n., as indicated by the corresponding increase in the percentage of snout length to predorsal length, with the overlap in range due to the progressively lower values of smaller S.macrostoma sp.n. specimens. The characteristics of this trend are more clearly defined by the comparison of their regressions in the plot of snout length to predorsal length (Figure 5.5). Although the S.macrostoma sp.n. sample is comparatively small, both regressions are accompanied by high correlation coefficients and are clearly divergent. Therefore, in addition to the strongly significant difference shown in the monovariate analysis, where S.macrostigma is distinguishable below the proportional snout length of 37,4% and S.macrostoma sp.n. above 36,5%, its diagnostic value increases with size.

Limited differentiation of S.nebulosus from S.macrostigma is possible using this character, indicated by their significant difference in mean values (t = 5,78, df = 74, p > 0,001) and non-overlapping ranges in standard deviation. The diagnostic value of this character, however, is reduced by their overlap in total range by 1,56%, constituting more than half the (2,7%) range of S.nebulosus.

4. Interorbital length (Figure 5.6)

The intraspecific variation of this character is large, a feature that is especially noticeable for S.zambezensis, S.macrostigma and S.leopardinus.

Among the five largest samples of S.zambezensis, the ratio of interorbital length to head length shows a positive correlation to latitude. The

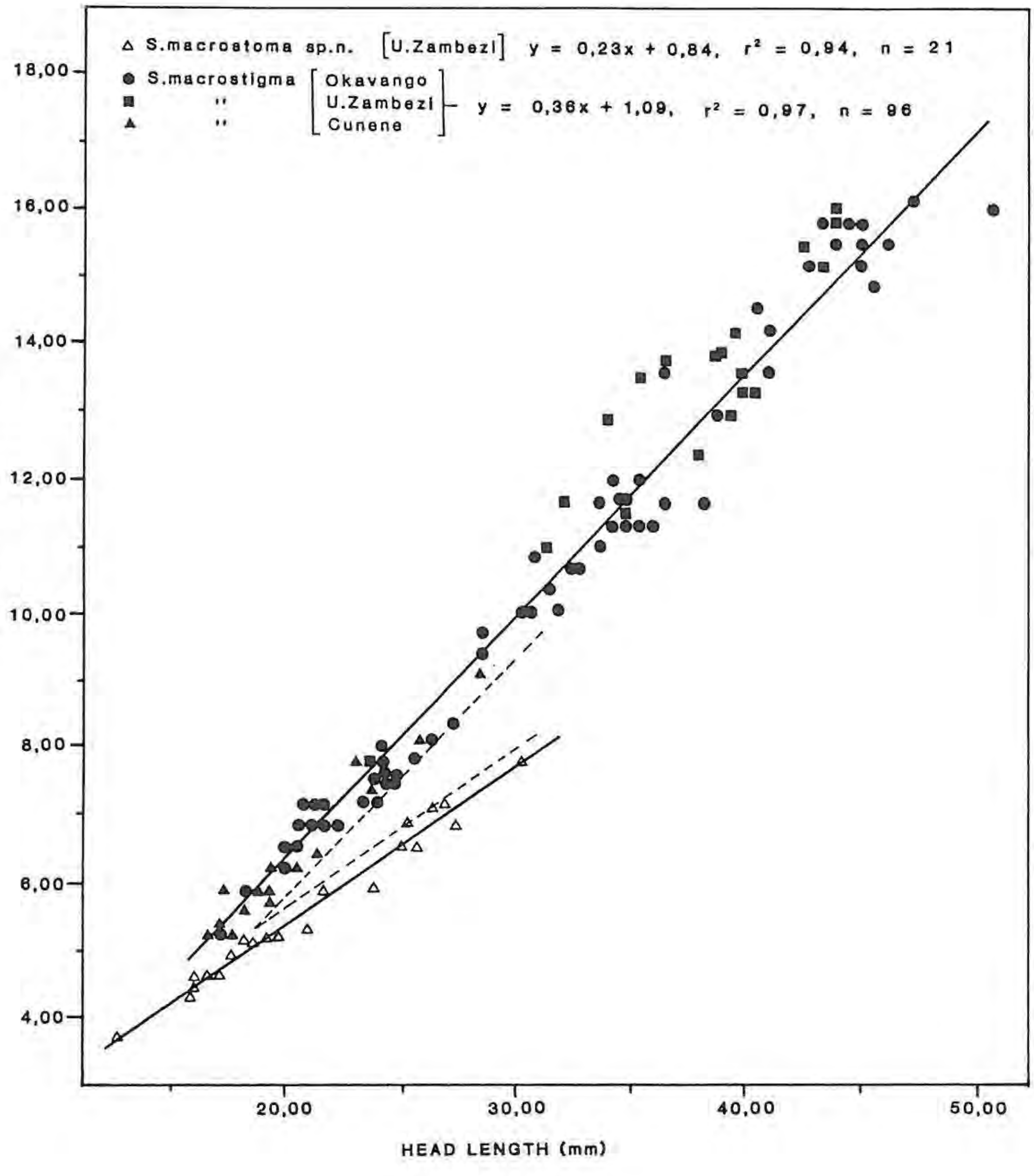

Figure 5.7 Comparison of the regressions of S.macrostoma sp.n. and S.macrostigma in the relationship of interorbital length to head length. Dashed lines represent 95% confidence limits.

difference of 3,28% between the mean values of the Middle Zambezi and Pongolo samples of this species is significant (t = 4,31, df = 36, p > 0,001). The difference (5,33%) in sample means between the Upper Zambezi and Cunene populations of S.macrostigma is even more pronounced, in comparison with their average standard deviation of 1,91%. In this species, both the Upper Zambezi and Cunene populations are significantly different from the Okavango population (t = 5,77, df = 79, p > 0,001 and t = 4,28, df = 74, p > 0,001, respectively).

Although the large intraspecific variation of this character would seem to allay its potential as a diagnostic feature, it is still useful to differentiate between S.macrostoma sp.n. and S.macrostigma. The very clear distinction between the Upper Zambezi populations of these two species is reduced by the lower values of the Cunene S.macrostigma population, and although significantly different (t = 6,23, df = 34, p > 0,001), they overlap by 0,51%. As with the previous character, the significantly lower mean value of the Cunene S.macrostigma population is due to the smaller number and smaller overall size of these specimens. The regression analysis of interorbital length to head length shows strongly divergent slopes in these species (Figure 5.7). The 95% confidence limits of these regressions, however, curtail the diagnostic use of this character in specimens with a head length smaller than 18,5 mm, corresponding to an average standard length in S.macrostigma of 55,5 mm and in S.macrostoma sp.n. of 56,0 mm (Appendix 3).

5. Dorsal to coracoid (Figure 5.8)

The expression of this measurement differes noticeably between Group I and Group II. The most widely separated mean values in S.zambezensis represented by the Middle Zambezi and Pongolo populations differ by only 2,22%, in comparison with the average standard deviation for the five largest samples of 3,47%. The mean values of the remaining species in Group I all fall within

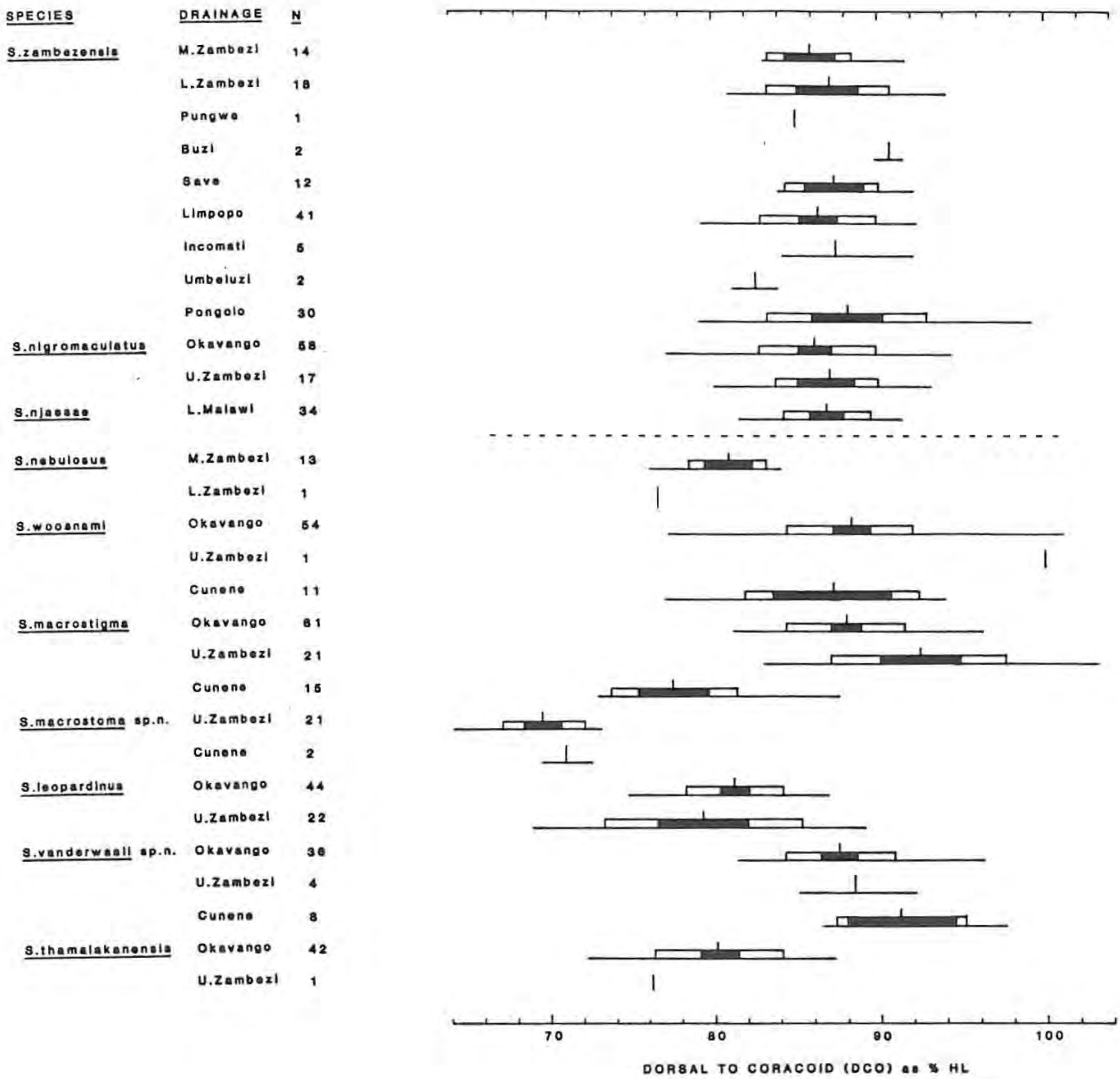

Figure 5.8 Dorsal to coracoid (DCO) expressed as a percentage of head length. Data given in Appendix Table 2.5

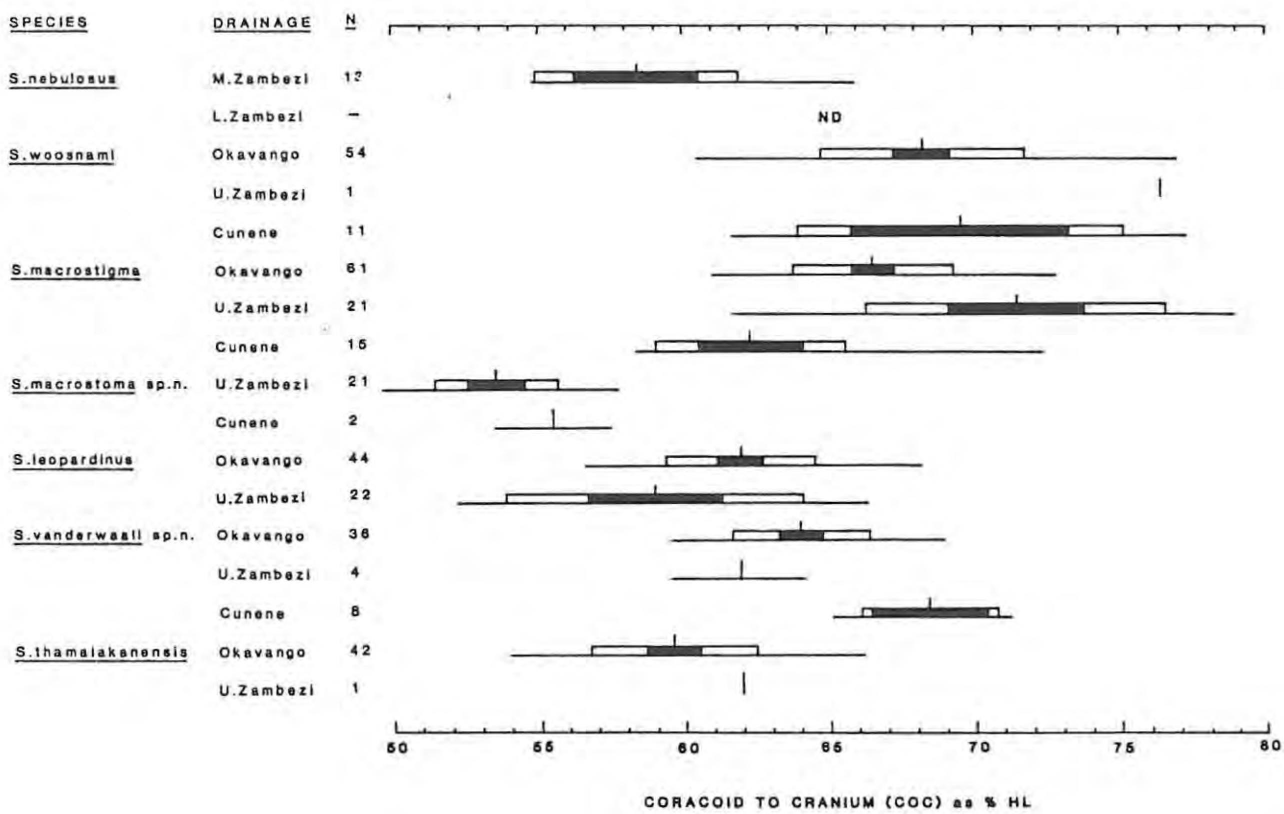

Figure 5.9 Coracoid to cranium (COC) expressed as a percentage of head length. Data given in Appendix Table 2.6.

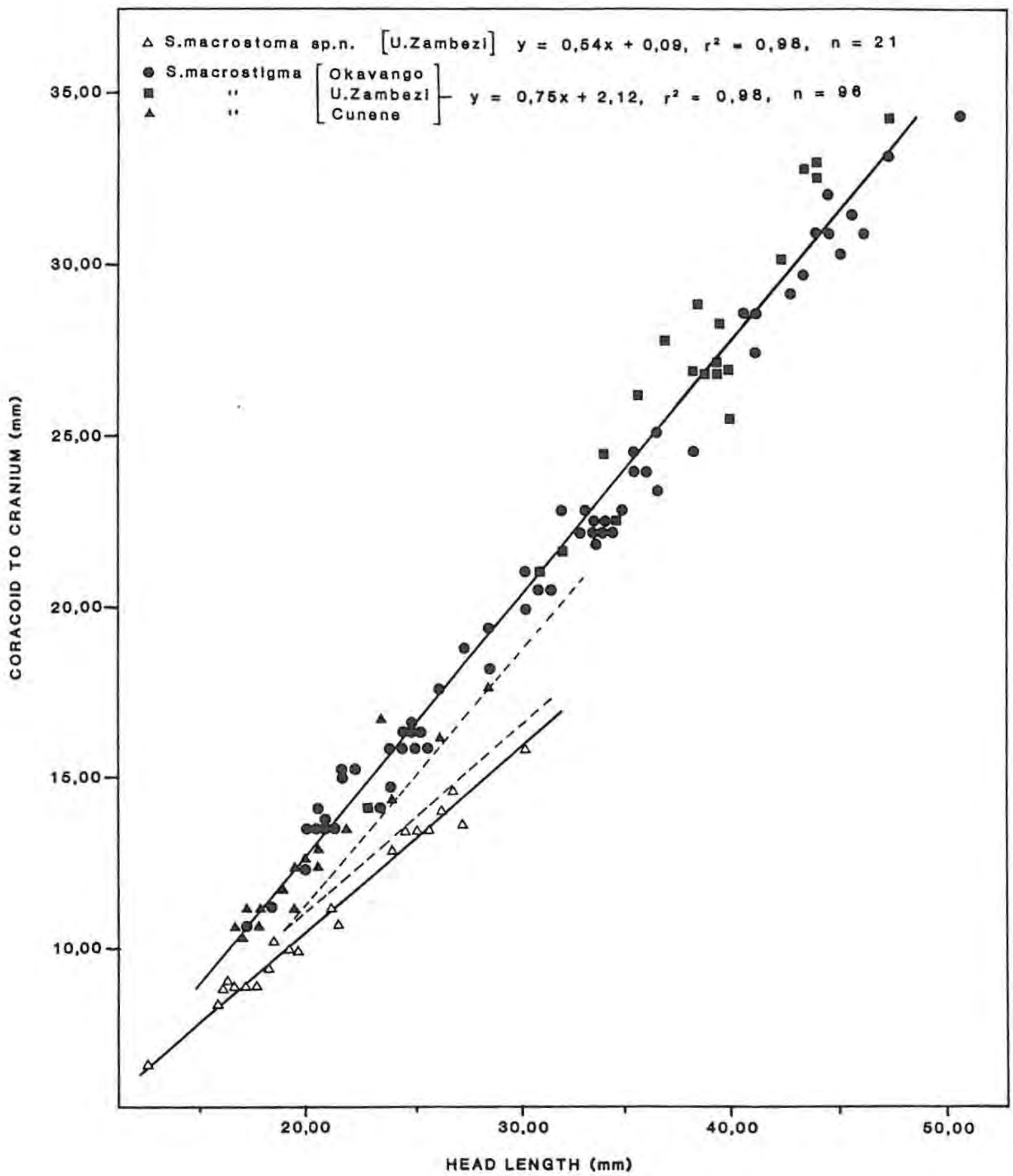

Figure 5.10 Comparison of the regressions of S.macrostoma sp.n. and S.macrostigma in the relationship of coracoid to cranium. Dashed lines represent 95% confidence limits.

this range. Both the intra- and interspecific variation is larger in Group II.

As with the interorbital length, S.macrostigma has the largest intra- specific variation in the dorsal to coracoid measurement among the species of Group II, with a significant difference ($t = 10,16$, $df = 76$, $p > 0,001$) between the Cunene and Okavango populations. The large variation within this species, however, does not limit the diagnostic value of this character in distinguishing it from S.macrostoma sp.n.

To a lesser extent it is also possible using the dorsal to coracoid measurement to differentiate S.vanderwaali sp.n. from S.leopardinus and from S.thamalakanensis, but both distinctions are marred by overlapping ranges.

6. Coracoid to cranium (Figure 5.9)

The measurements of coracoid to cranium (COC) and dorsal to coracoid (DCO) are similar in that both describe the relative distance between the pectoral girdle and the dorsal surface of the cranium, although not in the same plane. Not surprisingly, they also show a very similar pattern in the distribution of population means.

The distinction between S.macrostoma sp.n. and S.macrostigma is greater in the coracoid to cranium measurement than in the dorsal to coracoid measurement, as there is no overlap in range in the former and the means are more widely separated.

The regressional analysis of coracoid to cranium with head length again shows the strongly divergent slopes in these species (Figure 5.10). The convergence of the 95% confidence limits of each regression at 18,0 mm HL curtail the diagnostic use of this character below this value, which in S.macrostigma

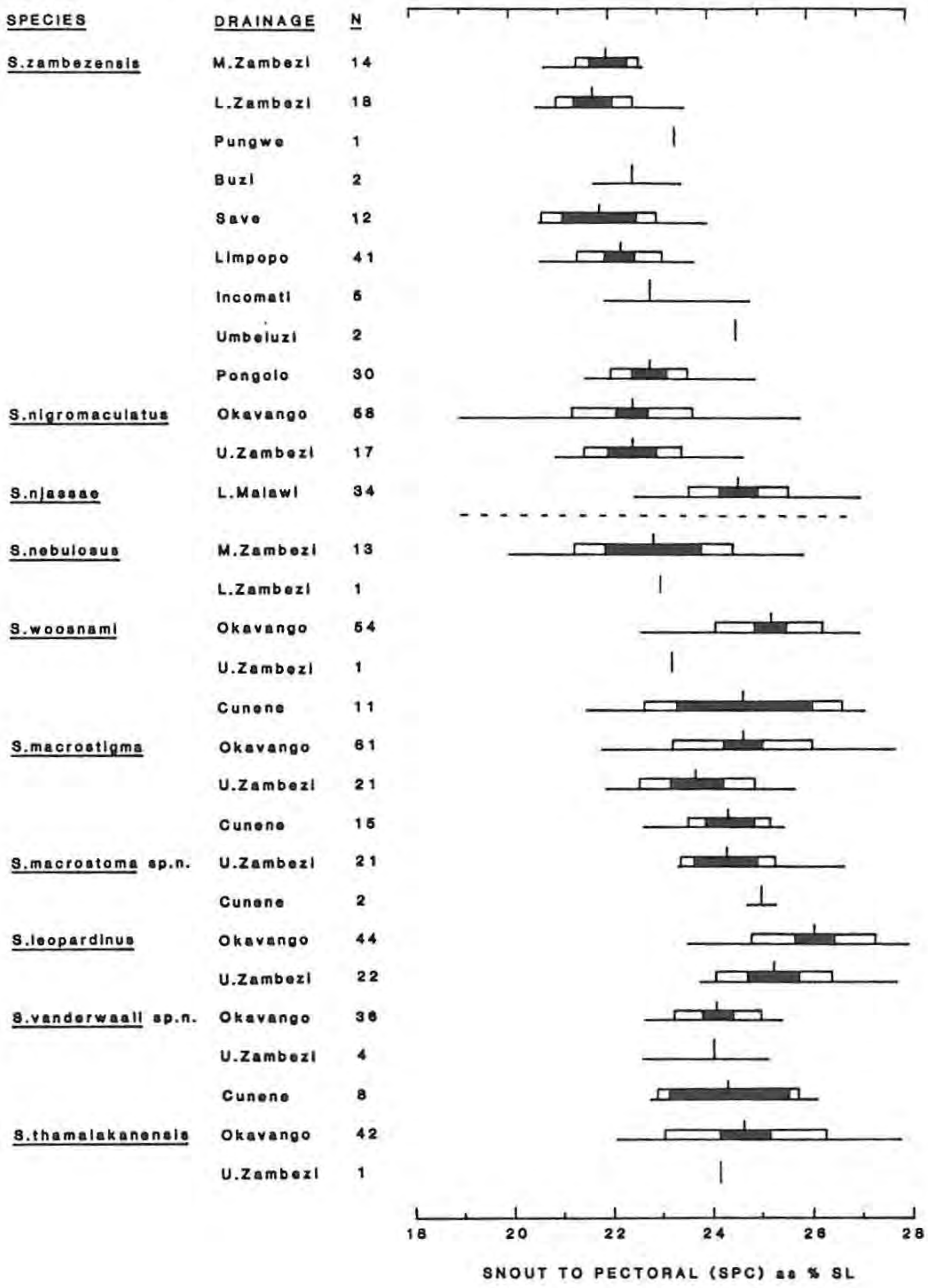

Figure 5.11 Snout to pectoral (SPC) expressed as a percentage of standard length. Data given in Appendix Table 2.7.

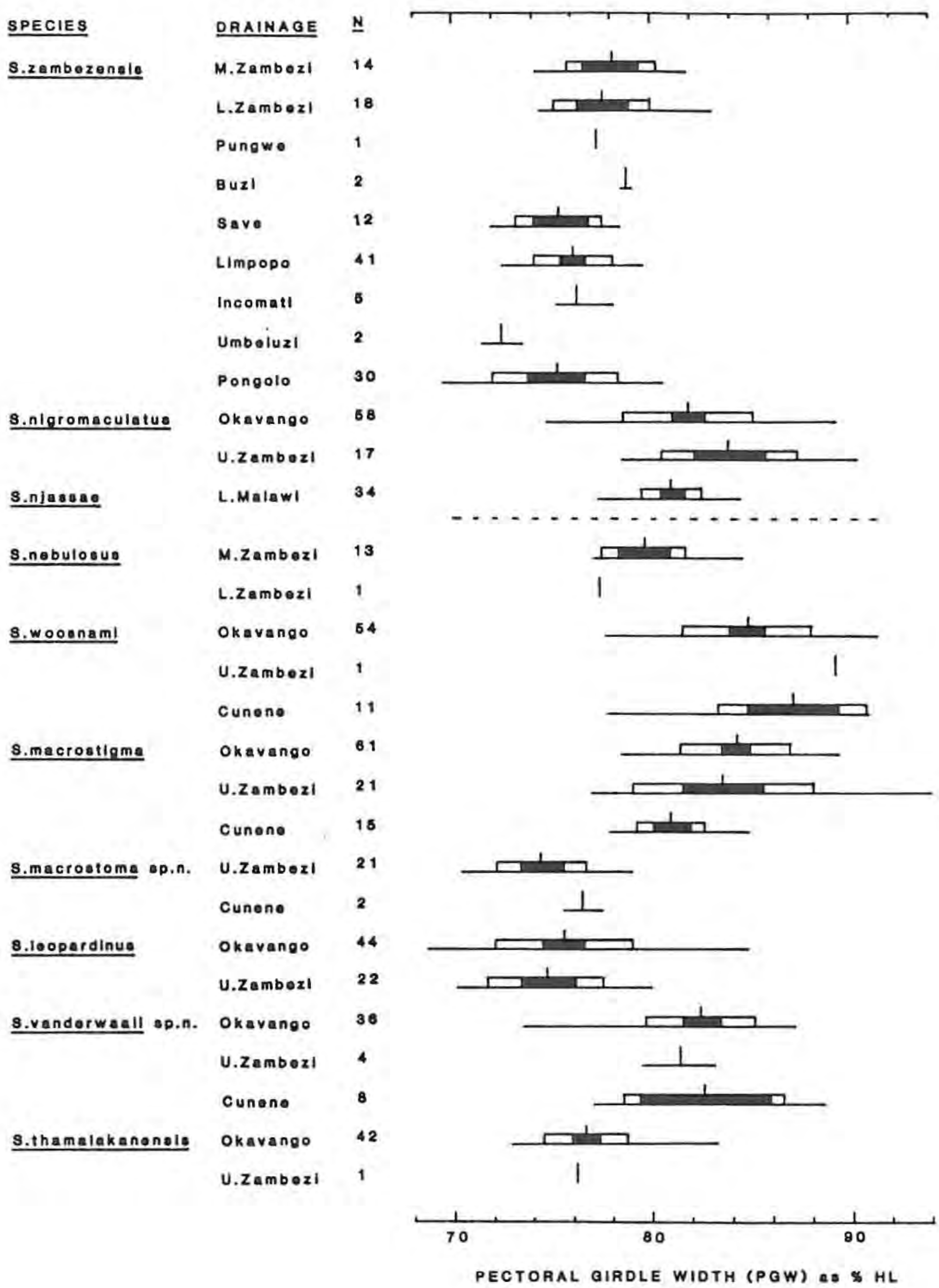

Figure 5.12 Pectoral girdle width (PGW) expressed as a percentage of head length. Data given in Appendix Table 2.8.

corresponds to a standard length of 54,0 mm and in S.macrostoma sp.n. of 54,5 mm (Appendix 3). Similar to the results of interorbital length, the reduced mean value in the Cunene population of S.macrostigma can be attributed to the small overall size of the specimens in this sample.

In contrast to the above results, the differentiation of S.vanderwaali sp.n. from S.leopardinus and S.thamalakanensis is substantially reduced.

7. Snout to pectoral (Figure 5.11)

The comparatively low intraspecific variation of this measurement is best exemplified in the five largest samples of S.zambezensis, where the difference in extreme mean values is only 1,13% in comparison with an average of their standard deviations of 0,83%.

Although interspecific differences are similarly low, differentiation is possible between S.njassae and S.zambezensis, with S.njassae showing a strongly significant difference between S.zambezensis from the adjacent drainage basin of the Lower Zambezi ($t = 11{,}58$, $df = 43$, $p > 0{,}001$).

Largely overlapping ranges in standard deviation of the remaining species, however, indicate the lack of any further differentiation.

8. Pectoral girdle width (Figure 5.12)

The lateral rigidity of the pectoral girdle allows this measurement to be taken with high precision and has certainly contributed to the relatively low intraspecific variation of this character. Although a slightly positive correlation with latitude is evident among S.zambezensis, the most widely separated mean values between the Middle Zambezi and Pongolo populations differ by only 2,41% in comparison with an average of their standard deviations of 2,82%. The overall range in S.zambezensis, however, almost totally

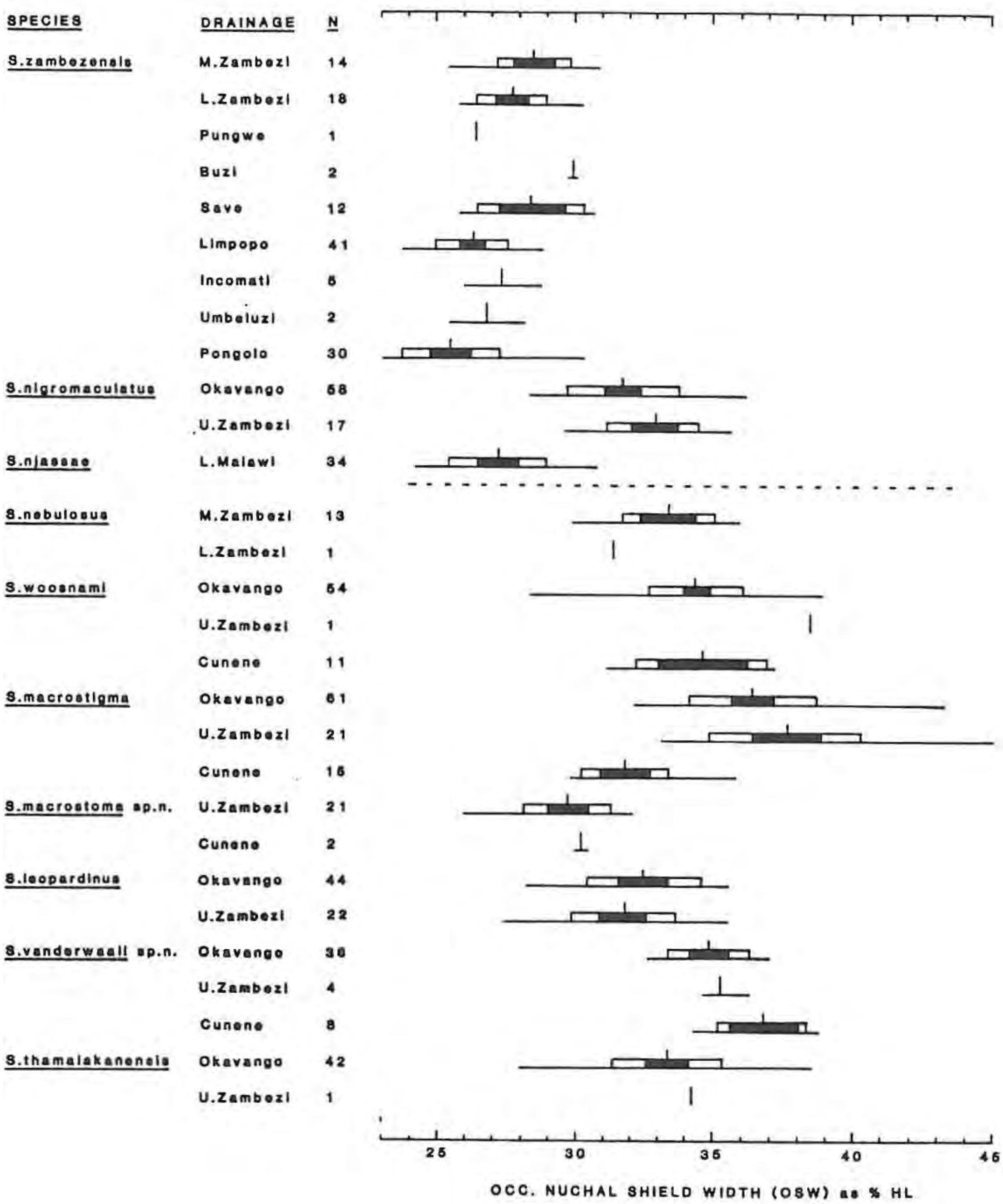

Figure 5.13 Occipito-nuchal shield width (OSW) expressed as a percentage of head length. Data given in Appendix Table 2.9.

overlaps the range in S.njassae.

Among the species of Group II, S.macrostoma sp.n., S.leopardinus, and to a lesser extent also S.thamalakanensis, are identified by their generally lower mean values. The only noteworthy difference in these results, however, is between S.macrostigma and S.macrostoma sp.n. with an overlap in range of only 2,11%.

The difference between mean values of S.vanderwaali sp.n. and S.leopardinus are highly significant ($t = 9{,}66$, $df = 78$, $p > 0{,}001$). While this clearly indicates the distinctness of each species, the large overlap in the ranges of this measurement severely diminishes its taxonomic value.

9. Occipito-nuchal shield width (Figure 5.13)

The differences in intraspecific variation are large in this character and range from 6,12% in S.macrostoma sp.n. to 15,17% in S.macrostigma. The variation in S.zambezensis shows a generally negative correlation with latitude, resulting in the significant difference between the mean values of the Middle Zambezi and Pongolo populations ($t = 5{,}95$, $df = 33$, $p > 0{,}001$). This difference, however, is overshadowed by their largely overlapping ranges.

In the proportional measurement of occipito-nuchal shield width the Okavango and Upper Zambezi populations of S.macrostoma sp.n. and S.macrostigma are clearly different, but the mean of the Cunene population of S.macrostigma is much closer to that for S.macrostoma sp.n. Among the species of Group I, S.nigromaculatus is identified by its generally higher values, but the largely overlapping ranges of this group do not allow for the reliable diagnosis of any one species.

10. Humeral process length (Figure 5.14)

The intraspecific variation in S.zambezensis shows a generally negative

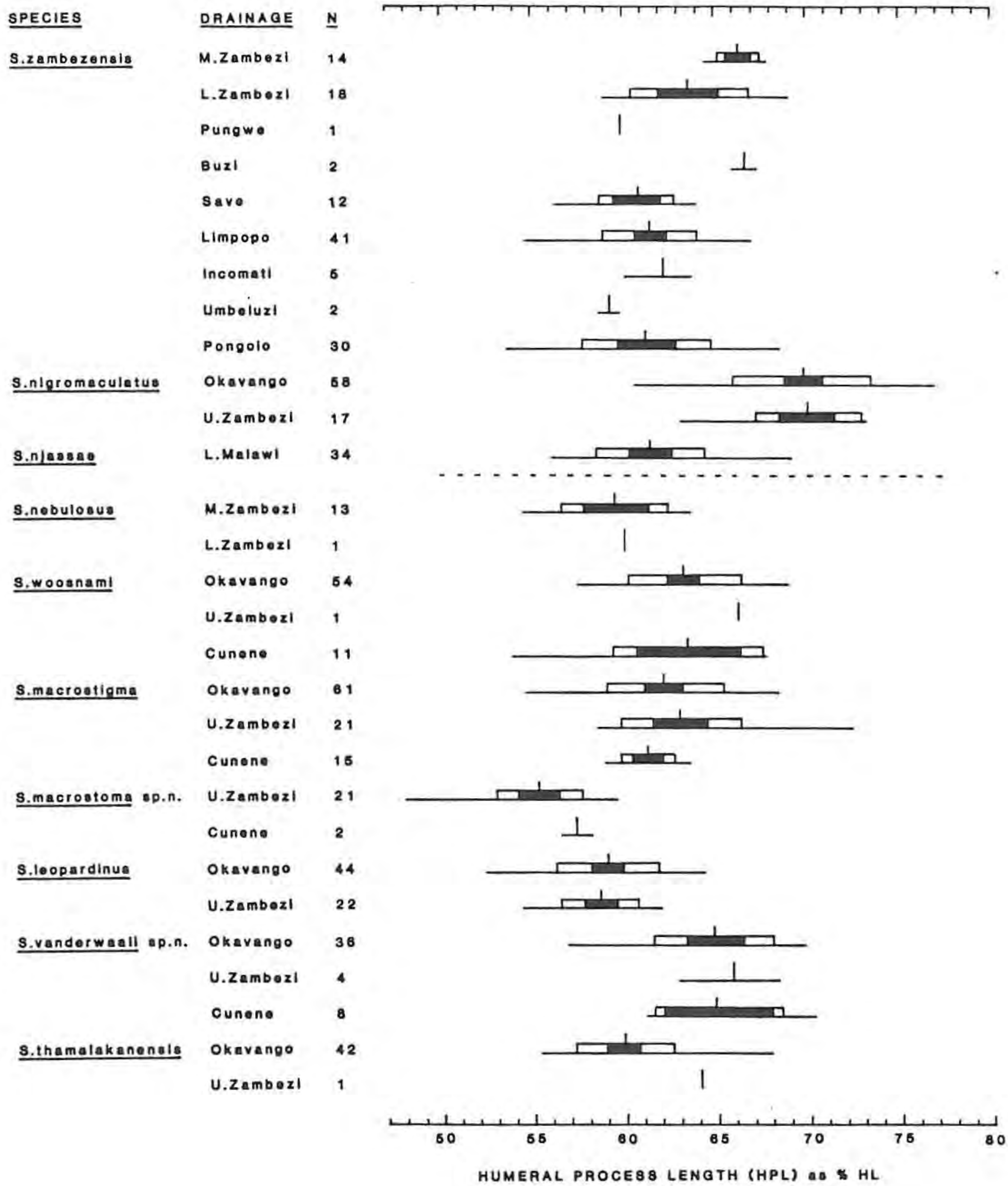

Figure 5.14 Humeral process length (HPL) expressed as a percentage of head length. Data given in Appendix Table 2.10.

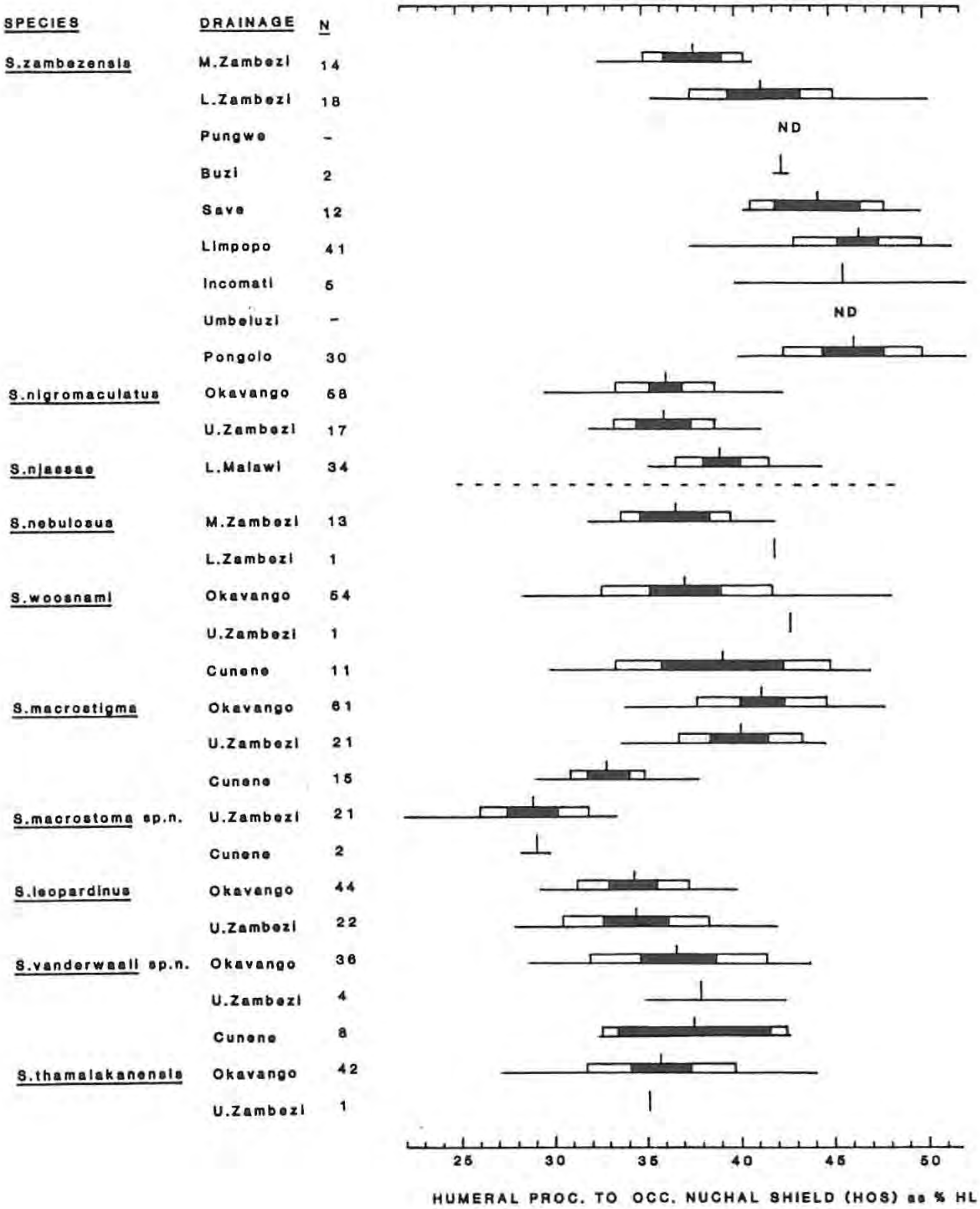

Figure 5.15 Humeral process to occipito-nuchal shield (HOS) expressed as a percentage of head length. Data given in Appendix Table 2.11.

correlation with latitude, where the ranges of the two most widely separated populations in the Middle Zambezi and Save are quite distinct and non-overlapping. This difference, however, is completely covered by the large variation within the Pongolo population. Due to the large overlap in ranges among the species of Group I, limited differentiation of only S.nigromaculatus is possible.

The difference between all three populations of S.macrostigma and that of S.macrostoma sp.n. is significant (t = 9,34, df = 46, p > 0,001). The diagnostic value of this character, however, is reduced by their overlap in range, with S.macrostigma distinguishable only at a humeral process length greater than 58,56% and S.macrostoma sp.n. at less than 56,52%.

The proportional measurement of humeral process length is also useful to distinguish between S.leopardinus and S.vanderwaali sp.n., but an overlap of 7,49% must be taken into account.

11. Humeral process to occipito-nuchal shield (Figure 5.15)

S.zambezensis shows the largest intraspecific variation in this character with a strongly positive correlation with latitude. The most widely separated mean values in this species differ by 8,78% in comparison with an average of their standard deviations of 3,05%. The most widely separated mean values in sequence shown between the Lower and Middle Zambezi populations, however, are not significantly different at 0,01% probability (t = 3,25, df = 27, 0,01 < p > 0,001). Due to this large variation in S.zambezensis no differentiation is possible among the species of Group I.

A very clear distinction exists between the Upper Zambezi and Okavango populations of S.macrostigma and S.macrostoma sp.n. Similar to the results of occipito-nuchal shield width, however, the mean value for the Cunene

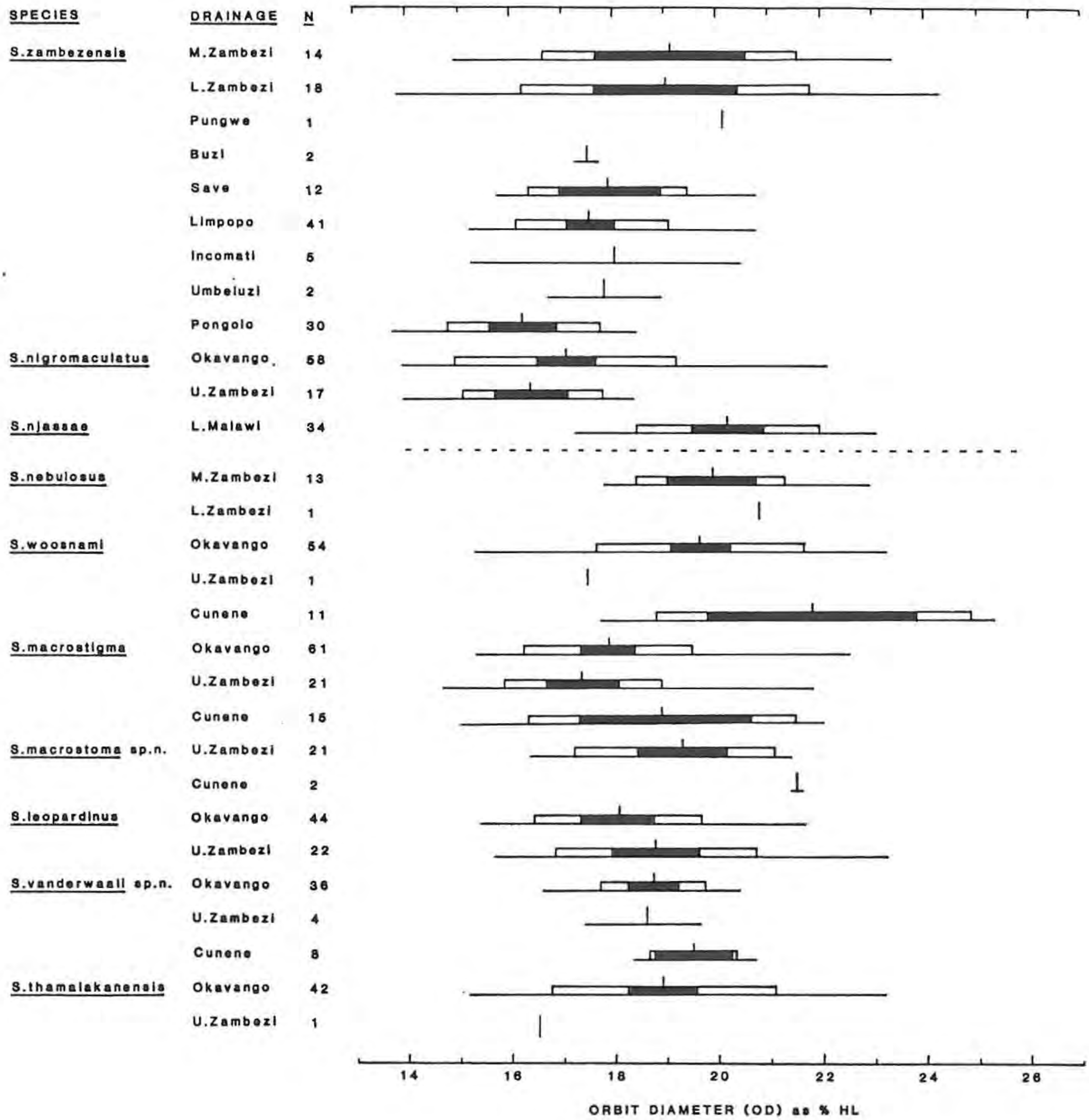

Figure 5.16 Orbit diameter (OD) expressed as a percentage of head length. Data given in Table 2.12.

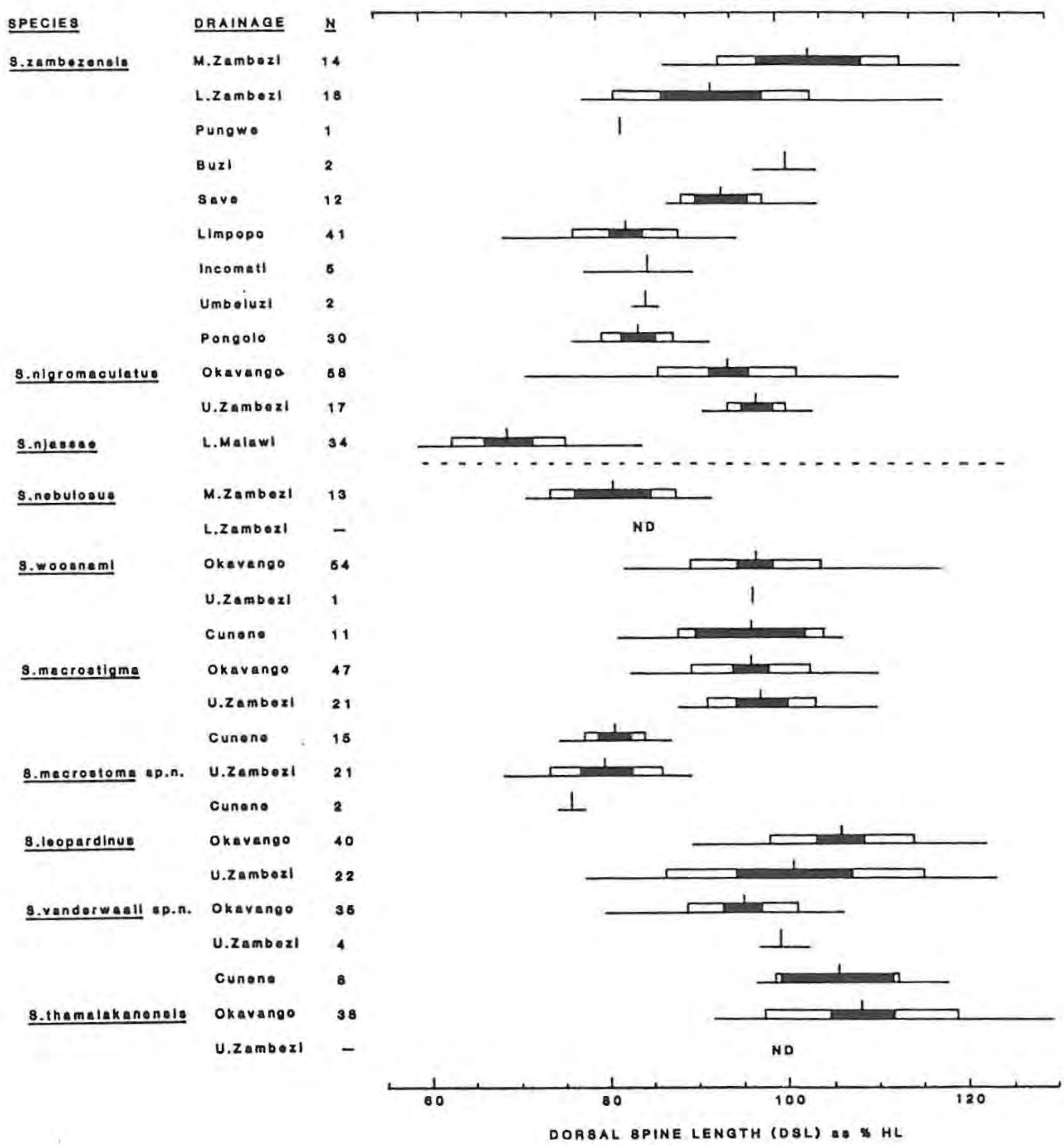

Figure 5.17 Dorsal spine length (DSL) expressed as a percentage of head length. Data given in Appendix Table 2.13.

population of S.macrostigma is closer to S.macrostoma sp.n.

The intra- and interspecific variation of the remaining species are very small, preventing any possible use of this character in their differentiation.

12. Orbit diameter (Figure 5.16)

The most striking feature of these results is the exceptionally large variation that exists in almost all species. The four largest ranges in S.zambezensis, S.woosnami, S.nigromaculatus and S.thamalakanensis account for 90%, 87%, 70% and 68%, respectively, of the total range of all ten species. From the comparison of computer-generated scattergrams, it is evident that this variation is attributable to varying degrees of negative allometry in all species, which, together with consistently small interspecific differences, prevent any possible use of this character as a diagnostic character among the southern African Synodontis.

The relatively small range of the Cunene population of S.vanderwaali sp.n. is almost certainly the result of the very small size of this sample in addition to the very similar standard length of these specimens (Table 4.3).

13. Dorsal spine length (Figure 5.17)

In relation to the measurement of other bony elements, this character shows a particularly large discrepancy in intrapopulational variation among conspecifics. In S.zambezensis, for example, the Lower Zambezi and Limpopo populations have standard deviations that are twice as large and standard errors that are three times as large as the Pongolo population. Although these data are not directly comparable due to their differences in sample size, this discrepancy is still relevant as the samples were taken from a similar size range (Figure 4.3). The large discrepancy in variation between drainages in the proportional measurement of dorsal spine length is also exhibited by

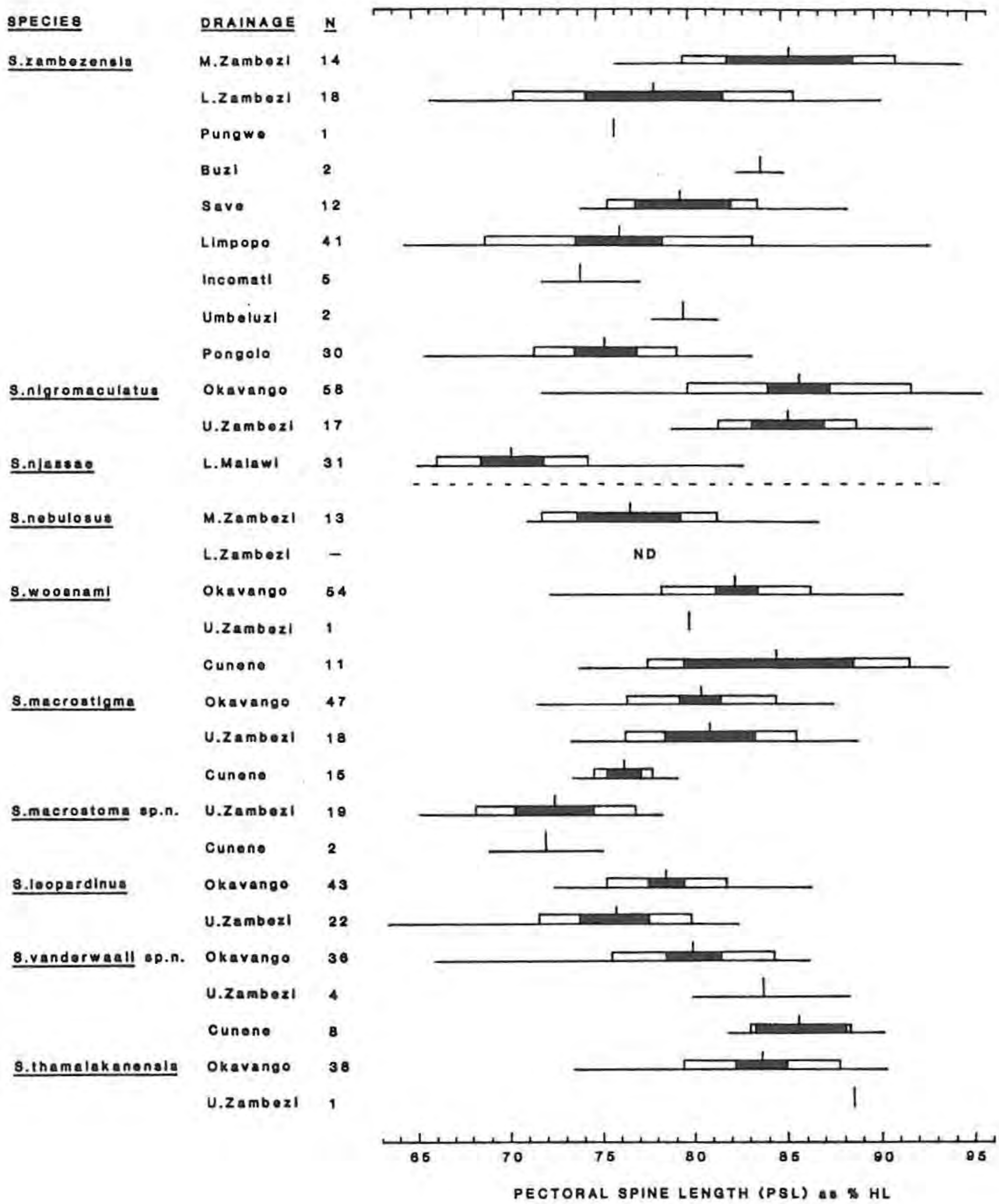

Figure 5.18 Pectoral spine length (PSL) expressed as a percentage of head length. Data given in Appendix Table 2.14.

S.nigromaculatus.

Another feature of this character is the equally large differences in intraspecific variation. S.zambezensis shows the largest such variation with a strongly negative correlation with latitude in population means, the two most widely differing samples in this species showing a strongly significant difference ($t = 7{,}22$, $df = 55$, $p > 0{,}001$).

Among the species of Group I, S.njassae is distinguishable from S.zambezensis and S.nigromaculatus by a generally shorter dorsal spine, and although overlapping in range with S.zambezensis from the adjacent drainage basin (Lower Zambezi) by 5,95%, their means are significantly different even at 0,1% probability ($t = 8{,}86$, $df = 42$, $p > 0{,}001$).

The most noteable difference among the species of Group II is that between the Upper Zambezi and Okavango populations of S.macrostigma and S.macrostoma sp.n., but the range of the Cunene population of S.macrostigma again closely approximates the range for S.macrostoma sp.n.

14. Pectoral spine length (Figure 5.18).

The most noteable feature of this character in comparison with the results of dorsal spine length is the larger overall variation shown by almost all species, but particularly in Group II. The range in S.zambezensis and S.nigromaculatus, for example, account for as much as 30,13% and 23,11% respectively, in comparison with the total range for all ten species of 32,25%. Differentiation among Group II species, however, is still possible as shown by the widely separated 95% limits between S.nigromaculatus and S.njassae.

The interspecific differences among the species of Group II are, on the whole, too small to allow any reasonable differentiation.

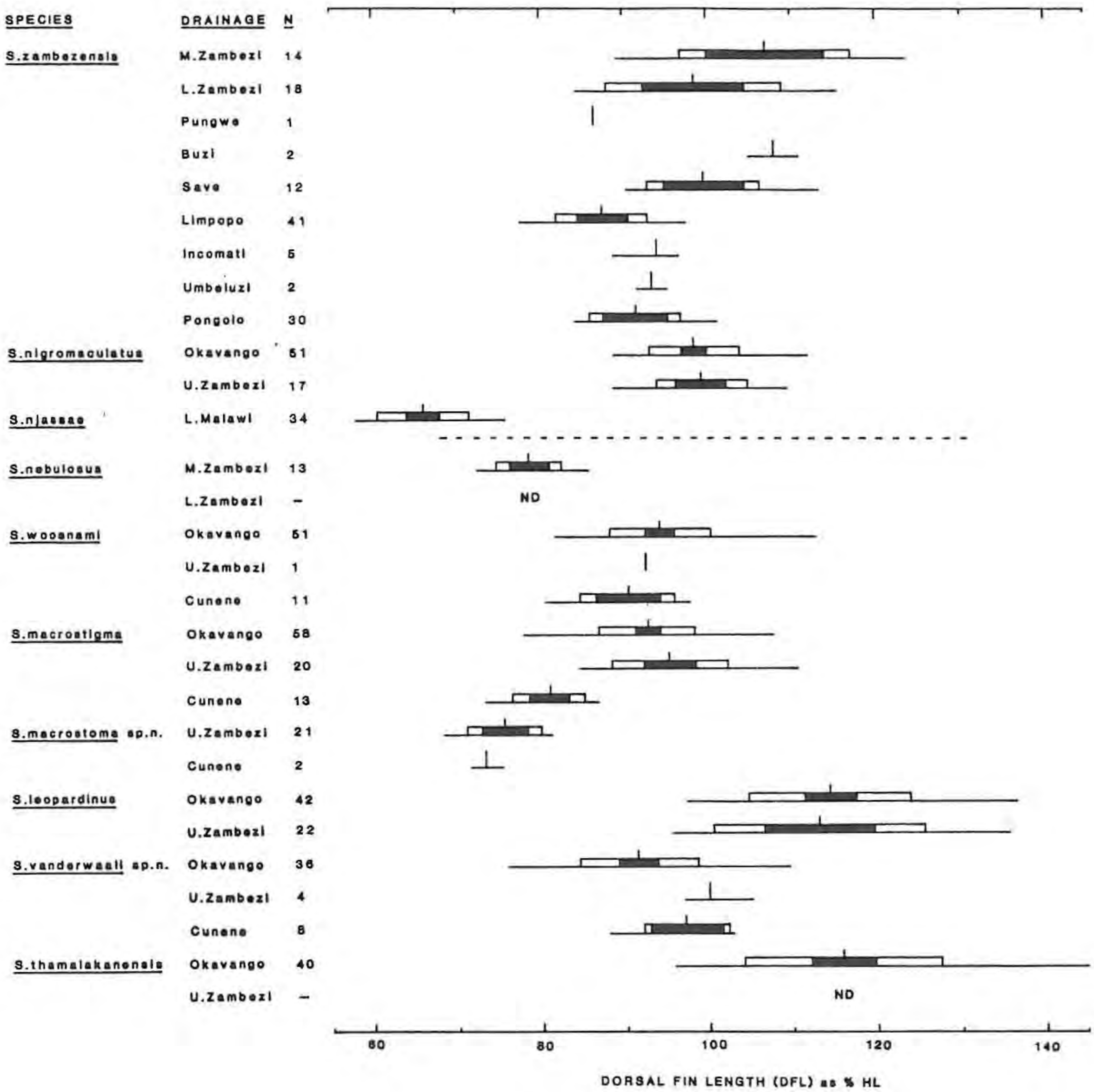

Figure 5.19 Dorsal fin length (DFL) expressed as a percentage of head length. Data given in Appendix Table 2.15.

15. Dorsal fin length (Figure 5.19)

As expected, this character shows a very similar pattern in the distribution of population means to the proportional measurement of dorsal spine length. The intraspecific variation shown by these two characters is also very similar, but the taxonomic value of dorsal fin length is, in general, considerably improved by larger interspecific differences.

The most striking example of the improved diagnostic value of this character is shown in the differentiation of S.njassae from the other two Group I species --- a distinction accentuated by the proportionally longer head length of S.njassae (p.44). Both comparisons are non-overlapping in range with extreme values differing by as much as 13,28% between this species and S.nigromaculatus. The distinction between S.njassae and S.zambezensis is of particular taxonomic importance in its comparison with the Lower Zambezi population of the latter species, where their ranges differ by 8,64%.

The differentiation of S.thamalakanensis and S.leopardinus from S.vanderwaali sp.n. is another example of the improved discriminating power of this character over the proportional measurement of dorsal spine length. The range of S.vanderwaali sp.n., however, overlaps S.leopardinus by 13,95% and S.thamalakanensis by 13,68%. The exceptionally large standard deviation and range in S.thamalakanensis cannot be explained in term of sexual dimorphism, as there is no significant difference between the data of each sex ($t = 0{,}04$, $df = 22$, $p = 0{,}97$).

The differentiation of S.nebulosus from S.macrostigma is marred by the largely overlapping range in the Cunene population of the latter species. A clear trend is discernible, however, between S.nebulosus and S.macrostigma from the adjacent basin of the Upper Zambezi, where their ranges overlap by only 1,13%.

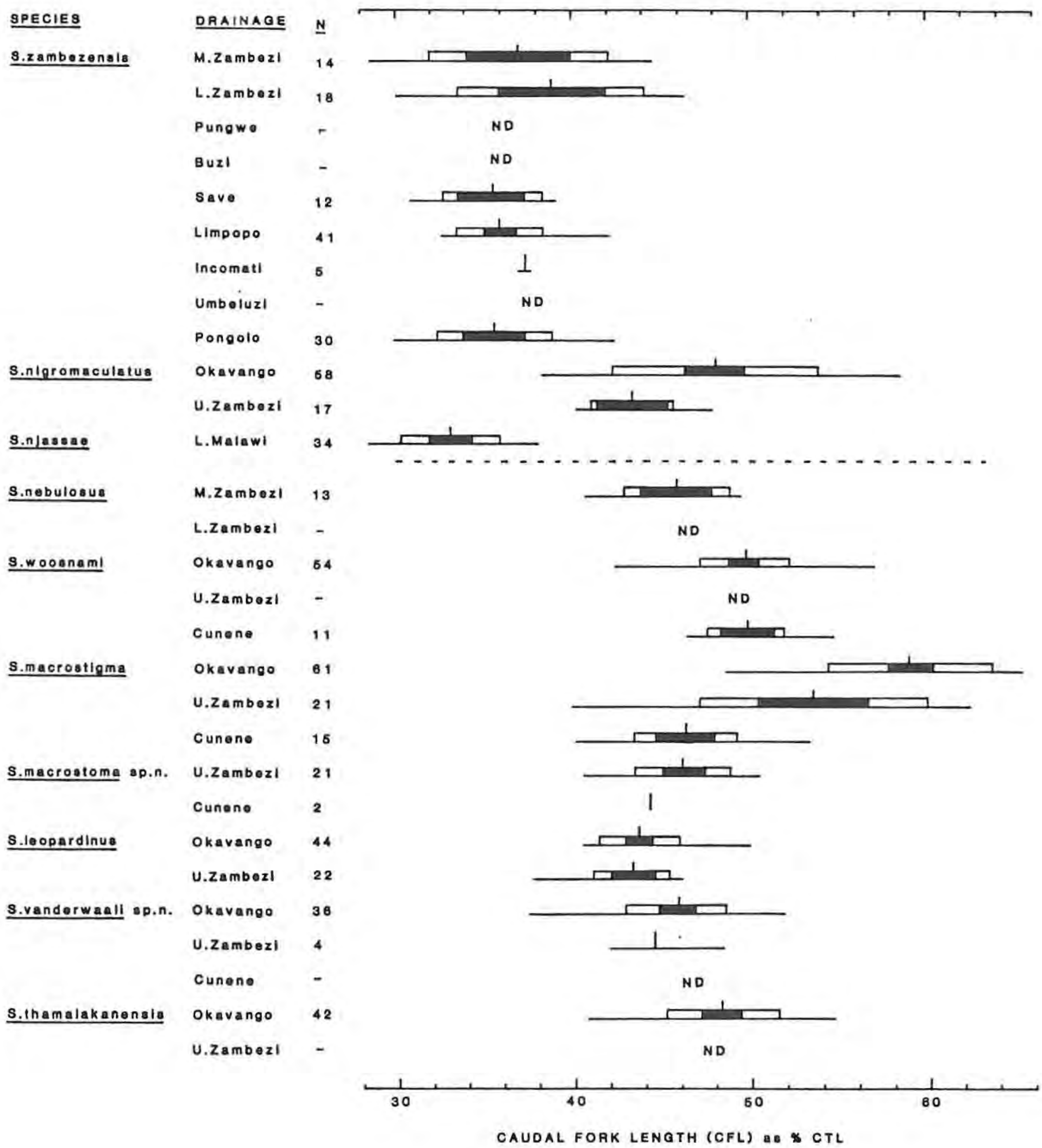

Figure 5.20 Caudal fork length (CFL) expressed as a percentage of caudal total length. Data given in Appendix Table 2.16.

S.macrostoma sp.n. is distinguishable from most other southern African species by a number of unique morphometric and meristic features. The consistently lower values in the proportional measurement of dorsal spine length and dorsal fin length in this species, is a valuable feature of particular relevance in the Upper Zambezi where it coexists with five other Synodontis species.

16. Caudal fork length (Figure 5.20)

The proportional measurement of this character to caudal total length is inversely related to the size (depth) of the caudal fin fork. The only clear trends in these results are shown in the generally larger values of S.nigromaculatus and S.macrostigma in relation to their respective groups.

The distinction between S.nigromaculatus and S.njassae is of particular taxonomic significance as no overlap exists between their ranges. The 95% limits in variation of the Save, Limpopo and Pongolo populations of S.zambezensis are clearly distinct from S.nigromaculatus with an overlap in range of only 4,16%. An increase in both the mean value and overall variation in the Middle and Lower Zambezi populations of S.zambezensis, however, increases this overlap to 8,19%, accounting for almost the entire range of the Upper Zambezi population of S.nigromaculatus. Over two thirds of the S.nigromaculatus specimens examined from the Okavango drainage were nonetheless still distinguishable at a proportional caudal fork length greater than 46,4%.

Apart from S.macrostigma, the intraspecific variations of the other Group II species are generally too large and their interspecific differences too small to allow any meaningful differentiation. The potentially important diagnostic value of this character in S.macrostigma, as indicated by the higher values of the Okavango population, is markedly reduced by the

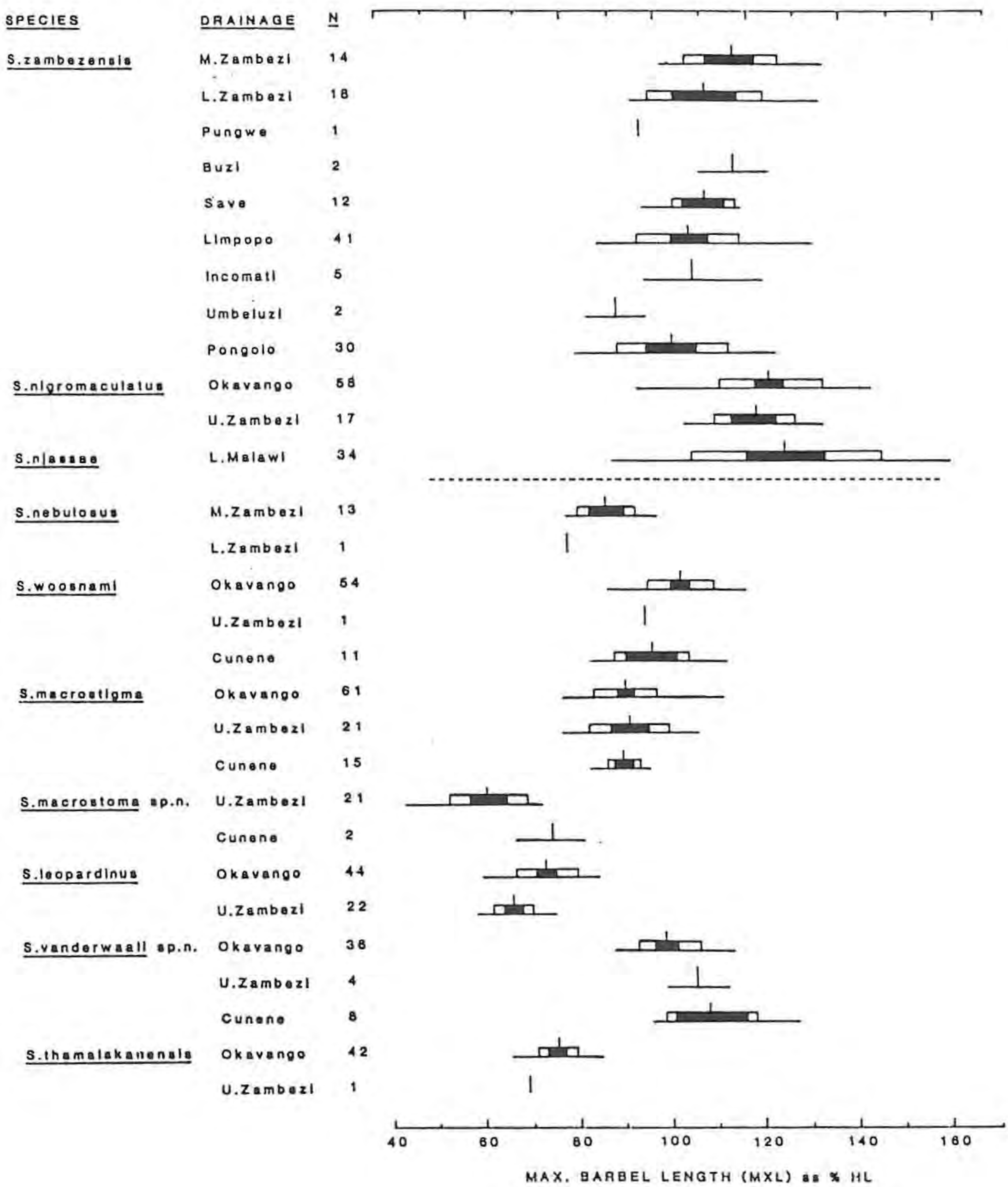

Figure 5.21 Maxillary barbel length (MXL) expressed as a percentage of head length. Data given in Appendix Table 2.17.

exceptionally large intraspecific variation in this species. Differences in caudal fork length are yet still useful in the differentiation of S.macrostigma from the other four species from the Okavango basin.

No sexual dimorphism was detected in this character. Mean values for each sex in the largely varying Upper Zambezi population of S.macrostigma, for example, differ by only 2,22% in comparison to an average of their standard deviations of 6,94%.

17. Maxillary barbel length (Figure 5.21)

Species in Group I are characterized by larger intraspecific variation and generally higher mean values than species in Group II, a trend that can be partly explained by their difference in barbel morphology. Synodontis are predominantly omnivorous, nocturnal bottom-feeders (Bishai & Gideiri, 1965), and, although they possess relatively large eyes in comparison with many other catfishes, the high concentration of taste buds on these barbels suggests an important tactile role for these circumoral appendages. While actively foraging for food the erect barbels are held slightly anteriorly, with the tips of all three pairs making contact with the substrate (pers. obs.). As the maxillary barbels of Group II species are noticeably thinner than those in Group I (Table 4.2), particularly towards the tips, a possible explanation of the above trend may be the greater susceptibility of the barbels in the former group to mechanical abrasion.

The largest intraspecific variation is exhibited by S.zambezensis, exemplified by the slight but progressive reduction in population means with decreasing latitude, where the most widely separated means within this species are not significantly different at the 0,01% level of confidence ($t = 3,50$, $df = 31$, $0,01 < p > 0,001$). The total range in variation of this species largely overlaps other Group I species, preventing any possible differentiation.

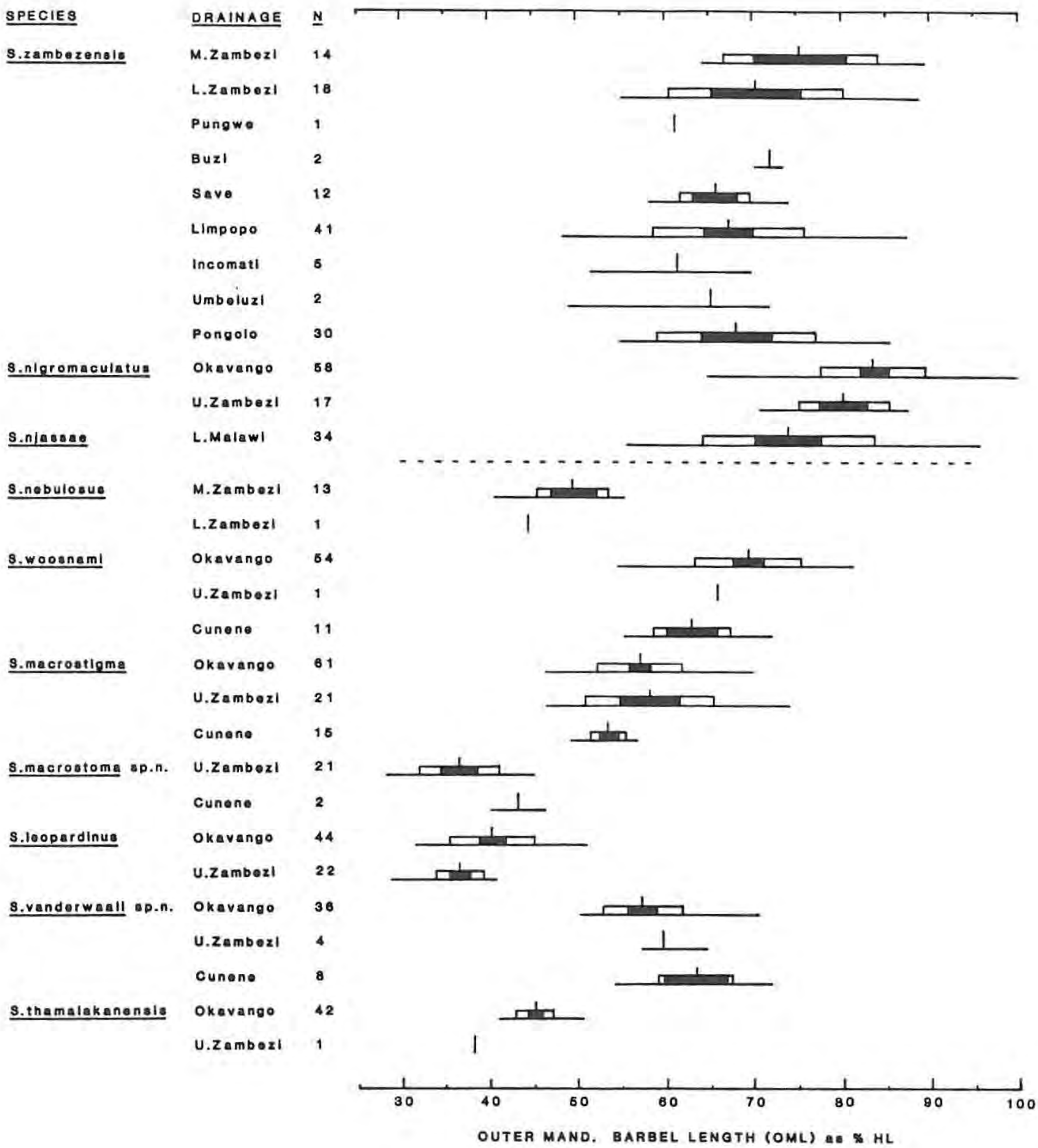

Figure 5.22 Outer mandibular barbel length (OML) expressed as a percentage of head length. Data given in Appendix Table 2.18.

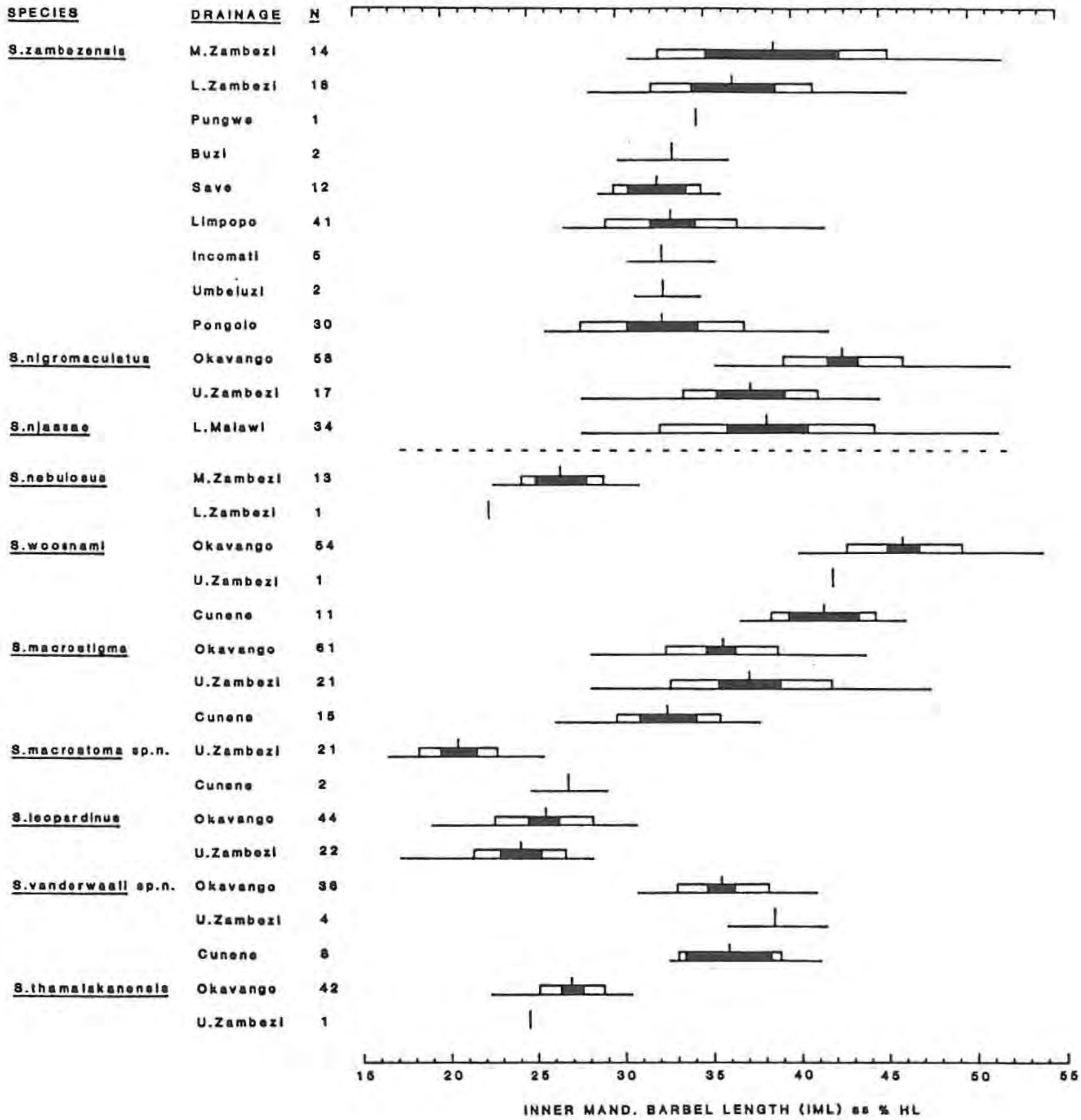

Figure 5.23 Inner mandibular barbel length (IML) expressed as a percentage of head. Data given in Appendix Table 2.19.

In contrast, a number of very distinct differences of taxonomic importance exist among the species of Group II. S.macrostigma, for example, shows consistently higher values than S.macrostoma sp.n. The large combined sample size and small intraspecific variation in S.macrostigma as well as a range that does not overlap with the Upper Zambezi population of S.macrostoma sp.n. would suggest the high diagnostic value of this character. The value of this character in their overall comparison, however, is slightly reduced by the intermediate lengths of the maxillary barbel of the Cunene population of S.macrostoma sp.n. Further specimens are required to confirm this result as the Cunene sample consisted of only two specimens.

Another example of the diagnostic value of maxillary barbel length among species that share a close resemblance to one another is shown in the very distinct difference between S.vanderwaali sp.n., S.leopardinus and S.thamalakanensis.

18. Outer mandibular barbel (Figure 5.22)

In comparison with the previous character, all species show a noticeably larger intraspecific variation, with the combined range in S.zambezensis again overlapping the other species of Group I, so preventing any possible differentiation.

The pattern in distribution of means among the species of Group II is very similar to the previous character resulting in its similar diagnostic value.

19. Inner mandibular barbel length (Figure 5.23)

The very similar pattern in distribution of means shown by the previous two characters is repeated in the proportional length of the inner mandibular barbels. In comparison with the other two sets of barbels, this measurement

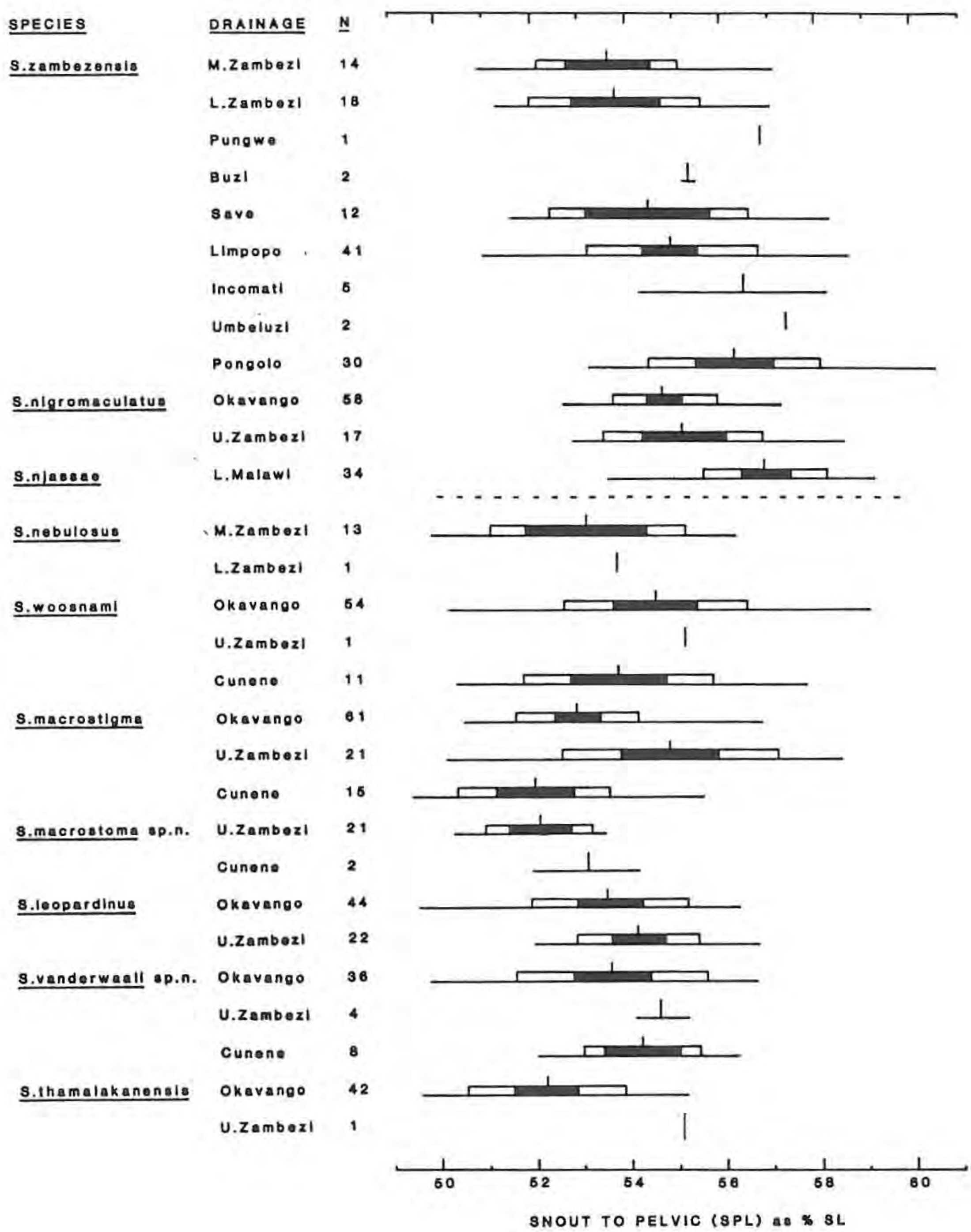

Figure 5.24 Snout to pelvic (SPL) expressed as a percentage of standard length. Data given in Appendix Table 2.20.

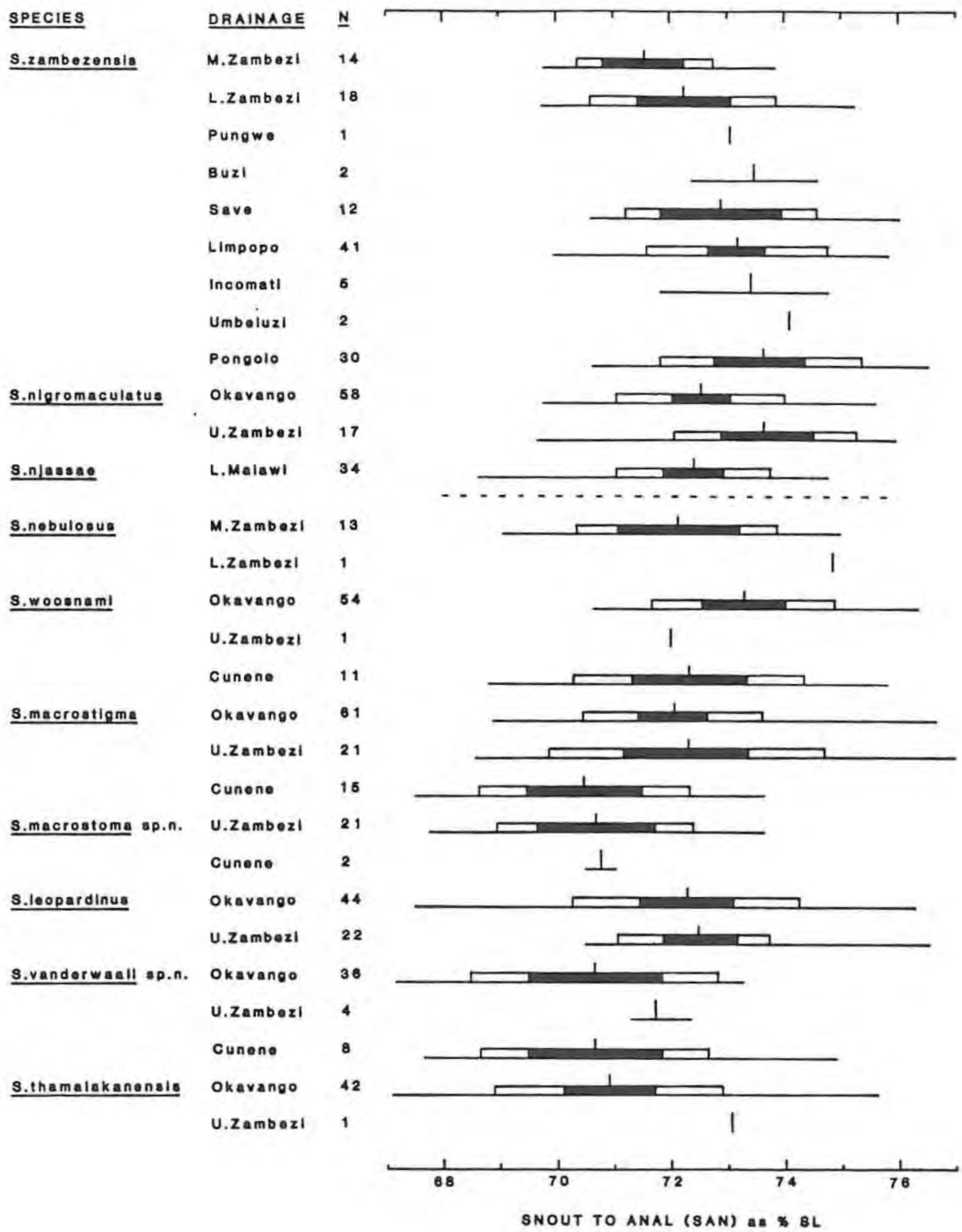

Figure 5.25 Snout to anal (SAN) expressed as a percentage of standard length. Data given in Appendix Table 2.21.

shows the largest intraspecific variation, with the combined range in S.zambezensis again overlapping the other Group I species. Some of the interspecific differences among Group II species shown by lengths of the maxillary and outer mandibular barbels, however, are accentuated in the inner mandibular barbels.

The very distinct difference between S.woosnami from S.leopardinus and S.thamalakanensis, for example, although evident in all barbel lengths is best expressed by the inner mandibular barbels.

Although S.zambezensis and S.nebulosus are easily distinguishable on a number of other characters, hence their initial allocation to separate groups, the difference between these two species is often less marked in juveniles. Consistently significant differences in the lengths of all three barbels throughout the size range studied is therefore a useful diagnostic feature between these two species and of particular relevance to specimens from the Lower Zambezi where they are sympatric.

20. Snout to pelvic, Snout to anal. (Figure 5.24 & 5.25)
The percentage ratio of these two measurements to standard length are considered together as their means show very similar distributional trends. In S.zambezensis both characters are positively correlated with latitude, the overall range in this species accounting for the total variation of the other Group I species.

Intraspecific variation is high in both sets of results but noticeably larger in the snout to anal data. The five species showing the largest intraspecific variation in the snout to pelvic measurement, for example, are S.zambezensis, S.macrostigma, S.woosnami, S.leopardinus and S.nebulosus, which account for 88,1%, 77,3%, 63,8%, 61,7% and 61,1% (respectively) of the total range of all

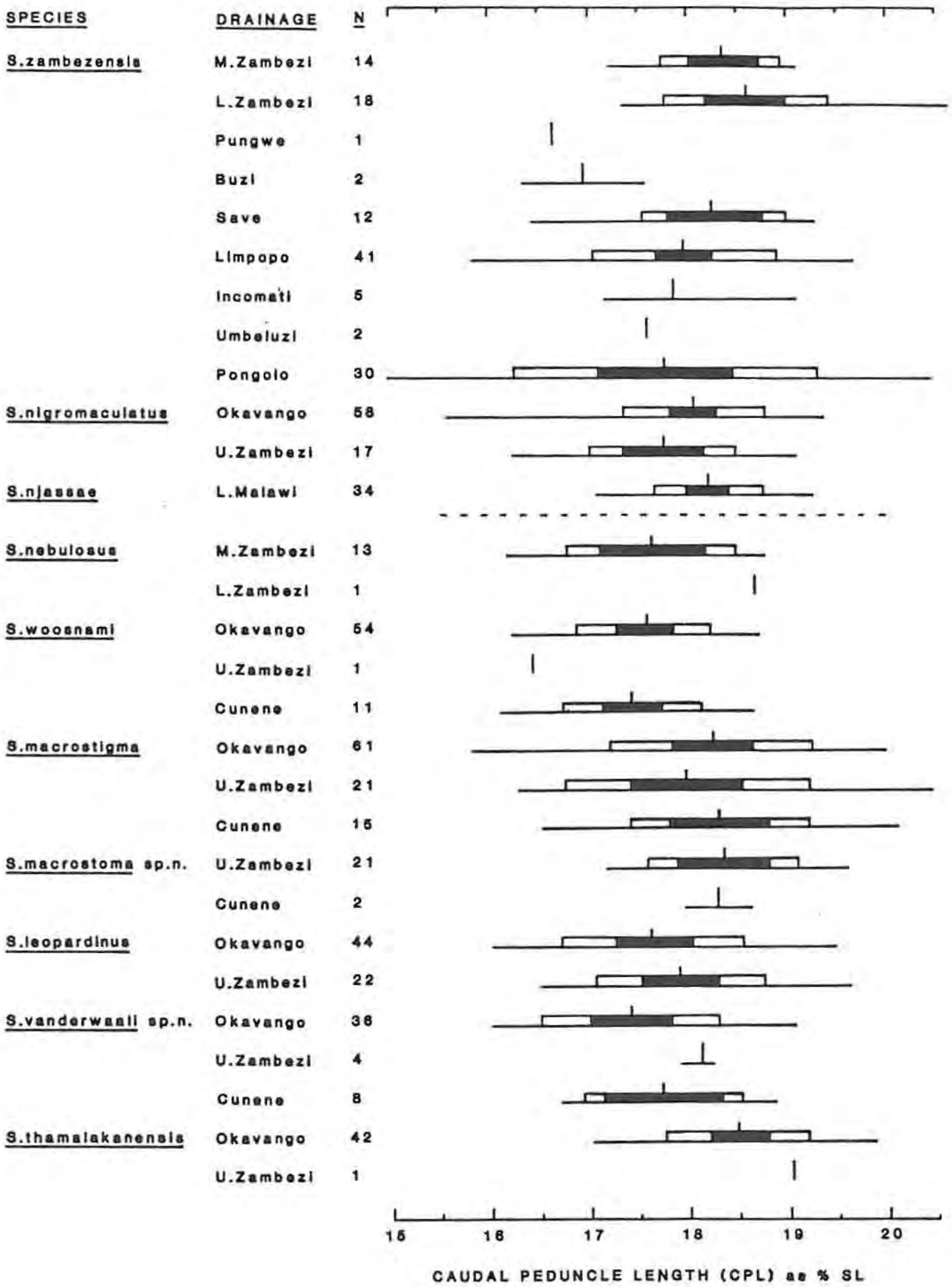

Figure 5.26 Caudal peduncle length (CPL) expressed as a percentage of standard length. Data given in Appendix Table 2.22.

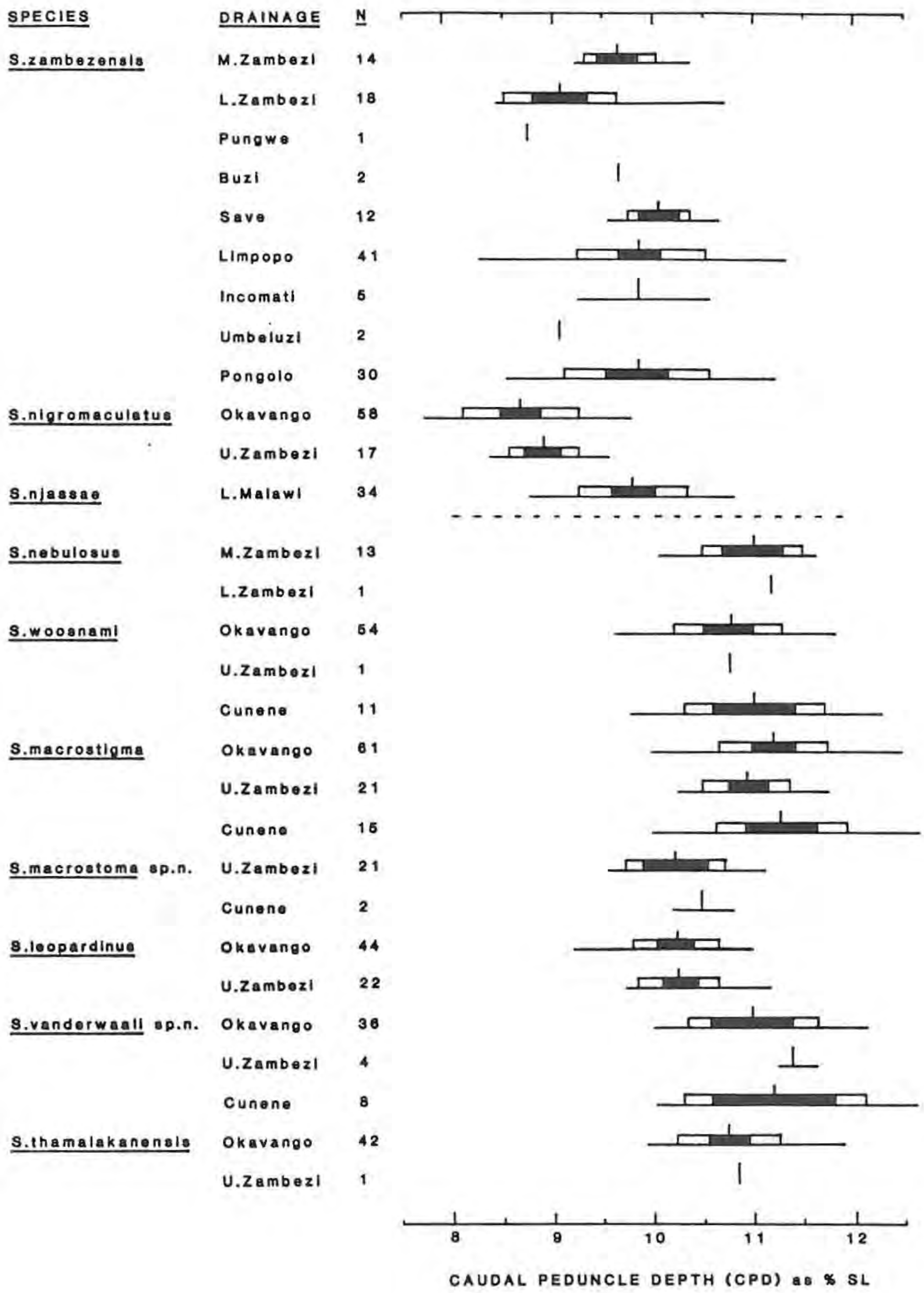

Figure 5.27 Caudal peduncle depth (CPD) expressed as a percentage of standard length. Data given in Appendix Table 2.23.

species. These same species account for 68,4%, 88,7%, 75,7% and 91,7% (respectively) of the total range of all species for the snout to anal measurement.

This large intraspecific variation coupled with consistently small interspecific differences preclude the use of these characters as diagnostic features among the southern African Synodontis.

21. Caudal peduncle length (Figure 5.26)

The most widely separated mean values between the species of Group I and Group II, represented by the Cunene population of S.macrostigma and the Okavango population of S.vanderwaali sp.n., differ by only 1,30% in comparison with an average standard deviation for all species of 1,89%. In addition, the ranges of all but a few species are of very similar size. No diagnostic value of any significance can thus be attributed to this character.

22. Caudal peduncle depth (Figure 5.27).

No clear trend is discernible among the five largest populations of S.zambezensis. The two most widely separated means in this species between the Lower Zambezi and Save populations are significantly different ($t = 5,32$, $df = 28$, $p > 0,001$), although the range of the Limpopo population accounts for the overall variation in this species. The only clear differentiation from this character is between S.nigromaculatus and all the species of Group II, a feature of limited taxonomic value, however, as these two groups are already clearly differentiated by a number of other characters.

Although certain tends are evident among the species of Group II, their largely overlapping ranges reduce the value of this character for diagnostic purposes.

23. Dorsal to adipose (Figure 5.28)

S.zambezensis has the largest intraspecific variation in this very variable

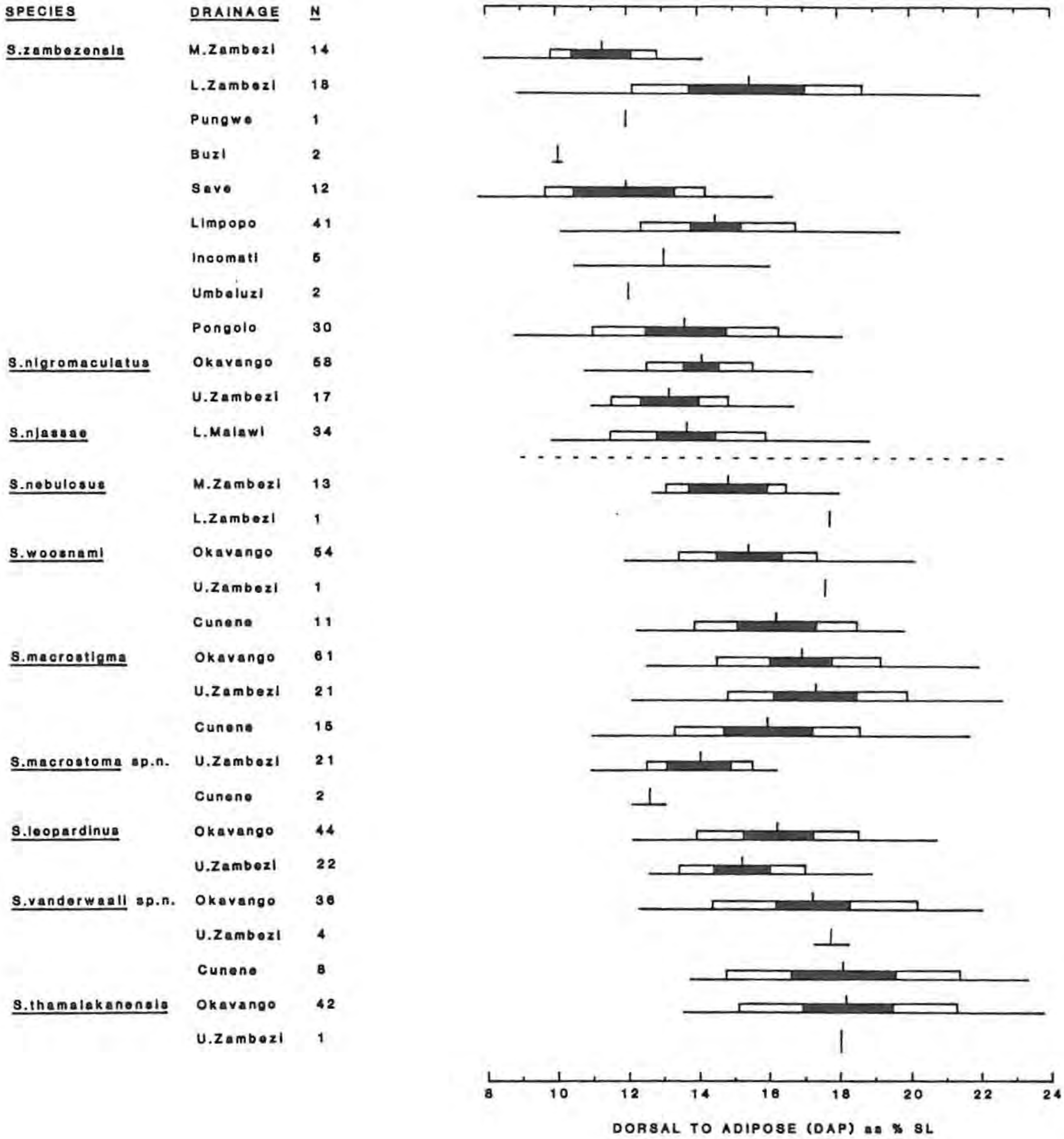

Figure 5.28 Dorsal to adipose (DAP) expressed as a percentage of standard length. Data given in Appendix Table 2.24.

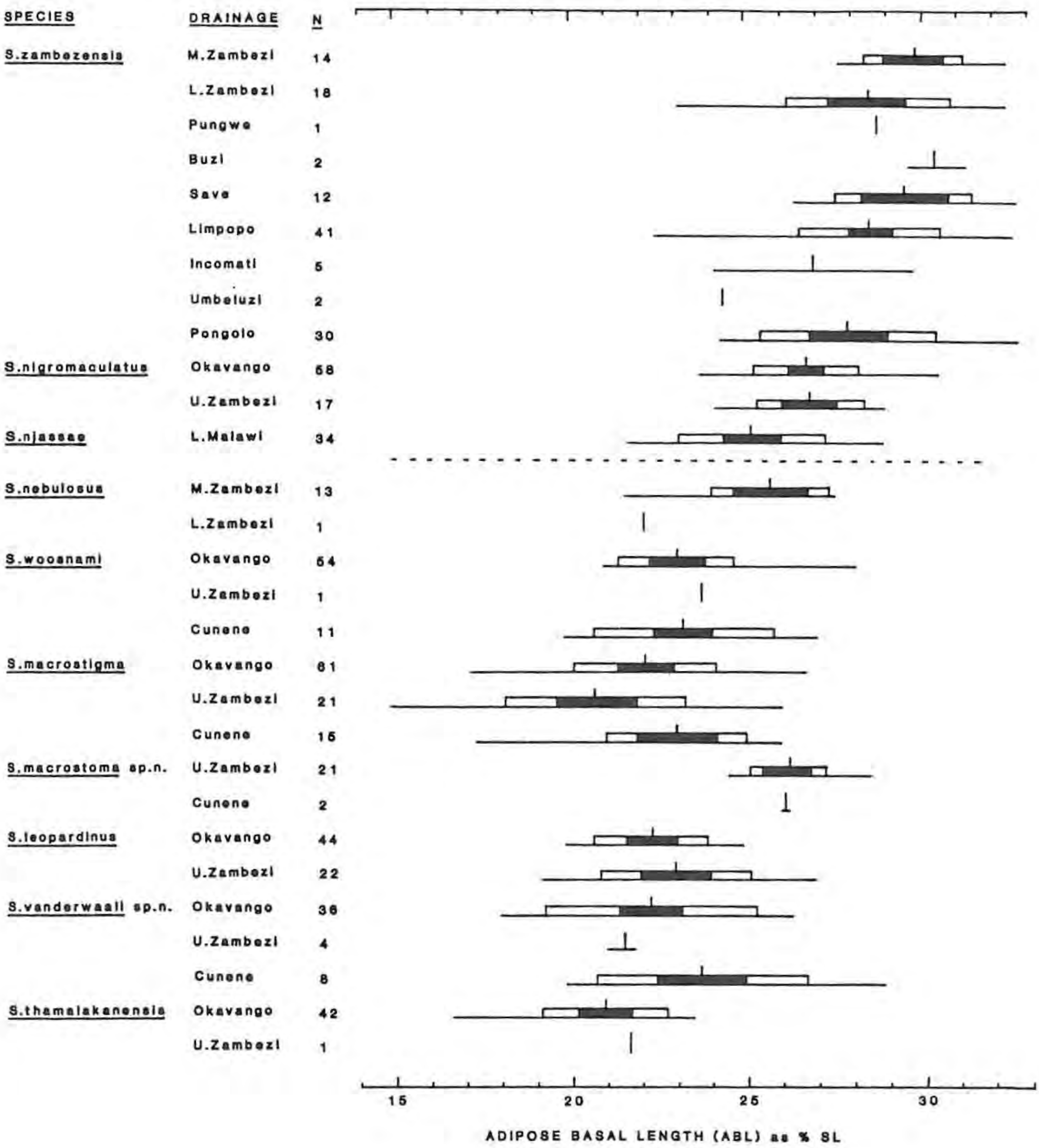

Figure 5.29 Adipose basal length (ABL) expressed as a percentage of standard length. Data given in Appendix Table 2.25.

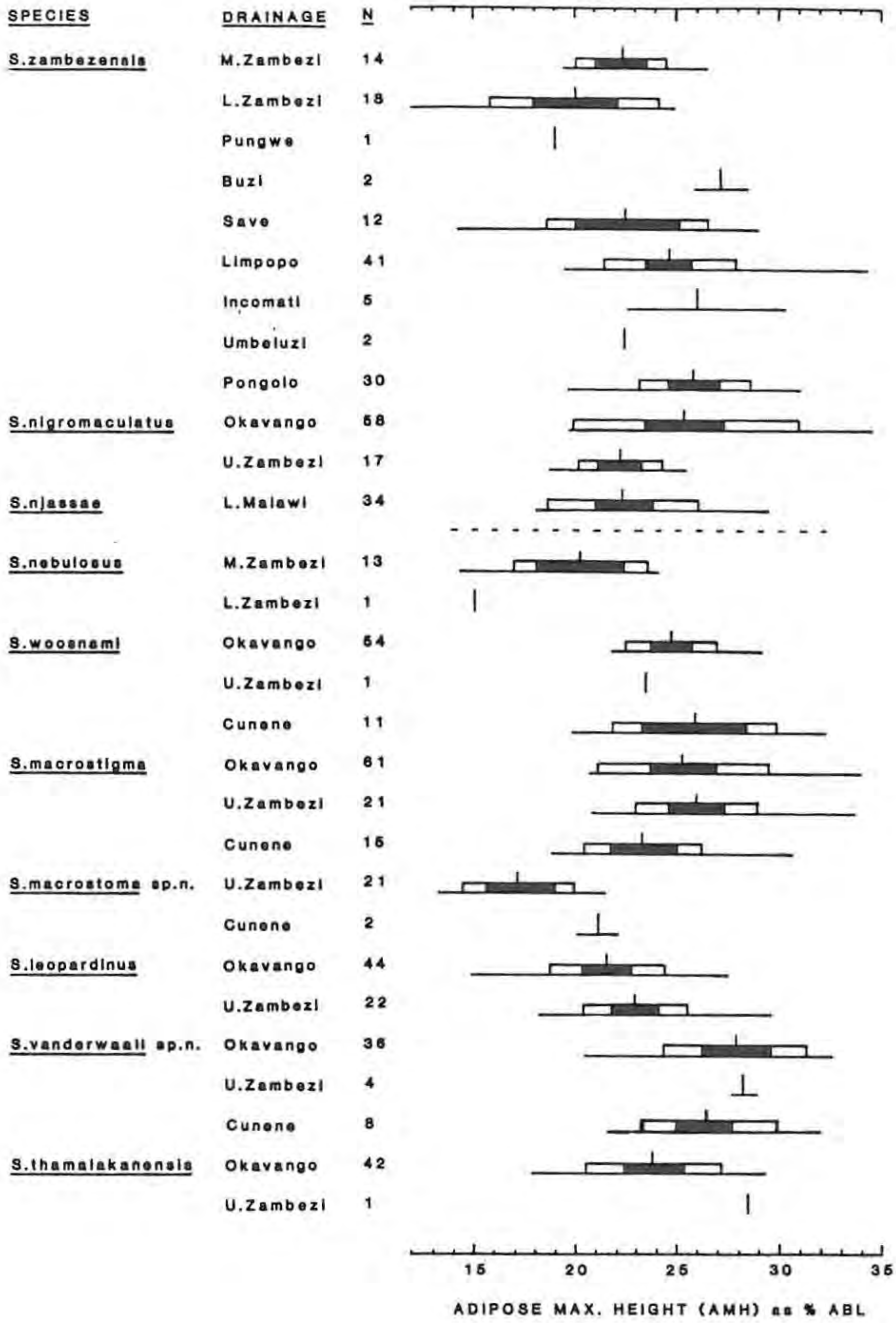

Figure 5.30 Adipose maximum height (AMH) expressed as a percentage of adipose basal length. Data given in Appendix Table 2.26.

character with the two most widely separated mean values between the Middle and Lower Zambezi populations differing by 4,10% in comparison with an average of their standard deviations of 2,40%. The latter population, however, accounts for 94% of the total variation in this species. No differentiation is possible between the remaining two species of Group I.

Although certain trends are discernible among the remaining species, the taxonomic value of their differences in dorsal to adipose measurement is negligible.

24. Adipose basal length (Figure 5.29)

In general, species of Group I are characterized by longer adipose fins than species in Group II with S.njassae, S.nebulosus and S.macrostoma sp.n. holding an intermediate position.

This measurement is characterized by high intraspecific variation and low interspecific differences. There is, however, a significant difference between the Upper Zambezi populations of S.macrostoma sp.n. and S.macrostigma ($t = 8,26$, $df = 27$, $p > 0,001$). An overlap of 2,21% between their ranges, though, markedly detracts from the diagnostic value of this character in distinguishing S.macrostoma sp.n.

25. Adipose maximum height (Figure 5.30)

S.zambezensis shows the largest intraspecific variation in this character. The most widely separated mean values between successive populations in this species are not significantly different, even at 5% probability ($t = 1,74$, $df = 25$, $0,1 < p < 0,05$). Their combined ranges, however, account for the total variation of the two remaining Group I species.

The only evident taxonomic differences between the species of Group II are the

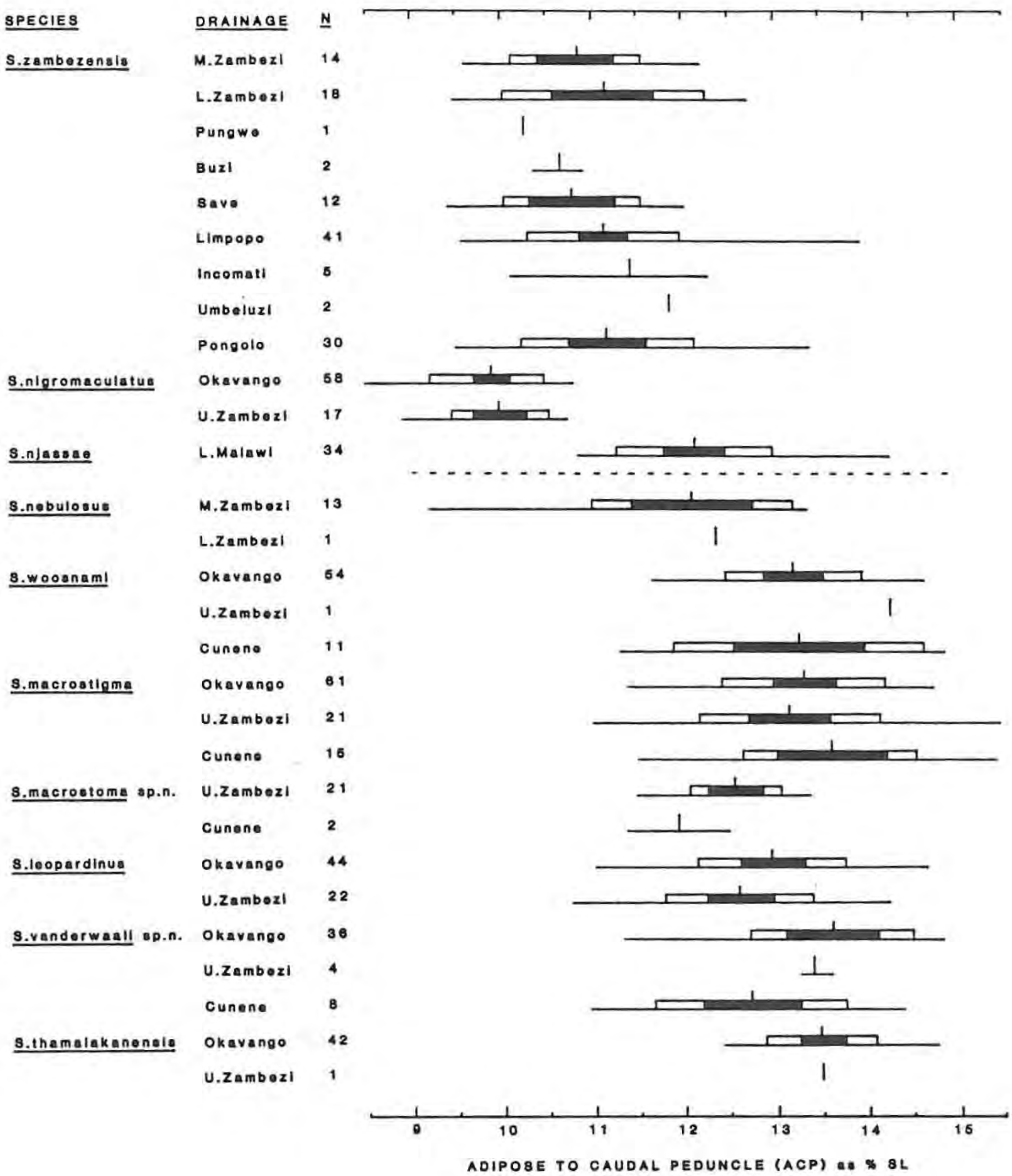

Figure 5.31 Adipose to caudal peduncle (ACP) expressed as a percentage of standard length. Data given in Appendix Table 2.27.

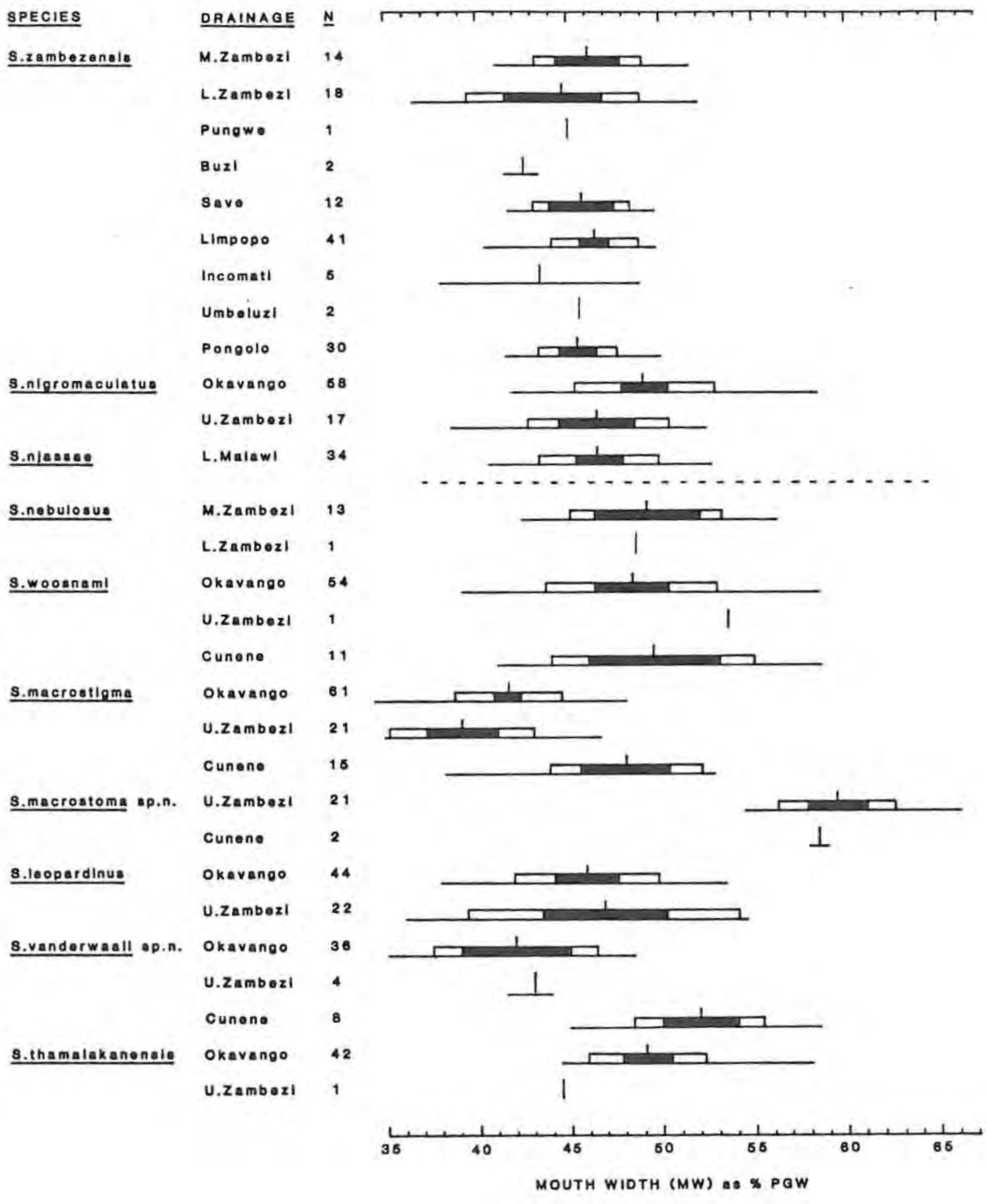

Figure 5.32 Mouth width (MW) expressed as a percentage of pectoral girdle width. Data given in Appendix Table 2.28.

generally smaller values of S.nebulosus and S.macrostoma sp.n., particularly in their comparison with S.macrostigma.

The species with the largest standard deviation, namely S.nigromaculatus, was tested for possible sexual dimorphism in this character. No significant difference, however, exists between the mean values for the two sexes ($t = 1{,}16$, $df = 25$, $p < 0{,}1$).

26. Adipose to caudal peduncle (Figure 5.31)
In general, this measurement is characterized by high intraspecific variation and low interspecific differences. One noticeable exception is the small variation in both populations of S.nigromaculatus, providing a useful distinction between this species and S.njassae. No differences of any diagnostic significance exist between the remaining species.

27. Mouth width (Figure 5.32).
This measurement is expressed as a proportion of pectoral girdle width rather than head length, as the former is taken at a similar orientation to mouth width, so facilitating their comparison.

Mouth width is taken at the outer perimeter of the lips and, as can be expected of a measurement of the 'soft' anatomy, is characterized by a relatively large intraspecific variation. Differentiation between certain Group II species, however, is still possible using this character. No useful pattern is evident in the distribution of mean values in Group I.

S.macrostoma sp.n. has the widest mouth of all southern African Synodontis, providing a useful diagnostic feature, but is particularly relevant in the differentiation of this species from S.macrostigma. The plot of mouth width to pectoral girdle width for these two species illustrates this variation in

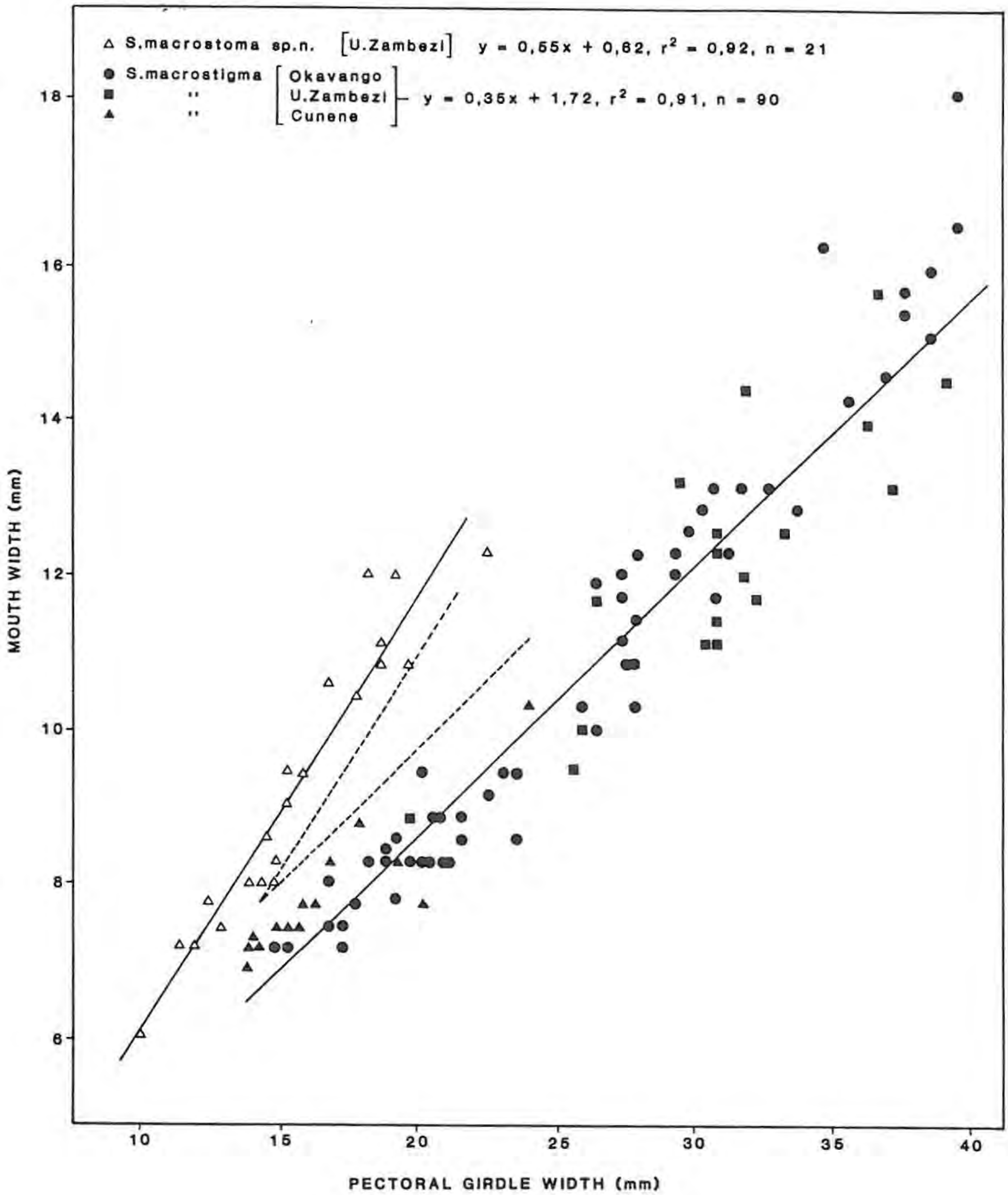

Figure 5.33 Comparison of the regressions of selected populations of S.macrostoma sp.n. and S.macrostigma in the relationship of mouth width to pectoral girdle width.

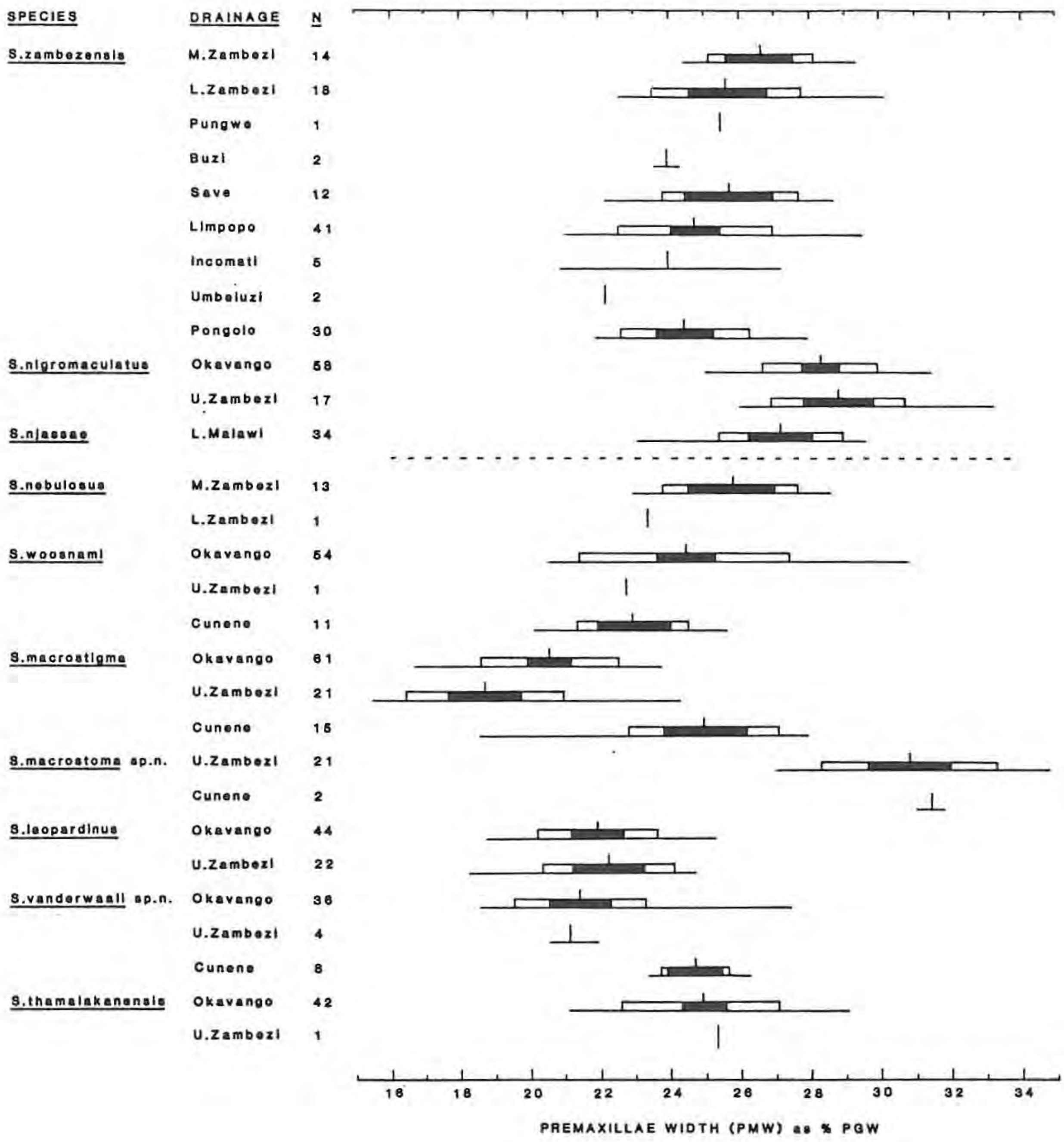

Figure 5.34 Premaxillae width (PMW) expressed as a percentage of pectoral girdle width. Data given in Appendix Table 2.29.

greater detail (Figure 5.33). Strongly divergent slopes of their regressions indicate a corresponding increase in the diagnostic value of this character with size, but, more importantly, the converse is also true. The point of convergence of the 95% confidence limits of the regressions of S.macrostoma sp.n. (0,80) and S.macrostigma (1,12), although not taking into account the decreased scatter of points about the mean with decreasing size, gives an estimate of the smallest measurement of pectoral girdle width at which the expected range in mouth width for each species overlaps by 5%. This value is set at 14,15 mm PGW, which corresponds to an estimated standard length in S.macrostoma sp.n. of 57,3 mm and in S.macrostigma of 50,2 mm.

A very clear distinction also exists between the data of S.macrostoma sp.n. and that of S.leopardinus and S.vanderwaali sp.n. The differentiation between S.macrostoma sp.n. and S.thamalakanensis is obscured by a slight overlap (4,60%) in range.

28. Premaxillae width (Figure 5.34)
As this measurement is taken at the same orientation as mouth width, it is also expressed as a proportion of pectoral girdle width.

The five largest populations of S.zambezensis show a distinctly positive correlation to latitude but with no significant difference between successive samples, indicating the clinal variation of this character. The overall range of this species largely overlaps the ranges of the other two species in this group, so obscuring the slightly broader premaxillae of S.nigromaculatus and S.njassae evident in Figure 5.34.

The most notable difference between the species of Group II is shown in the non-overlapping ranges of the Upper Zambezi populations of S.macrostigma and S.macrostoma sp.n., where the closest values from each differ by 2,77%. The

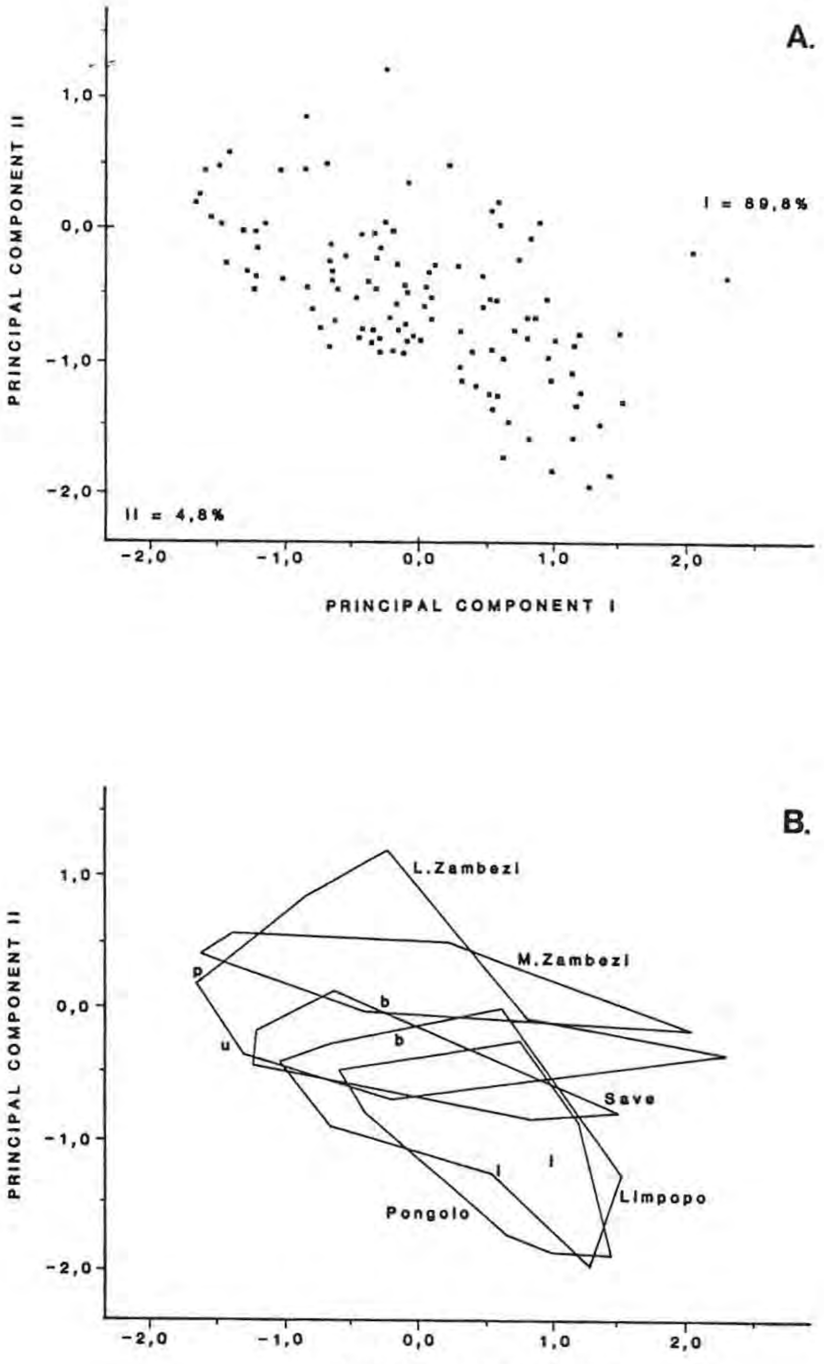

Figure 5.35 A. Individual projection scores on the first two principal components of <u>S.zambezensis</u> from selected populations.
B. Area occupied by individuals of each population shown in the above diagram; circumscribed by joining outlying points. b,i,p,u = individual scores of specimens from Buzi, Incomati,Pungwe and Umbeluzi Rivers, respectively.

higher values of the Cunene population of S.macrostigma, however, decrease the overall difference between these two species. The taxonomic value of this character is nonetheless still evident as their ranges overlap by only 0,89%. S.macrostoma sp.n. has the consistently wider premaxillae among the species of Group II. This distinction is most useful against S.leopardinus whose range differs from the former by 1,76%. S.macrostoma sp.n. is also distinguishable from S.vanderwaali sp.n. above 27,42% with an overlap in range of only 0,41%, and from S.thamalakanensis above 29,09% with an overlap of 2,08%.

Multivariate analysis of S.zambezensis morphometrics

The initial analysis of the preceding 29 proportional measurements have revealed the consistently large intraspecific variation of S.zambezensis. This species also has the largest range in latitudinal distribution. The univariate analysis of the five largest samples of S.zambezensis has shown the progressive shift of the mean in relation to latitude, where the difference between extreme mean values is often significant. The difference between successive populations in some of these characters, however, is not significant, which suggests a clinal variation.

The question now arises whether any of the discontinuities identified in the previous results are sufficient grounds to recognize infraspecific groups, or whether this variation can be explained on the basis of clinal variation in a single species. A principal components analysis of the first 21 morphometric characters (Table 4.1) was used to test these hypotheses.

Correlation between morphometric characters and the first two principal components indicate the strong relation to size in the first component which accounts for 89,8% of the variation in the multivariate system. The plot of individual projection scores on the first two principal components (Figure

Table 5.1 Frequency distribution of vertebral counts, pleural ribs and anal pterygiophores.

			Total vertebrae						Precaudal vertebrae				Caudal vertebrae						Preanal vertebrae						Pleural ribs				Anal pterygiophores			
Species	Drainage	n	37	38	39	40	41	42	11	12	13	14	25	26	27	28	29	30	19	20	21	22	23	24	8	9	10	11	10	11	12	13
<u>S.zambezensis</u>	M.Zambezi	20				10	10			8	11	1		1	4	11	4				1	17	2			2	14	3	2	13	5	
	L.Zambezi	13			2	6	5			11	2				3	6	4			1	4	7	1			1	6	6		10	3	
	Buzi	2				2				1	1				1	1					1	1					1	1		1	1	
	Save	20			6	11	3		2	15	3				4	11	5				8	14					16	4		10	10	
	Limpopo	25		2	12	11			1	15	9			2	17	6				2	8	15				2	19	4		14	11	
	Incomati	10			2	8			1	7	2				2	8					2	8					10			3	7	
	Umbeluzi	4				4				1	3				3	1					1	3					4			2	2	
	Pongolo	25			6	11	3			19	5	1			10	12	3				11	12	2			2	18	5		15	10	
<u>S.nigromaculatus</u>	Okavango	40				25	12	3	9	20	10	1			4	23	12	1			11	18	10	1		1	23	16	12	20	8	
<u>S.njassae</u>	L.Malawi	23			5	16	4		8	15						9	14				16	7				3	20		9	14		
<u>S.nebulosus</u>	M.Zambezi	11	5	6					3	8			4	5	2					9	2					11			1	4	6	
<u>S.woosnami</u>	Okavango	30	2	22	6				12	18			3	15	12				1	21	8					14	16		3	8	19	
<u>S.macrostigma</u>	Okavango	30	7	18	5				6	23	1		6	14	9	1			1	13	16				3	22	5			20	10	
<u>S.macrostoma</u> sp.n.	U.Zambezi	21	13	8						18	3		7	14						14	7					15	6		6	12	3	
<u>S.leopardinus</u>	Okavango	31		25	6					24	7		5	22	4					7	24					17	14		4	21	6	
<u>S.vanderwaali</u> sp.n.	Okavango	25		10	15				1	12	12		3	13	7	2				5	19	1				17	7	1	1	8	14	2
<u>S.thamalakanensis</u>	Okavango	30		9	20	1				24	6		3	12	15					16	14					23	7			7	19	4

5.35A) can thus be viewed as having size increasing from left to right on the horizontal axis. The second component accounts for 4,80% of the variation, with diagonal trends reflecting changes in the morphology with growth (Humphries et al., 1981). The cluster of individual scores representing each population is identified by joining outlying points (Figure 5.35B). Besides the horizontal component of each population which is indicative of its size range, the five largest populations all show a similar diagonal component suggesting analogous allometric trends in these morphometric characters. Another observable trend is the generally lower vertical scores of individuals from lower latitudes, where the area occupied by the most geographically separated populations of the Middle Zambezi and Pongolo do not overlap. The proportional area overlapped by successive populations, however, is very large.

These results would thus suggest that the large intraspecific variation in S.zambezensis is a product of clinal variation in morphology, with no obvious discontinuities in variation throughout this species' large latitudinal range.

SKELETAL MERISTICS

In general, species in Group I are characterized by 2 more vertebrae than species of Group II, with a particularly clear distinction between S.nigromaculatus and the latter group (Table 5.1). The range in S.zambezensis varies from 38-40 vertebrae in the Limpopo population and from 40-41 vertebrae in the Middle Zambezi population, the modal number for all eight populations, however, remaining constant at 40 vertebrae. The largely overlapping ranges in the remaining Group I species excludes any possible use of this character in

Table 5.2 Frequency distribution of pectoral and anal fin rays.

Species	Drainage	n	Pectoral Rays 7	Pectoral Rays 8	Pectoral Rays 9	Anal Rays n	Unbranched 4	Unbranched 5	Unbranched 6	Branched 7	Branched 8	Branched 9	Branched 10
S.zambezensis	M.Zambezi	26		8	18	20		20			6	6	8
	L.Zambezi	19		8	11	13		8	5		5	7	1
	Pungwe	1		1		1		ND				1	
	Buzi	2		2		2		1	1		1	1	
	Save	43		36	7	20		16	4		8	12	
	Limpopo	41		36	5	25		14	11		6	19	
	Incomati	5		3	2	10		10			7	3	
	Umbeluzi	4		3	1	4		3	1		1	3	
	Pongolo	30		20	10	25		9	16	2	6	17	
S.nigromaculatus	Okavango	98		55	43	40	9	21	10	1	31	8	
S.njassae	L.Malawi	34		12	22	23		18	5		18	5	
S.nebulosus	M.Zambezi	13		12	1	11		10	1	2	7	2	
S.woosnami	Okavango	54	38	16		30		22	8	3	20	7	
S.macrostigma	Okavango	61	54	7		30	2	20	8	2	15	13	
S.macrostoma sp.n.	U.Zambezi	21		20	1	21		19	2	2	19		
S.leopardinus	Okavango	44		43	1	31		28	3		15	14	2
S.vanderwaali sp.n.	Okavango	36	2	34		25		20	5	2	10	13	
S.thamalakanensis	Okavango	42	1	41		30		15	15		23	7	

their diagnosis.

The only difference of diagnostic importance among Group II species is that of S.macrostoma sp.n., where less than 38 vertebrae were recorded in 62% of the sample, in comparison with 38 or more vertebrae in S.leopardinus, S.vanderwaali sp.n. and S.thamalakanensis. Taking the relatively small sample size of these data into account, in addition to the potentially large variation exhibited by S.zambezensis, their difference of only one vertebra must be considered an unreliable diagnostic feature.

The above trends are reflected in the results of the other vertebral counts where Group I possess an average of two more caudal vertebrae, one more preanal vertebra and one more pleural rib than Group II. The species within each group, however, have very similar ranges, and no differentiation is discernible of any taxonomic importance.

The similar modal number of 12 precaudal vertebrae and the relatively large variation exhibited by most species in the number of anal pterygiophores also exclude these two characters as possible diagnostic features. Skeletal meristics, in general, offer very little in the diagnosis of these southern African species except to identify groups that are already separable on a number of other morphometric and meristic characters.

FIN RAYS

Only the largest sample of each species is examined in this preliminary analysis, with the exception of S.zambezensis from whose data an estimate of the expected intraspecific variation was determined (Table 5.2).

Seven dorsal fin rays were recorded in all 574 specimens without exception. Interestingly, Poll (1971: 237) recorded the dorsal fin rays of the S.zambezensis type series as ranging from seven to nine. This confusing anomaly is explained by the presence of two deformed rays in one of the paralectotypes (ZMB 3115), the nine rays in this specimen stemming from seven distinct bases which are clearly distinguishable in radiographs.

Seventeen principal caudal rays were recorded in all species without exception.

The range of pectoral fin rays is standard at eight to nine in all Group I species. The modal number in Group II varies between seven and eight, with nine rays recorded by one specimen each in S.nebulosus and S.macrotoma sp.n. The only species showing sufficient difference in this character to warrant mention is that of S.macrostigma and to a lesser extent S.woosnami. 89% of the S.macrostigma sample and 70% of the S.woosnami sample are distinguishable from S.nebulosus, S.macrostoma sp.n. and S.leopardinus by having less the eight pectoral rays.

The number of unbranched anal rays differs little from a modal number of five in all species, offering no diagnostic value in this character. The branched rays in this fin similarly differ little from a modal number of eight to nine.

BARBEL MORPHOLOGY

In the statistical analysis of barbel branching only the largest samples of each species are compared.

Maxillary barbels.

A comparative summary of maxillary barbel features is given in Table 5.3.

Table 5.3 A comparative summary of maxillary barbel features.

Species	Leading edge	Basal membrane: Presence	Basal membrane: Max. width (ratio of barbel width)	Basal membrane: Colour
S.zambezensis	smooth	present (narrow but distinct)	< 1/2	slightly darker than barbels
S.nigromaculatus	smooth	usually absent (v. narrow & indistinct in some)	< 1/3	slightly more yellow than barbels
S.njassae	smooth	usually absent (v. narrow & indistinct in some	< 1/3	similar to or slightly darker than barbels
S.nebulosus	smooth	absent or indistinct	< 1/3	similar to or slightly darker than barbels
S.woosnami	usually smooth (papillae: v.short, widely-spaced in a few specimens)	present (narrow)	1/3 - 3/4	darkly pigmented
S.macrostigma	papillose (papillae: widely-spaced moderately to very short but distinct)	present	1/2 - 1	darkly pigmented
S.macrostoma sp.n.	smooth	absent	-	-
S.leopardinus	usually smooth (papillae: v.short, squat, closely-packed in a few specimens)	present (narrow)	1/4 - 1/2	darkly pigmented
S.vanderwaali sp.n.	smooth	present (narrow)	1/4 - 1/2	darkly pigmented
S.thamalakanensis	strongly papillose (papillae: numerous, prominent, widely-spaced, 1/3-4/5 x barbel width in length, distributed singly or in couplets)	present (moderately to very wide)	4/5 - 8/5	darkly pigmented

Table 5.4 Frequency distribution of branching on the outer mandibular barbels.

Species	Drainage	n	1° branches												1° branches with 2° branching									2° branches / 1° branch						
			3	4	5	6	7	8	9	10	11	12	13	14	0	1	2	3	4	5	6	7	8	0	1	2	3	4	5	6
<u>S.zambezensis</u>	Limpopo	41		7	32	2									41									41						
<u>S.nigromaculatus</u>	Okavango	65		1	18	17	19	7	2	1					65									65						
<u>S.njassae</u>	L.Malawi	27		6	15	5	1								27									27						
<u>S.nebulosus</u>	M.Zambezi	13					1	1	2	4	3	1	1		2	3	5	2	1					2	10	1				
<u>S.woosnami</u>	Okavango	54	1	2	4	8	24	10	3	2					51	3								51	3					
<u>S.macrostigma</u>	Okavango	51					3	10	17	13	7	1			18	11	9	5	4	2	1	1		18	23	6	1	1	1	1
<u>S.macrostoma</u> sp.n.	U.Zambezi	21	2	8	5	4	2	1							19	2								19	2					
<u>S.leopardinus</u>	Okavango	49			1	7	11	17	5	7	1					12	20	17							43	5	1			
<u>S.vanderwaali</u> sp.n.	Okavango	36			2	12	15	3	3	1					12	15	4	4	1					12	18	6				
<u>S.thamalakanensis</u>	Okavango	41				2	6	4	7	10	6	4	1	1	2	5	15	10	2	2	2	2	1	2	26	8	3	1	1	

The most distinct differences of taxonomic significance in this feature are the strongly papillose leading edge and broad basal membrane of S.thamalakanensis in comparison with the usually smooth leading edge and narrow basal membranes of S.leopardinus and S.vanderwaali sp.n. The row of papillae in S.thamalakanensis may also extend across the antero-ventral rim of the lips in specimens where this ornamentation is moderately to well developed.

The complete absence of any basal membrane in S.macrostoma sp.n. is a very useful diagnostic feature in its differentiation from S.macrostigma, in which the basal membrane is always present, distinct and darkly pigmented. The difference in maxillary barbel morphology between S.macrostigma and S.nebulosus is less distinct than the above example yet is still an easily identifiable diagnostic feature between these two morphologically similar species.

A layer of mucus is exuded over the body in most fishes in response to the stress of capture. In Synodontis, this layer may be as much as 1 mm thick in adult specimens and is particularly noticeable on the head. On preservation, this (usually) opaque layer often conceals the row of small papillae on the leading edge of the maxillary barbels in certain species. Specimens of S.macrostigma with less well developed maxillary papillae are particularly good examples, the detection of these features often requiring removal of the overlying mucus with a finely-pointed instrument.

Outer mandibular barbels

The initial dichotomy in Farquharson's (1969) key to the southern African Synodontis is based on the branching of the outer mandibular barbels: the first group (A) having uniramous, simple, filamentous branches: and the second group (B) having biramous, compound, tuberculous branches. As previously mentioned

(p. 41) this division is retained, but the analysis of outer mandibular barbel branching in this study has shown certain of the above-mentioned criteria used by Farquharson (1969) to be incorrect or, at the least, ambiguous.

Farquharson (1969) did not define the terms "uniramous" and "biramous" as used in the above couplet. In the present study biramous refers to the existence of two sets of branches along the length of the barbel, set at two different planes. Uniramous thus refers to a single set in one plane. The uniramous condition was recorded in all species examined from Group I (comparable to Farquharson's (1969) Group A) but both the biramous and uniramous condition was recorded among the species of Group II (Group B). The biramous condition in S.woosnami is often not immediately obvious, as the inner set of branches may be very small, particularly in juveniles.

It is not clear what Farquharson (1969) means by "simple" as opposed to "compound", but from the illustration depicted in Figure 3 (p. 6/7) one must assume he is referring to the absence or presence of secondary branches. In accordance with the above description, secondary branching is absent from all Group I species, but the converse is not applicable to Group II. Six of the seven species in Group II all have some specimens in which secondary branching is lacking and in S.woosnami and S.macrostoma sp.n. this condition accounts for more than 90% of the sample (Table 5.4). S.leopardinus is the only species in Group II that does not have secondary branching.

The third criterion in Farquharson's (1969) division concerns the form of the outer mandibular barbel branches. All Group I species have filamentous branches. The branches of S.woosnami, a species of Group II, are noticable thicker than those of Group I but are also characterized by a progressive reduction in diameter towards a pointed tip and as such cannot be described as "tuberculous".

Table 5.5 Frequency distribution of branching on the inner mandibular barbels.

			1° branches									1° branches with 2° branching												2° branches / 1° branch						
Species	Drainage	n	5	6	7	8	9	10	11	12	13	0	1	2	3	4	5	6	7	8	9	10	11	0	1	2	3	4	5	6
S.zambezensis	Limpopo	41		2	7	19	12	1				1	2	5	21	11	1							1	40					
S.nigromaculatus	Okavango	65			2	14	19	24	4	2			1	7	16	25	12	4							60	4	1			
S.njassae	L.Malawi	27	1	10	11	4	1					14	2	4	5	2								14	12	1				
S.nebulosus	M.Zambezi	13			1	1	2	4	3	1	1			1	2	2	5	2	1						12	1				
S.woosnami	Okavango	54			1	4	11	16	15	6	1	24	15	12	1	1	1							24	28	2				
S.macrostigma	Okavango	51					3	8	23	11	6			1	5	12	13	15	3	1	1				43	3	2	1	1	1
S.macrostoma sp.n.	U.Zambezi	21			3	7	8	3				12	4	2	1	1	1							12	8	1				
S.leopardinus	Okavango	49				2	13	20	11	3					1	4	11	24	5	3	1				42	5	1	1		
S.vanderwaali sp.n.	Okavango	36				1	2	10	20	2	1			1	1	10	12	7	2	2	1				31	3	1	1		
S.thamalakanensis	Okavango	41					5	17	12	4	3				1	2	8	11	9	6	2	1	1		29	8	2	1	1	

Two aspects of outer mandibular barbel branching that are applicable in describing the above-mentioned dichotomy are the length and thickness of the primary branches. Group I species have very thin, filamentous branches, the longest of which is more than five times the diameter of the barbel stem; while Group II have relatively thick branches, of which the longest is less than three times the diameter of the barbel stem.

The form of outer mandibular barbel branching also has taxonomic implications at the species level. S.macrostoma sp.n., for example, is identified by its low number of (predominantly unbranched) primary branches which range from three to seven and, is distinguishable from those of S.macrostigma by six or less. S.macrostigma in comparison have seven to twelve primary branches with 65% of the sample showing secondary branching and with up to six secondary branches on each primary branch. In addition, the very low probability of secondary branching in S.woosnami is a useful diagnostic feature in its comparison with most of the other Group II species and in particular with S.leopardinus.

Inner mandibular barbels

The above-mentioned diffences in outer mandibular barbel branching between the species of Group I and Group II do not exist for the inner set of barbels. Interspecific differences within these groups, however, do allow a certain degree of differentiation.

S.woonami and S.macrostoma sp.n. are identified by their lower number of secondary branches. Although the range of this character is overlapping in all Group II species, 72% of the sample of S.woosnami and 77% of S.macrostoma sp.n. are still distinguishable from other Group II species in having a maximum of one primary branch with secondary branches.

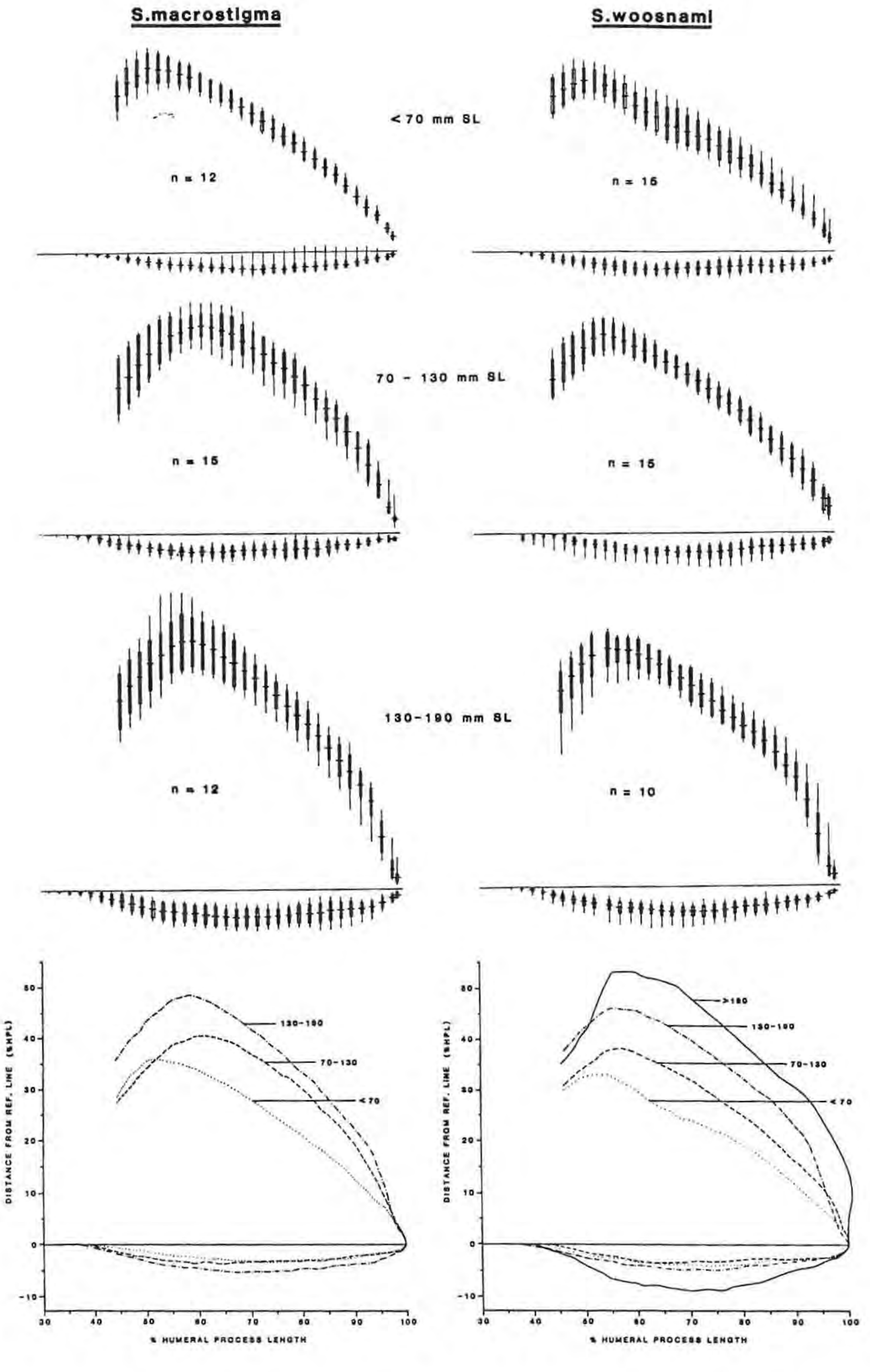

Figure 5.36 Variation in the shape of the humeral process in three size groups of S.macrostigma and S.woosnami and the comparison of the generalized outlines of each.

In contrast to the outer mandibular barbels all species of Group I have secondary branches on the inner mandibular barbels, although unbranched primary branches are also encountered (representing 2% in S.zambezensis and 52% in S.njassae). In Group I only the first two primary branches closest to the basal membrane are branched, the secondary branches situated at or near the base of the primary branch (see Figure 4.3). In Group II, the first two to three primary branches closest to the basal branch are usually unbranched.

The small number of specimens in S.macrostigma and S.thamalakanensis with more than four secondary branches in both the inner and outer mandibular barbels were all very large females. Many more specimens would be required, however, before this apparent sexual dimorphism in late adulthood could be confirmed.

HUMERAL PROCESS SHAPE

In the preliminary analysis of humeral process shape, 15 specimens (or less as availability would allow) from each of four size groups were compared between S.macrostigma and S.woosnami. These two species were chosen in particular, as the general shape of the humeral process appeared to be relatively similar, yet slight differences were apparent in the height and curvature of the postero-dorsal margin. Only one S.woosnami with a standard length of 205,15 mm represents the size group of specimens larger than 190 mm SL (Figure 5.36).

The height of the humeral process of both species, indicated by the distance between the dorsal margin and the reference line, increases with increasing size of the specimen. In contrast, the ventral margin in both species shows very little change with development. The noticeable difference in the ventral

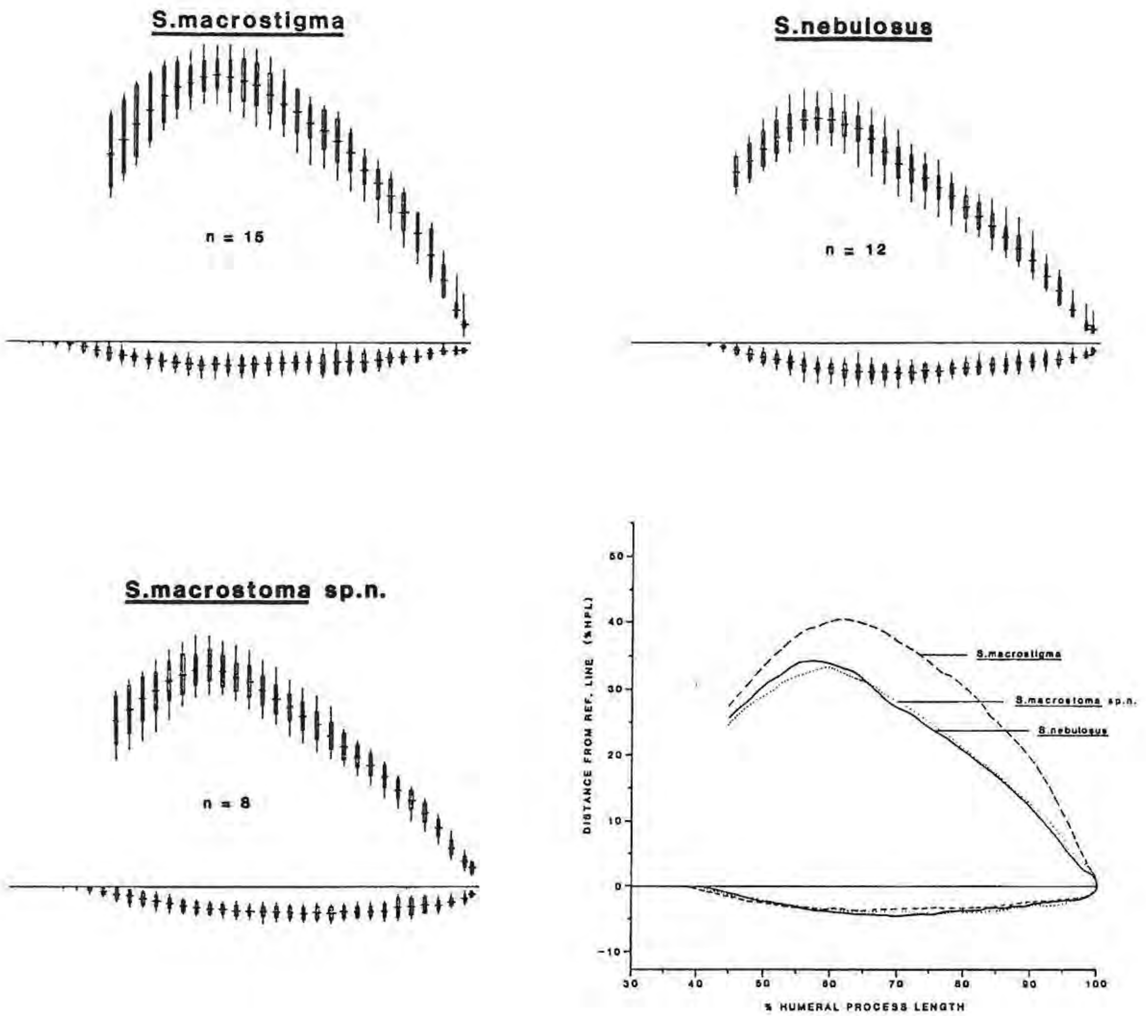

Figure 5.37 Variation in the shape of the humeral process in S.macrostigma, S.nebulosus and S.macrostoma sp.n. and the comparison of each species' generalized outline.

outline of the largest S.woosnami specimen is not considered to be representative of this size group, as it was derived from a single specimen and differs little from the lower range in variation of the 130-190 mm SL group. As a result of the consistently small inter- and intraspecific variation in the ventral margin between these and all subsequent species, no taxonomic value of any importance is attributed to this feature.

Of the three comparable size ranges in S.macrostigma and S.woosnami, the generalized outlines of the 130-190 mm SL group most closely resemble one another. The S.macrostigma outline, however, is slightly taller in the section between 56% and 86% of humeral process length, although also characterized by a larger degree of variation as indicated by larger values in standard deviation and range. Both outlines are obtusely pointed with a bilinear postero-dorsal margin, the apex of the angle at approximately 92% of humeral process length. The next most similar outlines are between the <70 mm SL groups. Here the S.macrostigma outline is taller along the entire length of the postero-dorsal margin. They differ further by a noticeably concave section between 56% and 86% of humeral process length in S.woosnami, although this section is also characterized by a higher degree of variability than S.macrostigma. The two most widely differing outlines are thus between the 70-130 mm SL groups. The S.woosnami outline still retains a slight bilinear element to its postero-dorsal margin, although the section closest to the tip is very much shorter than in the larger size group. The postero-dorsal margin in S.macrostigma, on the other hand, is more or less a continuous even curve and noticeably more rounded, with the section between 56% and 96% of humeral process length 2,75-7,85% taller than S.woosnami. As the generalized outline derived from specimens between 70 and 130 mm SL showed the greatest difference in height as well as in the shape of the postero-dorsal margin, up to 15 specimens of this size range were used in the comparison of the remaining species.

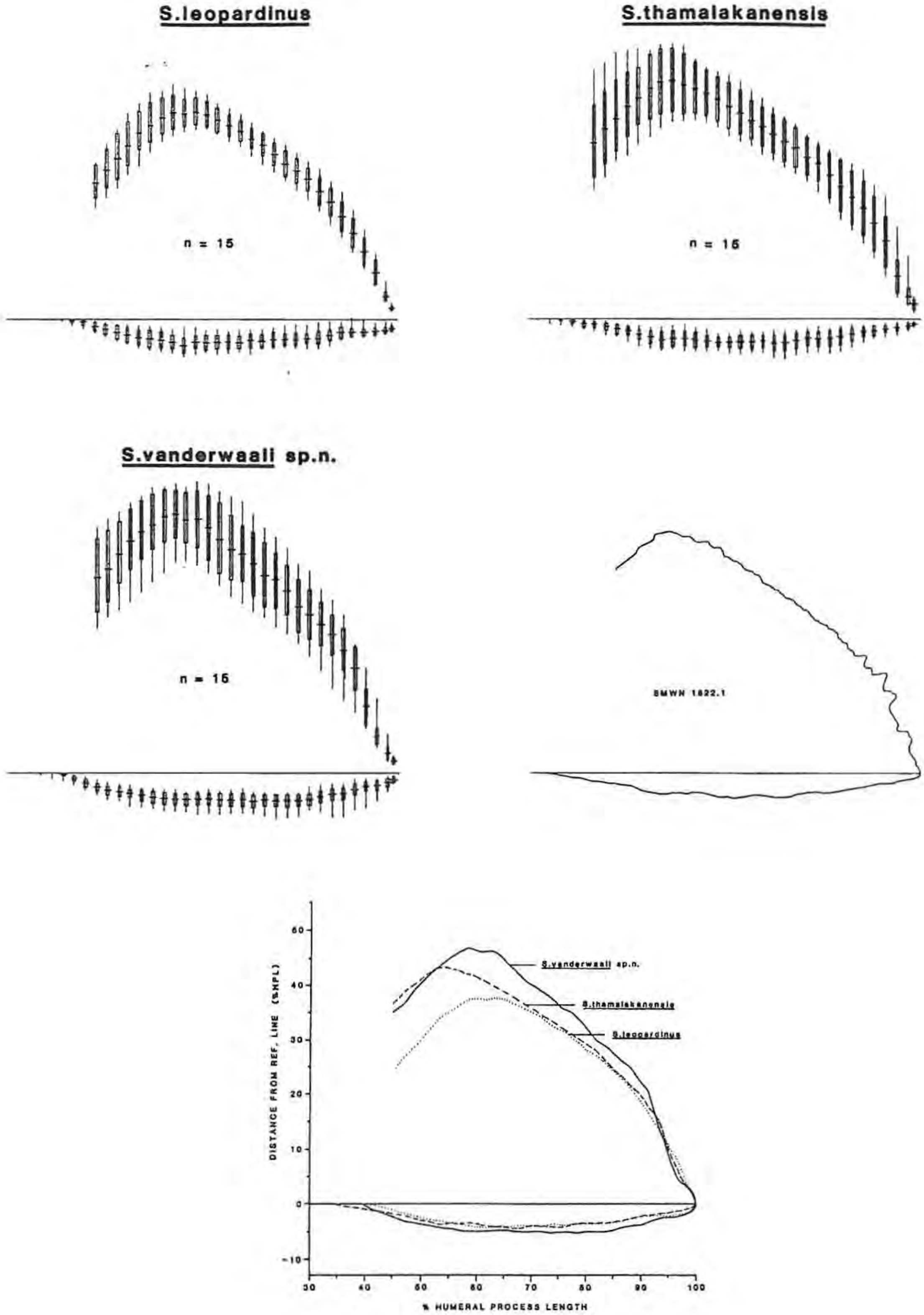

Figure 5.38 Variation in the shape of the humeral process in S.leopardinus, S.thamalakanensis and S.vanderwaali sp.n. and the comparison of each species' generalized outline.

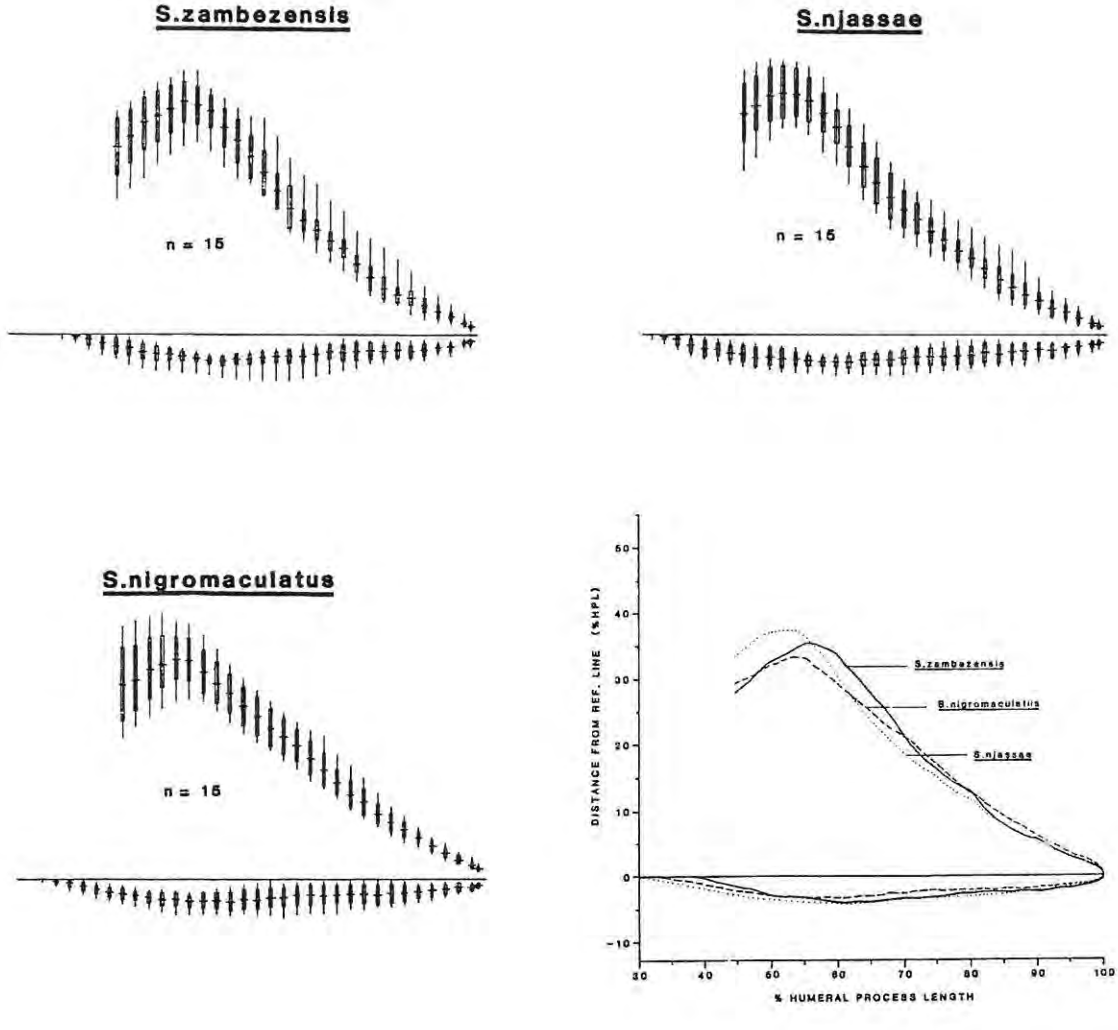

Figure 5.39 Variation in the shape of the humeral process in S.zambezensis, S.njassae and S.nigromaculatus and a comparison of each species' generalized outline.

The shape of the humeral process in S.macrostigma is compared with two further species due to their general resemblance in morphology and colour pattern, namely S.nebulosus and S.macrostoma sp.n. (Figure 5.37). The generalized outline of S.macrostigma is immediately distiguishable from the other two species by a noticeably taller dorsal margin, differing from 4,35-9,25 between 56% and 90% of humeral process length, in comparison with an average standard deviation in this section in S.nebulosus of 1,89 and in S.macrostoma sp.n. of 2,07. The outlines of S.nebulosus and S.macrostoma sp.n., however, are virtually indistinguishable, the slightly more concave section between 66% and 78% of humeral process length in S.nebulosus being of little significance considering the large degree of overlap in variation between these two species.

In the comparison of the generalized outlines of S.leopardinus, S.vanderwaali sp.n. and S.thamalakanensis, the first two species are distinguishable by a taller maximum height and longer postero-dorsal margin (Figure 5.38). The outlines of S.vanderwaali sp.n. and S.thamalakanensis are further distinguishable by the bilinear shape of the postero-dorsal margin, although this feature is very much more noticeable in the former. The outline in S.leopardinus, on the other hand, is uniformly curved with a noticeably smaller nipple at the tip of the process. The extent of the variation along the length of the ventral margin is also noticeably larger in S.thamalakanensis and S.vanderwaali sp.n. In the former this trend is explainable due to the presence of (often prominent) projections that are typical of adult specimens of this species and originate from the posterior third along the postero-dorsal margin, as illustrated in the outline of specimen SMWN 1822.1.

The sharply-pointed, triangular humeral processes with concave postero-dorsal

Table 5.6 Frequency distribution of the total number of moveable mandibular teeth

Species	Drainage	n	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
S.zambezensis	M.Zambezi	14																						2		2	2	1	4	1	2				
	L.Zambezi	17																2			2	2	2		2	2		1	2	1					
	Pungwe	1																																	
	Buzi	2																			1								1						
	Save	12																	2	1	2	3	3			1									
	Limpopo	37									1	1	2		2	6	9	2	4	4	2	3	1												
	Incomati	5															1	1	1			1	1												
	Umbeluzi	1																		1															
	Pongolo	21										2	1		3	2		2	7	1		1	1	1											
S.nigromaculatus	Okavango	100										1			4	5	7	10	5	4	11	13	5	4	7	3		7	8	1	1		1	1	
	U.Zambezi	16																		1		2	5	2		2	1	2					1		
S.njassae	L.Malawi	27											1		1	3	1	7	2	5	3	1	2							1					
S.nebulosus	M.Zambezi	13	1			1		4	2	1	3		1		1																				
	L.Zambezi	1					1																												
S.woosnami	Okavango	54			2	2	1	4	17	6	7	7	4	2	2																				
	U.Zambezi	1				1																													
	Cunene	11							1	2	4	2	1		1																				
S.macrostigma	Okavango	72						1	5	1	9	5	15	11	7	4	4	7	1	2															
	U.Zambezi	19				1			1	4				2	1	1	3	3	1	1	1														
	Cunene	30							1	3	4	7	5	6	2	1																			
S.macrostoma sp.n.	U.Zambezi	21		2		2	2	6	3	3	1	1																							
	Cunene	ND																																	
S.leopardinus	Okavango	49	2	1	5	10	9	9	6	3	2	1	1																						
	U.Zambezi	26		2	2	2	4	3	6	3	3		1																						
S.vanderwaali sp.n.	Okavango	36														1		2	2	2	4	8	2	2	3		4	2	2			2			
	U.Zambezi	4																							1					1		1		1	
	Cunene	8																							1			1	2	2	2				
S.thamalakanensis	Okavango	42						1	1	5	2	7	4	8	2	4	3	3	2																
	U.Zambezi	1										1																							

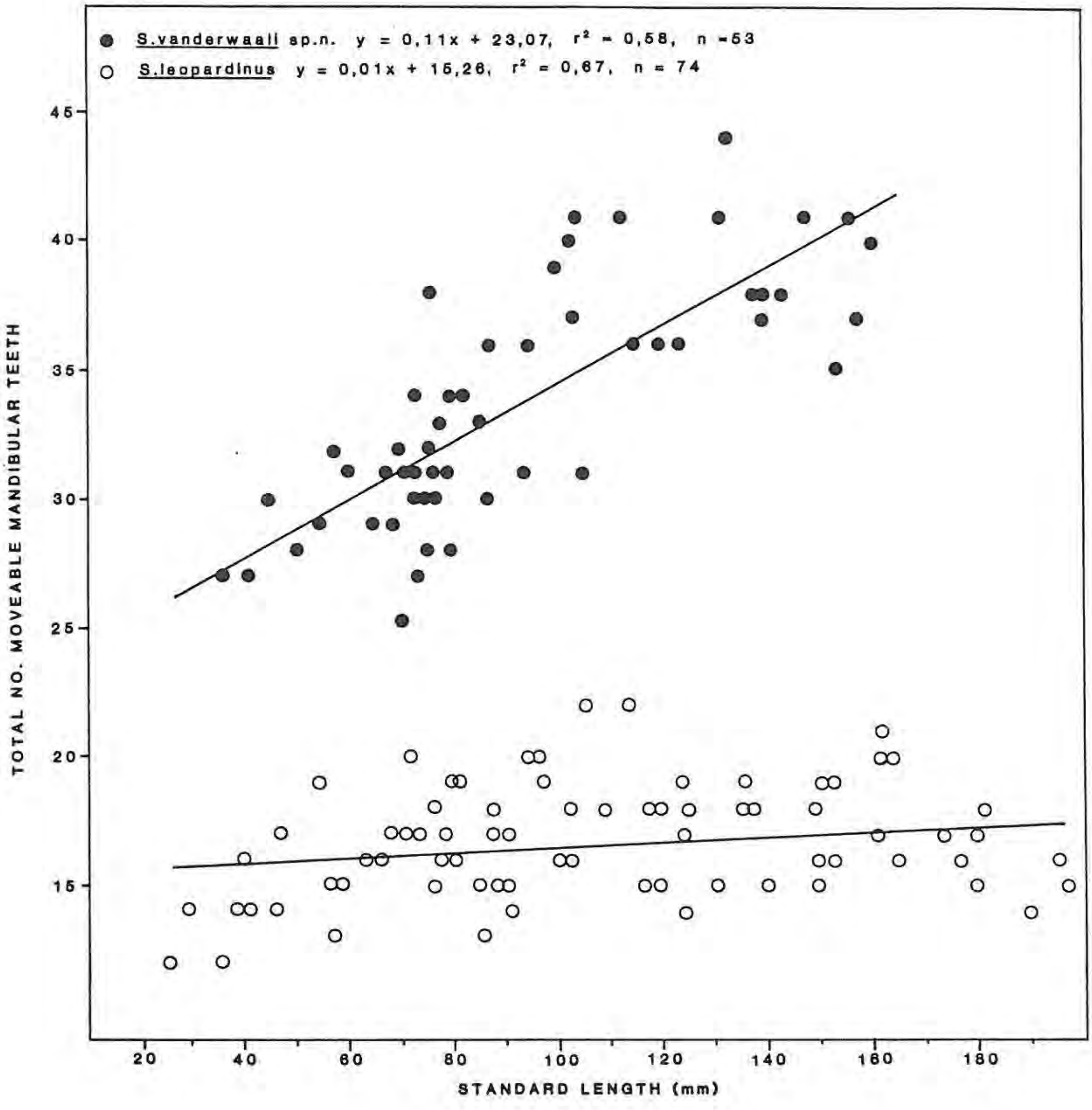

Figure 5.40 Scattergram of the total number of moveable mandibular teeth with standard length in S.vanderwaali sp.n. and S.leopardinus.

margins in species of Group I are readily distinguishable from other southern African Synodontis. The only important taxonomic difference within Group I species is the generally taller maximum height and longer postero-dorsal margin of S.njassae.

DENTITION

Moveable mandibular teeth.

A comparison of the frequency distributions of the total number of moveable mandibular teeth for each population is given in Table 5.6.

The most striking feature of the results is the very strong negative correlation of tooth number with latitude in S.zambezensis, to the extent that the ranges of the northern and southern populations do not overlap. No other species shows a similar range in geographic variation, although S.nigromaculatus, S.macrostigma and S.vanderwaali sp.n. share a similarly large range in tooth number. The extensive overlap in the tooth number of Group I species does not allow for taxonomic differentiation. A number of very distinct differences, however, are discernible among the species of Group II.

Taking into consideration the generally large intraspecific variation of mandibular tooth number, this character still allows the very clear diagnosis of S.vanderwaali sp.n. from most species except S.macrostigma and to a lesser extent also S.thamalakanensis. The distinction between S.vanderwaali sp.n. and S.leopardinus is particularly valuable due to the very close general resemblance of these two species shown. An estimate of the reliability of this character outside the size range studied was determined through bivariate

Table 5.7 Frequency distribution of functional moveable mandibular teeth.

Species	Drainage	n	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
S.zambezensis	M.Zambezi	14																			2	1	6	1	1	2		1		
	L.Zambezi	17															1	1	1	2	1	3	1	1	2		1		1	
	Pungwe	1																	1											
	Buzi	2																		1	1									
	Save	12																2	4	4			2							
	Limpopo	37									1		3	3	4	7	9	1	7	1		1								
	Incomati	5															1	1	2	1										
	Umbeluzi	1																1												
	Pongolo	21											1	2	2	2	7	4	1	2										
S.nigromaculatus	Okavango	100										1	2	2	8	9	11	13	7	8	5	8	3	5	6	8	2			
	U.Zambezi	16																2	2		7	1	2		1			1		
S.njassae	L.Malawi	27													1	4	8	5	3	4					1	1				
S.nebulosus	M.Zambezi	13	1					5	1	2	2	1			1															
	L.Zambezi	1									1																			
S.woosnami	Okavango	55					2		5	12	10	8	10	2	6															
	U.Zambezi	1						1																						
	Cunene	11							2		3	2	4																	
S.macrostigma	Okavango	72						1	1	4	9	17	14	5	9	5	4	1		2										
	U.Zambezi	19					1	1	1	1	2	1	1	2	3	2	2	1			1									
	Cunene	30							1	2	4	6	7	7	1	1	1													
S.macrostoma sp.n.	U.Zambezi	22				3	2	5	8	2	2																			
	Cunene	ND																												
S.leopardinus	Okavango	48			4	5	11	12	7	7	2																			
	U.Zambezi	26		1	1	3	5	4	6	4	1	1																		
S.vanderwaali sp.n.	Okavango	36													1		2	7	4	8	3	2	4		1	3				1
	U.Zambezi	4																						1		1		1	1	
	Cunene	8																						1	3	4				
S.thamalakanensis	Okavango	42					1		3	6	6	6	8	7	4	1														
	U.Zambezi	1											1																	

analysis. Although both regressions are accompanied by low correlation coefficients, these two sets of data show clearly divergent trends (Figure 5.40). The low correlation coefficients of both species does not allow the realistic comparison of their 95% confidence limits. From the extrapolation of lines joining outlying points, however, an estimate of the distinctness of these two species is possible down to approximately 15 - 20 mm SL, with a corresponding increase in the reliability of the diagnostic value of this character with size.

Species in Group I have already been shown to be clearly distinguishable from species in Group II on a number of morphometric features. Comparison of tooth number, however, is often easier than the subtle differences exhibited by some of the morphological characters, particularly in the field. This fact is particularly applicable to S.zambezensis and S.nebulosus which coexist in the Middle and Lower Zambezi systems. The very clear differentiation in tooth number of these two species is especially useful in identifying juveniles, where many of the differences in adults are not yet applicable or are much more difficult to measure.

In the analysis of this character, Farquharson (1969) considered both the total number and number of functional teeth. The comparison of the frequency distributions of these two values shows a reduction in the overall variation in the latter for almost all species (Table 5.7). This reduction, however, is not accompanied by a corresponding increase in interspecific differences, as one might reasonably expect. The size of the differences between S.vanderwaali sp.n. and S.woosnami and between the Lower and Middle Zambezi populations of S.zambezensis, for example, are even reduced slightly, the difference between S.vanderwaali sp.n. and S.leopardinus remaining unchanged.

As mentioned in page 31, the replacement teeth are usually situated in front of

Table 5.8 A comparative summary of premaxillae and associated primary tooth features.

Species	Ventral shelf			Gap between 1° and 2° teeth	Primary teeth		Illustration in Figure 5.41
	Length	Profile	Edge		Crown shape	Curvature	
<u>S.zambezensis</u>	moderately long	rounded	poorly defined	absent	tall, rounded to slightly posteriorly flattened, tip pointed	strongly to very strongly recurved	refer to a
<u>S.nigromaculatus</u>	moderately to very long	"	"	"	"	"	a
<u>S.njassae</u>	moderately long	"	"	"	"	"	refer to a
<u>S.nebulosus</u>	short	slightly rounded	slightly rounded	usually clear (narrow and indistinct in some)	posteriorly flattened, tip acutely pointed	slightly to moderately recurved	b
<u>S.woosnami</u>	usually absent (very short in some)	steeply sloping	absent	absent	rounded to slightly posteriorly flattened, tip pointed to bluntly pointed	straight to slightly recurved	c
<u>S.macrostigma</u>	very short	flat to slightly rounded	moderately to slightly rounded	usually distinguishable (narrow and indistinct in some)	posteriorly flattened, tip acutely pointed	slightly to moderately recurved	d
<u>S.macrostoma</u> sp.n.	moderately to very long	flat	well defined, often rectangular	very clear, often fairly wide	"	"	e
<u>S.leopardinus</u>	very short	ovate	indistinct	clear	round to slightly posteriorly flattened, tip pointed	straight to slightly recurved	f
<u>S.vanderwaali</u> sp.n.	short	flat to slightly rounded	well defined	"	posteriorly flattened, tip acutely pointed	strongly to very strongly recurved	g
<u>S.thamalakanensis</u>	"	rounded to ovate	poorly defined	usually clear (narrow and indistinct in some)	"	slightly to strongly recurved	h

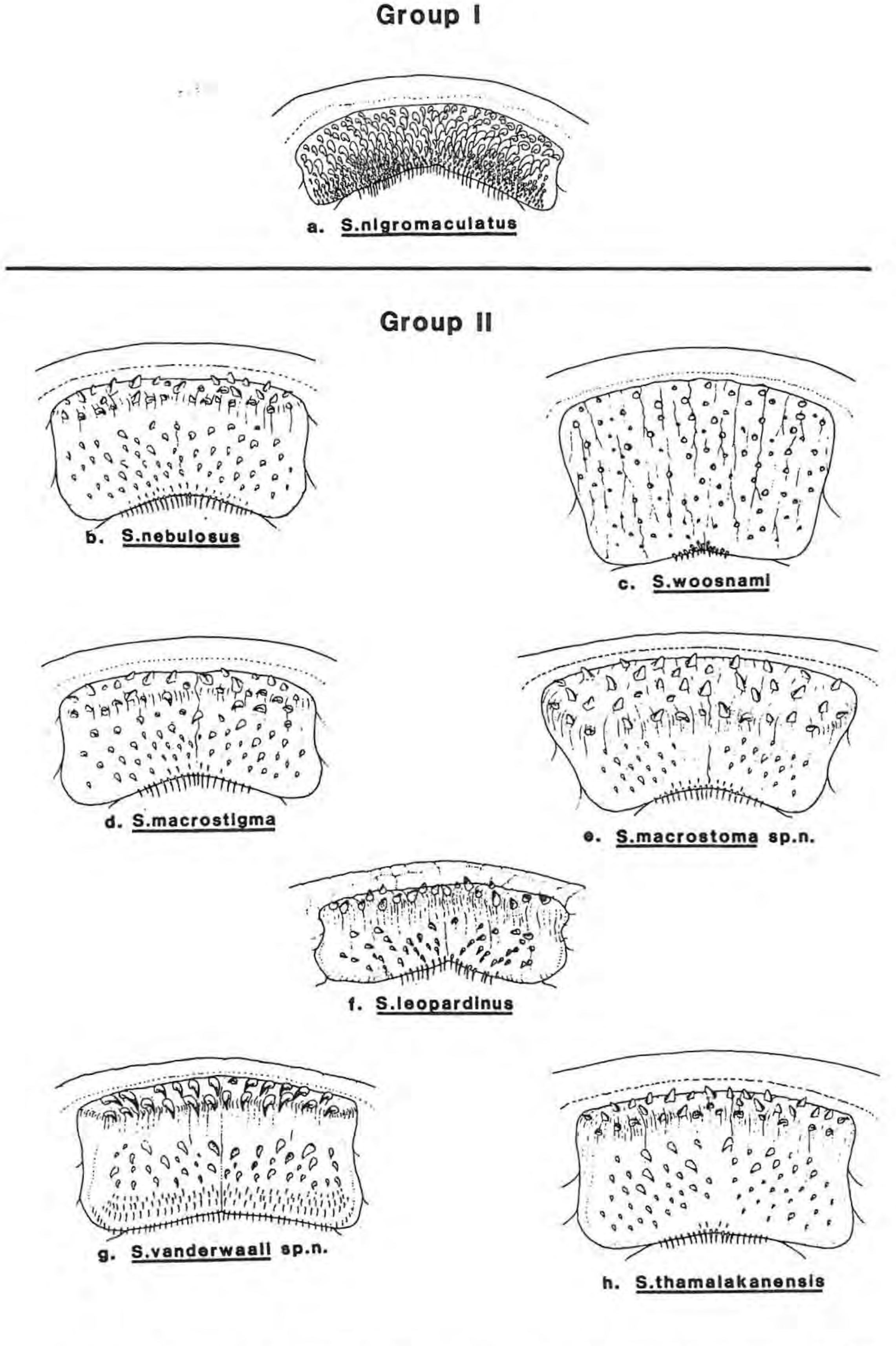

Figure 5.41 Premaxillae in postero-ventral view of representative specimens of Group II species and of S.nigromaculatus.

Table 5.9 Frequency distribution of primary premaxillary tooth number of selected populations of Group II species.

Species	Drainage	n	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
S.nebulosus	M.Zambezi	13																2		1		1	3	1		1	2	1	1								
S.woosnami	Okavango	54	primary teeth indistinguishable from secondary teeth																																		
S.macrostigma	Okavango	31									1	2	3	1	2	2	7	3	1	3	1	2	2	1													
S.macrostoma sp.n.	U.Zambezi	21													1	1				3		2		3	2		1	2		1	1	1	2	1			
S.leopardinus	Okavango	65	1	2	2	3	8	11	10	12	3	5	5	3	7		2	1																			
S.vanderwaali sp.n.	Okavango	36										1	2		2	2	4	2	6	5	4	2	2	1	1				1	1							
S.thamalakanensis	Okavango	42																1	1	4	2	3	3	2	2	9	4	2	1	3	1	1	1		1		1

a neat transverse row of functional teeth. An exception is seen in S.woosnami where these teeth occur in a distinctly curved band. Although this feature is unique among the southern African species, it is much less noticeable in juveniles.

Premaxillary teeth.

Group I species are excluded from the analysis of primary tooth number, because all three species lack a gap between the primary and secondary teeth, and there is no noticeable difference in size and shape that could distinguish these two tooth forms (5.8 and 5.41a). In addition, their ranges are largely overlapping with no discernible taxonomic difference. The number of primary and secondary teeth in this group together total 157(110-250), with 32(28-42) tertiary teeth arranged in one neat row (Figure 5.41 a).

In the analysis of Group II, only the largest populations of each species are compared. Apart from S.nebulosus, this brings together five of the six species coexisting in the Okavango basin. The sixth species, S.macrostoma sp.n., is from the adjacent and temporarily connected basin of the Upper Zambezi.

S.woosnami is immediately distinguishable from other Group II species in that no distinction exists between the primary and secondary teeth --- a feature similar to Group I (Table 5.8). These teeth are usually straight or slightly recurved, and shorter and more deeply set than any other southern African Synodontis, with a progressive reduction in size dorsally. Both tooth forms are situated on the posterior face, as the ventral shelf is usually absent or at the least extremely narrow (Figure 5.41 c).

A very noticeable distinction in number of primary teeth exists between S.leopardinus and S.thamalakanensis, with their ranges overlapping in extreme values only (Table 5.9). This difference is further enhanced by the generally

Table 5.10 Number of tertiary premaxillary teeth in selected populations of Group II species.

Species	Drainage	n	Row*	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
S.nebulosus	M.Zambezi	13	i																						1	2	2	4	1	1	1	1													
			ii						1			1		1		2	3	2	1	1	1	1	1																						
S.woosnami	Okavango	54	i												1		4	13	10	11	6	1		1	2																				
S.macrostigma	Okavango	50	i													1			2	4	3	4	6	9	7	5	2	3	2				1	1											
			ii	15	6	2	3	4	4	5	2	3	1	1	1	1		2																											
S.macrostoma sp.n.	U.Zambezi	21	i																		1	4	6	2	3	4		1																	
			ii	1				1		1		3	2	3	1	4		2		1		1																							
S.leopardinus	Okavango	51	i													1	1		2	8	5	4	3	11	11	2		2	1																
			ii	25		1	4	4	1	1	1	2	2	7	1	1	1																												
S.vanderwaali sp.n.	Okavango	30	i																								1	1	3	1	1	2	4	6	6	4	4	2	2	2	1		2		
			ii																				1	1	2	2		6	3	4	4	6	2	3	1	3			2			1		1	1
			iii							2		1	1	3	1		8	3	3	3	2	2	1	2			1		1		1	2			1	2			1						
			iv	14	3	5	6	2	2		2			2	1			1			1							1	1		1														
S.thamalakanensis	Okavango	42	i														1	1	2	3	4	4	4	5	5	3	2	1	1	4	1														
			ii	9	4	6	3	1	1	1			1																																

* i = first row on postero-dorsal margin; ii,iii & iv = sebsequent rows ventral to the first row.

more dorso-ventrally flattened and more recurved crowns of these teeth in S.thamalakanensis (Table 5.8 and Figure 5.41 f & h).

The ranges in primary tooth count between S.macrostigma and S.macrostoma sp.n. are largely overlapping with the latter distinguishable only above 31 (Table 5.9). The shape of the premaxillae between these two species, however, is markedly dissimilar with the most striking difference in the shape of the ventral shelf. In S.macrostoma sp.n. this feature is very wide, flat and moderately to very long with a well-defined often rectangular edge, and in S.macrostigma it is noticeably shorter with a less well defined edge (Table 5.8 and Figure 5.41 d & e).

Similar to the above example, the ranges in primary tooth number of S.leopardinus and S.vanderwaali sp.n. are largely overlapping, with the former distinguishable only below 19 and the latter above 25. The most striking difference between the premaxillary teeth of these two species, however, is in the number of tertiary teeth (Table 5.10). In S.leopardinus tertiary teeth are arranged in one or two rows concentrated near the centre and number between 14 and 33. In S.vanderwaali sp.n. they are much more numerous, totalling between 58 and 138 and arranged in three to four distinct rows, each extending the full width of the premaxillae. In addition, the primary teeth in S.vanderwaali sp.n. are more strongly recurved than S.leopardinus, and the ventral shelf is slightly longer and flatter with a more well defined edge.

In S.woosnami the tertiary teeth are usually larger in diameter than similar-sized specimens of the other species, fewer in number, concentrated near the centre and always arranged in only one neat row on the postero-dorsal rim. This feature further distinguishes the distinctive premaxillary teeth arrangement in this species.

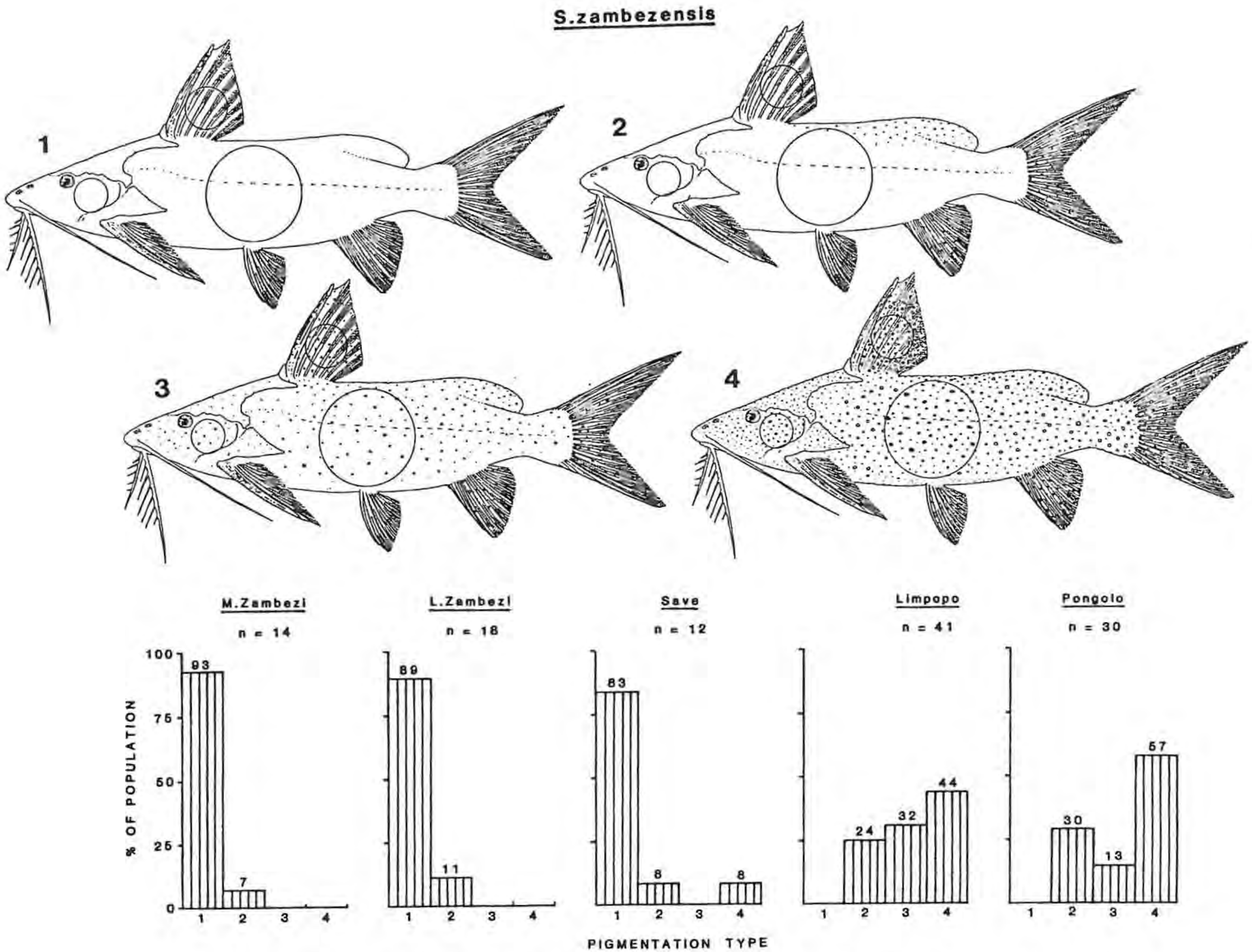

Figure 5.42 Illustration of four pigmentation types and their frequency distribution in selected populations of S.zambezensis.

COLOUR

Early in the study it became evident that the colour pattern was very variable resulting in the large degree of overlap between species, thus contributing little to their diagnosis. The inter- and intraspecific variation in the pattern of markings was nonetheless recorded, as this character remains one of the most frequently applied diagnostic features, especially in the field. Due to this large variation though, colour pattern was the last character to be analyzed, relying on the differentiation of species already decided upon from the comparison of their morphometric and meristic characters.

The particular pigmentation types illustrated are not meant to indicate the presence of such types only but serve merely as examples from the continuum of the overall range. The juveniles of all species have similar patterns to adults, though their individual markings are slightly larger, fewer in number and more widely distributed. All pigmentation types illustrated are of specimens larger than 70 mm SL. Sexual dimorphism in colour pattern was not recorded for any species.

Pattern of markings

The pattern of markings in S.zambezensis is by far the most confusing, as it varies from a form totally unspotted to one where small, closely-packed, predominantly spherical spots cover the entire body and fins, a pattern very similar to S.nigromaculatus. In the assessment of the five largest samples of this species, there is a general increase with increasing latitude in the percentage of spotted individuals, as well as an increase in the degree to which they are spotted (Figure 5.42). The more northerly populations of the Middle Zambezi, Lower Zambezi and Save systems are all characterized by a high percentage frequency of unspotted individuals, making up more than 83% in each, a form that is totally lacking in the more southerly populations of the

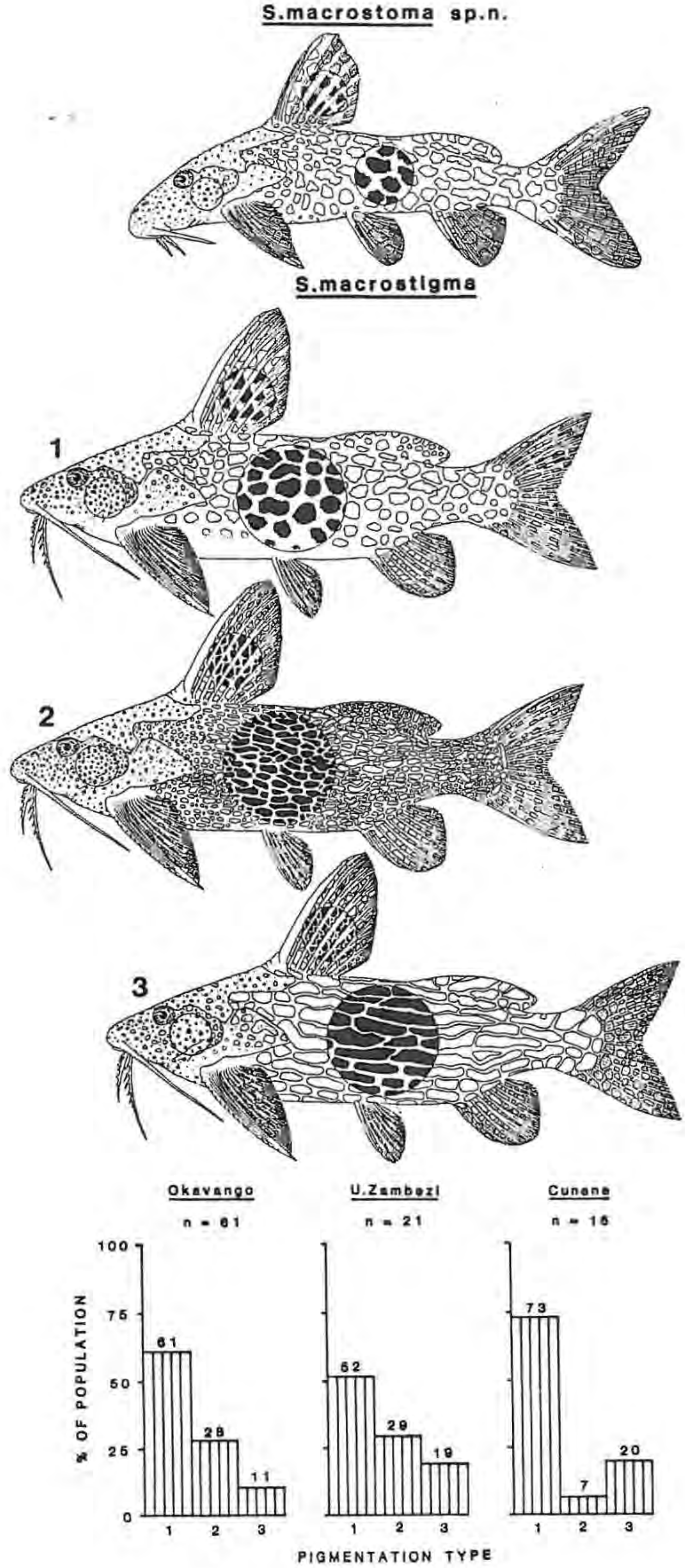

Figure 5.43 Illustration of three pigmentation types and their frequency distribution in selected populations of S.macrostigma. Also illustrated is the dominant pattern of markings in S.macrostoma sp.n.

Limpopo and Pongolo. The more highly spotted forms represented by pigmentation types 3 and 4 are absent in the Zambezi populations and poorly represented in the Save, but make up 76% and 70% of the Limpopo and Pongolo populations, respectively. In these last two populations the relatively high proportion of individuals having pigmentation type 2 was recorded in large adult specimens only. The spots of this form are usually only present on the adipose, caudal and anal fins. In the three more northerly populations, the chromatophores that make up the spots in this form are predominantly of a brown to brownish-yellow pigment and only slightly darker than the body colour, often making their detection difficult. In contrast, the markings of the two southerly populations are darkly pigmented throughout.

Pigmentation type 1 (Figure 5.43) is the dominant pattern of markings in all three populations of S.macrostigma, a pattern also exhibited by the holotype (Figure 5. 3). The specific name macrostigma, a noun in apposition from the Latin prefix macro-, meaning large and stigma-, meaning spot or mark, is a reference to this very characteristic pattern. The overall variation in this species, however, is too large to be able to be described from a single pigmentation type and varies from a form (type 2) where the spots are smaller, more numerous, slightly more elongated and very much more closely packed to one (type 3) with slightly fewer spots of similar depth but greatly elongated on the body and adipose fin. Markings may or may not extend over the ventral regions in type 1 and 3 but are always present there in type 2.

Though typical of larger adult specimens, the generalized outlines used to illustrate the different pigmentation types of each species tend to accentuate their morphological differences and so detract from their often very similar pattern of markings. This point is particularly relevant in the comparison of S.macrostigma and S.macrostoma sp.n., as their juvenile specimens much more closely resemble one another than depicted, particularly as a result of the

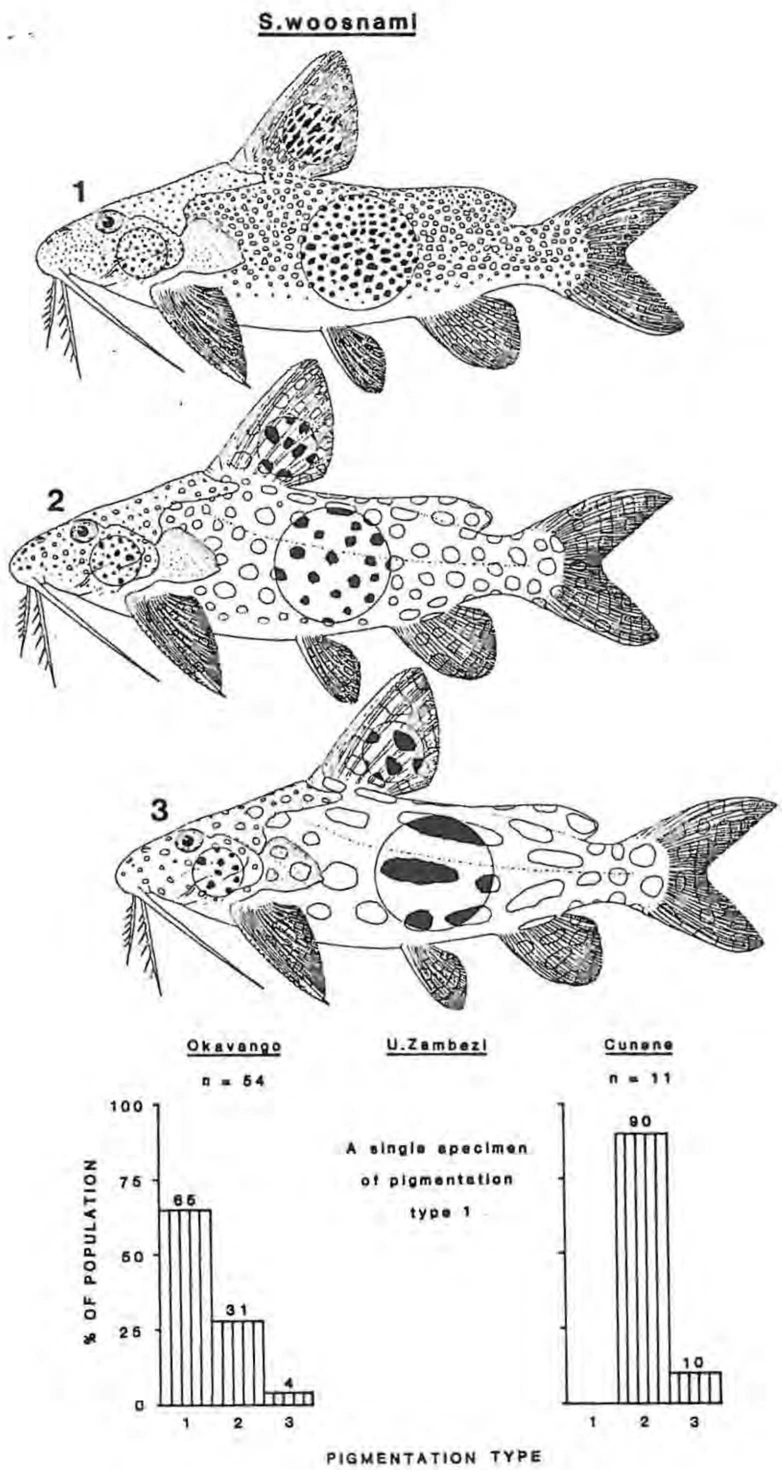

Figure 5.44 Illustration of three pigmentation types and their frequency distribution in selected populations of S.woosnami.

reduction in the proportional measurement of the snout in the latter species (p. 50). The pattern of markings in S.macrostoma sp.n. varies little from that illustrated in Figure 5.43, composed of large irregular-shaped blotches of similar relative size and distribution as pigmentation type 1 in S.macrostigma. This similarity in colour pattern, together with their morphological resemblance in the smaller size groups, has almost certainly contributed largely to the previous confusion of these two species.

A pattern of large, fairly widely spaced blotches is not only a characteristic of the two above-mentioned species, however, as it is also exhibited by S.woosnami, illustrated in pigmentation type 3 (Figure 5.44). Though this pattern accounts for only 4% and 10% of the Okavango and Cunene populations respecively, this overlap has resulted in many misidentifications. Specimen AMG 16305 photographed by Jubb (1967, Figure 157b), for example, and used to illustrate the colour pattern of S.macrostigma in the Cunene, has been identified as a S.woosnami with very typical dentition, humeral process shape and barbel morphology. Pigmentation type 2 in S.woosnami accounts for as much as 90% of the Cunene population and 31% of the Okavango population, and although the size of the markings are very similar they are more spherical and much more widely spaced in the former population. This rather slight difference, however, is progressively reduced in specimens smaller than 100 mm SL and indistinguishable below 70 mm SL. The dominant pattern of the Okavango population and also of the holotype of S.woosnami is that of type 1. The generally spherical and more closely packed spots of this pattern are all smaller than the diameter of the eye. The majority of specimens in all three pigmentation types lack markings along the ventral regions.

Among the southern African Synodontis no two species show a closer resemblance to one another in their pattern of markings than S.leopardinus and S.vanderwaali sp.n.. The size, shape, distribution and colour of the markings

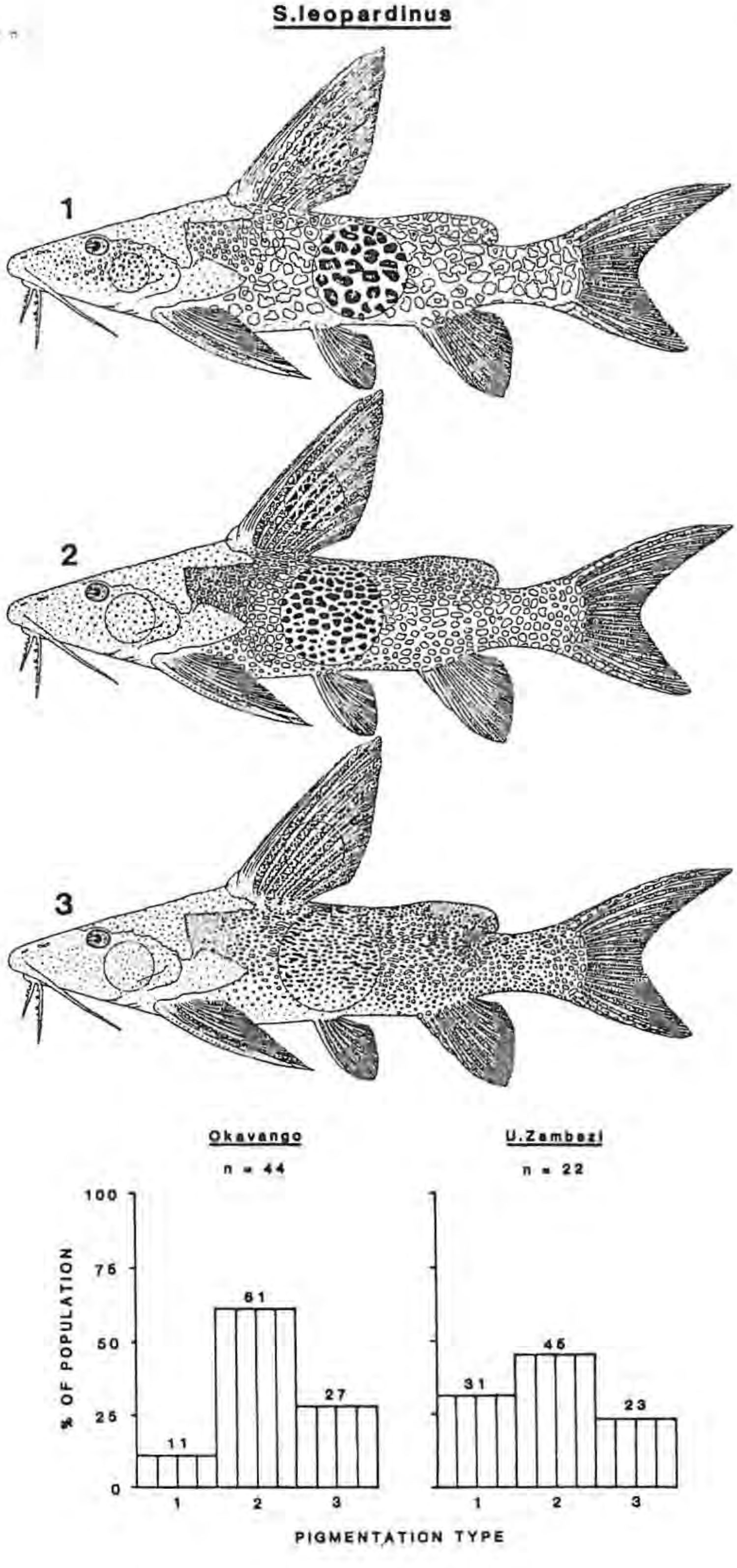

Figure 5.45 Illustration of three pigmentation types and their frequency distribution in two populations of S.leopardinus.

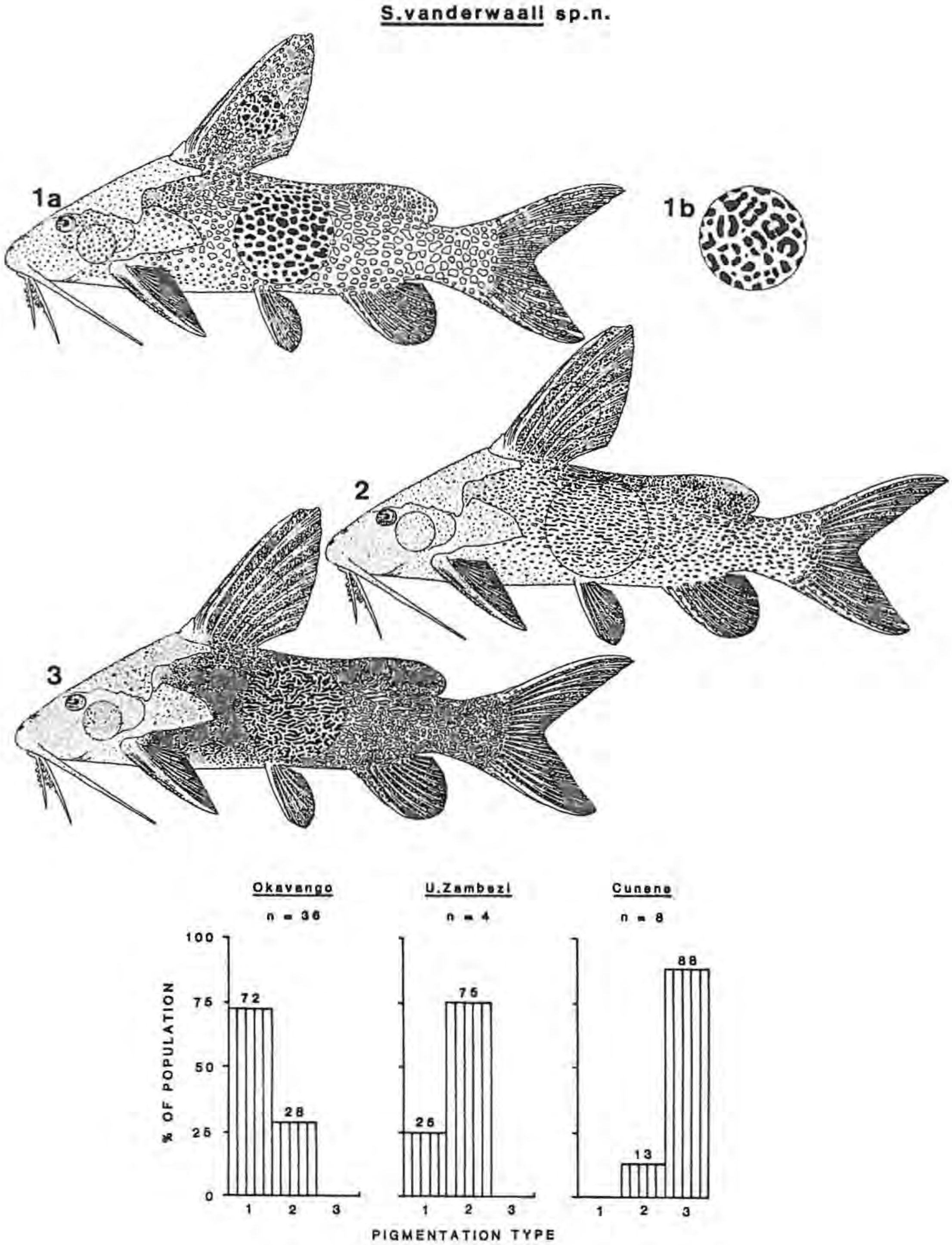

Figure 5.46 Illustration of three pigmentation types and their frequecy distribution in selected populations of S.vanderwaali sp.n..

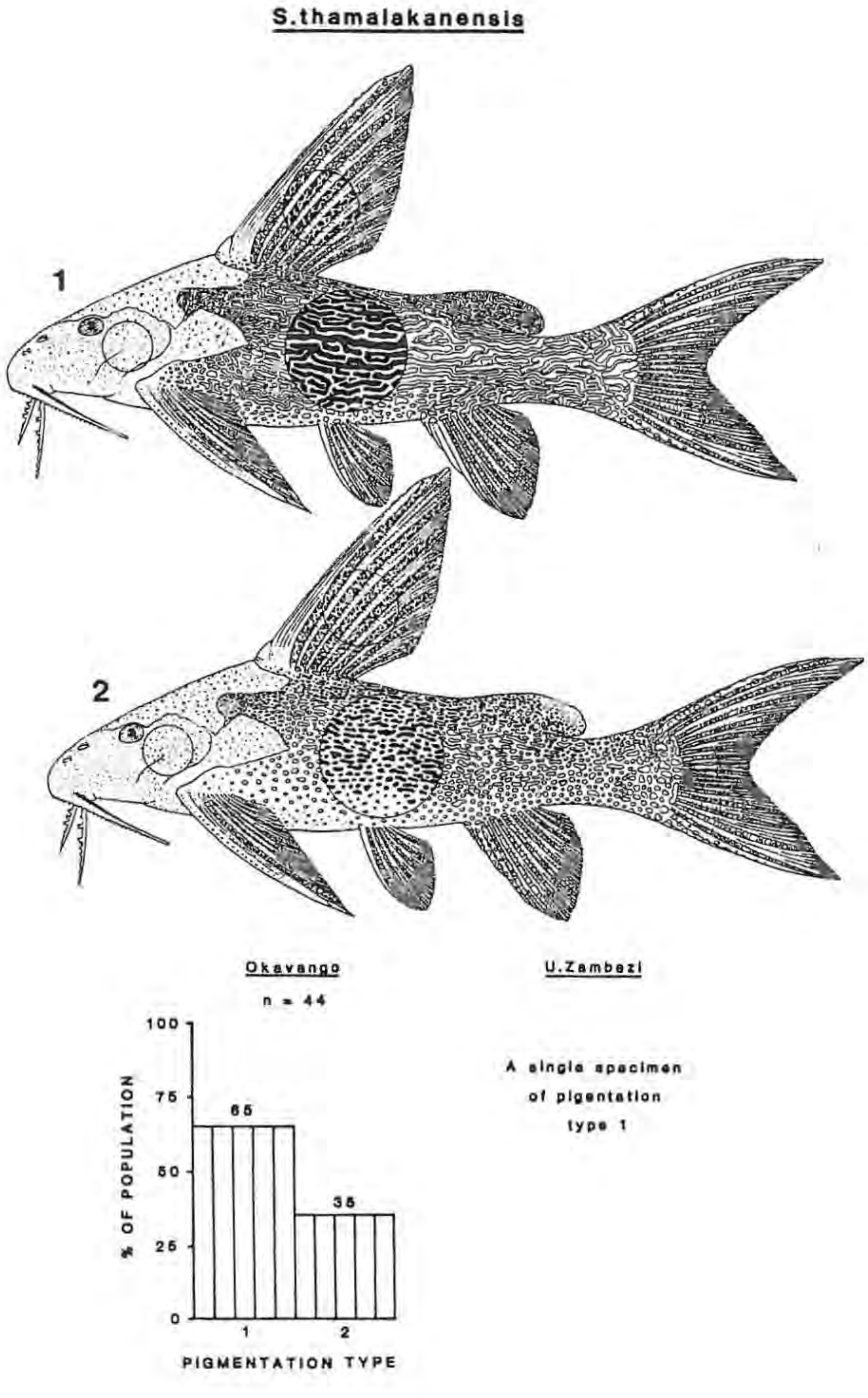

Figure 5.47 Illustration of three pigmentation types and their frequency distribution in selected populations of S.thamalakanensis.

of S.leopardinus type 2 and S.vanderwaali sp.n. type 1a, and of S.leopardinus type 3 and S.vanderwaali sp.n. type 2 are identical (Figures 5.45 and 5.46). In the Okavango and Upper Zambezi population this overlap accounts for as much as 100% in S.vanderwaali sp.n. and 72% and 76%, respectively, in S.leopardinus. This situation is further confused where the spots on the sides of the body in S.vanderwaali sp.n. may be grouped in a constellation of two to seven, as illustrated in type 1b (Figure 5.46). The area within these groups is usually of slightly darker pigment than body colour, giving an appearance very similar to type 1 in S.leopardinus. The only detectable difference between these two patterns is the slightly larger size and fewer number of spots in S.leopardinus, the majority of which occur singly and are circular to ovoid with lighter coloured centres. This difference, however, is reduced to insignificance in juveniles, where the discrepancy in size and distribution of markings in each species is indistinguishable. Morphologically S.leopardinus and S.vanderwaali sp.n. closely resemble one another, with the only readily identifiable diagnostic feature besides the shorter and wider head of the latter being significant difference in the lengths of all three barbels. By far the largest contributing factor responsible for the past confusion of these two species is their exceptionally large overlap in colour pattern.

Although the confusing use of colour as a diagnostic feature is typified in the above example, this situation is further exacerbated by yet another species whose pattern of markings overlap that of S.leopardinus, as seen in pigmentation type 2 in S.thamalakanensis (Figure 5.47). The more common pattern in S.thamalakanensis is illustrated in type 1, accounting for 65% of the Okavango population. Although this pattern of greatly elongated, reticulated lines is unique among the southern African species, the number and thickness of these lines varies considerably, an extreme example of which closely resembles pigmentation type 3 in S.macrostigma. The only distinction between these two types is the branched and more reticulated nature of these lines in S.thamalakanensis, a feature particularly evident on the mid-dorsal regions of the body.

The Cunene specimens of S.vanderwaali sp.n. have a pattern of markings that is also unique among the southern African species, composed of very closely packed, exceptionally fine, irregular-shaped spots and lines (Figure 5.46, type 2). Although the sample size of the Cunene and Upper Zambezi populations is very small, it is nonetheless interesting to note the complete absence of this pigmentation type in the Upper Zambezi and Okavango, with an overlap of only a single specimen of type 2.

The pattern of markings of S.nebulosus are similar to that illustrated for type 1 and 3 of S.macrostigma (Figure 5.43). The spots in this species are usually of a brown pigment in contrast to the brownish-yellow colouring of the body and fins. In a few specimens, however, the chromatophores of the markings are often smaller, more widely spaced and of a more yellowish pigment, making their detection difficult (Figure 6.2)

In contrast to the highly variable colour pattern of most of the species described above, the pattern of markings in S.nigromaculatus shows very little variation, both within and among the two populations examined (Figure 6.3). In addition, the background colouration of olive green in S.nigromaculatus is unique among the southern African Synodontis.

Partial albinism

Partial albinism has been recorded in a high percentage of juvenile (<70 mm SL) S.zambezensis specimens from the Pongolo River. Areas of the body showing this pigmentation abnormality are usually completely white and occur typically on the adipose fin and caudal peduncle. These areas appear devoid of any

Table 5.11 Selected morphometric and meristic data of the "S.kafuensis" type series.

Morphometrics	AMG 1530 Holotype	Paratypes AMG 1531 .1	.2	.3	.4	.5	.6	.7	.8	.9	.10	.11
Standard length	121,90	123,65	90,30	73,20	75,85	53,25	65,00	63,30	65,50	59,05	74,25	59,80
Predorsal length (% SL)	39,05	39,26	40,53	40,44	37,71	41,31	39,31	39,65	40,00	41,83	40,54	38,30
Snout length (% PDL)	37,95	41,40	36,88	37,84	38,11	35,23	36,40	31,47	37,36	35,02	37,21	37,15
Interorbital length (% HL)	31,04	24,76	31,00	28,97	27,37	31,20	29,91	31,90	36,32	29,66	30,74	29,72
Dorsal to coracoid (% HL)	74,05	63,58	81,33	74,45	72,02	81,05	78,50	83,54	77,59	75,74	80,42	74,68
Coracoid to cranium (% HL)	57,12	52,04	59,50	59,36	53,50	62,68	58,88	61,77	58,49	59,80	61,89	59,17
Snout to pectoral (% SL)	24,69	26,32	25,03	26,84	22,94	23,57	24,23	23,06	23,13	26,76	23,97	26,42
Pectoral girdle width (% HL)	77,61	70,55	80,67	77,26	74,49	83,09	81,07	83,54	79,72	80,39	80,00	79,07
Occ. nuchal shield width (% HL)	32,44	25,36	32,17	32,60	28,40	35,57	33,88	35,19	34,20	32,35	33,05	33,85
Humeral process length (% HL)	58,52	50,72	60,67	60,67	55,76	65,31	64,25	70,89	63,21	60,29	64,21	61,24
Hum.proc to occ.nuchal (% HL)	40,33	32,93	36,50	33,00	34,77	36,73	39,95	37,97	35,85	34,56	36,21	33,85
Dorsal spine length (% HL)	102,54	75,60	92,33	85,31	76,54	91,25	96,96	95,24	80,90	90,93	87,79	86,05
Pectoral spine length (% HL)	86,77	62,74	83,00	76,66	72,02	92,13	90,19	91,65	81,60	82,84	78,32	84,75
Dorsal fin length (% HL)	95,17	79,93	89,33	83,70	76,54	87,76	88,55	-	81,13	90,69	84,42	79,59
Max. barbel length (% HL)	73,79	56,73	70,50	67,61	76,13	86,30	90,65	87,85	87,03	80,64	74,11	87,86
Outer mand. length (% HL)	45,55	43,03	41,33	40,04	45,47	59,77	54,91	48,86	58,49	46,32	46,30	43,67
Inner mand. length (% HL)	24,17	30,29	27,00	28,17	26,75	34,40	32,24	30,89	32,31	30,15	28,00	25,84
Snout to anal (% SL)	72,35	71,29	73,98	75,27	72,71	73,24	72,54	74,72	73,74	73,07	73,27	74,58
Mouth width (% PGW)	53,44	65,76	52,07	51,30	58,29	53,33	46,11	47,58	54,73	46,04	52,89	-
Premaxillae width (% PGW)	26,56	60,99	22,52	23,70	30,94	24,91	23,63	24,85	26,92	21,04	25,53	26,14
Meristics												
Moveable mand. teeth (Total)	17	17	20	22	18	32	30	30	26	19	23	32
Premax. teeth (Primary)	24	22	21	26	33	26	25	28	27	20	28	27
.. .. (Tertiary) Row 1	27	19	22	21	18	24	32	-	26	22	19	26
.. .. .. Row 2	11	6	8	0	0	7	13	-	13	9	7	14

melanophores when viewed under a stereoscopic microscope at 40X magnification. No adult specimens exhibiting this type of colour pattern abnormality have been recorded from the Pongolo River in any of the large collections made over the last six years (la Hausse, pers. comm.). Although not within the aims of this study, it is nonetheless interesting to speculate how these melanophores manifest themselves later in development. An aspect of their existence which is of taxonomic importance, however, is that the only other southern African species to exhibit partial albinism, is S.nigromaculatus, a species that closely resembles S.zambezensis in many of the characters examined in this study.

Post-mortem change

No change in either the size or distribution of markings was noted before and after preservation in any of the specimens photographed when alive.

"S.KAFUENSIS"

As mentioned in Chapter 2 (p. 6), "S.kafuensis" was described from the Upper Kafue River by Farquharson (1969) in an MSc. thesis, but this account was never published. The criteria on which this species was erected are confusing as no diagnosis is given in the description. In addition, the accompanying key does not differentiate between the species of Group B (comparable to Group II in this study) but merely notes their (supposedly) non-overlapping geographic ranges, in which "S.kafuensis" is regarded as the only Synodontis species in the Upper Kafue River. This taxon was described by Farquharson (1969) on the grounds that the variation of certain morphometric and meristic characters is intermediate between that shown for S.leopardinus, S.woosnami and S.nebulosus although also largely overlapping.

On examining the "S.kafuensis" type series, I conclude the following: firstly, it is polyspecific; secondly, the holotype is identified as a S.macrostigma; and thirdly, only two specimens differ significantly from other recognized Synodontis species to warrant their recognition as new.

Twenty of the more important proportional measurements as well as the moveable mandibular and premaxillary tooth number of the "S.kafuensis" type series are given in Table 5.11. Sixteen of these morphometric values positively identify the holotype as a S.macrostigma, with snout length and barbel lengths differing only slightly from the range in this species. The proportional measurement of snout length (to predorsal length), for example, differs by only 0,51%. This discrepancy, though small, is explainable by the generally higher values of this character in Upper Kafue S.macrostigma with a mean of 36,07%, 1,09% higher than the combined mean of 34,98% for the other three populations. The tips of both maxillary barbels of the "S.kafuensis" holotype are broken, but a proportional measurement of 73,79% is estimated for the longest. All three pairs of barbels in this specimen are slightly shorter than the lowest values of the combined range of the Cunene, Okavango and Upper Zambezi populations of S.macrostigma. Similar to the above example, these differences are explained by the generally lower values of the Upper Kafue specimens, whose mean value deviates from the other three populations by 9,29% in maxillary barbel length, 7,37% in outer mandibular barbel length, and 6,04% in inner mandibular barbel length. The ranges of these three barbel lengths, however, (70,50 - 90,65%; 41,33 - 59,77%; 24,17 - 34,40%, respectively) largely overlap the range of the other three populations. In addition, the pattern of markings in the "S.kafuensis" holotype is comparable to S.macrostigma (Figure 5.43, pigmentation type 1) as is the shape and dentition of the premaxillae.

Three species are identified among the remaining paratypes. AMG 1531.1 and AMG 1531.4 are S.macrostoma sp.n., AMG 1531.3 is a S.leopardinus, and the rest are S.macrostigma. All eleven paratypes conform to the range of the species with which they are identified, with the exception of a few S.macrostigma specimens that have slightly shorter barbels, as explained above.

CHAPTER 6

TAXONOMY OF THE SOUTHERN AFRICAN SYNODONTIS

KEY TO SPECIES

1 a. Humeral process elongated, triangular and sharply-pointed with a concave postero-dorsal margin in all size groups. Outer mandibular barbels with very thin filamentous branches, the longest of which is more than 5 times diameter of barbel stem .... (2)

b. Humeral process broad and obtusely-pointed with a convex postero-dorsal margin in adults, convex section in juveniles may be restricted to posterior third only of the postero-dorsal margin. Outer mandibular barbels with relatively thick branches, the longest of which is less than 3 times diameter of barbel stem .... (4)

2 a. Markings composed of widely-separated, predominantly spherical spots, larger than pupil and as large as twice diameter of eye on sides of body and caudal peduncle. Dorsal fin length 58,3 - 75,7% head length. Dorsal spine length 59,3 - 84,2 % head length .... S.njassae

b. Markings may be absent but where present are composed of closely-packed, predominantly spherical spots, average size equal to or smaller than diameter of pupil on sides of body and caudal peduncle. Dorsal fin length 79,2 - 123,9% head length. Dorsal spine length 71,3 - 118,5% head length .... (3)

3 a. Spots often absent or sparse and indistinct; in heavily-spotted individuals, spots often absent or very indistinct along ventral regions. Average size of spots on sides of body and caudal peduncle less than half diameter of pupil and never overlapping (Figure 5.42). Live colouration of body and fins olive brown to slate grey; eggs orange to orange-yellow. Occipito-nuchal shield 23,1 - 30,7% head length. Caudal fork length 28,5 - 46,4% caudal total length .... S.zambezensis

b. Spots always present and numerous, covering entire body and fins. Average size of spots on sides of body and caudal peduncle larger than diameter of pupil, occasionally overlapping to form extended lines or grouped in a constellation of 3 - 5. Live colouration of body and fins olive green; eggs translucent, light green. Occipito-nuchal shield width 28,8 - 36,2% head length. Caudal fork length 38,2 - 58,6% caudal total length .... S.nigromaculatus

4 a. Long, slender mandibular barbel branches with sharply-pointed tips. No distinction between primary and secondary premaxillary teeth. Ventral shelf of premaxillae exceedingly narrow or absent (Figure 5.41c) .... S.woosnami

b. Short, thick, papilliform inner mandibular barbel branches with rounded tips. Clear distinction between size and position of primary and secondary premaxillary teeth, usually separated by a noticeable gap. Premaxillae with noticeable ventral shelf of varying thickness ... (5)

5 a. Ventral margin of mouth below horizontal level of ventral surface of pectoral girdle. Medial width of premaxillary ventral shelf large (Figure 5.41e). Snout length 37,0 - 41,7% predorsal length. Mouth width 53,5 - 66,1% pectoral girdle width. Width of premaxillae 27,0 - 34,7% pectoral girdle width .... S.macrostoma sp.n.

b. Ventral margin of mouth above horizontal level of ventral surface of pectoral girdle. Medial width of premaxillary ventral shelf small to very small. Snout length 29,4 - 39,4% predorsal length. Mouth width 34,4 - 58,6% pectoral girdle width. Width of premaxillae 15,4 - 29,1% pectoral girdle width .... (6)

6 a. Basal membrane prominent, maximum width 1 - 1 3/5 times diameter of barbel stem. Maxillary barbels with numerous, prominent (1/3 - 4/5 diameter of barbel stem in length), widely-spaced, single or double papillae on leading edge (Figure 6.9). Similar-sized papillae often extending across antero-ventral rim of mouth in large specimens .... S.thamalakanensis

b. Basal membrane may be absent; where present, maximum width is less than diameter of barbel stem. Maxillary barbels smooth or with moderately papillose leading edge; where papillae present, are narrowly-spaced and less than 1/4 diameter of barbel stem in length. Papillae never extending across antero-ventral rim of mouth .... (7)

7 a. Tertiary premaxillary teeth numerous (55 - 170) and arranged in 3 - 4 rows (Figure 5.41g). Moveable mandibular teeth 25 - 44 .... S.vanderwaali sp.n.

b. Tertiary premaxillary teeth less numerous (12 - 44) and arranged in 1 - 2 rows. Moveable mandibular teeth 12 - 30 .... (8)

8 a. Maxillary barbel length 58,7 - 85,3% head length. Pectoral girdle width 68,6 - 84,9% head length. Primary premaxillary teeth 9 - 24 .... S.leopardinus

b. Maxillary barbel length 77,5 - 112 , 6% head length. Pectoral girdle width 76,9 - 96,4% head length. Primary premaxillary teeth 17 - 35 .... (9)

9 a. Distinct, darkly-pigmented basal membrane on maxillary barbels, with finely to moderately papillose leading edge. Caudal fork length 39,8 - 66,5% caudal total length. Snout length 29,4 - 37,4% predorsal length .... S.macrostigma

b. Basal membrane on maxillary barbels absent, or indistinct and of similar colouring to barbel stem. Maxillary barbels with smooth leading edge. Caudal fork length 40,7 - 49,6% caudal total length. Snout length 35,9 - 38,6% predorsal length .... S.nebulosus

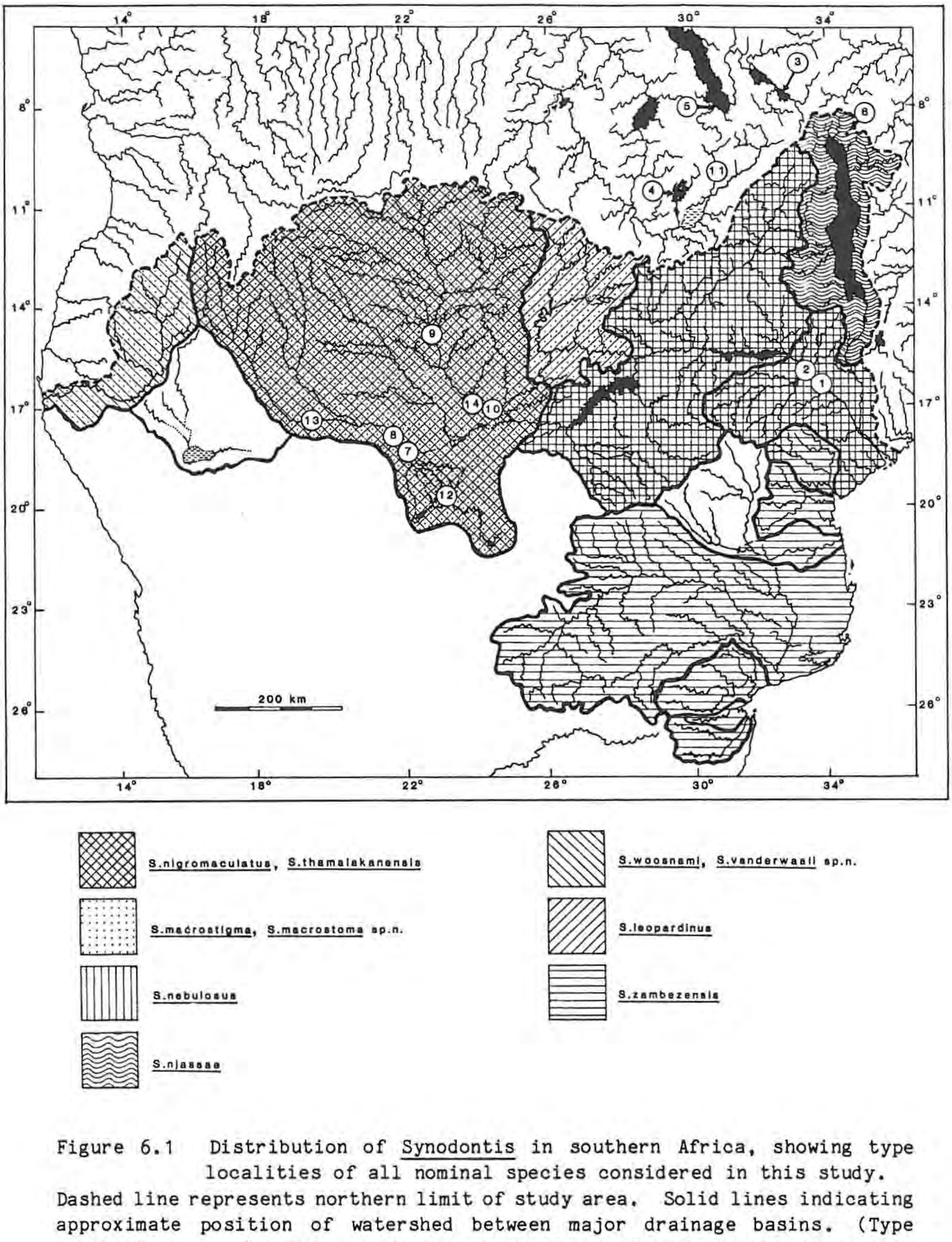

Figure 6.1 Distribution of _Synodontis_ in southern Africa, showing type localities of all nominal species considered in this study. Dashed line represents northern limit of study area. Solid lines indicating approximate position of watershed between major drainage basins. (Type localities: 1 = _S.nebulosus_, 2 = _S.zambezensis_, 3 = _S.zambezensis rukwaensis_, 4 = _S.nigromaculatus_, 5 = _S.melanostictus_, 6 = _S.njassae_, 7 = _S.woosnami_, 8 = _S.macrostigma_, 9 = _S.leopardinus_, 10 = _S.jallae_, 11 = _S.colyeri_, 12 = _S.thamalakanensis_, 13 = _S.vanderwaali_ sp.n., 14 = _S.macrostoma_ sp.n.)

DISTRIBUTION

The distribution of Synodontis in southern Africa and the type localities of all nominal species considered in this study are given in Figure 6.1.

S.zambezensis has the largest latitudinal distribution, which extends from the Luangwa River of the Middle Zambezi system southwards as far as the Pongolo River. A notable exception is the exclusion of this genus from the Upper Sabi River above the Selawandoma Falls and from the Upper Lundi River above the Chivirira Falls. These natural barriers have prevented the upward migration of 21 fish species in all, and it is postulated that their entry into this system was from the north via the low-lying Mocambique coastal plain before the existence of these falls (Bell-Cross, 1976). S.zambezensis is also known from river systems north of the study area, where it has been recorded from the Luangwe River, a tributary of Lake Mweru (Poll, 1971) and Lake Rukwa (Hilgendorf & Pappenheim, 1903; Ricardo, 1939). Hilgendorf & Pappenheim (1903) described the Lake Rukwa population as a new subspecies, S.zambezensis rukwaensis.

The extent of the geographical distribution of Synodontis species is very variable (Poll, 1971). This feature is best demonstrated in southern Africa by S.zambezensis and S.njassae, where the latter is resticted to Lake Malawi and its tributaries. The southern limit of distribution of S.njassae in the Shire River is effectively curtailed by the ecological barrier constituted by the Murchison Rapids and ultimately by the Kapachira Falls (Tweddle & Willoughby, 1979).

S.nebulosus is known from the Zambezi system below the Victoria Falls and is excluded from the Upper Kafue River by the Chasunta and Avumba Falls. This species is also recorded by Bell-Cross (1976) from the Mocambique section of the Buzi River.

S.macrostigma and S.macrostoma sp.n. have the largest longitudinal distributions among the southern African Synodontis, where they are recorded from the Upper Zambezi, Okavango and Cunene basins. Jubb (1967) mistakenly referred S.woosnami to the Kafue River in distribution tables. This is clearly an error, however, as he failed to identify this species from southern Africa though still recognizing this species as valid on the basis of the original description. In addition, the distribution of S.woosnami corresponds to that quoted in the text for S.macrostigma, which is excluded from the list.

Within southern Africa, S.nigromaculatus is known only from the Upper Zambezi and Okavango basins. Similar to S.zambezensis, the distribution of S.nigromaculatus extends into river systems north of the study area and was originally described from Lake Bangweulu. Two nominal species considered by the present study to be junior synonyms of S.nigromaculatus, namely, S.melanostictus and S.colyeri, were also described from central Africa; the former from Lake Tanganyika and the latter from the Mansa River, a tributary of the Chambezi River. Elsewhere in central Africa, S.nigromaculatus has been recorded from Lake Mweru (Boulenger, 1911a; Poll, 1933, 1971) and the Kasai-Zaire system (Poll, 1967, 1971). Poll (1971) further records S.nigromaculatus from the Limpopo River, referring to Jubb (1961), but overlooked a later amendment in which Jubb (1963a) refers these specimens to S.zambezensis. Poll (1971), Bell-Cross (1976), Jubb (1967) and Barnard (1948) have all recorded S.nigromaculatus from the Cunene River referring to Pellegrin (1936). This species, however, has never subsequently been recorded from this system and was absent in recent large collections made above the Ruacana Falls (van der Waal pers. comm.).

The two remaining species, S.leopardinus and S.thamalakanensis, are both recorded from the Upper Zambezi and Okavango basins. In addition, one of the "S.kafuensis" paratypes is identified as S.leopardinus, which constitutes a new distribution record of this species in the Upper Kafue River.

As an alpha taxonomic study, this revision does not attempt any phylogenetic analysis and therefore will not attempt any biogeographical analysis. Yet it is interesting to note the conformity between certain biogeographical hypotheses and the distribution of southern African Synodontis. Bell-Cross (1968) and Bowmaker et al. (1978), for example, have suggested that the Zambezian ichthyofauna originates from two major drainage basins that occurred in central Africa south of the Zaire. The western basin comprised the Cunene, Okavango, Upper Zambezi, Upper Kafue and Chambezi Rivers, whose fauna was of Zairean origin. The fauna of the eastern basin, which comprised the Lower and Middle Zambezi and the Shire River, was of Nilotic origin. This hypothesis would explain the distributional discontinuities that exist above and below the Victoria Falls and Kafue Gorge.

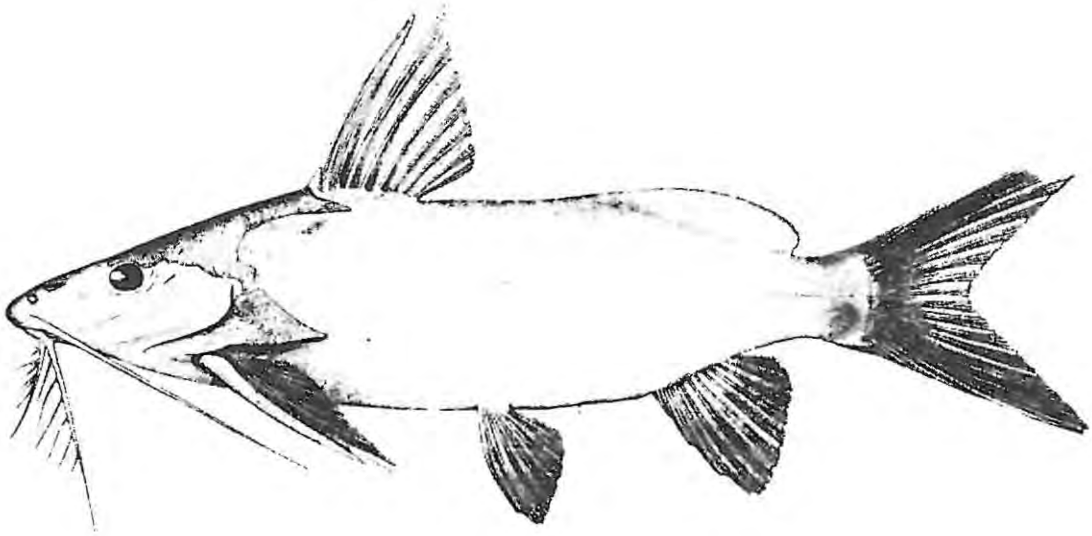

Figure 6.2 Synodontis zambezensis Peters 1852, Lectotype, ZMH 3119, female, 153,3 mm SL (after Poll, 1971: fig. 104).

SPECIES DESCRIPTIONS

Descriptions are presented in the above order of analysis.

Synodontis zambezensis Peters 1852

Figure 6.2, Table 6.1

Synodontis zambezensis Peters, 1852: 682, type locality: Tete, Lower Zambezi River; Peters, 1868: 31; Vaillant, 1896: 126; van der Horst, 1931: 246; Jubb, 1958: 181; Jubb, 1961: 116; Jackson, 1961a: 19, 84; Crass, 1964: 93; Jubb, 1967: 43, 141; Bell-Cross, 1976: 70, 192; Pienaar, 1978: 62.

Synodontis zambesensis, Günther, 1864: 214, unjustified amendment; Boulenger, 1911a: 415; Boulenger 1923: 438; Barnard, 1948: 441; Jubb, 1954: 692, 697; Poll, 1971: 220, 225.

Synodontis zambezensis rukwaensis Hilgendorf & Pappenheim, 1903: 267, type locality: Lake Rukwa.

Material examined

Lectotype: ZMH 3119 (female, 153,3 mm SL, Tete, Zambezi River, Mocambique, W.C.H. Peters).

Paralectotypes: ZMH 3118 (male, 122,0 mm SL, Tete, Zambezi River, Mocambique, W.C.H. Peters); ZMH 3117 (3 x females, 125,1, 137,6 & 159,9 mm SL, ditto); ZMH 3116 (female, 225,6 mm SL, ditto); ZMH 3115 (female, 179,8 mm SL, ditto).

Other material: given in Appendix 1.

Notes on taxonomy

The nine syntypes of S.zambezensis rukwaensis Hilgendorf & Pappenheim (1903)

Table 6.1 Morphometric and meristic data of S.zambezensis

Species	Lectotype	Paralectotypes (n = 7)	S.zambezensis (n = 116)		
			Mean	S.D.	Range
Standard length (mm)	153,30	121,95 - 225,55			72,70 - 225,55
Predorsal length (% SL)	37,18	34,89 - 37,62	37,09	1,72	32,61 - 40,28
Head length (% SL)	29,45	26,94 - 29,07	29,37	1,06	26,94 - 31,84
Snout length (% PDL)	35,70	32,67 - 35,62	34,03	1,13	30,97 - 36,71
Interorbital length (% HL)	34,44	30,59 - 37,20	33,94	2,30	28,03 - 40,25
Dorsal to coracoid (% HL)	89,81	83,19 - 94,37	86,94	3,69	79,30 - 99,46
Pectoral girdle width (% HL)	70,21	75,07 - 83,14	76,40	2,51	69,59 - 83,14
Occ. nuchal shield width (% HL)	110,52	26,95 - 30,26	26,95	1,82	23,09 - 31,74
Humeral process length (% HL)	58,91	59,63 - 64,08	62,44	3,17	53,62 - 69,17
Hum. proc. to occ. nuchal shield (% HL)	50,17	38,49 - 44,98	43,99	4,66	32,66 - 52,24
Orbit diameter (% HL)	13,84	15,22 - 18,98	17,83	2,09	13,75 - 24,26
Dorsal spine length (% HL)	81,40	87,35 - 118,52	92,26	15,98	71,17 - 120,84
Pectoral spine length (% HL)	73,42	79,51 - 90,42	77,94	6,71	64,60 - 100,00
Dorsal fin length (% HL)	-	- -	96,25	15,73	79,24 - 123,87
Caudal fork length (% CTL)	-	30,00 - 44,57	36,57	3,76	28,52 - 46,41
Maxillary barbel length (% HL)	112,07	97,72 -120,98	107,99	11,60	81,66 - 135,82
Outer mandibular barbel length (% HL)	74,86	60,10 - 76,86	68,26	9,05	44,59 - 89,43
Inner mandibular barbel length (% HL)	40,09	28,51 - 43,19	34,18	4,78	25,83 - 51,98
Snout to pectoral (% SL)	22,18	20,53 - 21,63	22,26	0,98	20,53 - 25,68
Snout to pelvic (% SL)	55,19	51,25 - 55,87	54,92	1,98	50,19 - 60,54
Snout to anal (% SL)	75,24	70,44 - 74,86	72,90	1,67	69,74 - 76,55
Caudal peduncle length (% SL)	18,33	17,80 - 20,66	18,07	1,04	14,95 - 20,66
Caudal peduncle depth (% SL)	9,20	8,43 - 8,95	9,71	0,65	8,26 - 11,32
Dorsal to adipose (% SL)	11,90	15,27 - 21,99	13,69	2,73	7,78 - 21,99
Adipose basal length (% SL)	9,98	29,16 - 30,68	28,61	2,18	22,48 - 32,88
Adipose maximum height (% ABL)	51,31	11,99 - 21,88	23,77	3,77	11,99 - 34,29
Adipose to caudal peduncle (% SL)	10,27	10,43 - 12,71	11,06	0,89	9,41 - 13,96
Mouth width (% PGW)	43,38	36,66 - 44,82	45,60	3,09	36,66 - 52,30
Premaxillae width (% PGW)	27,13	22,56 - 28,22	25,12	2,15	20,83 - 33,56
Meristics					
Total vertebrae	39	39 - 41			38 - 41
Precaudal vertebrae	12	12 - 13			11 - 14
Caudal vertebrae	27	27 - 29			26 - 29
Preanal vertebrae	20	20 - 23			20 - 23
Pleural ribs	10	9 - 11			9 - 11
Anal pterygiophores	11	11 - 12			10 - 12
Anal rays	V,9	V - VI, 8 - 9			V - VI, 7 - 10
Pectoral rays	8	8 - 10			8 - 9
Moveable mandibular teeth (Total)	39	27 - 38			20 - 40
Moveable mandibular teeth (First Row)	38	27 - 38			16 - 34

were not examined. The range of all diagnostic features given in the original description, however, are all within the total range of S.zambezensis from southern Africa. As these specimens are considered by Hilgendorf & Pappenheim (1903) to comply with the remaining characters quoted in the descriptions of Peters (1852) and Boulenger (1901), they are here tentatively referred to this species.

Diagnosis

Long, slender, filamentous barbel branches and an elongated, triangular humeral process with a concave postero-dorsal margin initially identifies this species together with S.nigromaculatus and S.njassae as members of Group I. S.zambezensis is distinguished from the former by a narrower occipito-nuchal shield, shorter humeral process and a shorter medial caudal fin ray. S.njassae is distinguished from S.zambezensis from the adjoining basin of the Lower Zambezi by a shorter dorsal spine and longer snout to pectoral distance. Markings in S.zambezensis are often absent or very few in number, particularly in the higher latitudes, but where present are equal to or smaller than the pupil and never overlap to form clusters or elongated lines.

Description

Largest of the southern African Synodontis, reaching 430 mm SL in Lake Kariba (Balon, 1974). Morphometric and meristic data summarized in Table 6.2

Mouth crescent to trapezoid-shaped with moderately broad, smooth to slightly rugose lips. Moveable mandibular teeth numerous (20 - 40), arranged in a single transverse band. Premaxillae broad with no distinction between the numerous (110-167) primary and secondary teeth (Figure 5.41a & Table 5.8).

Maxillary barbels with smooth leading edge, extending well beyond base of pectoral spine. Basal membrane distinct, maximum width less than or equal to half diameter of barbel stem, not extending further than half barbel length from base. Outer mandibular barbels also extending well beyond base of pectoral spine with 5 (4-6) unbranched primary branches. Inner mandibular barbels with 8-9 (6-10) primary branches, the first 3- 4(0-5) possessing a single secondary branch, at or near the base of the primary branch.

Humeral process with slightly to moderately concave (frequently biconcave) postero-dorsal margin and a shallow keel. Generalized shape depicted in Figure 5.39.

Dorsal spine stout, approximately equal to head length, smooth anterior margin, weakly serrated on upper half of posterior margin. Pectoral spines strongly serrated along whole length of inner margin, feebly serrated on outer margin. Pectoral fins not reaching anal fin. Anal fin with longer anterior rays. Caudal fin very deeply forked with long, pointed lobes of fairly similar length.

Colour of body uniform olive brown to slate grey, slightly paler ventrally. Presence of markings in adults variable, increasing in probability in lower latitudes (Figure 5. 2). Markings predominantly circular, decreasing in diameter and more numerous anteriorly. Juveniles (< 70 mm SL) spotted throughout range but showing a high incidence of partial albinism especially in Pongolo population. These pigmentation abnormalities, which confuse their identification, occur typically on the caudal peduncle and adipose fin, but also sometimes present on the sides of the body.

Distribution

Zambezi River below the Victoria Falls, southwards, including most east-flowing rivers up to and including the Pongolo River. Excluded from the Upper Lundi River above the Chivirira Falls and from the Upper Sabi above the

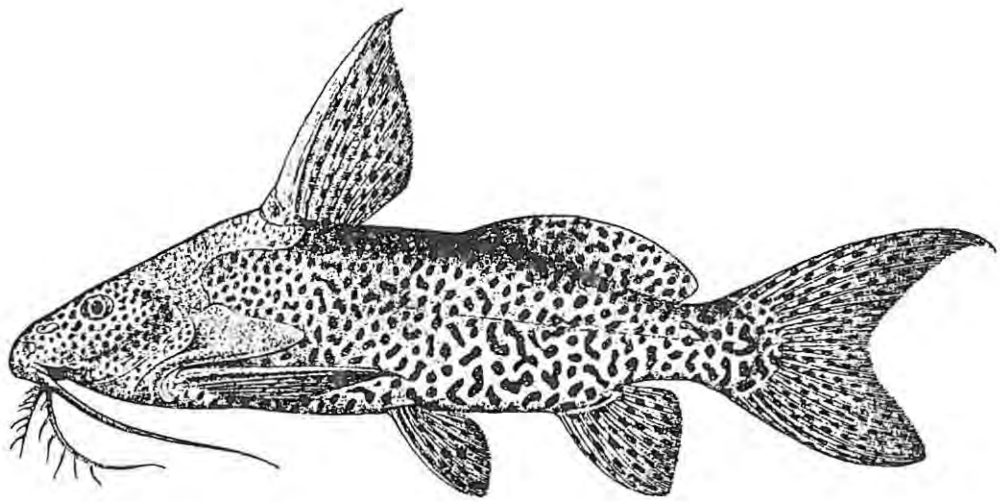

Figure 6.3 Synodontis nigromaculatus Boulenger 1905, Holotype, BMNH 1905.11.10.10, male, 182,6 mm SL (lateral and dorsal view after Boulenger, 1911a: fig. 313; ventral view after Poll, 1971: fig. 148).

Selawandoma Falls (Figure 6.1). The Middle Zambezi population is excluded from the Upper Kafue River by the Chasunta and Avumba Falls within the Kafue Gorge. This species is also known from the Zambian-Zaire system, where it has been recorded from Lake Rukwa (Hilgendorf & Pappenheim, 1903; Ricardo, 1939 and Hulot, 1950) and the Luangwe River, a tributary of Lake Mweru (Poll, 1971).

Synodontis nigromaculatus Boulenger 1905

Figure 6.3, Table 6.2

Synodontis nigromaculatus Boulenger, 1905: 645, type locality: Lake Banguelu; Boulenger 1911b: 416; Ricardo-Bertram, 1943: 187, 209; Jackson, 1961a: 20, 87; Jubb, 1963b: 28; De Kimpe, 1964: 77; Jubb, 1967: 43, 52, 141; Poll, 1971: 325.

Synodontis melanostictus Boulenger, 1906: 553, type locality: Lake Tanganyika; Boulenger 1911a: 418; Gilchrist & Thompson, 1913: 560; Poll, 1933: 134; Fowler, 1935: 273; Worthington & Ricardo, 1936: 1067, 1077; Pellegrin, 1936: 58; Ricardo-Bertram, 1940: 209; Barnard, 1948: 441; Jubb, 1954: 692; 1958: 181; Matthes, 1962: 41; De Kimpe, 1964: 195, 201, 222.

Synodontis colyeri Boulenger 1923: 438, original description, Mansa River, Zambia; Jackson, 1961a: 20, 88; De Kimpe, 1964: 77, 89.

Material examined

Holotype: BMNH 1905.11.10.10 (male, 182,6 mm SL, Lake Banguelu, Zambia, F.M. Melland).

Other material: given in Appendix 1; Holotype of S.melanostictus, male, 230,7 mm SL, Lofu, Lake Tanganyika, W.A.Cunnington; Holotype of

Table 6.2 Morphometric and meristic data of S.nigromaculatus, S.melanostictus and S.colyeri

Morphometrics	S.nigromaculatus Holotype	S.nigromaculatus (n = 75) Mean	S.D.	Range	S.melanostictus Holotype	S.colyeri Holotype
Standard length (mm)	182,60			27,15 - 219,25	230,70	125,30
Predorsal length (% SL)	38,66	37,86	0,98	35,10 - 40,15	37,06	37,51
Head length (% SL)	28,94	29,96	1,33	23,95 - 34,38	28,35	29,13
Snout length (% PDL)	34,35	34,36	1,34	27,54 - 37,70	36,32	33,19
Interorbital length (% HL)	36,99	34,13	1,61	30,48 - 38,01	38,00	31,51
Dorsal to coracoid (% HL)	-	86,16	3,36	77,41 - 93,23	92,28	85,75
Coracoid to neurocranium (% HL)	67,46	58,26	3,37	51,68 - 75,16	62,46	63,97
Pectoral girdle width (% HL)	78,90	82,08	3,55	73,05 - 90,30	91,21	85,89
Occ. nuchal shield width (% HL)	34,06	32,11	1,99	26,75 - 36,22	34,63	31,10
Humeral process length (% HL)	69,35	69,89	3,44	51,67 - 76,60	75,23	71,51
Hum. proc. to occ. nuchal shield (% HL)	42,09	36,03	2,65	29,60 - 42,47	41,06	42,19
Orbit diameter (% HL)	16,08	16,87	1,98	12,98 - 22,11	16,36	18,77
Dorsal spine length (% HL)	99,24	95,45	7,62	71,34 - 113,26	92,05	-
Pectoral spine length (% HL)	87,80	85,68	5,48	65,56 - 95,67	86,24	82,19
Dorsal fin length (% HL)	97,07	98,68	5,18	88,94 - 111,95	88,91	-
Caudal fork length (% CTL)	-	47,44	5,71	38,22 - 58,56	40,15	-
Maxillary barbel length (% HL)	121,29	122,75	10,45	94,55 - 144,59	128,44	95,89
Outer mandibular barbel length (% HL)	83,07	82,87	5,84	70,75 - 97,93	96,33	72,88
Inner mandibular barbel length (% HL)	36,71	41,71	3,79	34,62 - 52,22	48,62	37,27
Snout to pectoral (% SL)	22,32	22,42	1,10	18,26 - 24,94	23,47	23,50
Snout to pelvic (% SL)	51,78	54,90	1,29	52,65 - 58,61	55,87	58,62
Snout to anal (% SL)	71,96	72,89	1,60	69,70 - 75,97	76,16	73,58
Caudal peduncle length (% SL)	19,17	18,03	0,60	16,87 - 19,36	18,38	17,12
Caudal peduncle depth (% SL)	9,51	8,74	0,52	7,69 - 9,76	9,23	8,62
Dorsal to adipose (% SL)	11,39	13,84	1,61	10,77 - 17,25	12,25	10,85
Adipose basal length (% SL)	30,58	26,78	1,46	23,75 - 30,59	28,93	30,57
Adipose maximum height (% ABL)	21,51	23,98	2,68	18,95 - 30,49	26,97	19,40
Adipose to caudal peduncle (% SL)	10,12	9,91	0,57	8,48 - 10,79	10,73	9,38
Mouth width (% PGW)	44,60	48,30	3,90	38,53 - 58,42	41,49	46,09
Premaxillae width (% PGW)	24,82	28,46	1,74	25,00 - 33,23	26,66	27,11
Meristics						
Total vertebrae	40			40 - 42	42	40
Precaudal vertebrae	13			11 - 14	14	12
Caudal vertebrae	27			27 - 30	28	28
Preanal vertebrae	21			21 - 24	24	21
Pleural ribs	10			9 - 11	11	11
Anal pterygiophores	11			10 - 11	11	11
Anal rays	V,9			IV - VI, 7-9	V,8	V,8
Pectoral rays	8			8 - 9	9	8
Moveable mandibular teeth (Total)	31			21 - 43	36	24
,, ,, ,, (Functional)	25			17 - 33	28	18

S.colyeri, female, 125,3 mm SL, Mansa River, Zambia, Dr Colyer).

Notes on taxonomy

An illustration of the holotype of S.nigromaculatus in dorsal view published by Poll (1971) shows two prominent strongly recurved projections on the posterior half of each humeral process --- a feature found neither in any of the specimens examined in this study nor previously recorded for this species. I can only presume that this illustration, which closely resembles the holotype of S.omias Gunther, was transposed in error.

No significant differences were noted between the morphometric and meristic data of the types of S.nigromaculatus, S.melanostictus, S.colyeri and the range described by 75 specimens from the Upper Zambezi and Okavango. These three species were thus united under the oldest name, S.nigromaculatus. The slight discrepancy in the proportional measurement of predorsal length in S.melanostictus can be attributed to the very large size of this specimen, which is 11,45 mm longer in standard length than any other used in the description.

Diagnosis

This species closely resembles S.zambezensis and S.njassae in having long, slender, filamentous barbels and an elongated, triangular humeral process with a straight to slightly concave postero-dorsal margin (Figure 5.39). S.nigromaculatus is distinguished from S.zambezensis by a wider pectoral girdle and occipito-nuchal shield and from S.njassae by longer dorsal and pectoral spines, longer adipose to caudal peduncle distance, and a longer medial caudal ray. The greenish hue which covers the entire body and fins in live specimens is a unique characteristic among the southern African Synodontis.

Description

A large species with a maximum recorded size of 299 mm SL (Poll, 1971). Morphometric and meristic data summarized in Table 6.3.

Mouth rectangular, twice as wide as it is long, with moderately broad lips; smooth to slightly rugose in texture. Moveable mandibular teeth numerous (21-43), arranged in a broad transverse band. Premaxillae broad with no distinction between the numerous (120-225) primary and secondary teeth (Figure 5.41a & Table 5.8).

Maxillary barbels with smooth leading edge, extending beyond posterior base of pectoral fin. Basal membrane usually absent; when present is very narrow, not extending beyond 1/3 barbel length from base and of similar colouring to barbel stem. Outer mandibular barbels extend beyond base of pectoral spine with 5-8 (4-10) unbranched primary branches. Inner mandibular barbels with 8-10 (7-12) primary branches, the first 2-5 (1-6) possessing a single secondary branch, at or near the base of the primary branch.

Dorsal spine strong, ending in a short filament, approximately equal to length of head, anterior margin smooth except for 4 (1-4) serrations at the tip, serrated on the upper half of the posterior margin.

Caudal fin large, moderately to slightly forked, with a sharply-pointed upper lobe that is distinctly longer than the more rounded lower lobe.

Live colouration of body olive green dorsally to olive yellow ventrally with yellow to greenish yellow barbels. Fins slightly darker than body. Body and fins with numerous, separate black spots, a few of which may overlap on sides of body and on caudal peduncle to form short lines, or grouped in constellations of 3-5. Size of spots largest on the sides of body, caudal peduncle and

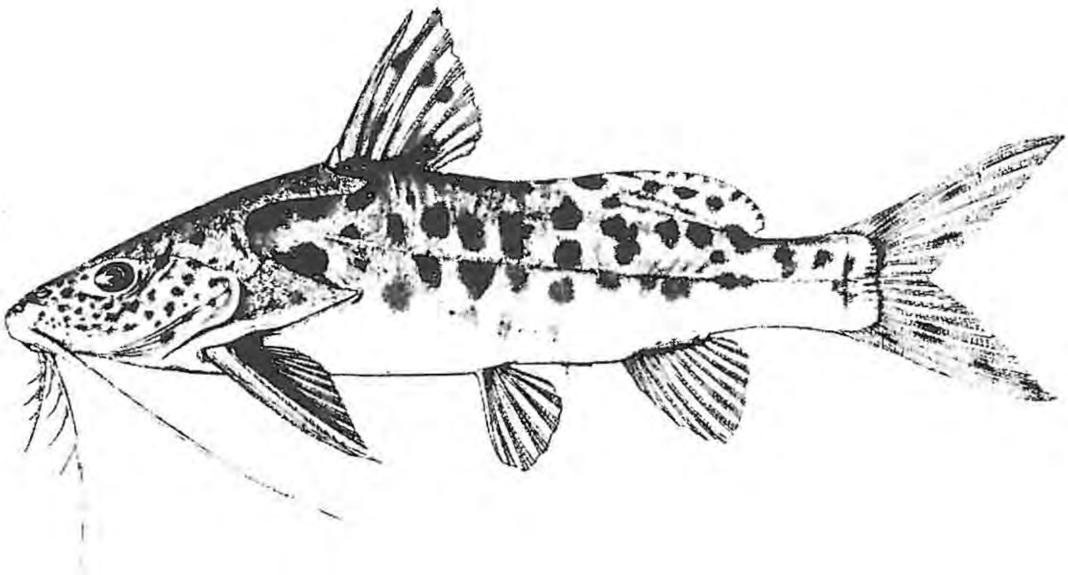

Figure 6.4 Synodontis njassae Keilhack 1908, Lectotype, ZMH 18191, male, 151,0 mm SL (after Poll, 1971: fig. 154).

adipose fin, decreasing progressively anteriorly. Spots slightly larger and less numerous in juveniles. Partial albinism has been recorded in specimens less than 70 mm SL and occurs typically on the caudal peduncle, adipose fin and sides of the body.

Distribution

Lake Banguelu, Lake Tanganyika, Okavango and Upper Zambezi systems (Figure 6.1). This species is also known from the Kasai-Zaire system where it has been recorded from the Chiumbe, Luembe, Kasai, Luachimo and Uamba Rivers (Poll, 1967, 1971 and David & Poll, 1937).

Synodontis njassae Keilhack 1908

Figure 6.4, Table 6.3

Synodontis njassae Keilhack, 1908: 168, type locality: Lake Njassa (Malawi); Jackson, 1959: 300; Jackson, 1961b: 556, 597; Poll, 1971: 215, 337; Bell-Cross, 1972: 6.

Synodontis zambesensis: Günther, 1894: 619; Boulenger, 1898: 4; Boulenger, 1911a: 451; Worthington, 1933b: 291, 294.

Material examined

Lectotype: ZMH 18191 (male, 151 mm SL, Lake Nyassa (Malawi) at Langenburg, Tanzania, S. Fulleborn).

Paratypes: ZMH 18192 (4 x 91-145 mm SL, ditto).

Other material: given in Appendix 1.

Diagnosis

S.njassae most closely resembles S.nigromaculatus and S.zambezensis,

Table 6.3 Morphometric and meristic data of S.njassae

Morphometrics	Lectotype	Paratypes (n = 4)	S.njassae (n = 29) Mean	S.D.	Range
Standard length (mm)	151,00	103,60 - 143,00			68,85 - 192,30
Predorsal length (% SL)	42,05	39,86 - 41,41	39,40	1,58	35,97 - 42,37
Head length (% SL)	32,12	30,91 - 34,63	31,44	1,13	28,86 - 33,53
Snout length (% PDL)	32,58	30,81 - 32,98	33,74	1,29	31,38 - 36,16
Interorbital length (% HL)	57,11	33,14 - 40,44	36,00	2,25	31,74 - 40,57
Dorsal to coracoid (% HL)	92,78	82,70 - 96,44	86,96	2,61	81,68 - 91,50
Coracoid to neurocranium (% HL)	54,64	54,71 - 61,33	60,77	2,27	56,45 - 65,65
Pectoral girdle width (% HL)	80,41	72,52 - 82,22	81,16	1,50	77,31 - 84,48
Occ. nuchal shield width (% HL)	30,96	30,21 - 32,58	27,24	0,74	24,20 - 30,80
Humeral process length (% HL)	61,86	56,74 - 64,52	61,58	2,97	56,16 - 69,21
Hum. proc. to occ. nuchal shield (%HL)	-	- -	39,22	2,49	35,20 - 44,52
Orbit diameter (% HL)	18,56	18,83 - 22,87	20,23	1,76	17,22 - 23,05
Dorsal spine length (% HL)	69,90	64,00 - 78,73	69,55	6,40	59,38 - 84,21
Pectoral spine length (% HL)	69,48	72,00 - 80,77	70,00	3,26	65,19 - 76,01
Dorsal fin length (% HL)	-	- -	65,98	5,23	58,30 - 75,66
Caudal fork length (% CTL)	32,45	29,89 33,33	33,05	2,79	28,37 - 38,11
Maxillary barbel length (% HL)	134,02	122,14 -133,33	126,59	20,30	89,35 - 161,35
Outer mandibular barbel length (% HL)	79,38	68,91 - 80,00	73,99	9,83	55,70 - 95,35
Inner mandibular barbel length (% HL)	41,24	31,81 - 45,45	38,44	6,13	27,91 - 51,65
Snout to pectoral (% SL)	-	- -	24,61	0,98	22,55 - 27,03
Snout to pelvic (% SL)	-	- -	56,98	1,26	54,54 - 59,46
Snout to anal (% SL)	-	- -	72,40	1,35	68,51 - 74,78
Caudal peduncle length (% SL)	-	- -	18,20	0,55	17,03 - 19,25
Caudal peduncle depth (% SL)	-	- -	9,79	0,56	8,74 - 10,80
Dorsal to adipose (% SL)	-	- -	13,73	2,17	9,89 - 18,81
Adipose basal length (% SL)	-	- -	25,22	2,05	21,70 - 28,82
Adipose maximum height (% ABL)	-	- -	22,45	3,70	18,16 - 29,50
Adipose to caudal peduncle (% SL)	-	- -	12,12	0,87	10,82 - 14,26
Mouth width (% PGW)	-	- -	46,60	3,22	40,61 - 52,58
Premaxillae width (% PGW)	25,90	22,57 - 25,96	27,13	1,77	22,19 - 29,53

Meristics

Meristics	Lectotype	Paratypes (n = 4)	S.njassae (n = 29) Range
Total vertebrae	40	39 - 41	39 - 41
Precaudal vertebrae	12	11 - 12	11 - 12
Caudal vertebrae	28	28 - 29	28 - 29
Preanal vertebrae	21	21	21 - 22
Pleural ribs	10	9 - 10	9 - 10
Anal pterygiophores	11	10 - 11	10 - 11
Anal rays	VI,8	V - VI, 7 - 9	V - VI, 8 - 9
Pectoral rays	9	8 - 9	7 - 8
Moveable mandibular teeth (Total)	24	25 - 32	22 - 32
,, ,, ,, (Functional)	23	20 - 24	20 - 31

particularly in having long, slender, filamentous barbels and an elongated, triangular humeral process with a concave postero-dorsal margin and shallow keel (Figure 5.39). S.njassae is distinguished from S.zambezensis by a larger snout to pectoral distance, shorter dorsal spine and shorter dorsal fin. It is distinguished from S.nigromaculatus by a narrower occipito-nuchal shield, shorter dorsal and pectoral spines, shorter dorsal fin, longer adipose to caudal peduncle distance and a more deeply forked caudal fin. The size of markings is significantly larger than either S.zambezensis or S.nigromaculatus and the markings are more widely spaced.

Description

A medium-sized species with a maximum recorded size of 192 mm SL (Poll, 1971). Morphometric and meristic data summarized in Table 6.4.

Mouth crescent to trapezoid-shaped, twice as broad as long with relatively narrow lips that are smooth to slightly rugose. Moveable mandibular teeth fairly numerous (22-32), arranged in a broad transverse band. Premaxillae broad with no distinction between the numerous (118-250) primary and secondary teeth (Figure 5.41a & Table 5.8).

Maxillary barbels with smooth leading edge, extending well beyond posterior base of pectoral fins. Basal membrane absent or indistinct, of similar colouring to barbel stem. Outer mandibular barbels extending beyond anterior base of pectoral spine with 4-7 unbranched primary branches. Inner mandibular barbels with 6-8 (5-9) primary branches, the first 0 (0-4) possessing a single secondary branch at or near the base of the primary branch. Dorsal spine ending in a short filament, smooth anterior margin except for 2 (2-5) small serrations at tip, finely serrated on upper half of posterior margin. Pectoral spines stout, ending in short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pectoral fins not

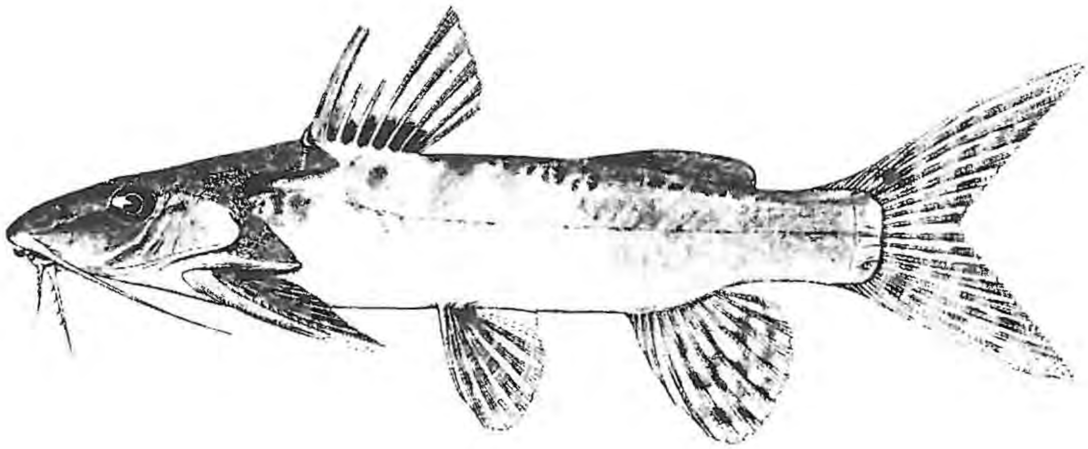

Figure 6.5 Synodontis nebulosus Peters 1852, Holotype, ZMH 3120, female, 116,2 mm SL (after Poll, 1971: fig. 102).

reaching anal fin. Anterior rays of the anal fin longer than posterior rays. Caudal fin deeply forked, with narrow, sharply-pointed lobes of similar length.

Live colouration of body light grey to slate grey dorsally, very pale grey to cream ventrally. Markings predominantly spherical, equal to or greater than the diameter of the eye on sides of the body, adipose and fins, decreasing progressively in size on the head. Spots widely separated on body, numerous and more concentrated on the head, absent or few in number on belly and absent from ventral surface of head. Juvenile markings slightly larger and less numerous.

Distribution

Lake Malawi and its tributaries; Shire River above the Kapachira Falls (Figure 6.1).

Synodontis nebulosus Peters 1852

Figure 6.5, Table 6.4

Synodontis nebulosus Peters, 1852: 682, type locality: Tete, Lower Zambezi River; Peters, 1868: 28; Günther, 1864: 213; Vaillant, 1896: in part 158, 167; Boulenger, 1911a: 423; Barnard, 1948: 442; Jackson, 1961a: 20, 86; Jubb, 1961: 43, 118; Jubb, 1963b: 7, 12, 28; Jubb, 1967: 43, 52, 141; Poll, 1971: 218, 222.

? Synodontis nebulosus: Pfeffer, 1889: 13; Vaillant, 1896: in part 158, 167.

Material examined

Holotype: ZMH 3120 (116,2 mm SL, Tete, Lower Zambezi River, Mocambique,

Table 6.4 Morphometric and meristic data of S.nebulosus

		S.nebulosus (n = 13)		
Morphometrics	Holotype	Mean	S.D.	Range
Standard length (mm)	116,20			69,95 - 118,00
Predorsal length (% SL)	36,75	37,88	0,73	36,55 - 38,81
Head length (% SL)	30,55	30,79	0,21	29,44 - 32,09
Snout length (% PDL)	36,07	37,22	0,86	35,88 - 38,58
Interorbital length (% HL)	33,38	30,81	0,94	29,05 - 33,38
Dorsal to coracoid (% HL)	79,15	80,99	0,64	76,17 - 84,28
Coracoid to neurocranium (% HL)	59,15	58,38	3,52	54,85 - 65,93
Pectoral girdle width (% HL)	77,50	79,70	2,04	77,16 - 84,60
Occ. nuchal shield width (% HL)	31,41	33,38	1,63	29,98 - 35,89
Humeral process length (% HL)	51,55	59,57	2,92	54,50 - 63,67
Hum. proc. to occ. nuchal shield (% HL)	42,60	36,78	2,99	32,01 - 42,68
Orbit diameter (% HL)	20,85	19,90	1,41	17,84 - 22,94
Dorsal spine length (% HL)	-	81,11	7,04	71,27 - 92,31
Pectoral spine length (% HL)	-	76,73	4,74	71,07 - 86,99
Dorsal fin length (% HL)	-	78,63	3,73	72,29 - 85,71
Caudal fork length (% CTL)	42,25	45,86	2,96	40,67 - 49,49
Maxillary barbel length (% HL)	74,93	87,91	6,08	74,93 - 98,69
Outer mandibular barbel length (% HL)	44,51	49,60	4,04	40,79 - 55,38
Inner mandibular barbel length (% HL)	22,82	26,70	2,39	22,54 - 31,10
Snout to pectoral (% SL)	22,03	22,86	1,59	19,97 - 25,83
Snout to pelvic (% SL)	53,79	53,15	2,07	49,56 - 56,26
Snout to anal (% SL)	74,90	72,12	1,74	69,05 - 75,00
Caudal peduncle length (% SL)	18,67	17,61	0,86	16,15 - 18,73
Caudal peduncle depth (% SL)	11,14	10,98	0,50	10,04 - 11,60
Dorsal to adipose (% SL)	20,39	14,85	1,68	12,71 - 20,40
Adipose basal length (% SL)	22,12	25,73	1,62	21,59 - 27,53
Adipose maximum height (% ABL)	15,18	20,39	3,33	14,43 - 24,26
Adipose to caudal peduncle (% SL)	12,35	12,09	1,10	9,20 - 13,35
Mouth width (% PGW)	-	49,15	4,09	42,34 - 56,20
Premaxillae width (% PGW)	-	25,78	1,94	22,99 - 28,60
Meristics				
Total vertebrae	37			37 - 38
Precaudal vertebrae	12			11 - 12
Caudal vertebrae	25			25 - 27
Preanal vertebrae	20			20 - 21
Pleural ribs	9			9
Anal pterygiophores	11			10 - 12
Anal rays	V,8			V - VI, 7 - 9
Pectoral rays	8			8 - 9
Moveable mandibular teeth (Total)	16			12 - 24
,, ,, ,, (Functional)	-			8 - 20
Premaxillary teeth (Primary)	-			25 - 36
,, ,, (Tertiary) Row 1	-			21 - 28
,, ,, ,, Row 2	-			5 - 19

W.C.H. Peters).

Other material: given in Appendix 1.

Diagnosis

S.nebulosus is known only from the Middle and Lower Zambezi drainages where it is distinguishable from S.zambezensis by shorter barbels, shorter outer mandibular barbels branches, a convex rather than concave postero-dorsal margin to the humeral process, fewer moveable mandibular teeth, and a pattern of markings composed of irregular shaped blotches rather than circular spots that are larger than the orbit.

Description

A medium-sized species with a maximum standard length of 290 mm recorded by Balon (1974) from Lake Kariba. Morphometric and meristic data summarized in Table 6.1.

Mouth crescent to trapezoid-shaped, 2-3 times as broad as long, with moderately broad, slightly rugose lips. Moveable mandibular teeth few in number (12-24) and arranged in a narrow transverse band. Premaxillae relatively broad with 24-35 primary teeth situated on a short, slightly rounded ventral shelf. Tertiary teeth arranged in two distinct rows (21-28, 5-19) (Figure 5.41b and Table 5.8).

Maxillary barbels with smooth leading edge extending beyond posterior base of pectoral spine. Basal membrane absent or indistinct, of similar colouring to barbel stem. Outer mandibular barbels not extending beyond anterior margin of pectoral spine; 7-13 primary branches, 0-4 of which possess a single secondary branch at or near tip of primary branch.

Dorsal spine short, ending in a short filament, smooth anterior margin except for 2-4 fine serrations at tip; posterior margin finely serrated throughout whole length. Pectoral spine ending in a short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pectoral fins not reaching base of anal fin. Anal fin with longer anterior rays. Caudal fin deeply forked with sharply-pointed lobes of similar length. Shallow, long-based adipose fin.

Live colouration olive green to brown with markings over entire body surface, finely spotted on head, large irregular-shaped blotches larger than diameter of eye on the sides of the body and adipose. Markings usually of a brown pigment but sometimes light yellowish-brown, which makes their detection difficult, especially on the ventral surface. Fins with evenly distributed spots, approximately equal to pupil of eye.

Distribution

Lower and Middle Zambezi systems, excluding Kafue River above the Chasunta and Avumba Falls (Figure 6.1). An unconfirmed report of specimens collected in the Mocambique section of the Buzi River by Mr Renato Morais is noted by Bell-Cross (1976).

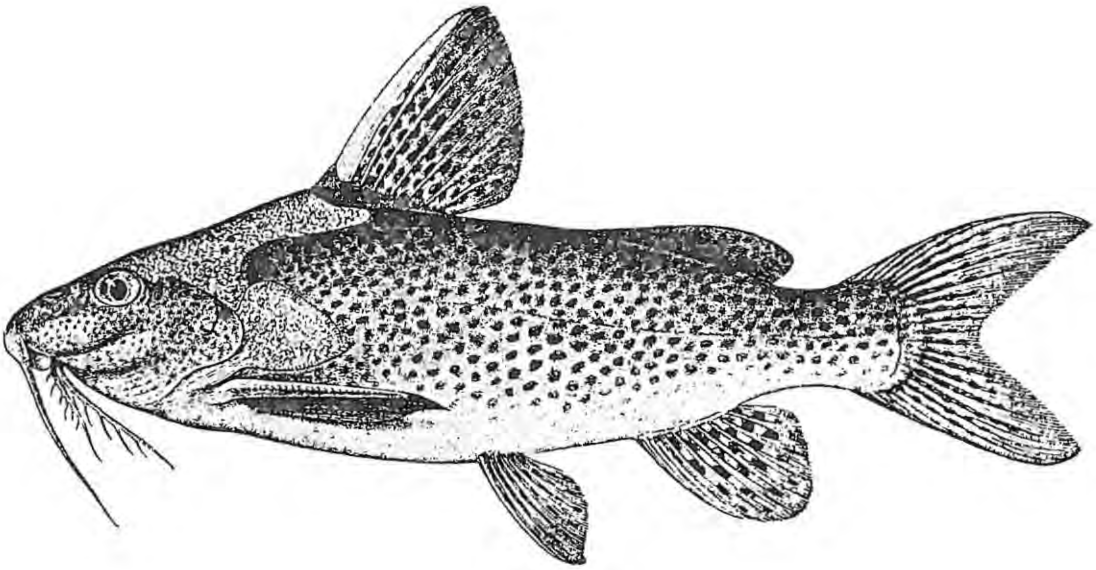

Figure 6.6 Synodontis woosnami Boulenger 1911, Holotype, BMNH 1910.5.31.36, male, 131,2 mm SL (lateral and dorsal view after Boulenger, 1911a: fig. 319; ventral view after Poll,1971: fig. 156).

Synodontis woosnami Boulenger 1911

Figure 6.6, Table 6.5

Synodontis woosnami Boulenger, 1911b: 424, type locality, Okavango River; Gilchrist & Thompson, 1913: 459; Fowler, 1931: 236; Fowler, 1935: 275; Pellegrin, 1936: 58; Jubb, 1958: 181; Jubb, 1961: 39, 43, 118; Jubb, 1963b: 7, 12, 28; Jubb, 1967: 43, 141; Poll, 1971: 216, 342; Bell-Cross, 1976: 191.

Synodontis macrostigma: Jubb, 1961: 39, 118; Jubb, 1967: in part, 143, Figure 157b.

Material examined

Holotype: BMNH 1910.5.31.36 (male, 131,2 mm SL, Okavango River, R.B. Woosnam).

Other material: given in Appendix 1.

Diagnosis

A large, broad, obtusely-pointed humeral process, with a strongly convex postero-dorsal margin in adults that is progressively narrower and more elongated in smaller specimens (Figure 5.36) initially places this species in Group II. The most valuable diagnostic features that distinguish S.woosnami from other species of this group are its long, slender, filamentous (Group I-like) barbels in comparison with the short thick, papilliform mandibular barbels more generally characteristic of Group II species. S.woosnami can be further differentiated by its dentition, where no distinction exists between primary and secondary premaxillary teeth, in comparison with a clear distinction in Group II species, where primary teeth are all arranged on a distinct ventral shelf (Figure 5.41c & Table 5.8). In addition, S.woosnami

Table 6.5 Morphometric and meristic data of S.woosnami

Morphometrics	Holotype	S.woosnami (n = 66) Mean	S.D.	Range
Standard length (mm)	131,20			45,35 - 204,10
Predorsal length (% SL)	37,61	39,09	1,69	35,07 - 42,65
Head length (% SL)	30,83	30,66	1,41	27,12 - 33,77
Snout length (% PDL)	36,58	34,99	1,29	32,41 - 38,32
Interorbital length (% HL)	33,13	33,28	2,30	29,77 - 38,49
Dorsal to coracoid (% HL)	92,34	88,48	4,40	77,14 - 101,15
Coracoid to neurocranium (% HL)	67,99	68,63	4,05	60,43 - 77,17
Pectoral girdle width (% HL)	80,47	85,38	3,48	73,92 - 91,43
Occ. nuchal shield width (% HL)	33,75	34,58	1,92	28,48 - 38,90
Humeral process length (% HL)	66,50	63,45	3,23	53,81 - 68,97
Hum. proc. to occ. nuchal shield (% HL)	48,20	37,27	4,54	28,48 - 48,21
Orbit diameter (% HL)	15,37	20,01	2,31	15,33 - 25,48
Dorsal spine length (% HL)	99,01	96,76	7,31	81,43 - 117,63
Pectoral spine length (% HL)	79,48	82,82	4,60	72,25 - 93,91
Dorsal fin length (% HL)	-	93,07	5,71	80,48 - 112,95
Caudal fork length (% CTL)	-	49,67	2,43	42,36 - 56,97
Maxillary barbel length (% HL)	83,95	101,96	7,57	83,94 - 117,40
Outer mandibular barbel length (% HL)	55,40	68,28	6,13	54,84 - 81,02
Inner mandibular barbel length (% HL)	41,29	45,25	3,72	36,72 - 54,07
Snout to pectoral (% SL)	24,28	25,01	1,35	21,51 - 27,10
Snout to pelvic (% SL)	57,09	54,58	1,93	52,19 - 59,12
Snout to anal (% SL)	76,30	73,27	1,60	70,64 - 76,33
Caudal peduncle length (% SL)	18,37	17,54	0,68	16,11 - 19,72
Caudal peduncle depth (% SL)	11,80	10,73	0,54	9,61 - 11,81
Dorsal to adipose (% SL)	17,30	15,46	1,98	11,98 - 20,17
Adipose basal length (% SL)	21,19	23,04	1,68	20,93 - 28,18
Adipose maximum height (% ABL)	23,74	24,85	2,24	21,84 - 29,21
Adipose to caudal peduncle (% SL)	13,03	13,19	0,75	11,63 - 14,61
Mouth width (% PGW)	38,56	48,32	4,64	39,08 - 58,54
Premaxillae width (% PGW)	20,58	24,10	2,85	20,11 - 32,50
Meristics				
Total vertebrae	38		37 - 39	
Precaudal vertebrae	12		11 - 12	
Caudal vertebrae	26		25 - 27	
Preanal vertebrae	20		19 - 21	
Pleural ribs	9		9 - 10	
Anal pterygiophores	11		10 - 12	
Anal rays	V,9		V - VI, 7 - 9	
Pectoral rays	7		7 - 8	
Moveable mandibular teeth (Total)	22		14 - 24	
,, ,, ,, (Functional)	20		12 - 20	
Premaxillary teeth (Tertiary) Row 1	20		11 - 21	

can be distinguished from S.vanderwaali sp.n. by fewer moveable mandibular teeth.

Description

A moderately large species with a maximum recorded size of 204,1 mm SL. Morphometric and meristic data summarized in Table 6.5.

Mouth rectangular to semi-circular, not more than twice as broad as long. Lips moderately broad, slightly to moderately rugose. Moveable mandibular teeth few in number (14-24), arranged typically in a narrow semi-circular band. No distinction between primary and secondary premaxillary teeth, which are all short and situated on posterior face; the ventral shelf usually very narrow or absent (Figure 5.41c). Tertiary premaxillary teeth short, relatively thick, few in number (11-12) and arranged in only one row.

Maxillary barbels usually with smooth leading edge, extending well beyond anterior base of pectoral spine; a few small widely-separated papillae occasionally present in very large specimens. Basal membrane narrow and darkly pigmented, with a maximum width usually 1/2 but occasionally 3/4 width of barbel stem. Outer mandibular barbels equal to or extending beyond anterior margin of pectoral spine, with 6-8 (3-10) usually unbranched primary branches; secondary branching present in only 6% of the specimens studied and only in one primary branch. Inner mandibular barbels with 9-11 (7-13) primary branches, the first 1-2 (1-5) possessing a single secondary branch.

Dorsal spine very stout, shorter than predorsal length and ending in a short filament, with a smooth anterior margin except for 2 (2-4) serrations at tip, finely serrated on posterior margin. Pectoral spines stout, ending in short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pelvic fins not reaching anal fin. Anal fin distinctly rounded

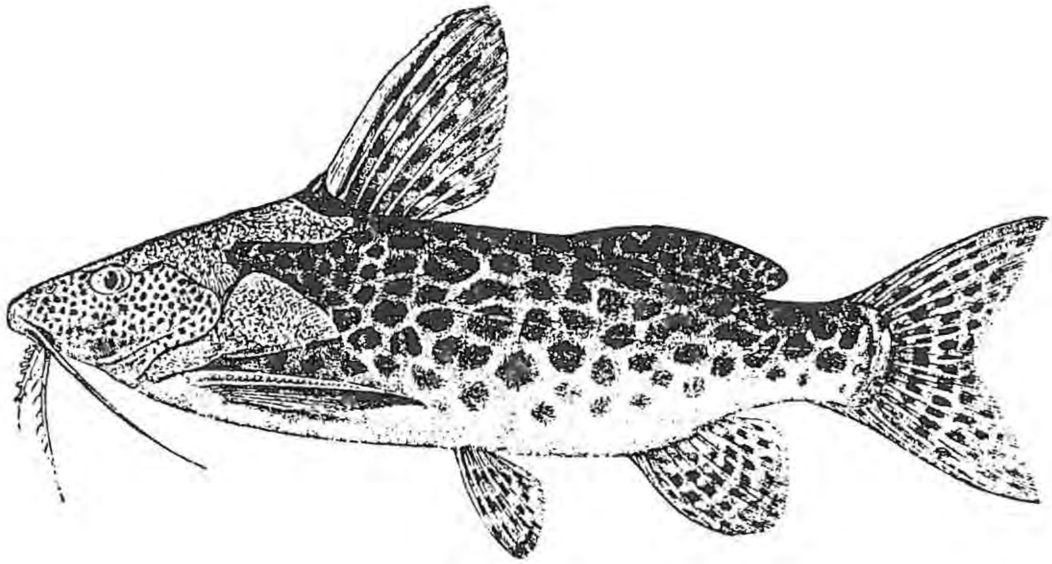

Figure 6.7 Synodontis macrostigma Boulenger 1911, Lectotype, BMNH 1910.5.31.37, female, 135,0 mm SL (lateral and dorsal view after Boulenger, 1911a: fig. 325; ventral view after Poll, 1971: fig. 158).

with first ray equal to or shorter than second and third rays.

Natural colouration variable, usually dark brown dorsally extending to lighter brown to olive brown on sides of body and very pale brown to cream ventrally. An additional yellow pigment may be present over entire body and fins in certain populations. Pattern of markings very variable, ranging from numerous small predominantly circular spots, equal to or smaller than pupil, to fewer, larger spherical to ovoid spots, larger than the diameter of the eye on sides of the body (Figure 5.44). Ventral regions usually unspotted.

Distribution

Upper Zambezi, Okavango and Cunene drainages (Figure 6.1).

Synodontis macrostigma Boulenger 1911

Figure 6.7, Table 6.6

Synodontis macrostigma Boulenger, 1911b: 432, type locality, Okavango River; Gilchrist & Thompson, 1913: 462; Boulenger, 1914: 385; Boulenger, 1916: 318; Fowler, 1935: 275; Pellegrin, 1936: 58; Barnard, 1948: 442; Jubb, 1954: 692, 697; Jubb, 1958: 181; Jackson, 1961a: 20, 86; Bell-Cross, 1965: 13, 17, 97, 106; Jubb, 1967: 43, 52, 143; Poll, 1971: 213, 345.

Synodontis woosnami: Jubb, 1961: 39; Farquharson, 1969: 61 in part.

Material examined

Lectotype: BMNH 1910.5.31.37 (female, 135,0 mm SL, Okavango River, R.B.

Table 6.6 Morphometric and meristic data of S.macrostigma

Morphometrics	Lectotype	Paralectotype	S.macrostigma (n = 96) Mean	S.D.	Range
Standard length (mm)	135,00			-	48,75 - 158,55
Predorsal length (% SL)	36,37	38,50	38,82	1,61	35,75 - 39,94
Head length (% SL)	30,11	31,50	32,02	1,23	29,39 - 35,12
Snout length (% PDL)	36,46	35,19	34,98	1,36	29,40 - 37,44
Interorbital length (% HL)	35,42	30,86	32,92	2,56	27,57 - 41,17
Dorsal to coracoid (% HL)	91,76	87,45	87,25	5,99	72,92 - 103,44
Coracoid to neurocranium (% HL)	70,73	68,72	66,72	4,36	58,33 - 78,89
Pectoral girdle width (% HL)	85,33	86,83	83,58	3,25	76,89 - 96,41
Occ. nuchal shield width (% HL)	39,36	37,86	35,82	3,09	29,89 - 45,06
Humeral process length (% HL)	64,44	60,08	62,22	2,95	56,52 - 72,31
Hum. proc. to occ. nuchal shield (%HL)	47,23	38,48	39,32	4,50	29,14 - 47,98
Orbit diameter (% HL)	15,74	18,52	19,10	3,23	14,61 - 26,44
Dorsal spine length (% HL)	99,02	86,42	92,01	11,35	74,81 - 110,55
Pectoral spine length (% HL)	77,74	75,72	79,74	4,13	71,63 - 89,82
Dorsal fin length (% HL)	94,46	-	91,76	9,52	73,27 - 110,55
Caudal fork length (% CTL)	63,17	-	55,95	6,54	39,83 - 66,45
Maxillary barbel length (% HL)	80,93	76,13	91,34	6,77	77,54 - 112,62
Outer mandibular barbel length (% HL)	51,17	44,03	56,80	5,28	46,43 - 73,92
Inner mandibular barbel length (% HL)	33,70	29,84	35,48	4,02	26,17 - 53,21
Snout to pectoral (% SL)	23,70	25,79	24,41	1,32	21,80 - 27,71
Snout to pelvic (% SL)	54,67	52,75	54,77	1,95	50,09 - 58,55
Snout to anal (% SL)	74,15	76,67	72,19	1,94	68,58 - 77,00
Caudal peduncle length (% SL)	18,44	18,08	18,12	1,12	15,82 - 20,45
Caudal peduncle depth (% SL)	11,52	11,54	11,10	0,55	9,81 - 12,49
Dorsal to adipose (% SL)	15,67	15,81	16,66	2,77	8,37 - 22,65
Adipose basal length (% SL)	24,30	22,81	22,03	2,85	14,86 - 30,57
Adipose maximum height (% ABL)	24,24	21,88	25,24	3,87	18,53 - 34,01
Adipose to caudal peduncle (% SL)	12,22	13,09	13,16	0,92	10,98 - 15,46
Mouth width (% PGW)	38,74	40,28	42,21	4,30	34,38 - 52,89
Premaxillae width (% PGW)	20,61	20,38	21,09	2,88	15,72 - 27,90
Meristics					
Total vertebrae	38	37			37 - 39
Precaudal vertebrae	11	12			11 - 13
Caudal vertebrae	27	25			25 - 28
Preanal vertebrae	19	20			19 - 21
Pleural ribs	9	9			8 - 10
Anal pterygiophores	12	11			11 - 12
Anal rays	V,8	VI,8			IV - VI, 7 - 9
Pectoral rays	8	8			7 - 8
Moveable mandibular teeth (Total)	27	23			15 - 34
,, ,, ,, (Functional)	25	17			12 - 26
Premaxillary teeth (Primary)	25	24			17 - 30
,, ,, (Tertiary) Row 1	-	-			12 - 30
Row 2	-	-			0 - 14

Woosnam).

Paralectotype: BMNH 1910.5.31.38 (77,2 mm SL, ditto).

Other material: given in Appendix 1.

Diagnosis

As previously mentioned (p.129, Figure 5.43), the name of this species was derived from its characteristic markings of large blotches. The present study has shown, however, that this species is not able to be diagnosed within Group II using this character. S.macrostoma sp.n. and S.woosnami, for example, from the Cunene, share very similar markings. S.macrostigma can be distinguished from S.macrostoma sp.n. by a shorter snout, larger interorbital length and longer barbels, the maxillary barbels possessing a distinct basal membrane. S.macrostigma differs from S.woosnami in having a papillose leading edge to the maxillary barbels and short, thick, tuberculose branches on the mandibular barbels. One further diagnostic feature enabling this species to be differentiated from all other Group II species is the markedly shallow fork of the caudal fin, shown in the large ratio of caudal fork length to caudal total length, particularly noticeable in adult specimens.

Description

A relatively small species with a maximum recorded size of 171 mm SL (Poll, 1971). Morphometric and meristic data summarized in Table 6.6.

Mouth relatively small, crescent to trapezoid-shaped, twice as wide as long. Lips moderately broad, usually slightly to moderately rugose but papillose in large specimens. Moveable mandibular teeth 18-27 (15-34) arranged in a single transverse band. Premaxillae relatively narrow with a moderately to well defined edge to the ventral shelf and flat to slightly rounded in profile. Primary premaxillary teeth flattened posteriorly and pointed, slightly to moderately recurved with a clear distinction between primary and secondary teeth (Figure 5.41d & Table 5.8). Tertiary premaxillary teeth few in number (12-30, 0-14), arranged in one or two rows.

Maxillary barbels with papillose leading edge, extending beyond posterior base of pectoral spine. Distinct, darkly-pigmented basal membrane, 1/2 to 1 times width of barbel stem. Outer mandibular barbels equal to or extending beyond ventral limit of gill openings, with 7-12 primary branches, the first 0-4 (0-7) with one (rarely two) secondary branches; 3-6 secondary branches have been recorded in a few very large specimens. Inner mandibular barbels with 9-13 primary branches, the first 3-7 (2-9) possessing 1 (rarely 2 or 3) secondary branches; 4-6 secondary branches have been recorded in a few very large specimens.

Humeral process relatively large, obtusely-pointed, with a convex postero-dorsal margin. Generalized shape depicted in Figure 5.36.

Dorsal spine stout, approximately equal to length of head, ending in a short filament; smooth anterior margin except for 4 (2-5) serrations at tip, finely serrated on posterior margin. Pectoral spines stout, ending in a short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pectoral fins not reaching anal fin. Anal fin rounded with first ray equal to or shorter than second and third rays. Caudal fin relatively short with moderate to very broad lobes of similar length, moderately to weakly forked.

Live colouration of body yellowish brown, paler ventrally and on the fins. Pattern of markings variable, with dominant colour composed of large irregular-shaped spots over entire body and fins, larger than diameter of the eye on sides of body, progressively smaller on the head. Variation ranging from spots which are slightly more elongate and very much more closely packed

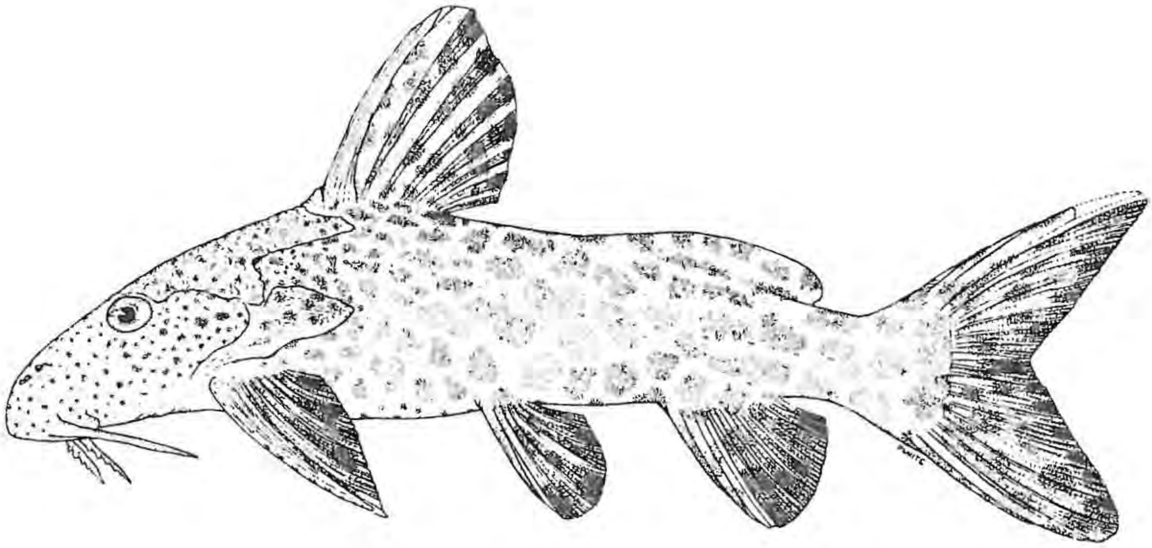

Figure 6.8 Synodontis macrostoma sp.n., Holotype, AMG 3398.3, female, 92,0 mm SL.

to a pattern with fewer spots of similar size to dominant pattern but greatly elongated on body and adipose fin. Ventral regions may or may not be spotted.

Distribution

Drainage basins of the Upper Zambezi, Okavango, Cunene and Upper Kafue (Figure 6.1).

Synodontis macrostoma sp.n.

Figure 6.8, Table 6.7

Material examined

Holotype: AMG 3398.3 (female, 92,0 mm SL, Katima Mulilo, Eastern Caprivi, Upper Zambezi River, B.C.D. van der Waal, 26 August 1975).

Paratypes: AMG 3398.4 - .14 (11 x 38,3 - 75,7 mm SL, ditto).

Other material: given in Appendix 1.

Diagnosis

The most distinguishing characteristic of this new species in its differentiation from other southern African Synodontis is an elongated head with a noticeably decurved profile. The mouth lies below the ventral horizontal level of the pectoral girdle. Additional diagnostic features include a large mouth, short maxillary and mandibular barbels, narrow pectoral girdle, and a short coracoid to cranium distance.

Description

The smallest of the southern African Synodontis with a maximum recorded size of 92,0 mm SL. Morphometric and meristic data summarized in Table 6.10.

Table 6.7 Morphometric and meristic data of S.macrostoma sp.n.

Morphometrics	Holotype	Paratypes (n = 11) Mean	S.D.	Range	S.macrostoma sp.n. (n = 11) Mean	S.D.	Range
Standard length (mm)	92,00	-	-	38,30 - 75,65	-	-	49,05 - 83,55
Predorsal length (% SL)	39,51	40,35	0,80	39,06 - 41,79	39,49	1,21	37,40 - 40,63
Head length (% SL)	32,93	33,40	0,58	32,74 - 34,39	32,86	0,98	31,22 - 34,33
Snout length (% PDL)	40,03	39,17	1,04	37,41 - 40,49	39,40	2,01	35,51 - 41,70
Interorbital length (% HL)	25,74	27,77	1,40	25,39 - 30,74	26,83	1,50	24,07 - 29,51
Dorsal to coracoid (% HL)	71,29	69,44	2,13	65,60 - 73,96	69,87	2,81	64,35 - 73,18
Coracoid to neurocranium (% HL)	51,82	52,75	1,51	49,54 - 54,86	54,77	2,40	50,28 - 58,51
Pectoral girdle width (% HL)	75,25	74,77	2,43	70,64 - 78,99	74,47	2,42	70,42 - 78,04
Occ. nuchal shield width (% HL)	29,21	30,10	1,54	27,25 - 32,13	29,52	1,61	26,01 - 31,56
Humeral process length (% HL)	55,45	55,16	3,22	47,94 - 59,56	55,63	1,66	53,25 - 58,23
Hum. proc. to occ. nuchal shield (%HL)	26,90	29,91	1,77	25,98 - 32,23	28,11	3,41	21,99 - 33,44
Orbit diameter (% HL)	17,82	20,08	1,61	16,74 - 21,83	19,89	1,84	17,01 - 22,57
Dorsal spine length (% HL)	84,32	81,35	6,78	68,42 - 89,47	79,61	6,54	70,38 - 86,70
Pectoral spine length (% HL)	67,16	74,89	3,30	68,12 - 78,41	70,98	4,04	65,19 - 77,46
Dorsal fin length (% HL)	74,59	75,49	4,48	68,11 - 81,23	75,27	4,37	68,11 - 81,23
Caudal fork length (% CTL)	40,50	46,47	2,60	42,11 - 50,36	46,22	2,33	42,89 - 50,56
Maxillary barbel length (% HL)	73,27	63,54	7,06	45,90 - 72,30	60,87	10,94	43,78 - 82,58
Outer mandibular barbel length (% HL)	41,75	35,66	4,31	28,13 - 42,42	38,23	4,99	31,54 - 46,30
Inner mandibular barbel length (% HL)	18,98	20,41	2,12	16,60 - 23,60	22,08	3,45	17,69 - 29,12
Snout to pectoral (% SL)	24,24	24,75	1,54	23,34 - 28,19	24,34	0,78	23,40 - 25,93
Snout to pelvic (% SL)	52,28	51,29	0,95	50,32 - 52,21	52,48	1,17	50,38 - 54,20
Snout to anal (% SL)	71,14	68,76	1,10	67,74 - 69,93	71,16	1,38	68,60 - 73,61
Caudal peduncle length (% SL)	18,10	18,99	0,57	18,38 - 19,50	18,19	0,71	17,15 - 19,60
Caudal peduncle depth (% SL)	9,78	10,18	0,13	10,10 - 10,33	10,32	0,55	9,54 - 11,11
Dorsal to adipose (% SL)	16,25	15,02	1,23	13,64 - 16,01	13,31	1,25	10,97 - 15,25
Adipose basal length (% SL)	25,71	26,08	1,26	24,72 - 27,19	26,15	1,04	24,47 - 28,44
Adipose maximum height (% ABL)	14,38	19,17	1,58	17,37 - 20,32	17,87	3,05	13,32 - 22,22
Adipose to caudal peduncle (% SL)	12,72	12,69	0,31	12,46 - 13,05	12,37	0,62	11,34 - 13,35
Mouth width (% PGW)	53,51	59,47	2,28	54,42 - 62,00	59,77	3,20	55,21 - 66,12
Premaxillae width (% PGW)	28,51	31,09	2,66	28,08 - 34,74	30,55	2,29	27,01 - 34,71

Meristics

Meristics	Holotype	Paratypes (n = 11)	S.macrostoma sp.n. (n = 11)
Total vertebrae	38	37 - 38	37 - 38
Precaudal vertebrae	12	12 - 13	12 - 13
Caudal vertebrae	26	25 - 26	25 - 26
Preanal vertebrae	21	20 - 21	20 - 21
Pleural ribs	9	9 - 10	8 - 10
Anal pterygiophores	10	10 - 12	10 - 11
Anal rays	VI,7	V - VI, 7 - 8	V, 7 - 8
Pectoral rays	8	8 - 9	8
Moveable mandibular teeth (Total)	15	13 - 21	15 - 20
,, ,, ,, (Functional)	14	11 - 16	11 - 15
Premaxillary teeth (Primary)	31	23 - 42	22 - 29
,, ,, (Tertiary) Row 1	24	17 - 24	18 - 23
Row 2	11	0 - 18	5 - 15

Head elongate with decurved profile where mouth extends below ventral horizontal level of the pectoral girdle. Mouth large and crescent-shaped with broad, fairly rugose lips. Moveable mandibular teeth very few in number (13-21), arranged in usually one narrow transverse band. Premaxillae wide with a well-defined (often rectangular) edge to a broad, flat ventral shelf (Figure 5.41e & Table 5.8). Primary premaxillary teeth (17-30) flattened posteriorly and pointed, slightly to moderately recurved. Very distinct gap between primary and secondary teeth. Tertiary teeth few in number and fairly widely separated (17-24, 0-18), arranged in two rows.

Maxillary barbels short and thick with smooth leading edge, not extending beyond posterior base of the pectoral fin. Basal membrane absent. Outer mandibular barbels with 7-12 short, thick primary branches, very rarely secondarily branched, not extending beyond ventral limit of gill openings. Inner mandibular barbels with 7-10 very short papillae-like primary branches, the first 1 (1-5) with one, very rarely two, secondary branches.

Humeral process relatively narrow, short, triangular with a straight or slightly convex postero-dorsal margin. Generalized shape depicted in Figure 5.37.

Dorsal spine moderately stout, shorter than length of head, ending in an extremely short filament, smooth anterior margin, serrated along entire length of posterior margin. Pectoral spines moderately stout, serrations on outer margin approximately half the size and slightly fewer in number than serrations on the inner margin. Pectoral fins not reaching anal fin. Anterior rays of anal fin longer than posterior rays. Caudal fin large, deeply forked, with moderately broad lobes of similar length.

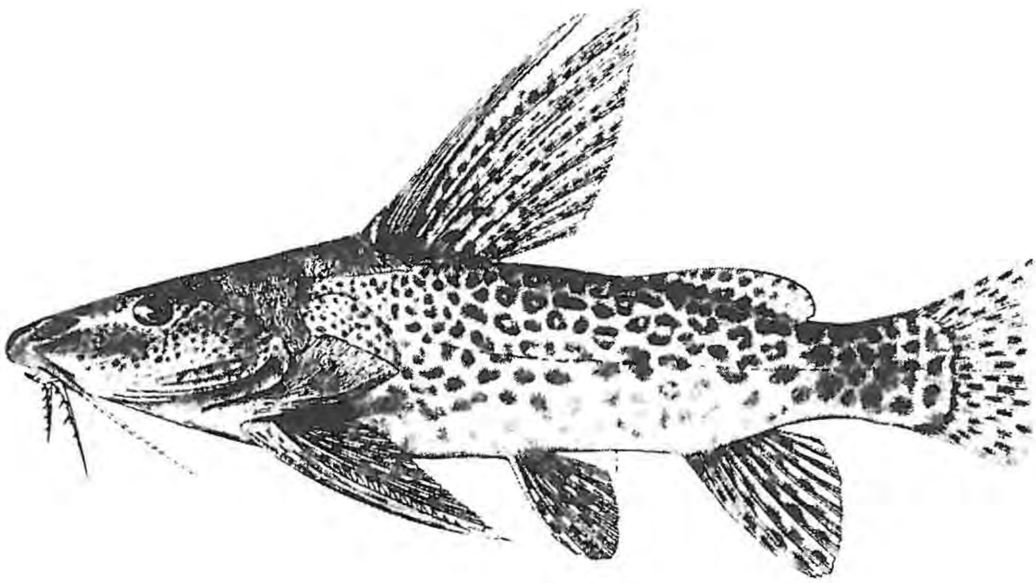

Figure 6.9 Synodontis leopardinus Pellegrin 1914, Holotype, MNHN 13/321, male, 119,1 mm SL (after Poll,1971: fig. 162).

No record available of live colouration. Body and fins entirely spotted except for ventral surface of the head which is usually unspotted. Markings predominantly spherical to ovoid, a few overlapping to form larger irregular-shaped blotches. Size of spots on posterior half of body equal to or larger than diameter of eye, decreasing in size anteriorly. Spots of head smaller than pupil. Markings on fins variable in size but all larger than pupil, evenly distributed on fins. Juvenile markings slightly larger and fewer in number.

Distribution

Drainage basins of the Okavango, Upper Zambezi, Cunene and Upper Kafue Rivers (Figure 6.1).

Synodontis leopardinus Pellegrin 1914

Figure 6.9, Table 6.8

Synodontis leopardinus Pellegrin, 1914: 26, type locality: Lealui, Upper Zambezi River; Boulenger, 1916: 320; Jubb, 1967: 43, 52, 143; Poll, 1971: 220, 351.

Synodontis jallae Gilchrist & Thompson, 1917: 561, type locality: Shesheke, Upper Zambezi River; Barnard, 1948: 444; Jubb, 1958: 181; Jubb, 1961: 39; Jubb, 1963b: 15, 28; 1967: 43, 143.

Synodontis woosnami: Jubb, 1961: 39; Jackson, 1961a: in part, 87; Jubb, 1963b: in part, 15,28; Poll, 1967: 249;

Synodontis thamalakanensis: Barnard, 1948: 444; Jubb, 1967: 43.

Material examined

Holotype: MNHN 13/321 (male, 119,1 mm SL, Lealui, District of Barotses, Upper

Table 6.8 Morphometric and meristic data of S.leopardinus and S.jallae

Morphometrics	S.leopardinus Holotype	S.leopardinus (n = 69) Mean	S.D.	Range	S.jallae Holotype
Standard length (mm)	119,10			25,22 - 195,95	163,70
Predorsal length (% SL)	40,55	41,06	1,61	38,11 - 44,25	38,55
Head length (% SL)	34,17	33,42	1,30	30,80 - 36,05	31,09
Snout length (% PDL)	38,62	36,06	1,04	33,43 - 38,62	35,42
Interorbital length (% HL)	30,71	30,31	2,32	25,46 - 34,48	34,68
Dorsal to coracoid (% HL)	80,59	80,59	4,27	69,06 - 89,24	87,13
Coracoid to neurocranium (% HL)	64,50	60,91	3,88	51,83 - 68,17	-
Pectoral girdle width (% HL)	69,41	75,31	3,31	68,64 - 84,91	72,79
Occ. nuchal shield width (% HL)	32,19	32,18	2,00	27,39 - 35,61	31,14
Humeral process length (% HL)	53,32	58,94	2,55	52,36 - 64,29	57,66
Hum. proc. to occ. nuchal shield (% HL)	34,64	34,43	3,48	27,81 - 41,99	41,36
Orbit diameter (% HL)	15,50	18,42	1,80	15,43 - 23,25	18,07
Dorsal spine length (% HL)	105,16	104,32	12,97	77,49 - 123,59	101,98
Pectoral spine length (% HL)	74,69	77,65	3,77	63,42 - 86,25	78,59
Dorsal fin length (% HL)	109,20	113,75	11,02	95,45 - 136,66	-
Caudal fork length (% CTL)	-	43,59	2,20	37,63 - 49,91	-
Maxillary barbel length (% HL)	-	71,45	6,69	58,66 - 85,27	66,01
Outer mandibular barbel length (% HL)	30,47	39,13	4,46	28,82 - 51,28	39,88
Inner mandibular barbel length (% HL)	18,67	25,04	2,83	17,32 - 30,77	21,61
Snout to pectoral (% SL)	28,55	25,79	1,26	23,48 - 27,98	27,24
Snout to pelvic (% SL)	56,00	53,86	1,49	49,57 - 56,71	56,26
Snout to anal (% SL)	74,48	72,37	1,72	67,47 - 76,56	75,93
Caudal peduncle length (% SL)	17,30	17,76	0,89	16,00 - 19,60	18,08
Caudal peduncle depth (% SL)	10,50	10,25	0,41	9,21 - 11,17	10,38
Dorsal to adipose (% SL)	14,95	15,76	2,12	12,06 - 20,76	13,81
Adipose basal length (% SL)	19,98	22,60	1,90	19,10 - 26,93	21,87
Adipose maximum height (% ABL)	21,85	22,36	2,74	14,96 - 28,47	17,60
Adipose to caudal peduncle (% SL)	13,52	12,78	0,83	10,73 - 14,65	13,81
Mouth width (% PGW)	38,26	46,82	4,22	36,00 - 54,45	-
Premaxillae width (% PGW)	23,31	21,84	1,78	17,64 - 25,25	23,75
Meristics					
Total vertebrae	38			38 - 39	38
Precaudal vertebrae	12			12 - 13	13
Caudal vertebrae	26			25 - 27	25
Preanal vertebrae	21			20 - 21	21
Pleural ribs	9			9 - 10	9
Anal pterygiophores	11			10 - 12	11
Anal rays	V,8			V,8 - 10	V,8
Pectoral rays	8			8 - 9	8
Moveable mandibular teeth (Total)	22			12 - 22	16
,, ,, ,, (Functional)	18			9 - 17	16
Premaxillary teeth (Primary)	-			9 - 25	-
,, ,, (Tertiary) Row 1	-			12 - 25	-
Row 2	-			0 - 13	-

Zambezi River, Zambia, M.V. Ellenberger).

Other material: given in Appendix 1; Holotype of S.jallae AMG 14290 (male, 163,7 mm SL, Sesheke, Upper Zambezi River, Zambia, Rev. Jalla).

Diagnosis

S.leopardinus most closely resembles S.vanderwaali sp.n. and S.thamalakanensis, the colour pattern of the former, in particular, being very similar. S.leopardinus is distinguished from S.vanderwaali sp.n. by its significantly shorter barbels, narrower occipito-nuchal shield, shorter dorsal to coracoid distance, longer dorsal fin and fewer moveable mandibular teeth. The distinction between S.leopardinus and S.thamalakanensis is less obvious, S.leopardinus having fewer primary premaxillary teeth, fewer moveable mandibular teeth, a markedly narrower basal membrane, and markings that do not converge to form elongated lines.

Description

A moderately large species with a maximum recorded size of 196 mm SL. Morphometric and meristic data summarized in Table 6.7.

Mouth crescent-shaped, twice as broad as long, with moderately broad lips that are slightly to moderately rugose. Moveable mandibular teeth very few in number (12-22), arranged in a narrow transverse band. Premaxillae relatively narrow with a narrow ventral shelf. Posterior edge of ventral shelf largely indistinct or absent (Figure 5.41f). Primary teeth large, round to posteriorly flattened and pointed, straight to slightly recurved and few in number (9-25). Clear distinction between primary and secondary teeth, which are usually separated by a noticeable gap. Tertiary teeth few in number (12-25, 0-13), arranged in one or two narrow rows.

Maxillary barbels with (usually) smooth or finely papillose leading edge, not extending beyond posterior base of pectoral spine. Basal membrane narrow and darkly-pigmented, maximum width 1/6 to 1/2 width of barbel stem. Outer mandibular barbels equal to or shorter than ventral limit of gill openings with 5-11 short, thick primary branches, 1-3 of which have usually one (rarely 2 or 3) secondary branch.

Humeral process relatively small, short and obtusely-pointed, with an evenly but strongly convex postero-dorsal margin. Generalized shape depicted in Figure 5.38.

Dorsal spine tall and stout, ending in a short filament, longer than length of head, smooth anterior margin except for 4 (1-5) serrations at tip, serrated along entire posterior margin. Pectoral spines stout, ending in a short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pectoral fins not reaching anal fin. Anal fin with longer anterior rays. Caudal fin with fairly broad lobes, the upper noticeably longer than the lower.

Live colouration dark brown dorsally, lighter brown to olive brown on sides of body, extending to very pale brown to cream ventrally. Pattern of markings variable, dominant pattern composed of numerous small spherical to ovoid spots over entire body and fins, approximately equal to diameter of eye on sides of body. Variation ranging from fewer, larger leopard-like spots typical of the type specimen to a form where the spots are more numerous, generally more elongate than the dominant pattern and smaller than the pupil in width. Ventral region may or may not be spotted.

Distribution

Drainage basins of the Upper Zambezi, Okavango and Upper Kafue Rivers (Figure 6.1).

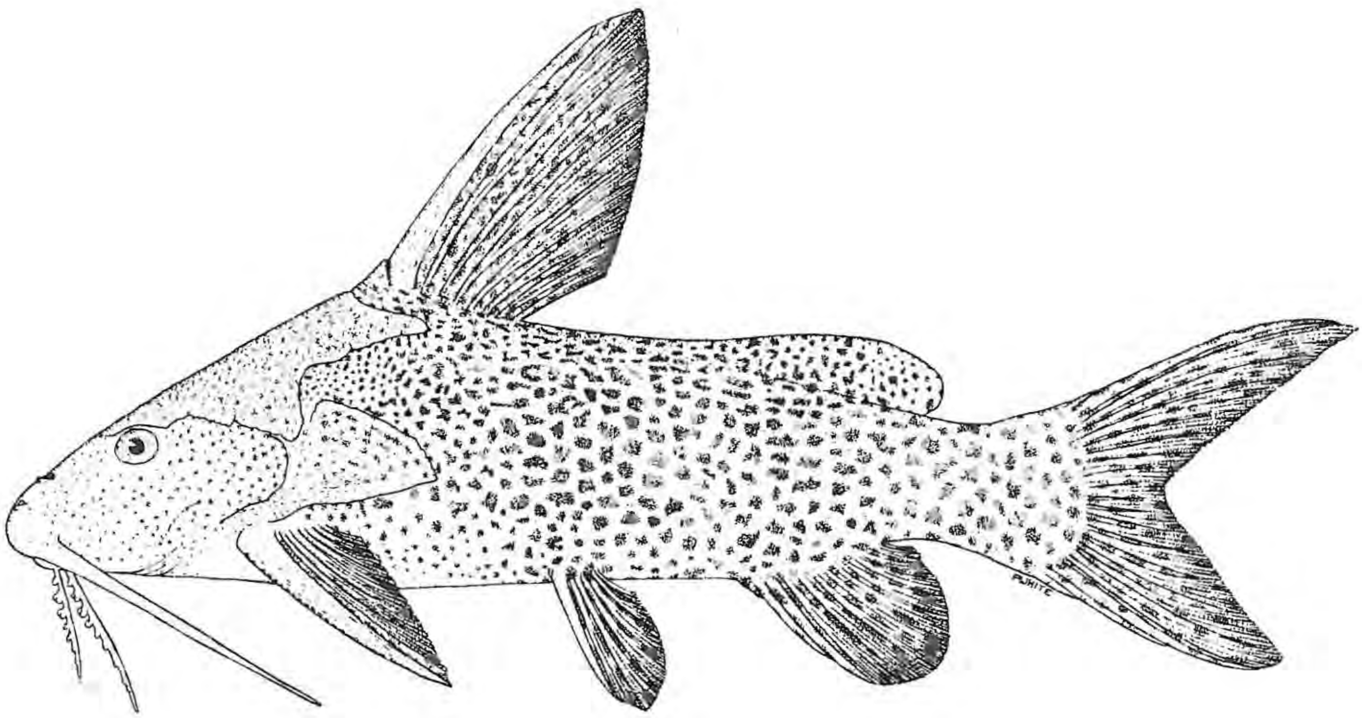

Figure 6.10 Synodontis vanderwaali sp.n., Holotype, AMG P5796.6, male, 119,5 mm SL.

Synodontis vanderwaali sp.n.

Figure 6.10, Table 6.9

Material examined

Holotype: AMG P5796.6 (male, 119,5 mm SL, Okavango River, South West Africa, B.C.D. van der Waal, 20 November 1977).

Paratype: AMG P5796.11 (male, 139,5 mm SL, Okavango River, South West Africa, B.C.D. van der Waal, 20 November 1977); RUSI 18734 (1 x female, 112,4 mm SL, Nxamaceri, Okavango River, M.N. Bruton et al., 24 October 1984); RUSI 25521 (3 x juveniles, 72,8, 73,0 & 75,5 mm SL, Boro River, canalized area, Okavango Delta, G.S. Merron, 16 May 1985); RUSI 2237 (1 x male, 114,5 mm SL; 2 x females, 139,5 & 156,1 mm SL, Kavango, Okavango River, South West Africa, P.H.Skelton et al., 26 October 1984).

Other material given in Appendix 1.

Diagnosis

This species most closely resembles S.leopardinus and to a lesser extent also S.thamalakanensis. The large overlap in the colour patterns of S.vanderwaali and S.leopardinus has almost certainly been the largest contributing factor responsible for this species being previously overlooked. The most striking diagnostic features of S.vanderwaali sp.n. from which it can be clearly distinguished from both S.leopardinus and S.thamalakanensis are its longer maxillary and mandibular barbels. S.vanderwaali sp.n. can be further distinguished from S.leopardinus by a shorter snout to pectoral distance, wider occipito-nuchal shield and larger number of moveable mandibular teeth. S.vanderwaali sp.n. differs from S.thamalakanensis in having a shorter dorsal spine, shorter dorsal fin, narrower mouth, larger dorsal to coracoid distance and a larger number of moveable mandibular teeth.

Morphometrics	Holotype	S.vanderwaali sp.n. (n = 47) Mean	S.D.	Range
Standard length (mm)	119,50			57,20 - 160,30
Predorsal length (% SL)	40,00	39,94	1,29	36,64 - 42,19
Head length (% SL)	32,72	32,68	0,91	30,48 - 34,32
Snout length (% PDL)	35,15	35,06	0,99	32,74 - 37,80
Interorbital length (% HL)	34,78	32,59	0,34	29,64 - 39,61
Dorsal to coracoid (% HL)	87,98	87,70	3,23	81,78 - 96,40
Coracoid to neurocranium (% HL)	63,81	63,80	2,39	59,49 - 68,97
Pectoral girdle width (% HL)	80,69	82,35	2,63	73,48 - 87,28
Occ. nuchal shield width (% HL)	35,55	34,97	1,34	32,60 - 36,99
Humeral process length (% HL)	67,01	65,06	3,11	56,80 - 69,77
Hum. proc. to occ. nuchal shield (% HL)	43,09	37,00	4,70	28,50 - 43,60
Orbit diameter (% HL)	16,88	18,71	1,01	16,59 - 20,44
Dorsal spine length (% HL)	108,57	97,67	8,02	79,71 - 117,92
Pectoral spine length (% HL)	85,17	80,39	4,47	65,80 - 89,28
Dorsal fin length (% HL)	105,75	93,51	5,83	75,94 - 101,83
Caudal fork length (% CTL)	42,56	45,66	2,82	37,32 - 52,00
Maxillary barbel length (% HL)	99,87	99,89	6,46	87,53 - 113,93
Outer mandibular barbel length (% HL)	59,46	57,58	4,43	50,33 - 70,56
Inner mandibular barbel length (% HL)	31,20	35,94	2,72	30,78 - 41,53
Snout to pectoral (% SL)	23,39	24,12	0,88	22,62 - 25,41
Snout to pelvic (% SL)	52,55	53,95	1,96	49,91 - 56,63
Snout to anal (% SL)	70,46	70,70	1,03	67,20 - 74,95
Caudal peduncle length (% SL)	17,20	17,65	0,89	16,02 - 19,22
Caudal peduncle depth (% SL)	11,30	11,15	0,72	10,00 - 12,56
Dorsal to adipose (% SL)	16,86	17,78	3,10	12,30 - 23,30
Adipose basal length (% SL)	23,72	22,86	2,98	17,97 - 28,86
Adipose maximum height (% ABL)	26,46	27,10	3,32	20,45 - 32,60
Adipose to caudal peduncle (% SL)	12,97	13,10	0,97	10,95 - 13,60
Mouth width (% PGW)	35,18	48,93	4,02	35,09 - 58,62
Premaxillae width (% PGW)	18,86	21,36	1,71	18,59 - 27,42
Meristics				
Total vertebrae	38			38 - 39
Precaudal vertebrae	12			11 - 13
Caudal vertebrae	26			25 - 28
Preanal vertebrae	21			20 - 22
Pleural ribs	10			9 - 11
Anal pterygiophores	11			10 - 13
Anal rays	V,8			V - VI, 7 - 9
Pectoral rays	8			7 - 8
Moveable mandibular teeth (Total)	36			25 - 41
,, ,, ,, (Functional)	25			20 - 35
Premaxillary teeth (Primary)	25			18 - 36
,, ,, (Tertiary) Row 1	28			23 - 39
Row 2	32			19 - 41
Row 3	28			6 - 35
Row 4	15			0 - 27

Description

A moderately small species with a maximum recorded size of 156 mm SL. Morphometric and meristic data summarized in Table 6.9.

Mouth crescent-shaped, two to three times as wide as long, with relatively narrow lips that are smooth to slightly rugose. Moveable mandibular teeth numerous (25-44), arranged in one transverse band. Premaxillae relatively narrow with a distinct ventral shelf that is flat to slightly rounded in profile with a well-defined posterior edge. Primary teeth fairly numerous (18-36), posteriorly flattened, acutely pointed and strongly to very strongly recurved (Figure 5.41g & Table 5.8). Clear differentiation possible between primary and secondary teeth, separated by a distinct gap. Tertiary teeth exceptionally numerous (23-39, 19-41, 6-35, 0-27), arranged in up to four rows, extending the full width of the premaxillae. In the Cunene specimens these rows are less distinct but cover a similar area on the premaxillae.

Maxillary barbels with smooth leading edge, extending beyond posterior base of the pectoral fin. Basal membrane darkly pigmented and narrow, maximum width 1/4 to 1/2 width of barbel stem. Outer mandibular barbels extending beyond anterior base of pectoral spine, 0-4 of which possess (usually) one or two secondary branches. Inner mandibular barbels with 8-13 very short, thick, papilliform primary branches, the first 2-9 possessing 1 (rarely 2-4) secondary branch.

Humeral process large, tall and obtusely-pointed with a strongly convex postero-dorsal margin. Generalized shape depicted in Figure 5.38.

Dorsal spine stout, approximately equal to head length, ending in a very short filament, anterior margin smooth except for 1-2 fine serrations at tip, finely

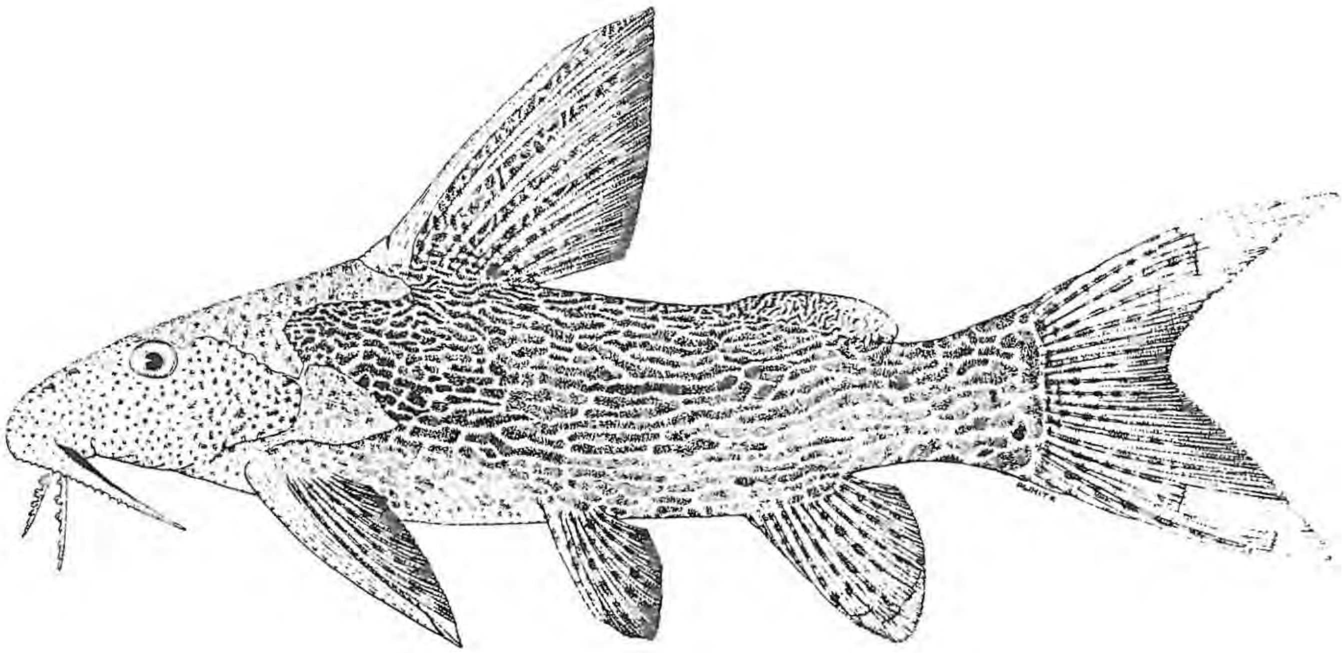

Figure 6.11 Synodontis thamalakanensis Fowler 1935, Paratype, TMP 15305, male, 140,0 mm SL.

serrated on posterior margin. Pectoral spines stout, ending in a short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pectoral fins not reaching anal fin. Anal fin with distinctly rounded ventral margin, the first three anterior rays of very similar length. Caudal fin with broad lobes of similar length, the upper lobe slightly more pointed than the distinctly rounded lower lobe.

Live colouration brown to olive brown, lighter ventrally. Pattern of markings very variable, ranging from irregular-shaped spots over entire body and fins, approximately equal to diameter of the eye to a form where the spots are more numerous and extended into bars of varying lengths and smaller in width than the pupil on the sides of the body. Specimens from the Cunene River exhibit a pattern similar to the latter but where the lines are generally more elongate, convoluted, considerably more numerous and more tightly packed. In the first example the spots may be grouped in a constellation of 2-7 with lighter coloured centres, similar to the 'leopard spotting' in S.leopardinus. Juveniles show similar variation but spots are larger and fewer in number.

Distribution

Drainage basins of the Upper Zambezi, Okavango and Cunene Rivers (Figure 6.1).

Synodontis thamalakanensis Fowler 1935

Figure 6.11, Table 6.10

Synodontis thamalakanensis Fowler, 1935: 274, type locality: Maun, Thamalakane River, Botswana.

Synodontis woosnami: Jubb, 1961: 39; 1963b: 15,28; Poll, 1971: in part 342.

Table 6.10 Morphometric and meristic data of S.thamalakanensis

		S.thamalakanensis (n = 43)		
Morphometrics	Paratype	Mean	S.D.	Range
Standard length (mm)	140,00			49,40 - 174,50
Predorsal length (% SL)	37,61	40,24	1,97	37,03 - 44,97
Head length (% SL)	31,82	33,16	1,56	30,92 - 37,00
Snout length (% PDL)	36,94	37,17	0,91	35,17 - 39,37
Interorbital length (% HL)	34,34	31,04	2,41	26,98 - 35,58
Dorsal to coracoid (% HL)	83,61	80,22	3,88	72,36 - 87,41
Coracoid to neurocranium (% HL)	65,10	59,63	2,84	53,90 - 65,78
Pectoral girdle width (% HL)	74,19	76,62	2,12	72,93 - 83,13
Occ. nuchal shield width (% HL)	31,43	33,39	1,98	27,99 - 38,44
Humeral process length (% HL)	54,88	59,91	2,64	55,29 - 67,99
Hum. proc. to occ. nuchal shield (%HL)	40,63	35,76	4,00	27,19 - 43,94
Orbit diameter (% HL)	17,51	18,91	2,17	15,17 - 23,19
Dorsal spine length (% HL)	99,21	108,29	10,63	91,60 - 129,33
Pectoral spine length (% HL)	73,97	83,61	4,16	73,32 - 90,32
Dorsal fin length (% HL)	112,79	115,86	11,77	95,72 - 144,74
Caudal fork length (% CTL)	-	48,32	3,18	40,73 - 54,66
Maxillary barbel length (% HL)	78,79	74,70	4,53	65,85 - 84,59
Outer mandibular barbel length (% HL)	45,12	45,03	2,08	35,22 - 50,83
Inner mandibular barbel length (% HL)	25,93	26,92	1,89	22,31 - 30,41
Snout to pectoral (% SL)	25,00	24,66	1,62	22,07 - 27,80
Snout to pelvic (% SL)	52,00	52,19	1,65	49,56 - 55,18
Snout to anal (% SL)	73,57	70,91	2,00	67,09 - 75,61
Caudal peduncle length (% SL)	18,36	18,49	0,72	17,01 - 19,87
Caudal peduncle depth (% SL)	11,21	10,75	0,50	9,94 - 11,91
Dorsal to adipose (% SL)	15,46	18,19	3,11	13,19 - 23,75
Adipose basal length (% SL)	21,64	20,92	1,80	16,62 - 23,49
Adipose maximum height (% ABL)	23,93	23,95	3,28	17,95 - 29,36
Adipose to caudal peduncle (% SL)	12,82	13,48	0,60	12,40 - 14,76
Mouth width (% PGW)	48,11	49,08	3,17	43,15 - 58,08
Premaxillae width (% PGW)	26,78	24,95	2,08	21,10 - 29,09
Meristics				
Total vertebrae	38		38 - 40	
Precaudal vertebrae	12		12 - 13	
Caudal vertebrae	26		25 - 27	
Preanal vertebrae	20		20 - 21	
Pleural ribs	9		9 - 10	
Anal pterygiophores	12		11 - 13	
Anal rays	VI,8		V - VI, 8 - 9	
Pectoral rays	8		7 - 8	
Moveable mandibular teeth (Total)	19		17 - 28	
,, ,, ,, (Functional)	18		12 - 21	
Premaxillary teeth (Primary)	30		25 - 43	
,, ,, (Tertiary) Row 1	24		13 - 27	
Row 2	0		0 - 9	

Synodontis leopardinus: Jubb, 1967: in part 43, 143.

Synodontis jallae: Barnard, 1948: 442, 444; Maar, 1960: 7.

Material examined

Paratype: TMP 15305 (male, 140,0 mm SL, Maun, Thamalakane River, Bechuanaland Protectorate, de Schauensee South Africa Expedition, 1930).

Other material: given in Appendix 1.

Diagnosis

This species most closely resembles S.leopardinus and S.vanderwaali sp.n. The most prominent diagnostic features of S.thamalakanensis are its large basal membrane, extensively papillose leading edge to the maxillary barbels and a pattern of markings where individual spots converge to form very long convoluted lines on the sides of the body and caudal peduncle. S.thamalakanensis can be further distinguished from S.leopardinus by a significantly larger number of primary premaxillary teeth, and from S.vanderwaali sp.n. by shorter barbels, wider mouth, taller dorsal fin, taller dorsal spine and a smaller dorsal to coracoid distance.

Description

A medium to large species with a maximum recorded size of 175 mm SL. Morphometric and meristic data summarized in Table 6.8.

Mouth crescent shaped, three to four times as broad as wide, with moderately broad lips that are strongly rugose in front, with a row of prominent papillae on antero-ventral rim in larger specimens. Moveable mandibular teeth (17-28) arranged in a single transverse band. Premaxillae relatively wide, with a narrow but distinct ventral shelf, rounded to ovate in profile with a poorly defined posterior edge (Figure 5.41h & Table 5.8). Primary teeth numerous

(25-43), flattened posteriorly, acutely pointed with slightly to strongly recurved crowns. Clear distinction between primary and secondary teeth but often separated by a small, indistinct gap. Tertiary teeth few in number (13-27, 0-9), arranged in one or two rows.

Maxillary barbels with numerous, prominent (1/3 - 4/5 width barbel stem in length), widely-spaced, single or double papillae on leading edge. Basal membrane very large and darkly pigmented, maximum width 4/5 - 8/5 width of barbel stem. Outer mandibular barbels not extending beyond ventral limit of gill openings with 6-14 relatively short primary branches, 0-8 of which possess 1 (1-5) secondary branch. Inner mandibular barbels with 9-13 short, thick, papilliform primary branches, the first 4-9 (3-11) possessing 1 (1-5) secondary branch.

Humeral process large and obtusely pointed, with a strongly convex postero-dorsal margin. Larger specimens often with prominent, conical-shaped projections on the posterior half of this margin. Generalized shape depicted in Figure 5.38.

Dorsal spine very tall and stout, longer than length of head, ending in short filament, anterior margin smooth except for 4 (2-5) serrations at tip, finely serrated on posterior margin. Pectoral spines stout, ending in short filament, numerous fine serrations on outer margin, fewer larger serrations on inner margin. Pectoral fins not reaching anal fin. Anal fin with longer anterior rays. Caudal fin with broad though sharply-pointed lobes of fairly similar length.

Live colouration dark brown dorsally, lighter brown to olive brown on the sides of the body, slightly paler ventrally. Pattern of markings variable but typically composed of greatly elongated, often highly convoluted vermicular lines, equal to or less than diameter of the eye in width on the sides of the body. Variation also includes a form where the spots are spherical to ovoid, very numerous and equal to or smaller than the pupil on the sides of the body. Ventral regions may or may not be spotted. Fins with numerous, evenly distributed small spots. Juveniles showing similar pattern but with fewer, larger markings.

Distribution

Drainage basins of the Upper Zambezi and Okavango Rivers (Figure 6.1).

Chapter 7

DISCUSSION

The present study was specifically undertaken due to the inability of available keys to diagnose the southern African *Synodontis* species, in spite of the fact that the taxonomy of this group was revised twice within the past two decades. A detailed analysis of the characters traditionally used in *Synodontis* taxonomy was thus a necessary prerequisite to this third revision. To my knowledge, Farquharson (1969) is the only other author to have seriously considered the value of characters traditionally used in *Synodontis* taxonomy, based on a knowledge of their intra- and interspecific variation. Only limited comparison with this study is possible, however, as certain of the taxa recognized by Farquharson (1969) are shown by the present study to be polyspecific.

Character analysis

Historically, keys to the identification of *Synodontis* species have consistently used four main characters, namely, colour pattern, humeral process shape, barbel morphology and moveable mandibular tooth number.

The large variation in colour pattern has been recorded in many of the African catfishes, but particularly in species of *Clarias*, *Synodontis*, *Amphilius* (Jubb, 1963b) and *Chiloglanis* (Bell-Cross, 1976). The persistent use of this character as a diagnostic feature among the southern African *Synodontis* stems from the fact that five of the eight species described from the Zambezi system were assigned names referring to their pattern of markings (p.2 ; Jubb, 1967). The detailed analysis of colour pattern in the present study has shown this character to be extremely variable and largely overlapping, but of greater taxonomic significance is the finding that this variability is not shared by all species. S.nigromaculatus, for example, has an uncharacteristically small variation in the pattern of markings and a background colouration that is unique among the southern African Synodontis.

The shape of the humeral process has long been used to diagnose Synodontis species. Vaillant (1895, 1896) was the first to assess the taxonomic value of this character, but this study contributed little to our understanding of the variation as it merely involved the documentation of humeral process features previously considered diagnostic among the nominal taxa, based on mainly published descriptions. Farquharson (1969) did not compare humeral process shape but did include this character in species descriptions, recording the postero-dorsal margin as convex, straight or concave, and the tip as either blunt or pointed. Poll (1971) has provided the most comprehensive descriptions of this character to date, recording the shape of both the postero-dorsal and ventral margins as well as the development of the lateral flange and form of granulation on the lateral face. Poll's (1971) descriptions, however, were derived from very few specimens (p.3), so providing little additional information of this character's taxonomic value.

The southern African Synodontis are divisible into two groups on the basis of humeral process shape, the first group having a concave postero-dorsal margin and the second group a convex margin. Farquharson (1969) considered this distinction only applicable to adults, as a straight postero-dorsal margin was recorded in all the juvenile specimens he examined. The findings of the present study concur with Jubb (1967, 1982) who does recognize this distinction but acknowledges that it is far less apparent in small specimens (<59 mm SL). The present study has shown that the postero-dorsal margin of the humeral process in species of the first group is consistently concave throughout the size range studied, but in small specimens of the second group the convex section may be limited to the posterior half of the postero-dorsal margin only. The largest difference in humeral process shape within these two groups is shown by the present study to exist in specimens of a standard length between 70 and 130 mm. Within this size range, however, differences are generally too small and the variation too large to allow any reasonable differentiation. Among the southern African Synodontis, the most important taxonomic value of humeral process shape is its ability to divide the species into two distinct groups. At the descriptive taxonomic level, this character is therefore particularly useful in keys.

The dimensions of the humeral process are usually recorded by its length and height (or depth). The exact measurement of these two distances, however, has been interpreted differently by various authors, making comparison difficult. Humeral process length (HPL) for example, was defined by Farquharson (1969) as the length of the postero-dorsal margin and by Poll (1971) as the distance along the median longitudinal axis from the anterior margin to the posterior tip. Due to the difficulty in estimating the midpoint on the anterior margin of the humeral procress, which in some species may be inclined at an angle of more than 45° from the vertical, the latter measurement is undoubtledly the less reliable. By taking the anterior point of this measurement from the leading edge of the base of the (erect) pectoral spine, a greater degree of consistency is achieved. Humeral process length expressed as a proportion of head length is a character of variable diagnostic value and, compared with most other skeletal measurements, this character shows a particularly large variation in range. To justify interspecific comparisons using this character, the full extent of the intraspecific variation must be accounted for.

One of the features that distinguish Synodontis from other mochokids is the presence of branched mandibular barbels. All three pairs of barbels in this genus are characterized by a large diversity in form, allowing their use as diagnostic features at the specific level. Previous descriptions of Synodontis barbels have usually concentrated on four morphological aspects: length, form of the mandibular barbel branches, presence of a basal membrane, and development of papillae on the leading edge of the maxillary barbels.

The initial dichotomy in Farquharson's (1969) key to the southern African Synodontis is based on characters originally recognized by Jubb (1967) and concern the number, form and arrangement of outer mandibular barbel branches (p.68). The variation of all four characters, however, is shown by the present study to be larger than that previously documented and inapplicable to the above dichotomy. One aspect of the outer mandibular barbels that is applicable to this dichotomy is the length of its (primary) branches. In Group I they are five times the diameter of the barbel stem and in Group II are less than three times the diameter of the barbel stem. With the exception of this distinction, barbel branching shows little taxonomic significance among the southern African Synodontis.

The presence of a basal membrane and papillae on the maxillary barbels are frequently used to diagnose Synodontis species. The abnormally small development of these epidermal features in certain specimens for which these characters generally exist often conceals their potentially diagnostic value. Among the southern African Synodontis this condition is most relevant to S.macrostigma but is not applicable to the whole size range, as all adult specimens examined in this study were reliably diagnosed by the presence of these two characters. In a small percentage of juveniles, however, the papillae are small enough to be totally covered by the overlying layer of mucus, their detection often requiring microscopic examination.

The taxonomic value of barbel lengths to the southern African Synodontis is very variable. No differentiation is possible using these characters among the species of Group I, yet among certain Group II species they constitute one of the most discriminating of the non-skeletal based measurements.

The description of Synodontis dentition has traditionally involved only the moveable mandibular teeth for which the number and (lateral) shape were recorded. This preference is partly due to the smaller number and greater accessibility of these teeth in comparison with the more numerous and less accessible premaxillary teeth. The number of moveable mandibular teeth is shown by the present study to be a character of variable taxonomic value, resulting from greatly differing magnitudes of intraspecific variation (Table 5.6 & 5.7). Large variation of this character is attributed to an increase in tooth number with size (Figure 5.40), a relationship also noted by Barnard (1948), Jackson (1961a) and Farquharson (1969). The first two authors, however, did not have sufficient specimens to demonstrate that this relationship is limited to certain species only.

In all southern African Synodontis, replacement moveable mandibular teeth at various stages of development are situated in front of a usually regular transverse row of functional teeth (Figure 4.5). The intraspecific variation in the number of functional teeth is slightly smaller than that for the total count, but interspecific differences remain similar for both characters. Scanning electron examination of the bases of these teeth show a wedge-shaped band of collagen with the dentine extending to the attachment bone anteriorly (Fink, 1981). This results in the frequent misplacement of functional teeth, making their distinction from replacement teeth more difficult, a condition also noted by Farquharson (1969) and Crass (1960). As the taxonomic value of each set is fairly similar and to avoid problems of positional assessment, the total count is recommended.

The premaxillae of most catfish groups have only one tooth-bearing surface which is usually flat and orientated ventrally (Alexander, 1966). As the teeth of these bones are predominantly of uniform shape and size, the characters derived from these features are usually limited to various dimensions of the premaxillae or their tooth bands. Among the southern African Synodontis the proportional measurement of premaxillary width (to pectoral girdle width) shows a large degree of overlap, allowing the differentiation of S.macrostoma sp.n. only. Further species differentiation is possible, however, owing to additional characters that can be derived from these features. The premaxillae in Synodontis are inclined postero-ventrally with teeth orientated in such a way as to project both ventrally and posteriorly. In addition, the variations in the size and position of teeth on the premaxillae allow the recognition of three tooth types (Figure 4.6). Features of taxonomic value include the primary and tertiary tooth counts and the lateral profile of the ventral shelf of the premaxillae. Among the southern African Synodontis certain features of these characters show sufficient specificity to be used alone, as shown by the exceptionally high number of tertiary teeth in S.vanderwaali sp.n. which are characteristically arranged in four distinct rows (Figure 5.41). No differentiation in premaxillary teeth is evident among the species of Group II, yet their common pattern is unique mong the southern African species, providing a very useful character in initial identification.

Within the Ostariophysi, the roof of the cranium attains its broadest dimensions in the catfishes (Alexander, 1966). Further cranial specialization in certain catfish groups is shown in the presence of a nuchal shield, formed from the expansion and coalescence of the bony supports of the first three rays of the dorsal fin together with the posterior process of the supraoccipital (Gregory, 1933). The nuchal shield is well developed in the Mochokidae, attaining its greatest proportions in Synodontis where it extends beyond the base of the dorsal fin. Due to the lack of overlying muscle, the entire roof of the cranium in Synodontis is visible through the skin. Furthermore, the rigidity of the cranium allows a high level of precision in measurement and is thus an obvious feature of taxonomic interest.

In the present study, the dimensions of the cranium are recorded by six linear measurements of which only three appear to be of any taxonomic importance at the species level, namely, snout length (SNL), interorbital length (INL) and occipito-nuchal shield width (OSW). The greatest diagnostic value of all three characters is in the differentiation of S.macrostoma sp.n. from S.macrostigma. The proportionately larger snout length of S.macrostoma sp.n. in comparison to the other southern African species is a feature that is readily observable without measurement and, as shown in the bivariate analysis (Figure 5.4 & 5.5), is applicable in its differentiation from S.macrostigma down to small juveniles (10 - 20 mm SL). The diagnostic importance of the dimensions of the snout to S.macrostoma sp.n. are improved by yet another characteristic, in that it is noticeably decurved. The ventral margin of the mouth in S.macrostoma sp.n. extends below the level of the ventral surface of the pectoral girdle --- a feature that is unique among the southern African Synodontis. Together, these characteristics form two of the most recognizable field identification features of this new species.

The remaining three cranial measurements include predorsal length (PDL), head length (HL) and orbit diameter (OD). Both predorsal length and head length show little discriminatory value among the southern African Synodontis but still have important application in morphometric analysis as denominators to other measurements of the head. Of these two measurements, head length has the generally smaller intraspecific variation, suggesting its greater suitability for this purpose. One exception shown in the present study is that of snout length, in which predorsal length as the denominator contributed to the greater discrimination between S.macrostoma sp.n. and S.macrostigma.

Orbit diameter is not strictly a cranial measurement, as the posterior limit is taken against the inner margin of the posterior circumorbital bone. The slight lack of rigidity between these two bones in comparison with other cranial measurements, however, cannot alone explain this character's consistently large intraspecific variation. In addition to the negative allometric growth (p.53; Farquharson, 1969) and largely overlapping ranges shown by all species, orbit diameter shows little taxonomic value among the southern African Synodontis. This character has, however, proved useful in the identification of Synodontis species from more northerly river systems. S.comoensis for example, was described by Daget & Leveque (1981) using the proportional measurement of orbit diameter to head length to distinguish this species from S.schall (Bloch-Schneider, 1801). Furthermore, the combination of orbit diameter and maxillary barbel length was used by Poll (1971) to distiguish S.alberti Schiltuis 1891 from other Synodontis from the Zaire Basin.

Characters used in the present study to record the distance between the cranium and pectoral girdle involve the measurements of dorsal to coracoid (DCO), cranium to coracoid (COC) and snout to pectoral (SPC). The present analysis has shown the first two characters to have no diagnostic value among the species of Group I but reveal some marked differences in lateral head profile between certain Group II species. The most striking differentiation created by both these measurements is that between S.macrostigma and S.macrostoma sp.n. This differentiation, however, is not equally applicable to the entire size range studied. The first and more obvious reason is that of disproportionate growth as exemplified in Figure 5.10, where the diagnostic use of the coracoid to cranium measurement is curtailed for specimens below a head length of 18,0 mm. The second reason concerns the measurement itself. In small specimens (< 50 mm SL), the slight pressure exerted on the coracoid during this measurement is often enough to displace the pectoral girdle slightly, so contributing to an increased margin of error.

In the present study the definition of pectoral girdle width is similar to the 'head width' used by Poll (1971) and the 'head breadth' used by Whitehead (1962) but differs from both in that it is not taken at the base of the pectoral spines. Neither of these previous definitions specify the required position of these spines during measurement, although the illustration by Poll (1971: Figure 1) shows the fins in an erect position. In preserved material considerable pressure is often needed to erect the fins. For measurements such as humeral process length which require the erection of only one fin, this rarely causes a problem. The difficulty of erecting two fins whilst the measurement is taken, however, severely reduces the accuracy with which this measurement can be taken. For this reason the present study adopted the definition of 'head width' used by Farquharson (1969), which simply measures the maximum width of the girdle, irrespective of pectoral spine position. In contrast to the measurements between the pectoral girdle and cranium, the pectoral girdle itself is relatively rigid, allowing a level of precision equal to that of the cranial measurements.

Dorsal fin length (DFL) is a standard measurement used in the taxonomy of many fish groups, but in Synodontis previous workers have consistently referred to the dorsal spine in recording the height of this fin. This preference stems from the greater ease and precision with which this measurement can be made in comparison to that of the first dorsal ray. The present study, however, has found dorsal fin length to be the taxonomically more useful measurement. In Synodontis the dorsal fin is usually of similar length to its spine, which explains the close pattern in distribution of population means between these two characters (Figure 5.17 & 5.19). The smaller intraspecific variation and larger interspecific differences in dorsal fin length in comparison to the length of its spine, increase the diagnostic value of the dorsal fin measurement.

Measurements derived from the adipose fin hold little to no taxonomic value among the southern African Synodontis. The interspecific differences noted in both the adipose basal length and dorsal to adipose measurements are impaired by consistently large intraspecific variations in all species (Figures 5.28 & 5.29). This variability is partly explained by the difficulty in determining the origin of the adipose fin in preserved material (Whitehead, 1962), an aspect also noted in Chiloglanis (Poll, 1952: Crass, 1960). The adipose fin of Synodontis is also unsupported by cartilage (Matsuoka & Iwai, 1983). Furthermore, Johnels (1954: 371) has shown that the height and length of the adipose fin, as well as its position relative to the dorsal, may vary with the nutritional state of the fish.

Phylogenetics

As an alpha taxonomic study this revision does not attempt any analysis above the level of species, yet certain indications of phylogenetic significance are evident at this stage.

As previously mentioned, the southern African Synodontis are divisible into two groups on the shape of the humeral process. The preceding character analysis has shown that species within each group show many more morphological and meristic similarities than species between these groups, which may indicate a closer phylogenetic relationship between species that share a common humeral process shape. The large diversity of humeral process shapes among the remaining Synodontis species (see Poll, 1971: plates 8 - 12) would also indicate the suitability of this character as certainly worthy of examination in future phylogenetic studies.

Fossil remains of most catfishes found thus far comprise fragments of fin spines and crania, which are difficult, sometimes impossible, to assign to genera (Greenwood, 1972: Roberts, 1975). The identification of Synodontis among these remains is made possible by certain unique osteological features, in particular, stout, longitudinally-striated fin spines and a large, triangular humeral process (von den Driesch, 1983). Greater understanding of the variation in humeral process shape in living species through a quantitative analysis similar to that described above could prove the means to diagnose fossil species more accurately, as well as allowing the fossil record to be incorporated into a phylogenetic analysis.

As the present study involves the comparison of very few and only external osteological features, in addition to the very limited knowledge of the distribution of characters between and among the nine currently recognized genera of the Mochokidae (Greenwood, 1963; Howes, 1980), any judgement on the relationships of the southern African Synodontis is highly speculative. In this regard, the only comparison worthy of mention is that between S.nigromaculatus and S.zambezensis, which are shown by the present study to closely resemble one another. From the comparison of the descriptions of species from more northerly drainages, S.nigromaculatus and S.zambezensis would seem to show more similarities to each other than to any other Synodontis species, suggestive of a sister group.

The state of southern African Synodontis taxonomy and recommendations for future research.

In Synodontis the mouth opens ventrally, which must be interpreted as an adaptation to bottom feeding (Alexander, 1966). There is some evidence, however, to suggest that certain species of this genus are more pelagic than most other catfishes (Cott, 1957; Jackson, 1961b; Willoughby, 1974). Feeding habits are adapted accordingly and range from normally-orientated benthos eaters to inverted plankton eaters (Green, 1977). Further feeding specialization is noted in S.victoriae and S.afrofischeri, both specialized mollusc eaters, the former able to extract the gastropods from their shells with the aid of suitably adapted mandibular teeth (Corbet, 1961). In this regard, some of the most striking anatomical differences noted in the present study are those associated with feeding, e.g. length and form of the barbels, mouth size, and the number and arrangement of the moveable mandibular and premaxillary teeth. Differences in feeding behaviour have also been recorded among the southern African Synodontis. Of the Synodontis species studied by van der Waal (1985) from Lake Liambezi, the diet of S.nigromaculatus shows a significantly higher component of fish than either S.leopardinus or S.macrostigma. In aquaria, S.nigromaculatus is also noticeably more aggressive than most other southern African Synodontis species (pers.obs.). A need to investigate the taxonomic significance of other aspects of the trophic apparatus is thus clearly evident.

Given the morphological evidence presented above, there seems little doubt that (at least) ten species are represented among the specimens examined. The consistently large variation of S.macrostigma in relation to other Group II species of comparable geographic distribution, however, warrants closer examination. Much of this variation is attributable to the Cunene sample whose data shows little conformity to the Okavango and Upper Zambezi samples of this species. In all but a few characters, however, the values of the Cunene specimens fall within the ranges of the other two samples. As demonstrated by the regression analysis of the interorbital and coracoid to cranium measurements (Figure 5.7 & 5.10, respectively), this inconformity is partly explained by the limited range and smaller overall sizes of the Cunene specimens in addition to the disproportionate allometric relationship between these measurements. The variation of the Cunene S.macrostigma sample in dorsal fin length and dorsal spine length which closely approximates that for S.macrostoma sp.n. is not as easily explained, though this may reflect an ecophenotypic adaptation (sensu Hubbs, 1941). In the measurements of dorsal to coracoid, humeral process to occipito-nuchal shield and occipito-nuchal shield width, the Cunene S.macrostigma values lie intermediate between S.macrostoma sp.n. and the other two S.macrostigma samples. This combination of character states of both an intermediate and mosaic pattern is indicative of introgressive hybridization (Ross, 1974). The paucity of adult specimens and the poor state of preservation of much of the available material from the Cunene River did not allow this possibility to be investigated further. All 15 specimens are here tentatively referred to S.macrostigma as the majority of morphological characters in addition to barbel morphology and moveable mandibular tooth number conform to the Okavango and Upper Zambezi populations of this species.

A total of 591 specimens from 13 river systems were examined in the character analysis. Those populations poorly represented include S.nebulosus from the Lower Zambezi River, S.woosnami, S.vanderwaali sp.n. and S.thamalakanensis from the Upper Zambezi River, S.macrostoma sp.n. from the Cunene River and S.zambezensis from the Pungwe, Buzi, Incomati and Umbeluzi Rivers. All but two of the ten recognized species, however, have at least one statistically valid sample of more than 30 specimens. Greater knowledge of the variation in the above-mentioned populations must therefore be considered important research priorities for the beter understanding of the taxonomy of the southern African

Synodontis.

Many of the characters considered diagnostic among Synodontis species are shown in the present study to be more variable than previously documented. Of greater taxonomic significance, however, is the finding that certain of these characters have widely differing ranges in intraspecific and intrapopulational variation, resulting in an equally variable diagnostic value. Therefore, to justify the use of any one character in the differentiation of the southern African Synodontis species, the full extent of the intraspecific variation, both within and among drainages, must be accounted for.

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APPENDIX 1

MATERIAL EXAMINED

SYNODONTIS ZAMBEZENSIS

Lectotype: ZMH 3119 (female, 153,3 mm SL, Tete, Lower Zambezi, W.C.H. Peters, 1852).

Paralectotypes: ZMH 3118 (1 x male, 158,0 mm SL, ditto), ZMH 3117 (3 x females; 137,6, 159,9 & 125,1 mm SL, ditto), ZMH 3116 (1 x female, 225,6 mm SL, ditto), ZMH 3115 (1 x male, 179,8 mm SL, ditto).

Middle Zambezi

AMG PF1358 (7 x Sanyati W, Lake Kariba, L. Kariba Fisheries Research Institute, 6 March 1965); AMG P2023 (3 x Gache Gache River, Lake Kariba, P.H. Skelton, 14 August 1973); AMG PF1624 (4 x Tailrace below wall, Lake Kariba, B.G. Donnelly, 25 June 1967).

Lower Zambezi

AMG PF1471 (1 x Chikwawa Ferry, Lower Shire River, Malawi, D. Eccles, 3 October 1965); NMZB 1219 (4 x Ancuaze, Lower Zambezi, Mocambique, G.L. Guy, 30 November 1965); NMZB 1220 (5 x Chemba, L. Zambezi River, G.L. Guy, 4 December 1964); RUSI 74-2411 (1 x Fish farm, Lower Shire River, Malawi, Fisheries Department, 21 November 1973).

Pungwe

NMZB 3027 (1 x Muar River, Gorongosa, Mocambique, J. Tello, 30 August 1972).

Buzi

NMZB 2822 (2 x Revue River, Inchope, Mocambique, G. Bell-Cross, 11 August 1972).

Save

AMG PF1000 (1 x Lower Lundi River, Rhodesia, R.A. Jubb, May 1958); AMG 1635 (6 x Lower Lundi River, below falls, R.A. Jubb, May 1958); AMG PF333 (1 x Lundi River gorge, S. Rhodesia, R.A. Jubb, September 1956); AMG PF1408 (1 x Lower Lundi River, S. Rhodesia, R.A. Jubb, 1958); NMZB 0398 (1 x Marhumbini, Lower Lundi River, G.L. Guy, 27 February 1958); NMZB 2853 (2 x Alves de Lima, Save River, Mocambique).

Limpopo

AMG P1894 (4 x Beit Bridge, Limpopo R., B.G. Donnelly, 25 January 1972); AMG PF1631 (1 x Pafuri, Levubu R., 7 August 1959); RUSI 21826 (21 x Ga-Sefati trib., Crocodile River, B. van der Waal, 24 August 1984); TMP 8619 (1 x Hammanskraal Dam, A. Wolff, 12 May 1913); TMP 1820 (1 x ditto); TMP 1821 (1 x ditto); TMP 1822 (1 x ditto); TMP 1823 (1 x ditto); TMP 1824 (1 x ditto); TMP 1825 (1 x ditto); TMP 1830 (1 x ditto); TMP 1831 (1 x ditto); TMP 1832 (1 x ditto); TMP 1833 (1 x ditto); TMP 1839 (1 x ditto); TMP 1942 (1 x ditto); TMP 1943 (1 x ditto).

Incomati

AMG P4354 (1 x Komati River, I. Gaigher & van der Merwe, 25 July 1966); AMG P4355 (1 x ditto, I. Gaigher & van der Merwe, 19 January 1967); AMG P4356 (2 x Incomati R., I. Gaigher & van der Merwe, 30 September 1966); TMP 21784 (1 x Skukuza, Sabie R., Kruger National Park, 31 March 1947).

Umbeluzi

TMP 8647 (1 x Umbeluzi R., 48 km from Maputo, T. Jenkins, 13 December 1911).

Pongolo

RUSI 17444 (15 x Pongolo River below dam wall, Jozini, P. White & R. Jackson, 18 August 1982); AMG 521 (1 x Kangazini Pan, Pongolo flood plain, 14 September 1956); AMG 6712 (1 x Pongolo R., below dam wall, Transvaal Prov. Fish. Inst., August 1968); TMP 10989 (1 x Maputo R., Mocambique); TMP 10990 (1 x ditto); TMP 15327 (1 x Pongolo R., Zululand, A. Roberts, August 1933); TMP 15328 (1 x Pongolo R., Zululand, A. Roberts, August 1933); RUSI 25516 (3 x Mlawayana Pan, Pongolo flood plain, P. White, 15 September 1983); RUSI 26110 (1 x Pongolo River below dam wall, Jozini, P. White, 20 August 1982); RUSI 26111 (1 x Banzi Pan, Ndumu Game Reserve, Pongolo flood plain, P.White, 19 September 1983); RUSI 26112 (1 x Pongolo River, Ndumu Game Reserve, 21 September 1983); RUSI 26113 (1 x Mayazela Pan, Pongolo flood plain, P.White, 15 September 1983); RUSI 26114 (1 x Pongolo River below dam wall, Jozini, P.White, 19 August 1982); AM P4455 (1 x Namanini Pan, Pongolo flood plain, H.Kok).

SYNODONTIS NIGROMACULATUS

Holotype: BMNH 1905.11.10.10 (male, 182,60 mm SL, Lake Bangwelo, F.H. Melland).

Okavango

AMG PF 1642.1-5 (5 x Shashi R., 3 miles south of Maun, Botswana, I. Gaigher, April 1969); AMG 3414.2-.4 (3 x

AMG P5762 (1 x Katere, Okavango R., S.W.A., B. v.d. Waal, 20 November 1977); AMG P5797 (2 x Bunya, Okavango R., S.W.A., B. v.d. Waal, 20 November 1977); AMG P5798 (1 x Mazua, Okavango R., S.W.A., B. v.d. Waal, November 1977); AMG P 5979 (2 x Muhango Omuramba, Okavango R., S.W.A., B. v.d. Waal, 17 November 1977); RUSI 18790.2 (1 x Nxamaceri confluence with Okavango R., Botswana, M.N. Bruton et al., October 1984); RUSI 18862 (4 x Okavango R., 6 km upstream from Nxamaceri confluence, Okavango River, M.N.Bruton, October 1984); RUSI 21156 (1 x ditto), RUSI 26115 (4 x Okavango River, South West Africa, P.H.Skelton & G.S.Merron, 29 April 1984); RUSI 26116 (1 x Thamalakane River, Okavango Delta, P.White, 13 December 1982); RUSI 26117 (1 x Matlapaneng Bridge, Thamalakane River, Okavango Delta, P.White, 13 December 1982); RUSI (1 x ditto); RUSI 26119 (1 x Thamalakane River, Okavango Delta, P.White, 17 March 1984); RUSI 26119 (1 x ditto); SMWN P324 (1 x Okavango R., F. Meiring, 24 May 1957); SMWN P325 (1 x Kapaku, Okavango R., P. Buys, 19 July 1964); SMWN P766 (1 x Caiundo, Okavango R., Angola, 5 October 1972); SMWN P1088 (2 x Kapaku, Okavango River, P.C. Olivier, 25 June 1969); SMWN P1826 (1 x Kapaku, Okavango River); SMWN P1828 (1 x ditto); SMWN P1830 (1 x ditto); SMWN 1831 (2 x ditto); SMWN P1886 (1 x Popa Falls, Okavango R.) RUSI 26120 (1 x Okavango River, South West Africa, P.H.Skelton & G.S.Merron, 29 April 1984); RUSI 26121 (1 x ditto); RUSI 26122 (6 x ditto); RUSI 26123 (3 x Boro River, Okavango Delta, G.S.Merron April 1984); RUSI 26124 (1 x Chanogha Lagoon, Botletle River, Okavango Delta, G.S.Merron, 5 July 1984); AM 1642 (6 x ditto); RUSI 26125 (5 x Thamalakane River, Okavango Delta, P.White, 13 December 1982); RUSI 21156 (1 x dotto); RUSI 26126 (3 x Okavango River, South West Africa, P.H.Skelton, 29 April 1984); RUSI 26127 (1 x Thamalakane River, Okavango Dela, P.White, 13 July 1985).

<u>Upper Zambezi</u>

AMG PF 1474.1 & .2 (2 x Chavuma above Falls, U. Zambezi R., G. Bell-Cross, 7 May 1956); AMG PF 1639 (2 x U. Zambezi R. above Victoria Falls, G. Bell-Cross); AMG P2450 (1 x U. Zambezi R. above Victoria Falls, B.C. Hoare, 3 October 1964); AMG 3198.1 & .2 (2 x Katima Mulilo Rapids, U. Zambezi R., B. v.d. Waal, 29 September 1975); AMG 3220.1 (1 x Katimbeza, U. Zambezi R., B. v.d. Waal & P.M. Skelton, 26 September 1975); AMG 3388.1-.4 (4 x Katimbeza, U. Zambezi R., B. v.d. Waal & P.H. Skelton, 24 July 1975); AMG 3432 (1 x Lizauli, Kwando R., E. Caprivi, B. v.d. Waal, 17 July 1975); TMP 15123 (1 x Kasane, Chobe R., Botswana, V. Fitzsimons, 28 July 1930); TMP 15124 (1 x ditto); TMP 15125 (1 x ditto); TMP

15126 (1 x ditto).

SYNODONTIS NJASSAE

Lectotype: ZMH 18191 (male, 151,0 mm SL, L. Nyassa at Langenburg, Tanzania, S. Fulleborn, 1908).

Paralectotypes: ZMH 18192 (1 x female 143,0 mm SL; 3 x males 143,0, 113,5, & 103,6 mm SL, ditto).

L.Malawi

AMG PF1467 (7 x L. Malawi, D. Eccles, 23 March 1968); AMG PF1468 (6 x ditto); AMG PF1469 (2 x L. Malawi, D. Eccles, 23 June 1962); AMG PF1470 (5 x Upper Shire R., Liwonde Ferry, D. Eccles, 7 September 1965); AMG PF1472 (2 x L. Malawi, D. Eccles, 18 December 1967); AMG PF1638 (4 x L. Malawi, Nkata Bay, Joint Fisheries Res. Organisation, 1963); RUSI 74-246 (3 x L. Malawi, Fisheries Dept., 20 November 1973).

SYNODONTIS NEBULOSUS

Holotype: ZMH 3120 (116,2 mm SL, Tete, Zambezi R., Mocambique, W.C.H. Peters, 1852).

Middle Zambezi

AMG PF955 (1 x Lake Kariba, B.G. Donnelly, March 1968); AMG PF1419 (1 x L. Kariba, Sengwa, B.G. Donnelly, 10 August 1968); AMG PF1518 (1 x Chirundu, Middle Zambezi R., R. Boltt, January 1958); AMG PF1634 (4 x Gorge below L. Kariba, 3 December 1958); AMG PF1679 (1 x Chirundu, Middle Zambezi R., R. Boltt, January 1958); AMG P1957 (1 x L. Kariba, Senka, B. Donnelly, 20 November 1967); NMZB 0402 (1 x confluence of Sengwa & Middle Zambezi R's, September 1958); NMZB 1092 (1 x Chirundu, Middle Zambezi R., 1965); NMZB 1729 (1 x Sengwa, L. Kariba); RUSI 74-125.1 (1 x L. Malawi, Fisheries Dept., 1 June 1969).

SYNODONTIS WOOSNAMI

Holotype: BMNH 1910.5.31.36 (male, 131.2 mm SL, Okavango R., R.B. Woosnam).

Okavango

SMWN P1819 (3 x Popa Falls, Okavango River); SMWN P1825.1 (1 x Okavango River at Andara); RUSI 26128 (1 x Thamalakane River, Okavango Delta, P.White, 21 October 1983); RUSI 26129 (1 x ditto); SMWN P1832 (1 x Okavango River at Kapaku); SMWN P1833 (1 x Okavango River at Kapaku); AMG P5800 (1 x Okavango River at Mazua, 90 km west of Rundu, 17[50'S/19[07'30"S, B. v.d. Waal, November 1977); AMG P5801.1 (1 x ditto); AMG P5974.2 (1 x Muhango Omuramba, Okavango River, S.W.A. 1808'S/21 40'E, B. v.d. Waal, 17 November 1977); AMG P5977.1 & .6 (2 x ditto); RUSI 22072 (2 x Popa Rapids, Okavango River, P.H. Skelton, 21 October 1984); RUSI 22151.1-.3 (3 x Kavango, Mbambi, Okavango River, S.W.A., P.H. Skelton, 23 October 1984); RUSI 22158.1 (1 x Okavango River, S.W.A., B.C.D van der Waal); RUSI 22295.1 (1 x Kavango, Okavango River, S.W.A.); RUSI 26130 (1 x Chanogha Lagoon, Botletle River, Okavango, G.S.Merron, 23 October 1983); RUSI 26131 (1 x Okavango River, South West Africa, P.H.Skelton & G.S.Merron, 29 April 1984); RUSI 26132 (1 x Chanogha Lagoon, Botletle River, Okavango, G.S.Merron, 4 July 1984); RUSI (12 x Boro River, canalized area, G.S.Merron, 16 May 1985); RUSI 126134 (1 x ditto); RUSI 26135 (11 x Thamalakane River, Okavango Delta, G.S.Merron, 16 May 1985); RUSI 26136 (2 x ditto); RUSI 26137 (3 x ditto).

Upper Zambezi

AM 3433.1 (1 x Lizauli, Kwando R., B. v.d. Waal 17 July 1975)

Cunene

AMG PF1630.5 (1 x Cunene R., Angola, G. Bell-Cross); AMG 10683.1 & .2 (2 x Ogongo Dam, 17[41'S/15[28'E, B. v.d. Waal, 6 December 1984); AMG 10750.1 & .2

(2 x Calueque, above wall, 17[17'S/14[33'E, B. v.d. Waal, 7 December 1984); SMWN P921.1 & .2 (2 x Cunene R. at Folgares, Angola); SMWN P1257.2 (1 x Ondurnsa Falls, Cunene R., Angola); SMWN P1544.3-.5 (3 x Cunene R. at Jumba ia Homa, Angola, M.J. Penrith, 8 December 1973).

SYNODONTIS MACROSTIGMA

Lectotype: BMNH 1910.5.31.37 (female, 135,0 mm SL, Okavango R., R.B. Woosnam).

Paralectotype: BMNH 1910.5.31.38 (77,15 mm SL, Okavango R., R.B. Woosnam).

Okavango

AMG PF1421.1.-.3 (3 x Maun, Thawalakane R., Okavango, I.G. Gaigher, April 1969); AMG PF 1473.1 & .2 (2 x Maun, Thamalakane R., Botswana, B.G. Donnelly, 28 January 1964); AMG P5763 (5 x Katere, 300 m upstream from confluence of Okavango & Cuito Rivers, 18 01'S/20 46'E, B. v.d. Waal, 20 November 1977); NMZB 1279.1-.5, .7-.9 (8 x Kwai R., Okavango, A. Maar, 1963); RUSI 20878 (1 x Matlapaneng pool, Thamalakane R., Okavango, G. Merron, 12 March 1984); RUSI 20998 (1 x 3rd Bridge, Moremi Game Reserve, Okavango, G. Merron, 24 March 1984); RUSI 22158.2, .5 & .7 (3 x ditto); RUSI 22221 (2 x Kavango, Okavango R., 17 54'S/19 46'E, P.H. Skelton et al., 26-27 October 1984); RUSI 26138 (1 x Chanogha Lagoon, Botletle River, G.S.Merron, 7 November 1983); RUSI 26139 (1 x Chanogha Lagoon, Btletle River, Okavango, G.S.Merron, 11 November 1983); RUSI 26140 (1 x Thamalakane River, Okavango Delta, G.S.Merron, 16 May 1985); RUSI 26141 (3 x ditto); RUSI 26142 (1 x Thamalakane River, Okavango Delta, P.White, 20 October 1983); RUSI 26143 (4 x Matlapaneng Bridge, Thamalakane River, Okavango Delta, G.S.Merron, 19 June 1984); RUSI 26144 (6 x Xakanaxa Lagoon, Okavango Delta, G.S.Merron, 5 July 1984); RUSI 26145 (4 x ditto); RUSI 26146 (6 x Thokatsebe, Boro River, Okavango Delta, G.S.Merron, 18 May 1985); RUSI 26147 (9 x ditto).

Upper Zambezi

AMG P2320.1-.4 (4 x Sangwali, Linyanti R., E. Caprivi, 18[15'S/23[40'E, B. v.d. Waal, 27 September 1973); AMG P2321 (5 x Lake Laimbezi, Linyanti R., E. Caprivi, 17[55'S/24[25'E, B. v.d. Waal, 14 November 1973); AMG P2322 (3 x Kasiba Valley, Kwando R., E. Caprivi, B. v.d. Waal, 18 October 1973); AMG P2325.1-.4 (4 x Mulapo near Sangwali, Kwando-Linyanti R., E. Caprivi, B. v.d. Waal, 27 October 1973); AMG P2526.1 (1 x Sangwali, Linyanti R., E. Caprivi, B. v.d. Waal, 27 October 1973); AMG 3399.1 (1 x Katimo Mulilo, E. Caprivi, B. v.d. Waal, 26 August 1975); AMG P 8708.2 (1 x ditto); NMZB 3489 (1 x Batobaja, confluence of Chobe and Upper Zambezi Rivers, B. v.d. Waal, 16 October 1973).

Cunene

AMG P1630.4 (1 x Cunene R., Angola, G. Bell-Cross); AMG P5872 (1 x Olushandja Dam, N. Owambo, Oshana Etaka, 17[22'S/14[38'E, B. v.d. Waal, 30 May 1977); SMWN P884.1-.4 (4 x Folgares, Cunene R., Angola); SMWN P928.1-.9 (9 x Candonque, Cunene R., Angola).

SYNODONTIS MACROSTOMA SP.N.

Holotype: AMG 3398.3 (female, 92,0 mm SL, Katima Mulilo, E. Caprivi, Upper Zambezi R., B. van der Waal, 26 August 1975);

Paratypes: AMG 3398.4-.14 (11 x 00.00 mm to 00.00 mm SL, ditto).

Upper Zambezi

AMG PF228 (3 x Kabuta, Chobe R., July 1949); AMG 3199.1 (1 x Katima Mulilo Rapids, E. Caprivi, B. van der Waal & P.H. Skelton, 29 December 1975); AMG 3200.1 & .2 (2 x Katima Mulilo Rapids, E. Caprivi, B. van der Waal & P.H. Skelton, 29 September 1975); AMG 3411 (2 x Impalila, E. Caprivi, B. van der Waal, 7 August 1975); AMG P 8709 (1 x Caprivi, Upper Zambezi R., B. van der Waal).

Cunene

SMWN P928.18 & .19 (2 x Candonque, Cunene R., Angola).

SYNODONTIS LEOPARDINUS

Holotype: MNHN 13/321 (male, 119.1 mm SL, Lealui, District of Barotses, Zambia, M.V. Ellenberger, 1913).

Okavango

AMG P821 (1 x Caiundo, Okavango River, Angola, M.J. Penrith, 16 October 1972); AMG P1821 (3 x Popa Falls, Okavango River); AMG P5796 (7 x Bunya, 70 km West of Rundu, Okavango R., 17[52'S/19[24'E, B. v.d. Waal, 20 November 1977); AMG P5800.1 (1 x Mazua, Okavango R., S.W.A., B. v.d. Waal, November 1977); RUSI 20875.1-.3 (3 x Thamalakane R., Okavango Delta, G.S. Merron, 12 March 1984); RUSI 22105.1-.4 (4 x Kavango, Okavango R., P.H. Skelton et al., 21 October 1984); RUSI 26148 (1 x Thokatsebe, Boro River, Okavango, G.S.Merron, 16 May 1985); RUSI 26149 (4 x ditto); RUSI 26150 (3 x ditto); RUSI 26151 (3 x Thamalakane River, Okavango Delta, G.S.Merron, 18 May 1985); RUSI 26152 (2 x ditto) SMWN P1820.2 & .3 (2 x Popa Falls, Okavango River) SMWN 1825.2-.4 (3 x ditto); SMWN 1827.1-.3 (3 x Kapaku, Okavango R.); SMWN 1834 (1 x ditto); SMWN 1835.1 (1 x ditto); TMP 26752 (1 x Kurunkuru, Kavango, Okavango R., S.W.A., State Vet., July 1960).

Upper Zambezi

AMG PF 1527.1 & .3-.8 (7 x Chavuma, Upper Zambezi R., ...); AMG PF1677.1 (1 x Upper Zambezi R., R.A. Jubb, July 1959); AMG 3201.1-.9 (9 x Rapids at Katimam Mulilo, E. Caprivi, Upper Zambezi R., B. v.d. Waal & P.H. Skelton, 29 September 1975); AMG 3349.1 & .2 (2 x Malila Mulapo, E. Caprivi, Upper Zambezi R., B. v.d. Waal, 25 August 1975); AMG 3398.1 & .2 (2 x Katima Mulilo, E. Caprivi, Upper Zambezi R., B. v.d. Waal, 26 August 1975); NMZB 1291.1 (1 x Katima Mulilo, E.

Caprivi, A. Maar, December 1963).

SYNODONTIS VANDERWAALI SP.N.

Holotype: AMG P5796.6 (male, 119.5 mm SL, Okavango R., S.W.A., B. v.d. Waal, 20 November 1977).

Paratypes: AMG P5796.11 (male, 139.5 mm SL, ditto); RUSI 18734 (1 x female, mm SL, Nxamaceri, Okavango River, M.N.Bruton et al., 24 October 1984); RUSI 25521 (3 x juveniles, 72,8, 73,0 & 75,5 mm SL, Boro River, canalized area, Okavango Delta, G.S.Merron, 16 May 1985); RUSI 22237 (1 x male, 14,5 mm SL; 2 x females, 139,5 & 156,1 mm SL, Kavango, Okavango River, South West Africa, P.H.Skelton et al., 26 October 1984).

Okavango

RUSI 18735 (2 x Nxamaceri, Okavango River, M.N.Bruton et al., 24 October 1984); RUSI 20875.4 (1 x Thamalakane River, Okavango R., G.S. Merron et al., 12 March 1984); RUSI 22158.3, .4 & .6 (3 x Okavango R., S.W.A., B. van der Waal); 22177.1-.4 (4 x Kavango, Okavango, S.W.A., P.H. Skelton et al., 24 October 1984); RUSI 20875.4 (1 x Thamalakane River, Okavango Delta, P.White); RUSI 25517 (13 x Thamalakane River above Matlapaneng Bridge, Okavango Delta, P.White, 16 May 1985); RUSI 25520 (1 x Thamalakane River, Maun, Okavango Delta, G.S.Merron, 15 May 1985); RUSI 25522 (ditto); RUSI 25518 (1 x Boro River, canalized area, Okavango Delta, G.S.Merron, 16 May 1985).

Upper Zambezi

AMG P2327 (4 x Kwando River, trib. of Linyanti River, Chobe, B. v.d. Waal, October 1973).

Cunene

SMWN 1068 (3 x Cunene River, 20 km E Rochados, Angola); SMWN 965 (1 x Cunene River at Ruacana, Angola); SMWN (1 x ditto); SMWN 1067 (3 x Cunene River at

Calueque, Angola).

SYNODONTIS THAMALAKANENSIS

Paratype: TMP 15305 (1 x male, 140 mm SL, Thamalakane River, Maun, Bechuanaland Protectorate, de Schauensee South Africa Expedition, 1930).

Okavango

AMG P1641.6-.12 (7 x Shashi River, 3 miles South of Maun, Okavango, I. Gaigher, April 1959); AMG P1820.1 (1 x Popa Falls, Okavango River); AMG P1822.1 & .2 (2 x ditto); AMG P1829 (1 x Kapaku, Okavango River); AMG P1835 (2 x ditto); AMG 5977.7 & .8 (2 x Muhango, Okavango River, South West Africa, B. van der Waal); RUSI 18735.3 (1 x Nxamaceri confluence, Okavango River, M.N. Bruton et al., 15 February 1983); RUSI 19729 (1 x Boro River, Okavango Delta, G.S. Merron et al., 30 October 1983); RUSI 20875.5 (1 x Matlapaneng pool, Thamalakane River, Okavango Delta, G.S. Merron, 12 March 1984); RUSI 20877 (1 x ditto); RUSI 20997 (1 x 3rd Bridge, Moremi Game Reserve, Okavango Delta, G.S. Merron et al. 24 March 1984); RUSI 26153 (1 x Thamalakane River, Okavango Delta, P.White, 5 November 1983); RUSI 26154 (2 x Chanogha Lagoon, Botletle River, Okavango Delta, G.S.Merron 4 July 1984); RUSI 26155 (1 x ditto); RUSI 26156 (10 x Boro River, canalized area, Okavango Delta, G.S.Merron, 16 May 1985); RUSI 26157 (3 x ditto); RUSI 26158 (1 x Thokatsebe, Boro River, Okavango Delta, G.S.Merron, 18 May 1985); RUSI 26159 (2 x ditto); SMWN P518.1 (1 x Popa Falls, Okavango River, M.J. Penrith, 25 August 1971); SMWN 551 (1 x Popa Falls, Okavango River, M.J.Penrith).

Upper Zambezi

AMG P8708.1 (1 x Caprivi, Upper Zambezi River, B.C.D. van der Waal).

APPENDIX 2

TABLES OF MORPHOMETRIC DATA

TABLE 2.1 Predorsal length as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	38.33	0.27	1.00	36.63 - 40.23
	L.Zambezi	18	37.72	0.30	1.27	34.89 - 39.46
	Pungwe	1	39.68	-	-	- - -
	Buzi	2	39.30	-	-	38.31 - 40.28
	Save	12	37.76	0.26	0.91	36.72 - 39.79
	Limpopo	41	35.74	0.26	1.67	32.61 - 39.89
	Incomati	5	38.03	-	-	37.77 - 38.60
	Umbeluzi	2	38.96	-	-	38.28 - 39.64
	Pongolo	30	37.28	0.29	1.37	34.81 - 39.28
S.nigromaculatus	Okavango	58	37.81	0.13	1.00	35.10 - 40.15
	U.Zambezi	17	38.03	0.22	0.92	36.29 - 39.67
S.njassae	L.Malawi	34	39.40	0.29	1.58	35.97 - 42.37
S.nebulosus	M.Zambezi	13	37.88	0.20	0.73	36.55 - 38.81
	L.Zambezi	1	36.75	-	-	- - -
S.woosnami	Okavango	54	39.44	0.18	1.35	36.87 - 42.43
	U.Zambezi	1	37.41	-	-	- - -
	Cunene	11	37.82	0.70	2.33	35.07 - 41.65
S.macrostigma	Okavango	61	38.93	0.23	1.76	35.92 - 43.10
	U.Zambezi	21	37.95	0.25	1.12	35.75 - 39.94
	Cunene	15	39.50	0.26	0.99	37.45 - 41.06
S.macrostoma sp.n.	U.Zambezi	21	39.87	0.24	1.12	37.40 - 41.79
	Cunene	2	40.27	-	-	40.08 - 40.46
S.leopardinus	Okavango	44	41.19	0.27	1.79	38.11 - 44.25
	U.Zambezi	22	40.79	0.25	1.17	39.06 - 44.10
S.vanderwaali sp.n.	Okavango	36	39.91	0.22	1.31	36.64 - 42.19
	U.Zambezi	4	40.20	-	-	38.85 - 41.52
	Cunene	8	37,03	0,35	1,00	35,62 - 38,36
S.thamalakanensis	Okavango	42	40.24	0.30	1.97	37. 3 - 44.97
	U.Zambezi	1	40.04	-	-	- - -

TABLE 2.2 Head length as % standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	29,66	0,20	0,73	28,54 - 30,82
	L.Zambezi	18	29,48	0,266	1,13	26,94 - 31,44
	Pungwe	1	31,70	-	-	- - -
	Buzi	2	30,17	-	-	29,74 - 30,61
	Save	12	29,70	0,19	0,67	28,62 - 31,04
	Limpopo	41	28,77	0,16	1,04	27,32 - 31,77
	Incomati	5	30,25	-	-	29,37 - 31,63
	Umbeluzi	2	31,41	-	-	30,99 - 31,84
	Pongolo	30	29,51	0,17	0,80	27,56 - 31,07
S.nigromaculatus	Okavango	58	29,93	0,19	1,44	26,95 - 32,38
	U.Zambezi	17	30,06	0,22	0,89	28,55 - 31,62
S.njassae	L.Malawi	34	31,44	0,21	1,13	28,86 - 33,53
S.nebulosus	M.Zambezi	13	30,79	0,21	0,76	29,44 - 32,09
	L.Zambezi	1	30,55	-	-	- - -
S.woosnami	Okavango	54	30,86	0,15	1,12	28,28 - 33,77
	U.Zambezi	1	29,27	-	-	- - -
	Cunene	11	30,13	0,64	2,14	27,12 - 33,12
S.macrostigma	Okavango	61	32,22	0,17	1,30	29,71 - 35,12
	U.Zambezi	21	31,26	0,23	1,01	29,39 - 32,82
	Cunene	15	32,24	0,19	0,72	30,72 - 33,13
S.macrostoma sp.n.	U.Zambezi	21	33,13	0,19	0,85	31,22 - 34,39
	Cunene	2	33,03	-	-	32,91 - 33,15
S.leopardinus	Okavango	44	33,42	0,21	1,39	30,80 - 35,84
	U.Zambezi	22	33,42	0,24	1,14	31,59 - 36,05
S.vanderwaali sp.n.	Okavango	36	32,69	0,15	0,92	30,48 - 34,32
	U.Zambezi	4	32,58	-	-	31,33 - 33,60
	Cunene	8	30,29	0,26	0,72	29,35 - 31,34
S.thamalakanensis	Okavango	42	33,16	0,24	1,56	30,92 - 37,00
	U.Zambezi	1	32,47	-	-	- - -

TABLE 2.3 Snout length as % Predorsal length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	33,96	0,26	0,98	31,33 - 34,89
	L.Zambezi	18	34,07	00,31	-	31,60 - 36,65
	Pungwe	1	35,70	-	-	- - -
	Buzi	2	34,33	-	-	32,52 - 36,13
	Save	12	33,91	0,30	1,05	31,97 - 35,65
	Limpopo	41	34,01	0,19	1,20	30,97 - 36,39
	Incomati	5	33,28	-	-	32,21 - 34,20
	Umbeluzi	2	32,16	-	-	- - -
	Pongolo	30	34,10	0,23	1,07	31,94 - 36,71
S.nigromaculatus	Okavango	58	34,31	0,14	1,08	31,48 - 37,23
	U.Zambezi	17	34,84	0,27	1,13	33,31 - 37,70
S.njassae	L.Malawi	34	33,74	0,24	1,29	31,38 - 36,16
S.nebulosus	M.Zambezi	13	37,22	0,24	0,86	35,88 - 38,58
	L.Zambezi	1	36,07	-	-	- - -
S.woosnami	Okavango	54	35,07	0,18	1,34	32,41 - 38,32
	U.Zambezi	1	33,74	-	-	- - -
	Cunene	11	34,90	0,29	0,96	33,19 - 36,21
S.macrostigma	Okavango	61	35,15	0,17	1,29	31,99 - 37,44
	U.Zambezi	21	34,50	0,37	1,70	29,40 - 37,34
	Cunene	15	34,97	0,31	1,18	33.65 - 37,38
S.macrostoma sp.n.	U.Zambezi	21	39,46	0,33	1,53	36,50 - 41,70
	Cunene	2	37,30	-	-	37,05 - 37,55
S.leopardinus	Okavango	44	35,83	0,15	1,00	33,43 - 37,98
	U.Zambezi	22	36,53	0,21	0,99	34,37 - 38,62
S.vanderwaali sp.n.	Okavango	36	35,09	0,17	1,04	32,74 - 37,80
	U.Zambezi	4	34,87	-	-	34,51 - 35,36
	Cunene	8	35,44	0,32	0,90	33,68 - 36,41
S.thamalakanensis	Okavango	42	37,17	0,14	0,91	35,17 - 39,37
	U.Zambezi	1	36,83	-	-	- - -

TABLE 2.4 Interorbital length as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	32,10	0,65	2,44	28,03 - 36,41
	L.Zambezi	18	32,14	0,58	2,48	28,75 - 37,20
	Pungwe	1	30,52	-	-	- - -
	Buzi	2	35,54	-	-	35,35 - 35,72
	Save	12	34,11	0,54	1,87	30,31 - 36,81
	Limpopo	41	34,59	0,25	1,62	31,59 - 37,86
	Incomati	5	33,31	-	-	30,61 - 36,63
	Umbeluzi	2	34,86	-	-	34,54 - 35,17
	Pongolo	30	35,38	0,39	1,83	32,97 - 40,25
S.nigromaculatus	Okavango	58	33,89	0,19	1,45	30,48 - 36,97
	U.Zambezi	17	34,94	0,46	1,88	30,97 - 33,01
S.njassae	L.Malawi	34	36,00	0,42	2,25	31,74 - 40,57
S.nebulosus	M.Zambezi	13	30,81	0,26	0,94	29,05 - 32,45
	L.Zambezi	1	33,38	-	-	- - -
S.woosnami	Okavango	54	33,07	0,29	2,15	29,83 - 38,49
	U.Zambezi	1	36,08	-	-	- - -
	Cunene	11	33,78	0,87	2,87	29,77 - 37,47
S.macrostigma	Okavango	61	32,63	0,25	1,93	28,57 - 37,19
	U.Zambezi	21	35,70	0,55	2,45	31,98 - 41,17
	Cunene	15	30,37	0,35	1,27	28,57 - 33,40
S.macrostoma sp.n.	U.Zambezi	21	27,24	0,34	1,56	24,07 - 29,08
	Cunene	2	27,15	-	-	26,84 - 27,45
S.leopardinus	Okavango	44	31,07	0,28	1,85	27,35 - 35,93
	U.Zambezi	22	28,78	0,52	2,44	25,46 - 34,48
S.vanderwaali sp.n.	Okavango	36	32,50	0,38	2,25	29,64 - 39,61
	U.Zambezi	4	33,36	-	-	32,43 - 34,37
	Cunene	8	33,49	0,64	1,81	29,92 - 35,37
S.thamalakanensis	Okavango	42	31,04	0,37	2,41	26,98 - 35,58
	U.Zambezi	1	31,24	-	-	- - -

TABLE 2.5 Dorsal to coracoid as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	85,96	0,68	2,54	83,15 - 91,73
	L.Zambezi	18	87,07	0,87	3,68	81,06 - 94,37
	Pungwe	1	85,06	-	-	- - -
	Buzi	2	90,75	-	-	89,99 - 91,52
	Save	12	87,31	0,81	2,81	84,06 - 92,42
	Limpopo	41	86,42	0,55	3,52	79,75 - 92,79
	Incomati	5	87,47	-	-	84,60 - 92,39
	Umbeluzi	2	82,72	-	-	81,40 - 84,05
	Pongolo	30	88,18	1,02	4,80	79,30 - 99,46
S.nigromaculatus	Okavango	58	86,32	0,46	3,50	77,41 - 94,86
	U.Zambezi	17	87,03	0,76	3,15	80,23 - 93,23
S.njassae	L.Malawi	34	86,96	0,48	2,61	81,68 - 91,50
S.nebulosus	M.Zambezi	13	80,99	0,64	2,30	76,17 - 84,28
	L.Zambezi	1	76,34	-	-	- - -
S.woosnami	Okavango	54	88,35	0,52	3,80	77,67 - 101,15
	U.Zambezi	1	99,95	-	-	- - -
	Cunene	11	87,23	1,58	5,25	77,14 - 94,00
S.macrostigma	Okavango	61	88,01	0,45	3,53	81,36 - 96,58
	U.Zambezi	21	92,20	1,16	5,19	83,05 - 103,44
	Cunene	15	77,52	0,98	3,79	72,92 - 87,66
S.macrostoma sp.n.	U.Zambezi	21	69,59	0,53	2,44	64,35 - 73,96
	Cunene	2	71,01	-	-	69,46 - 72,55
S.leopardinus	Okavango	44	81,21	0,44	2,92	74,71 - 86,80
	U.Zambezi	22	79,35	1,29	6,04	69,06 - 89,24
S.vanderwaali sp,n.	Okavango	36	87,61	0,55	3,29	81,78 - 96,40
	U.Zambezi	4	88,49	-	-	85,27 - 92,17
	Cunene	8	91,15	1,37	3,88	86,50 - 97,49
S.thamalakanensis	Okavango	42	80,22	0,60	3,88	72,36 - 87,41
	U.Zambezi	1	76,21	-	-	- - -

TABLE 2.6 Coracoid to neurocranium as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.nigromaculatus	Okavango	58	58,48	0,49	3,55	51,68 - 75,16
	U.Zambezi	17	57,58	0,65	2,69	54,53 - 64,88
S.njassae	L.Malawi	34	60,77	0,42	2,27	56,45 - 65,65
S.nebulosus	M.Zambezi	13	58,38	0,98	3,52	54,85 - 65,93
	L.Zambezi	1	-	-	-	- - -
S.woosnami	Okavango	54	68,20	0,48	3,50	60,43 - 76,76
	U.Zambezi	1	78,04	-	-	- - -
	Cunene	11	69,53	1,68	5,58	61,67 - 77,17
S.macrostigma	Okavango	61	66,52	0,36	2,76	60,95 - 72,70
	U.Zambezi	21	71,15	1,14	5,10	61,67 - 78,89
	Cunene	15	62,28	0,85	3,29	58,33 - 72,34
S.macrostoma sp.n.	U.Zambezi	21	53,51	0,47	2,13	49,54 - 58,51
	Cunene	2	55,48	-	-	53,44 - 57,52
S.leopardinus	Okavango	44	61,92	0,40	2,59	56,49 - 68,17
	U.Zambezi	22	58,94	1,09	5,12	51,83 - 66,25
S.vanderwaali sp.n.	Okavango	36	64,01	0,40	2,37	59,49 - 68,97
	U.Zambezi	4	61,94	-	-	59,52 - 64,06
	Cunene	8	70,45	0,83	2,35	67,09 - 73,29
S.thamalakanensis	Okavango	42	59,63	0,44	2,84	53,90 - 65,78
	U.Zambezi	1	62,01	-	-	- - -

TABLE 2.7 Snout to pectoral as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	21,98	0,17	0,62	20,74 - 22,71
	L.Zambezi	18	21,68	0,18	0,75	20,53 - 23,28
	Pungwe	1	23,35	-	-	- - -
	Buzi	2	22,49	-	-	21,69 = 23,29
	Save	12	21,81	0,34	1,17	20,61 - 24,01
	Limpopo	41	22,22	0,13	0,84	20,61 - 23,77
	Incomati	5	22,84	-	-	21,94 - 24,82
	Umbeluzi	2	24,57	-	-	- - -
	Pongolo	30	22,81	0,17	0,78	21,48 - 24,94
S.nigromaculatus	Okavango	58	22,41	0,15	1,15	18,26 - 24,94
	U.Zambezi	17	22,47	0,23	0,95	20,92 - 24,69
S.njassae	L.Malawi	34	24,61	0,18	0,98	22,55 - 27 03
S.nebulosus	M.Zambezi	13	22,86	0,44	1,59	19,97 - 25,83
	L.Zambezi	1	22,03	-	-	- - -
S.woosnami	Okavango	54	25,18	0,15	1,07	22,60 - 27,08
	U.Zambezi	1	23,22	-	-	- - -
	Cunene	11	24,67	0,60	1,98	21,51 - 27,10
S.macrostigma	Okavango	61	24,65	0,18	1,40	21,80 - 27,71
	U.Zambezi	21	23,68	0,26	114	21,92 - 25,65
	Cunene	15	24,37	0,22	0,83	22,62 - 25,45
S.macrostoma sp.n.	U.Zambezi	21	24,47	0,27	1,21	23,34 - 28,19
	Cunene	2	25,01	-	-	24,72 - 25,29
S.leopardinus	Okavango	44	26,05	0,19	1,24	23,48 - 27,98
	U.Zambezi	22	25,26	0,25	1,16	23,78 - 27,70
S.vanderwaali sp.n.	Okavango	36	24,12	0,15	0,88	22,62 - 25,41
	U.Zambezi	4	24,07	-	-	22,66 - 25,15
	Cunene	8	24,29	0,50	1,43	22,75 - 26,23
S.thamalakanensis	Okavango	42	24,66	0,250	1,62	22,07 - 27,80
	U.Zambezi	1	24,15	-	-	- - -

TABLE 2.8 Pectoral girdle width as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	78,08	0,62	2,30	74,24 - 81,84
	L.Zambezi	18	77,59	0,58	2,46	74,41 - 83,14
	Pungwe	1	77,27	-	-	- - -
	Buzi	2	78,84	-	-	78,66 - 79,03
	Save	12	75,43	0,64	2,20	71,96 - 78,52
	Limpopo	41	76,13	0,31	1,95	72,53 - 79,69
	Incomati	5	76,28	-	-	75,20 - 78,12
	Umbeluzi	2	72,60	-	-	71,57 - 73,62
	Pongolo	30	75,27	0,67	3,16	69,59 - 80,86
S.nigromaculatus	Okavango	58	81,89	0,43	3,22	74,83 - 89,39
	U.Zambezi	17	83,97	0,82	3,39	78,56 - 90,30
S.njassae	L.Malawi	34	81,16	0,28	1,50	77,31 - 84,48
S.nebulosus	M.Zambezi	13	79,70	0,57	2,04	77,16 - 84,60
	L.Zambezi	1	77,50	-	-	- - -
S.woosnami	Okavango	54	84,82	0,44	3,20	73,92 - 91,43
	U.Zambezi	1	89,28	-	-	- - -
	Cunene	11	87,12	1,14	3,76	77,86 - 90,87
S.macrostigma	Okavango	61	84,26	0,35	2,72	78,52 - 89,44
	U.Zambezi	21	83,48	1,01	4,52	76,89 - 96,41
	Cunene	15	80,97	0,44	1,72	77,87 - 84,89
S.macrostoma sp.n.	U.Zambezi	21	74,41	0,52	2,27	70,33 - 79,00
	Cunene	2	76,51	-	-	75,53 - 77,79
S.leopardinus	Okavango	44	75,61	0,52	3,48	68,64 - 84,91
	U.Zambezi	22	74,72	0,63	2,94	70,12 - 80,00
S.vanderwaali sp.n.	Okavango	36	82,46	0,45	2,71	73,48 - 87,28
	U.Zambezi	4	81,34	-	-	79,46 - 83,20
	Cunene	8	82,59	1,39	3,93	76,89 - 88,70
S.thamalakanensis	Okavango	42	76,62	0,33	2,12	72,93 - 83,13
	U.Zambezi	1	76,20	-	-	- - -

TABLE 2.9 Occipito-nuchal shield width as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	28,53	0,36	1,33	25,48 - 30,92
	L.Zambezi	18	27,69	0,30	1,27	25,85 - 30,26
	Pungwe	1	26,41	-	-	- - -
	Buzi	2	29,87	-	-	29,69 - 30,04
	Save	12	28,42	0,56	1,93	25,86 - 31,74
	Limpopo	41	26,30	0,20	1,30	23,75 - 28,83
	Incomati	5	27,32	-	-	- - -
	Umbeluzi	2	26,83	-	-	25,43 - 28,22
	Pongolo	30	25,49	0,37	1,72	23,09 - 30,33
S.nigromaculatus	Okavango	58	31,75	0,34	2,04	26,75 - 36,22
	U.Zambezi	17	32,91	0,40	1,66	29,64 - 35,61
S.njassae	L.Malawi	34	27,24	0,32	1,74	24,20 - 30,80
S.nebulosus	M.Zambezi	13	33,38	0,45	1,63	29,98 - 35,89
	L.Zambezi	1	31,41	-	-	- - -
S.woosnami	Okavango	54	34,42	0,23	1,70	28,48 - 38,90
	U.Zambezi	1	39,25	-	-	- - -
	Cunene	11	34,63	0,71	2,34	31,19 - 37,27
S.macrostigma	Okavango	61	36,42	0,37	2,28	32,08 - 43,30
	U.Zambezi	21	37,65	0,61	2,75	33,19 - 45,06
	Cunene	15	31,83	0,40	1,56	29,89 - 35,75
S.macrostoma sp.n.	U.Zambezi	21	29,74	0,35	1,60	26,01 - 32,13
	Cunene	2	30,24	-	-	30,07 - 30,40
S.leopardinus	Okavango	44	32,52	0,43	2,08	28,23 - 35,61
	U.Zambezi	22	31,80	0,40	1,89	27,39 - 35,59
S.vanderwaali sp.n.	Okavango	36	34,90	0,32	1,43	32,60 - 36,99
	U.Zambezi	4	35,32	-	-	34,67 - 36,32
	Cunene	8	36,81	0,54	1,52	34,43 - 38,74
S.thamalakanensis	Okavango	42	35,32	-	-	34,67 - 36,32
	U.Zambezi	1	34,21	-	-	- - -

TABLE 2.10 Humeral process length as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	66,34	0,31	1,14	64,52 - 67,85
	L.Zambezi	18	63,67	0,75	3,17	58,92 - 69,17
	Pungwe	1	59,96	-	-	- - -
	Buzi	2	66,66	-	-	66,07 - 67,25
	Save	12	60,81	0,60	2,07	56,37 - 64,02
	Limpopo	41	61,57	0,41	2,60	54,69 - 67,14
	Incomati	5	62,28	-	-	60,11 - 63,81
	Umbeluzi	2	59,21	-	-	58,49 - 59,94
	Pongolo	30	61,34	0,75	3,51	53,62 - 68,60
S.nigromaculatus	Okavango	58	69,69	0,50	3,78	56,67 - 76,60
	U.Zambezi	17	70,57	0,45	1,84	67,61 - 73,22
S.njassae	L.Malawi	34	61,58	0,55	2,97	56,16 - 69,21
S.nebulosus	M.Zambezi	13	59,57	0,81	2,92	54,50 - 63,67
	L.Zambezi	1	51,55	-	-	- - -
S.woosnami	Okavango	54	63,30	0,42	3,04	57,47 - 68,97
	U.Zambezi	1	66,27	-	-	- - -
	Cunene	11	63,54	1,25	4,15	53,81 - 67,52
S.macrostigma	Okavango	61	62,18	0,51	3,14	56,52 - 68,39
	U.Zambezi	21	63,01	0,74	3,31	58,55 - 72,31
	Cunene	15	61,26	0,38	1,46	58,85 - 63,62
S.macrostoma sp.n.	U.Zambezi	21	55,21	0,55	2,38	49,90 - 58,56
	Cunene	2	57,38	-	-	56,53 - 58,23
S.leopardinus	Okavango	44	59,05	0,42	2,78	52,36 - 64,29
	U,Zambezi	22	58,71	0,44	2,07	54,42 - 62,00
S.vanderwaali sp.n.	Okavango	36	64,90	0,74	3,24	56,80 - 69,77
	U.Zambezi	4	65,82	-	-	62,82 - 68,32
	Cunene	8	64,98	1,21	3,43	61,03 - 70,21
S.thamalakanensis	Okavango	42	59,91	0,41	2,64	55,29 - 67,99
	U.Zambezi	1	64,19	-	-	- - -

TABLE 2.11 Humeral process to occipito-nuchal shield as % Head length.

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	37,75	0,71	2,64	32,66 - 40,97
	L.Zambezi	18	40,76	0,61	2,57	35,50 - 44,98
	Pungwe	ND	-	-	-	- - -
	Buzi	2	42,38	-	-	42,08 - 42,67
	Save	12	44,35	1,03	3,57	40,42 - 49,88
	Limpopo	41	46,53	0,54	3,45	37,68 - 51,68
	Incomati	5	45,70	-	-	39,81 - 52,24
	Umbeluzi	ND	-	-	-	- - -
	Pongolo	30	46,27	0,79	3,72	40,05 - 52,20
S.nigromaculatus	Okavango	58	36,25	0,44	2,69	29,60 - 42,47
	U.Zambezi	17	36,13	0,67	2,70	32,10 - 41,27
S.njassae	L.Malawi	34	39,22	0,46	2,49	35,20 - 44,52
S.nebulosus	M.Zambezi	13	36,78	0,83	2,99	32,01 - 41,81
	L.Zambezi	1	42,68	-	-	- - -
S.woosnami	Okavango	54	37,27	0,93	4,54	28,48 - 48,21
	U.Zambezi	1	42,88	-	-	- - -
	Cunene	11	39,00	1,65	5,75	29,60 - 46,80
S.macrostigma	Okavango	61	41,29	0,56	3,45	33,96 - 47,98
	U.Zambezi	21	40,38	0,68	3,06	33,17 - 44,64
	Cunene	15	32,95	0,53	2,05	29,14 - 37,81
S.macrostoma sp.n.	U.Zambezi	21	28,91	0,63	2,90	21,99 - 33,44
	Cunene	2	29,05	-	-	28,27 - 39,83
S.leopardinus	Okavango	44	34,38	0,63	3,07	29,25 - 39,83
	U.Zambezi	22	34,50	0,84	3,96	27,81 - 41,99
S.vanderwaali sp.n.	Okavango	36	36,50	1,10	4,87	28,50 - 43,60
	U.Zambezi	4	37,90	-	-	34,89 - 42,40
	Cunene	8	37,52	1,75	4,95	32,28 - 42,64
S.thamalakanensis	Okavango	42	35,76	0,79	4,00	27,19 - 43,94
	U.Zambezi	1	35,13	-	-	- - -

TABLE 2.12 Orbit diameter as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	19,10	0,67	2,49	14,79 - 23,38
	L.Zambezi	18	19,02	0,654	2,78	13,84 - 24,26
	Pungwe	1	20,13	-	-	- - -
	Buzi	2	17,48	-	-	17,22 - 17,73
	Save	12	17,92	0,45	1,55	15,78 - 20,73
	Limpopo	41	17,59	0,23	1,47	15,20 - 20,73
	Incomati	5	18,04	-	-	15,22 - 20,59
	Umbeluzi	2	17,88	-	-	16,77 - 18,98
	Pongolo	30	16,27	0,31	1,46	13,75 - 18,61
S.nigromaculatus	Okavango	58	17,08	0,28	2,15	13,93 - 22,11
	U.Zambezi	17	16,43	0,33	1,35	13,97 - 18,40
S.njassae	L.Malawi	34	20,23	0,33	1,76	17,22 - 23,05
S.nebulosus	M.Zambezi	13	19,90	0,39	1,41	17,84 - 22,94
	L.Zambezi	1	20,85	-	-	- - -
S.woosnami	Okavango	54	19,68	0,28	2,00	15,33 - 23,20
	U.Zambezi	1	17,52	-	-	- - -
	Cunene	11	21,85	0,90	3,00	17,77 - 25,48
S.macrostigma	Okavango	61	17,88	0,27	1,65	15,34 - 22,53
	U.Zambezi	21	17,43	0,35	1,55	14,61 - 21,84
	Cunene	15	24,22	0,56	2,16	19,23 - 26,44
S.macrostoma sp.n.	U.Zambezi	21	19,65	0,34	1,57	16,74 - 21,83
	Cunene	2	21,50	-	-	21,43 - 21,57
S.leopardinus	Okavango	44	18,07	0,33	1,62	15,43 - 21,65
	U.Zambezi	22	18,80	0,41	1,94	15,67 - 23,25
S.vanderwaali sp.n.	Okavango	36	18,73	0,23	1,04	16,59 - 20,44
	U.Zambezi	4	18,61	-	-	17,41 - 19,65
	Cunene	8	19,51	0,31	0,88	18,34 - 20,67
S.thamalakanensis	Okavango	42	18,91	0,34	2,17	15,17 - 23,19
	U.Zambezi	1	16,59	-	-	- - -

TABLE 2.13 Dorsal spine length as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	103,68	2,71	10.13	87.47 -120.84
	L.Zambezi	18	92.78	2.59	10.98	78.26 -118.52
	Pungwe	1	82.47	-	-	- - -
	Buzi	2	100.97			97.56 -104.37
	Save	12	93.85	1.31	4.53	87.64 -104.66
	Limpopo	41	83.03	0.92	5.92	71.17 - 95.27
	Incomati	5	85.48	-	-	78.11 - 90.60
	Umbeluzi	2	85.09	-	-	83.68 - 86.50
	Pongolo	30	84.19	0.87	4.07	76.97 - 92.16
S.nigromaculatus	Okavango	58	94.25	1.10	7.71	71.34 -113.26
	U.Zambezi	17	97.45	0.77	3.19	91.26 103.51
S.njassae	L.Malawi	34	69.55	1.26	6.40	59.38 - 84.21
S.nebulosus	M.Zambezi	13	81.11	1.95	7.04	71.27 - 92.31
	L.Zambezi	ND				
S.woosnami	Okavango	54	97.04	0.99	7.28	82.19 -117.63
	U.Zambezi	1	96.73			
	Cunene	11	96.45	2.70	8.09	81.43 -106.78
S.macrostigma	Okavango	61	96.40	0.96	6.59	82.97 -110.55
	U.Zambezi	21	-	-	-	- - -
	Cunene	15	80.95	0.85	3.28	74.81 - 87.35
S.macrostoma sp.n.	U.Zambezi	21	79.95	1.38	6.31	68.09 - 89.47
	Cunene	2	75.95	-	-	74.46 - 77.43
S.leopardinus	Okavango	44	106.17	1.26	7.98	89.43 -122.37
	U.Zambezi	22	100.89	3.05	14.29	77.49 -123.59
S.vanderwaali sp.n.	Okavango	36	95.10	1.03	6.11	79.71 -106.23
	U.Zambezi	4	99.18	-	-	96.81 -102.37
	Cunene	8	105.54	2.57	6.81	96.60 -117.92
S.thamalakanensis	Okavango	42	108.29	1.73	10.63	91.60 -129.33
	U.Zambezi	ND				

TABLE 2.14 Pectoral spine length as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	85,43	1,53	5,73	76,01 - 94,73
	L.Zambezi	18	78,12	1,79	7,58	65,97 - 90,42
	Pungwe	1	75,97	-	-	- - -
	Buzi	2	83,82	-	-	82,52 - 85,12
	Save	12	79,63	1,18	4,07	74,19 - 88,54
	Limpopo	41	76,20	1,18	7,21	64,60 - 93,00
	Incomati	5	74,04	-	-	71,80 - 77,33
	Umbeluzi	2	79,70	-	-	77,80 - 81,60
	Pongolo	30	75,47	0,81	3,82	65,51 - 83,20
S.nigromaculatus	Okavango	58	85,82	0,84	5,98	65,56 - 95,67
	U.Zambezi	17	85,27	0,90	3,71	79,01 - 92,92
S.njassae	L.Malawi	34	70,00	0,64	3,26	65,19 - 76,01
S.nebulosus	M.Zambezi	13	76,73	1,31	4,74	71,07 - 86,99
	L.Zambezi	ND				
S.woosnami	Okavango	54	82,43	0,56	4,02	72,25 - 91,34
	U.Zambezi	1	79,87	-	-	- - -
	Cunene	11	84,69	2,22	7,01	73,81 - 93,91
S.macrostigma	Okavango	61	80,51	0,55	4,00	71,63 - 87,56
	U.Zambezi	21	80,68	1,12	4,61	73,38 - 89,82
	Cunene	15	76,27	0,40	1,57	73,50 - 79,14
S.macrostoma sp.n.	U.Zambezi	21	72,52	0,99	4,32	65,19 - 78,41
	Cunene	2	72,02	-	-	68,97 - 75,06
S.leopardinus	Okavango	44	78,59	0,49	3,21	72,36 - 86,25
	U.Zambezi	22	75,79	0,89	4,17	63,42 - 82,42
S.vanderwaali sp.n.	Okavango	36	80,02	0,73	4,39	65,80 - 86,21
	U.Zambezi	4	83,76	-	-	79,85 - 89,28
	Cunene	8	85,68	0,98	2,60	81,72 - 90,18
S.thamalakanensis	Okavango	42	83,61	0,68	4,16	73,32 - 90,32
	U.Zambezi	1	88,56	-	-	- - -

TABLE 2.15 Dorsal fin length as % Predorsal length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	106.98	3.50	10.03	89.28 -123.87
	L.Zambezi	18	97.60	3.05	10.55	84.30 -115.65
	Pungwe	1	86.50	-	-	- - -
	Buzi	2	108.00	-	-	- - -
	Save	12	99.75	2.37	6.73	90.46 -113.35
	Limpopo	41	87.55	1.52	5.53	79.24 - 97.78
	Incomati	5	93.97	-	-	- - -
	Umbeluzi	2	93.50	-	-	- - -
	Pongolo	30	91.57	1.96	5.57	84.17 -101.35
S.nigromaculatus	Okavango	58	98.45	0.73	5.20	88.94 -111.95
	U.Zambezi	17	99.16	1.41	5.46	89.84 -109.85
S.njassae	L.Malawi	34	65.98	0.97	5.23	58.30 - 75.66
S.nebulosus	M.Zambezi	13	78.63	1.08	3.73	72.29 - 85.71
	L.Zambezi	ND				
S.woosnami	Okavango	51	94.28	0.85	6.10	81.61 -112.95
	U.Zambezi	1	92.51	-	-	- - -
	Cunene	11	90.35	1.70	5.63	80.48 - 97.83
S.macrostigma	Okavango	58	92.78	0.74	5.67	77.95 -107.88
	U.Zambezi	21	95.36	1.54	6.87	84.58 -110.55
	Cunene	15	80.91	1.10	4.25	73.27 - 86.86
S.macrostoma sp.n.	U.Zambezi	21	75.49	1.24	4.48	68.11 - 81.23
	Cunene	2	73.19	-	-	71.27 - 75.20
S.leopardinus	Okavango	44	114.30	1.47	9.53	97.12 -136.66
	U.Zambezi	22	113.01	3.24	12.53	95.45 -135.75
S.vanderwaali sp.n.	Okavango	36	91.50	1.16	6.93	75.94 -109.40
	U.Zambezi	4	100.01	1.78	3.56	97.02 -105.12
	Cunene	8	97.14	1.74	4.61	88.16 -101.83
S.thamalakanensis	Okavango	42	115.86	1.86	11.77	95.72 -144.74
	U.Zambezi	ND				

TABLE 2.16 Caudal fork length as % Caudal total length.

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	36.99	1.34	5.02	28.52 - 44.55
	L.Zambezi	18	38.88	1.37	5.29	30.00 - 46.41
	Pungwe	ND				
	Buzi	ND				
	Save	12	35.54	0.86	2.84	30.80 - 39.05
	Limpopo	41	35.94	0.44	2.42	32.64 - 42.03
	Incomati	5	37.37	-	-	36.98 - 37.76
	Umbeluzi	ND				
	Pongolo	30	35.68	0.81	3.25	29.83 - 42.38
S.nigromaculatus	Okavango	58	48.08	0.83	5.84	38.22 - 58.56
	U.Zambezi	17	43.42	0.82	2.31	40.21 - 47.84
S.njassae	L.Malawi	34	33.05	0.59	2.79	28.37 - 38.11
S.nebulosus	M.Zambezi	13	45.86	0.89	2.96	40.67 - 49.59
	L.Zambezi	ND				
S.woosnami	Okavango	54	49.73	0.37	2.52	42.36 - 56.97
	U.Zambezi	ND				
	Cunene	11	49.82	0.65	2.15	46.40 - 54.75
S.macrostigma	Okavango	61	59.11	0.57	4.24	48.11 - 65.45
	U.Zambezi	21	54.14	1.44	6.12	39.83 - 62.45
	Cunene	15	46.29	0.76	2.94	40.12 - 53.33
S.macrostoma sp.n.	U.Zambezi	21	46.17	0.59	2.70	40.50 - 50.56
	Cunene	2	44.27	-	-	- - -
S.leopardinus	Okavango	44	43.72	0.38	2.24	40.50 - 49.91
	U.Zambezi	22	43.29	0.57	2.13	37.63 - 46.07
S.vanderwaali sp.n.	Okavango	36	45.80	0.50	2.84	37.32 - 52.00
	U.Zambezi	4	44.55	-	-	42.00 - 48.37
	Cunene	ND				
S.thamalakanensis	Okavango	42	48.32	0.54	3.18	40.73 - 54.66
	U.Zambezi	ND				

TABLE 2.17 Maxillary barbel length as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	116,35	2,59	9,69	101,32 - 135,82
	L.Zambezi	18	110,73	3,16	12,63	95,00 - 135,21
	Pungwe	1	96,54	-	-	- - -
	Buzi	2	116,61	-	-	109,13 - 124,09
	Save	12	110,07	1,89	6,55	96,77 - 117,99
	Limpopo	41	106,79	1,74	11,17	86,35 - 132,93
	Incomati	5	107,25	-	-	97,03 - 121,69
	Umbeluzi	2	90,50	-	-	84,44 - 96,90
	Pongolo	30	102,76	2,50	11,73	81,66 - 124,35
S.nigromaculatus	Okavango	58	123,53	1,42	10,84	94,55 - 144,59
	U.Zambezi	17	120,08	2,13	8,77	105,16 - 134,40
S.njassae	L.Malawi	34	126,59	3,84	20,30	89,35 - 161,35
S.nebulosus	M.Zambezi	13	87,91	1,69	6,08	79,74 - 98,69
	L.Zambezi	1	74,93	-	-	- - -
S.woosnami	Okavango	54	103,37	0,95	6,94	87,52 - 117,40
	U.Zambezi	1	95,56	-	-	- - -
	Cunene	11	96,89	2,41	7,98	83,94 - 113,38
S.macrostigma	Okavango	61	91,23	0,88	6,80	77,62 - 112,62
	U.Zambezi	21	92,07	1,93	8,61	77,54 - 106,89
	Cunene	15	90,86	0,89	3,43	83,14 - 95,98
S.macrostoma sp.n.	U.Zambezi	21	61,53	1,83	8,39	43,78 - 73,27
	Cunene	2	74,90	-	-	67,22 - 82,58
S.leopardinus	Okavango	44	73,99	0,96	6,39	60,08 - 85,27
	U.Zambezi	22	66,39	0,81	3,81	58,66 - 75,10
S.vanderwaali sp.n.	Okavango	36	99,27	1,05	6,29	87,53 - 113,93
	U.Zambezi	4	105,44	-	-	98,72 - 112,78
	Cunene	8	108,00	3,35	9,49	95,75 -126,83
S.thamalakanensis	Okavango	42	74,70	0,70	4,53	65,85 - 84,59
	U.Zambezi	1	69,57	-	-	- - -

TABLE 2.18 Outer mandibular barbel length as % Head length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	75,39	2,41	6,69	64,12 - 89,43
	L.Zambezi	18	70,39	2,41	9,93	55,09 - 88,92
	Pungwe	1	61,04	-	-	- - -
	Buzi	2	71,90	-	-	70,05 - 73,75
	Save	12	65,78	1,16	4,02	58,26 - 74,17
	Limpopo	41	67,32	1,35	8,62	48,66 - 87,53
	Incomati	5	61,58	-	-	51,67 - 69,91
	Umbeluzi	2	65,32	-	-	49,30 - 72,00
	Pongolo	30	68,08	1,91	8,98	54,99 - 85,53
S.nigromaculatus	Okavango	58	83,62	0,77	5,86	65,00 - 100,00
	U.Zambezi	17	80,28	1,24	5,12	70,75 - 87,86
S.njassae	L.Malawi	34	73,99	1,83	9,83	55,70 - 95,35
S.nebulosus	M.Zambezi	13	49,60	1,12	4,04	40,79 - 55,38
	L.Zambezi	1	44,51	-	-	- - -
S.woosnami	Okavango	54	69,51	0,81	5,92	54,84 - 81,02
	U.Zambezi	1	66,01	-	-	- - -
	Cunene	11	63,08	1,30	4,33	55,25 - 72,10
S.macrostigma	Okavango	61	57,15	0,62	4,82	46,43 - 69,98
	U.Zambezi	21	58,15	1,62	7,22	46,66 - 73,92
	Cunene	15	53,56	0,51	1,98	49,71 - 57,29
S.macrostoma sp.n.	U.Zambezi	21	36,58	0,97	4,43	28,13 - 45,20
	Cunene	2	43,22	-	-	40,14 - 46,30
S.leopardinus	Okavango	44	40,34	0,71	4,72	31,52 - 51,28
	U.Zambezi	22	36,70	0,56	2,60	28,82 - 40,57
S.vanderwaali sp.n.	Okavango	36	57,33	0,75	4,50	50,33 - 70,56
	U.Zambezi	4	59,76	-	-	57,19 - 64,86
	Cunene	8	63,40	1,49	4,22	59,07 - 72,03
S.thamalakanensis	Okavango	42	45,03	0,32	2,08	41,00 - 50,83
	U.Zambezi	1	38,22	-	-	- - -

TABLE 2.19 Inner mandibular barbel length as % Head length.

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	38,99	1,76	6,57	30,74 - 51,98
	L.Zambezi	18	36,65	1,11	4,59	28,51 - 46,60
	Pungwe	1	34,63	-	-	- - -
	Buzi	2	33,24	-	-	30,08 - 36,40
	Save	12	32,34	0,73	2,53	28,90 - 35,98
	Limpopo	41	33,12	0,59	3,75	26,93 - 41,72
	Incomati	5	32,66	-	-	30,64 - 35,69
	Umbeluzi	2	32,60	-	-	30,98 - 34,91
	Pongolo	30	32,57	0,99	4,64	25,83 - 42,00
S.nigromaculatus	Okavango	58	42,77	0,44	3,37	35,52 - 52,22
	U.Zambezi	17	38,10	0,69	2,84	34,62 - 44,98
S.njassae	L.Malawi	34	38,44	1,14	6,13	27,91 - 51,65
S.nebulosus	M.Zambezi	13	26,70	0,66	2,39	22,72 - 31,10
	L.Zambezi	1	22,54	-	-	- - -
S.woosnami	Okavango	54	46,18	0,45	3,30	40,04 - 54,07
	U.Zambezi	1	42,09	-	-	- - -
	Cunene	11	41,58	0,90	2,98	36,72 - 46,33
S.macrostigma	Okavango	61	35,72	0,40	3,16	28,24 - 43,95
	U.Zambezi	21	36,92	1,31	5,87	26,62 - 53,21
	Cunene	15	32,61	0,75	2,90	26,17 - 37,76
S.macrostoma sp.n.	U.Zambezi	21	20,59	0,49	2,25	16,60 - 25,68
	Cunene	2	26,91	-	-	24,70 - 29,12
S.leopardinus	Okavango	44	25,51	0,43	2,85	19,01 - 30,77
	U.Zambezi	22	24,12	0,56	2,62	17,32 - 28,38
S.vanderwaali sp.n.	Okavango	36	35,65	0,44	2,63	30,78 - 40,91
	U.Zambezi	4	38,52	-	-	35,85 - 41,53
	Cunene	8	35,95	1,03	2,93	32,33 - 41,10
S.thamalakanensis	Okavango	42	26,92	0,29	1,89	22,31 - 30,41
	U.Zambezi	1	24,60	-	-	- - -

TABLE 2.20 Snout to pelvic as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	53,60	0,40	1,48	50,88 - 57,07
	L.Zambezi	18	53,78	0,44	1,81	51,23 - 57,03
	Pungwe	1	56,81	-	-	- - -
	Buzi	2	55,32	-	-	55,17 - 55,47
	Save	12	54,66	0,60	2,08	51,54 - 58,29
	Limpopo	41	54,94	0,28	1,80	50,19 - 58,64
	Incomati	5	56,47	-	-	54,26 - 58,28
	Umbeluzi	2	57,34	-	-	- - -
	Pongolo	30	56,25	0,39	1,82	53,21 - 60,54
S.nigromaculatus	Okavango	58	54,78	0,18	1,09	52,65 - 57,26
	U.Zambezi	17	55,16	0,41	1,67	52,89 - 58,61
S.njassae	L.Malawi	34	56,98	0,24	1,26	54,54 - 59,46
S.nebulosus	M.Zambezi	13	53,15	0,57	2,07	49,56 - 56,26
	L.Zambezi	1	53,79	-	-	- - -
S.woosnami	Okavango	54	54,58	0,42	1,93	52,19 - 59,12
	U.Zambezi	1	55,20	-	-	- - -
	Cunene	11	53,75	0,58	2,08	50,40 - 57,85
S.macrostigma	Okavango	61	52,92	0,24	1,30	50,50 - 56,80
	U.Zambezi	21	54,90	0,52	2,33	50,09 - 58,55
	Cunene	15	54,22	0,15	0,31	53,99 - 54,66
S.macrostoma sp.n.	U.Zambezi	21	52,10	0,31	1,11	50,32 - 53,57
	Cunene	2	53,00	-	-	51,97 - 54,20
S.leopardinus	Okavango	44	53,57	0,34	1,65	49,57 - 56,34
	U.Zambezi	22	54,17	0,27	1,27	51,97 - 56,71
S.vanderwaali sp.n.	Okavango	36	53,59	0,41	2,01	49,91 - 56,63
	U.Zambezi	4	54,59	-	-	54,03 - 55,15
	Cunene	8	54,18	0,51	1,25	52,05 - 56,25
S.thamalakanensis	Okavango	42	52,19	0,32	1,65	49,56 - 55,18
	U.Zambezi	1	55,09	-	-	- - -

TABLE 2.21 Snout to anal as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	71,54	0,32	1,19	69,77 - 73,83
	L.Zambezi	18	72,21	0,39	1,64	69,74 - 75,25
	Pungwe	1	73,04	-	-	- - -
	Buzi	2	73,48	-	-	72,38 - 74,57
	Save	12	72,90	0,48	1,68	70,61 - 76,04
	Limpopo	41	73,16	0,25	1,58	69,94 - 75,84
	Incomati	5	73,41	-	-	71,83 - 74,77
	Umbeluzi	2	74,08	-	-	- - -
	Pongolo	30	73,60	0,38	1,78	70,60 - 76,55
S.nigromaculatus	Okavango	58	72,53	0,24	1,48	69,76 - 75,53
	U.Zambezi	17	73,67	0,39	1,60	69,70 - 75,97
S.njassae	L.Malawi	34	72,40	0,25	1,35	68,51 - 74,78
S.nebulosus	M.Zambezi	13	72,12	0,48	1,74	69,05 - 75,00
	L.Zambezi	1	75,00	-	-	- - -
S.woosnami	Okavango	54	73,27	0,35	1,60	70,64 - 76,33
	U.Zambezi	1	72,00	-	-	- - -
	Cunene	11	72,30	0,49	1,95	68,80 - 75,75
S.macrostigma	Okavango	61	72,02	0,29	1,56	68,85 - 76,67
	U.Zambezi	21	72,26	0,55	2,47	68,58 - 77,00
	Cunene	15	73,10	0,77	1,53	71,18 - 74,93
S.macrostoma sp.n.	U.Zambezi	21	70,67	0,47	1,71	67,74 - 73,61
	Cunene	2	70,74	-	-	70,47 - 71,01
S.leopardinus	Okavango	44	72,26	0,40	1,96	67,47 - 76,27
	U.Zambezi	22	72,49	0,31	1,44	70,51 - 76,56
S.vanderwaali sp.n.	Okavango	36	70,65	0,56	2,15	67,20 - 73,23
	U.Zambezi	4	71,82	-	-	71,28 - 72,35
	Cunene	8	70,65	0,58	1,93	67,68 - 74,95
S.thamalakanensis	Okavango	42	70,91	0,39	2,00	67,09 - 75,61
	U.Zambezi	1	73,03	-	-	- - -

TABLE 2.22 Caudal peduncle length as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	18,36	0,16	0,60	17,22 - 19,10
	L.Zambezi	18	18,60	0,19	0,82	17,33 - 20,66
	Pungwe	1	16,64	-	-	- - -
	Buzi	2	16,96	-	-	16,33 - 17,59
	Save	12	18,27	0,21	0,73	16,42 - 19,30
	Limpopo	41	17,97	0,14	0,92	15,86 - 19,71
	Incomati	5	17,87	-	-	17,14 - 19,11
	Umbeluzi	2	17,58	-	-	- - -
	Pongolo	30	17,77	0,33	1,54	14,95 - 20,45
S.nigromaculatus	Okavango	58	18,12	0,10	0,58	16,92 - 19,36
	U.Zambezi	17	17,84	0,16	0,62	16,87 - 19,07
S.njassae	L.Malawi	34	18,20	0,10	0,55	17,03 - 19,25
S.nebulosus	M.Zambezi	13	17,61	0,23	0,86	16,15 - 18,73
	L.Zambezi	1	18,67	-	-	- - -
S.woosnami	Okavango	54	17,54	0,14	0,68	16,20 - 18,70
	U.Zambezi	1	16,41	-	-	- - -
	Cunene	11	17,55	0,16	0,71	16,14 - 18,69
S.macrostigma	Okavango	61	18,24	0,19	1,02	15,82 - 20,00
	U.Zambezi	21	18,00	0,28	1,27	16,28 - 20,45
	Cunene	15	18,70	0,30	1,20	16,52 - 20,11
S.macrostoma sp.n.	U.Zambezi	21	18,35	0,21	0,76	17,15 - 19,60
	Cunene	2	18,29	-	-	17,95 - 18,62
S.leopardinus	Okavango	44	17,62	0,19	0,91	16,00 - 19,48
	U.Zambezi	22	17,90	0,18	0,86	16,48 - 19,60
S.vanderwaali sp.n.	Okavango	36	17,42	0,19	0,88	16,02 - 19,05
	U.Zambezi	4	18,12	-	-	17,90 - 18,25
	Cunene	8	17,43	0,30	0,91	16,64 - 18,82
S.thamalakanensis	Okavango	42	18,49	0,14	0,72	17,01 - 19,87
	U.Zambezi	1	19,02			

TABLE 2.23 Caudal peduncle depth as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	9,64	0,08	0,31	9,22 - 10,35
	L.Zambezi	18	9,07	0,13	0,56	8,43 - 10,71
	Pungwe	1	8,73	-	-	- - -
	Buzi	2	9,65	-	-	9,64 - 9,66
	Save	12	10,06	0,09	0,31	9,54 - 10,62
	Limpopo	41	9,87	0,10	0,64	8,26 - 11,32
	Incomati	5	9,85	-	-	9,27 - 10,56
	Umbeluzi	2	9,06	-	-	- - -
	Pongolo	30	9,84	0,16	0,73	8,52 - 11,22
S.nigromaculatus	Okavango	58	8,67	0,09	0,57	7,69 - 9,76
	U.Zambezi	17	8,90	0,09	0,34	8,36 - 9,56
S.njassae	L.Malawi	34	9,79	0,10	0,56	8,74 - 10,80
S.nebulosus	M.Zambezi	13	10,98	0,14	0,50	10,04 - 11,60
	L.Zambezi	1	11,14	-	-	- - -
S.woosnami	Okavango	54	10,73	0,12	0,54	9,61 - 11,81
	U.Zambezi	1	10,75	-	-	- - -
	Cunene	11	11,03	0,21	0,67	9,75 - 12,25
S.macrostigma	Okavango	61	11,21	0,10	0,54	10,00 - 12,49
	U.Zambezi	21	10,94	0,10	0,45	10,25 - 11,74
	Cunene	15	11,14	0,18	0,86	9,81 - 12,55
S.macrostoma sp.n.	U.Zambezi	21	10,22	0,14	0,50	9,54 - 11,11
	Cunene	2	10,50	-	-	10,21 - 10,79
S.leopardinus	Okavango	44	10,23	0,09	0,43	9,21 - 10,98
	U.Zambezi	22	10,26	0,09	0,40	9,72 - 11,17
S.vanderwaali sp.n.	Okavango	36	10,98	0,18	0,58	10,00 - 12,12
	U.Zambezi	4	11,31	-	-	11,25 - 11,55
	Cunene	8	11,20	0,28	0,85	10,03 - 12,56
S.thamalakanensis	Okavango	42	10,75	0,10	0,50	9,94 - 11,91
	U.Zambezi	1	10,85	-	-	- - -

TABLE 2.24 Dorsal to adipose as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	11,32	0,41	1,52	7,95 - 14,07
	L.Zambezi	18	15,42	0,77	3,28	8,63 - 21,99
	Pungwe	1	11,90	-	-	- - -
	Buzi	2	10,10	-	-	9,98 - 10,23
	Save	12	11,97	0,65	2,24	7,78 - 16,16
	Limpopo	41	14,57	0,35	2,21	10,10 - 19,70
	Incomati	5	13,10	-	-	10,52 - 16,04
	Umbeluzi	2	12,02	-	-	- - -
	Pongolo	30	13,68	0,56	2,62	8,78 - 18,17
S.nigromaculatus	Okavango	58	14,13	0,25	1,54	10,77 - 17,25
	U.Zambezi	17	13,21	0,39	1,62	11,00 - 16,75
S.njassae	L.Malawi	34	13,73	0,42	2,17	9,89 - 18,81
S.nebulosus	M.Zambezi	13	14,85	0,48	1,68	12,71 - 18,08
	L.Zambezi	1	20,40	-	-	- - -
S.woosnami	Okavango	54	15,46	0,43	1,98	11,98 - 20,17
	U.Zambezi	1	17,62	-	-	- - -
	Cunene	11	16,21	0,39	2,04	12,25 - 18,80
S.macrostigma	Okavango	61	16,96	0,41	2.22	12.52 - 22,59
	U.Zambezi	21	17,36	0,59	2,62	12,14 - 22,65
	Cunene	15	12,42	1,19	2,66	11,07 - 21,76
S.macrostoma sp.n.	U.Zambezi	21	14,04	0,42	1,52	10,97 - 16,25
	Cunene	2	12,60	-	-	12,18 - 13,01
S.leopardinus	Okavango	44	16,26	0,47	2,30	12,06 - 20,76
	U.Zambezi	22	15,23	0,38	1,80	12,66 - 18,87
S.vanderwaali sp.n.	Okavango	36	17,18	0,55	2,96	12,30 - 22,01
	U.Zambezi	4	17,76	-	-	17,25 - 18,21
	Cunene	8	18,03	0,77	3,37	13,76 - 23,30
S.thamalakanensis	Okavango	42	18,19	0,62	3,11	13,53 - 23,75
	U.Zambezi	1	18,01	-	-	- - -

TABLE 2.25 Adipose basal length as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	29,79	0,38	1,41	27,64 - 32,44
	L.Zambezi	18	28,53	0,54	2,30	23,09 - 32,30
	Pungwe	1	28,75	-	-	- - -
	Buzi	2	30,43	-	-	29,58 - 31,28
	Save	12	29,54	0,56	1,93	26,43 - 32,62
	Limpopo	41	28,56	0,32	2,02	22,48 - 32,52
	Incomati	5	26,95	-	-	24,17 - 29,72
	Umbeluzi	2	24,41	-	-	- - -
	Pongolo	30	27,92	0,53	2,49	24,30 - 32,88
S.nigromaculatus	Okavango	58	26,74	0,24	1,47	23,75 - 30,49
	U.Zambezi	17	26,87	0,36	1,48	24,20 - 28,96
S.njassae	L.Malawi	34	25,22	0,39	2,05	21,70 - 28,82
S.nebulosus	M.Zambezi	13	25,73	0,47	1,62	21,59 - 27,53
	L.Zambezi	1	22,12	-	-	- - -
S.woosnami	Okavango	54	23,04	0,37	1,68	20,93 - 28,18
	U.Zambezi	1	23,76	-	-	- - -
	Cunene	11	23,12	0,44	2,54	19,76 - 26,95
S.macrostigma	Okavango	61	22,10	0,39	2,09	17,19 - 26,68
	U.Zambezi	21	20,76	0,58	2,58	14,86 - 25,95
	Cunene	15	26,73	1,37	3,06	17,15 - 26,05
S.macrostoma sp.n.	U.Zambezi	21	26,13	0,30	1,08	24,47 - 28,44
	Cunene	2	26,06	-	-	25,96 - 26,16
S.leopardinus	Okavango	44	22,28	0,33	1,61	19,79 - 24,85
	U.Zambezi	22	22,95	0,46	2,16	19,10 - 26,93
S.vanderwaali sp.n.	Okavango	36	22,25	0,44	2,96	17,97 - 26,20
	U.Zambezi	4	21,47	-	-	- - -
	Cunene	8	23,70	0,64	3,01	19,85 - 28,86
S.thamalakanensis	Okavango	42	20,92	0,36	1,80	16,62 - 23,49
	U.Zambezi	1	21,66	-	-	- - -

TABLE 2.26 Adipose maximum height as % Adipose basal length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	22,35	0,59	2,20	19,52 - 26,63
	L.Zambezi	18	20,06	0,98	4,14	11,99 - 25,00
	Pungwe	1	19,14	-	-	- - -
	Buzi	2	27,27	-	-	25,99 - 28,55
	Save	12	22,66	1,13	3,91	14,21 - 29,00
	Limpopo	41	24,71	0,50	3,20	19,61 - 34,29
	Incomati	5	26,11	-	-	22,65 - 30,33
	Umbeluzi	2	22,52	-	-	- - -
	Pongolo	30	25,98	0,58	2,72	19,84 - 31,01
S.nigromaculatus	Okavango	58	25,48	0,92	5,62	19,79 - 34,50
	U.Zambezi	17	22,33	0,51	2,09	18,95 - 25,49
S.njassae	L.Malawi	34	22,45	0,70	3,70	18,16 - 29,50
S.nebulosus	M.Zambezi	13	20,39	0,96	3,33	14,43 - 24,26
	L.Zambezi	1	15,18	-	-	- - -
S.woosnami	Okavango	54	24,85	0,49	2,24	21,84 - 29,21
	U.Zambezi	1	23,67	-	-	- - -
	Cunene	11	26,03	1,12	3,92	19,95 - 32,45
S.macrostigma	Okavango	61	25,45	0,77	4,16	20,88 - 34,01
	U.Zambezi	21	26,06	0,68	3,03	20,99 - 33,72
	Cunene	15	20,78	0,97	2,17	18,53 - 30,75
S.macrostoma sp.n.	U.Zambezi	21	17,39	0,75	2,70	13,32 - 21,64
	Cunene	2	21,20	-	-	20,18 - 22,22
S.leopardinus	Okavango	44	21,71	0,57	2,81	14,96 - 27,62
	U.Zambezi	22	23,07	0,54	2,54	18,38 - 28,47
S.vanderwaali sp.n.	Okavango	36	27,90	0,35	3,50	20,45 - 32,60
	U.Zambezi	4	28,26	-	-	27,75 - 28,89
	Cunene	8	26,50	0,50	3,30	21,60 - 32,01
S.thamalakanensis	Okavango	42	23,95	0,66	3,28	17,95 - 29,36
	U.Zambezi	1	28,50	-	-	- - -

TABLE 2.27 Adipose to caudal peduncle as % Standard length

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	10,83	0,20	0,73	9,60 - 12,21
	L.Zambezi	18	11,13	0,27	1,12	9,48 - 12,71
	Pungwe	1	10,25	-	-	- - -
	Buzi	2	10,63	-	-	10,35 - 10,91
	Save	12	10,78	0,22	0,75	9,41 - 12,02
	Limpopo	41	11,13	0,13	0,84	9,54 - 13,96
	Incomati	5	11,41	-	-	10,09 - 12,28
	Umbeluzi	2	11,84	-	-	- - -
	Pongolo	30	11,17	0,21	0,96	9,49 - 13,40
S.nigromaculatus	Okavango	58	9,88	0,10	0,59	8,48 - 10,79
	U.Zambezi	17	9,97	0,13	0,54	8,89 - 10,71
S.njassae	L.Malawi	34	12,12	0,16	0,87	10,82 - 14,26
S.nebulosus	M.Zambezi	13	12,09	0,30	1,10	9,20 - 13,35
	L.Zambezi	1	12,35	-	-	- - -
S.woosnami	Okavango	54	13,19	0,15	0,75	11,63 - 14,61
	U.Zambezi	1	14,27	-	-	- - -
	Cunene	11	13,20	0,35	1,34	11,24 - 14,77
S.macrostigma	Okavango	61	13,30	0,17	0,89	11,36 - 14,74
	U.Zambezi	21	13,11	0,22	1,00	10,98 - 15,46
	Cunene	15	12,55	0,29	0,65	11,84 - 13,41
S.macrostoma sp.n.	U.Zambezi	21	12,54	0,14	0,50	11,47 - 13,35
	Cunene	2	11,92	-	-	11,34 - 12,49
S.leopardinus	Okavango	44	12,95	0,17	0,82	10,99 - 14,65
	U.Zambezi	22	12,59	0,17	0,81	10,73 - 14,23
S.vanderwaali sp.n.	Okavango	36	13,62	0,20	0,88	11,30 - 14,80
	U.Zambezi	4	13,43	-	-	13,25 - 13,60
	Cunene	8	12,72	0,27	1,03	10,95 - 14,37
S.thamalakanensis	Okavango	42	13,48	0,12	0,60	12,40 - 14,76
	U.Zambezi	1	13,48	-	-	- - -

TABLE 2.28 Mouth width as % Pectoral girdle width

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	46,14	0,78	2,93	41,18 - 51,49
	L.Zambezi	18	44,24	1,22	4,71	36,66 -
	Pungwe	1	45,00	-	-	- - -
	Buzi	2	42,54	-	-	41,61 - 43,46
	Save	12	45,76	0,76	2,64	41,76 - 49,77
	Limpopo	41	46,47	0,37	2,34	40,44 - 49,77
	Incomati	5	43,56	-	-	38,00 - 48,89
	Umbeluzi	2	45,75	-	-	- - -
	Pongolo	30	45,56	0,45	2,10	41,61 - 49,93
S.nigromaculatus	Okavango	58	49,05	0,62	3,74	41,96 - 58,42
	U.Zambezi	17	46,57	0,92	3,82	38,53 - 52,39
S.njassae	L.Malawi	34	46,60	0,60	3,22	40,61 - 52,58
S.nebulosus	M.Zambezi	13	49,15	1,23	4,09	42,34 - 56,20
	L.Zambezi	1	48,60	-	-	- - -
S.woosnami	Okavango	54	48,32	0,95	4,64	39,08 - 58,54
	U.Zambezi	1	53,50	-	-	- - -
	Cunene	11	49,52	1,70	5,50	41,02 - 58,53
S.macrostigma	Okavango	61	41,69	0,39	2,99	34,38 - 48,21
	U.Zambezi	21	39,14	0,90	3,93	35,02 - 46,79
	Cunene	15	48,07	1,11	4,15	38,29 - 52,89
S.macrostoma sp.n.	U.Zambezi	21	59,42	0,74	3,14	53,51 - 66,12
	Cunene	2	58,44	-	-	57,86 - 59,02
S.leopardinus	Okavango	44	45,85	0,82	4,00	57,86 - 59,02
	U.Zambezi	22	46,84	1,61	7,37	36,00 - 54,45
S.vanderwaali sp.n.	Okavango	36	41,95	1,49	4,48	35,09 - 48,52
	U.Zambezi	4	43,10	-	-	41,54 - 43,95
	Cunene	8	52,02	1,02	3,54	45,08 - 58,62
S.thamalakanensis	Okavango	42	49,08	0,62	3,17	44,54 - 58,08
	U.Zambezi	1	43,15	-	-	- - -

TABLE 2.29 Premaxillae width as % Pectoral girdle width

Species	Drainage	n	Mean	S.E.	S.D.	Range
S.zambezensis	M.Zambezi	14	26,83	0,44	1,65	24,41 - 29,81
	L.Zambezi	18	25,68	0,51	2,10	22,58 - 30,09
	Pungwe	1	25,49	-	-	- - -
	Buzi	2	23,99	-	-	23,63 - 24,35
	Save	12	25,71	0,56	1,93	22,20 - 28,65
	Limpopo	41	24,75	0,35	2,21	20,91 - 33,56
	Incomati	5	20,85	-	-	20,83 - 27,16
	Umbeluzi	2	22,16	-	-	- - -
	Pongolo	30	24,44	0,39	1,83	21,88 - 27,95
S.nigromaculatus	Okavango	58	28,31	0,27	1,66	25,00 - 31,42
	U.Zambezi	17	28,79	0,47	1,93	25,98 - 33,23
S.njassae	L.Malawi	34	27,13	0,33	1,77	22,19 - 29,53
S.nebulosus	M.Zambezi	13	25,78	0,56	1,94	22,99 - 28,60
	L.Zambezi	1	23,39	-	-	- - -
S.woosnami	Okavango	54	24,45	0,42	2,99	20,58 - 32,50
	U.Zambezi	1	22,84	-	-	- - -
	Cunene	11	22,95	0,47	1,57	20,11 - 25,63
S.macrostigma	Okavango	61	20,57	0,31	1,95	16,72 - 23,72
	U.Zambezi	21	18,71	0,50	2,24	15,41 - 24,24
	Cunene	15	24,99	0,53	2,14	18,55 - 27,90
S.macrostoma sp.n.	U.Zambezi	21	30,82	0,57	2,48	27,01 - 34,74
	Cunene	2	31,49	-	-	- - -
S.leopardinus	Okavango	44	21,93	0,35	1,69	18,78 - 25,25
	U.Zambezi	22	24,71	2,93	12,78	17,64 - 76,92
S.vanderwaali sp.n.	Okavango	36	21,41	0,42	1,87	18,59 - 27,42
	U.Zambezi	4	21,11	0,28	0,56	20,62 - 21,88
	Cunene	8	24,66	0,34	0,95	23,30 - 26,15
S.thamalakanensis	Okavango	42	24,95	0,32	2,08	21,10 - 29,09
	U.Zambezi	1	25,38	-	-	- - -

APPENDIX 3

REGRESSIONAL ANALYSIS OF SELECTED MORPHOMETRIC MEASUREMENTS

Species	n	Variable: Dependent	Variable: Independent	Regression	r^2
S.macrostigma	96	Head Length (HL)	Standard length (SL)	y = 0,30x + 1,74	0,98
,,	96	Interorbital (INL)	Standard length (SL)	y = 0,11x - 0,85	0,96
,,	96	Snout length (SNL)	Standard length (SL)	y = 0,12x + 0,97	0,97
S.macrostoma sp.n.	23	Head length (HL)	Standard length (SL)	y = 0,32x + 0,30	0,99
,,	23	Interorbital (INL)	Standard length (SL)	y = 0,08X + 0,82	0,97
,,	23	Snout length (SNL)	Standard length (SL)	y = 0,17x + 0,61	0,98

APPENDIX 4

TABLES OF HUMERAL PROCESS SHAPE DATA

Table 4.1 S.macrostigma < 70 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	30,5	26,0 - 34,7	5,8	-0,8	-0,4 - -1,5	0,5
48	33,0	28,6 - 37,7	5,4	-1,1	-0,1 - -2,0	0,5
50	34,4	30,0 - 39,0	5,3	-1,3	-0,5 - -2,4	0,6
52	35,9	31,0 - 39,7	5,9	-1,7	-0,4 - -3,0	0,8
54	35,5	31,5 - 39,2	5,7	-1,9	-6,5 - -3,5	0,7
56	35,4	32,0 - 38,4	4,9	-2,3	-0,6 - -3,7	0,7
58	34,7	31,5 - 37,4	4,4	-2,4	-1,0 - -3,7	0,7
60	34,0	31,0 - 37,0	4,4	-2,5	-0,9 - -3,6	1,1
62	33,0	30,4 - 35,3	3,4	-2,8	-0,7 - -3,8	0,7
64	31,9	29,1 - 33,8	3,5	-2,9	-0,8 - -4,0	0,7
66	30,9	28,3 - 33,1	3,4	-3,0	-0,6 - -4,1	0,7
68	29,7	27,1 - 31,9	3,5	-3,1	-0,5 - -4,0	0,6
70	28,2	25,8 - 30,2	3,3	-3,2	-0,6 - -4,6	0,6
72	27,0	24,5 - 29,2	3,8	-3,4	-0,2 - -4,8	0,8
74	25,5	23,0 - 28,2	3,8	-3,3	-0,1 - -4,5	0,8
76	24,0	21,4 - 26,6	3,9	-3,2	-0,3 - -4,3	0,8
78	22,5	20,3 - 25,0	3,6	-3,3	-0,5 - -4,3	0,8
80	21,1	19,0 - 23,4	3,5	-3,0	-0,8 - -4,1	0,8
82	19,5	17,5 - 22,0	3,5	-2,9	-1,2 - -4,1	0,8
84	18,0	15,9 - 20,3	3,4	-2,8	-1,0 - -4,0	0,9
86	16,3	14,4 - 18,2	3,3	-2,7	-1,1 - -3,7	0,9
88	15,0	13,0 - 17,2	3,0	-2,6	-1,0 - -3,5	0,8
90	12,7	11,3 - 15,2	2,8	-2,6	-0,8 - -3,5	0,7
92	10,7	8,8 - 12,8	2,7	-2,1	-0,9 - -3,0	0,7
94	8,6	6,7 - 10,9	3,0	-1,7	-0,9 - -3,0	0,7
96	7,0	5,3 - 8,9	2,0	-1,3	-0,5 - -2,3	0,7
98	4,4	3,2 - 5,6	1,8	-1,2	-0,3 - -1,9	0,6
99	2,9	2,3 - 4,0	1,5	-0,7	-0,3 - -1,4	0,3

Table 4.2 S.macrostigma 70 - 130 mm SL

% HPL	Dorsal margin			Ventral margin		
	Mean	Range	S.D.	Mean	Range	S.D.
46	28,6	22,0 - 3,3	10,9	-1,9	-0,1 - -3,2	1,0
48	30,8	24,5 - 37,7	11,0	-2,1	-0,4 - -3,6	0,8
50	33,2	26,9 - 39,5	10,7	-2,3	-1,0 - -4,0	0,7
52	35,3	29,7 - 41,2	10,1	-2,7	-1,2 - -4,1	0,8
54	37,4	32,2 - 42,7	8,4	-3,0	-1,5 - -4,6	1,0
56	38,8	34,0 - 43,5	6,9	-3,1	-1,7 - -4,9	0,9
58	39,4	35,5 - 44,4	4,7	-3,4	-1,6 - -5,3	0,9
60	40,3	36,3 - 45,3	4,7	-3,6	-2,0 - -5,6	0,9
62	40,6	36,2 - 45,0	4,5	-3,4	-2,2 - -5,7	1,0
64	40,3	35,1 - 45,2	4,9	-3,6	-1,6 - -5,4	1,0
66	39,8	34,3 - 44,7	6,4	-3,5	-1,8 - -5,5	1,2
68	39,1	32,9 - 44,7	6,5	-3,4	-2,0 - -5,4	1,1
70	37,6	32,5 - 43,5	6,0	-3,3	-1,5 - -5,2	1,0
72	36,3	31,5 - 41,5	6,4	-3,2	-1,1 - -5,2	1,0
74	35,1	29,0 - 38,7	6,4	-3,1	-1,4 - -4,8	1,0
76	33,4	27,1 - 37,4	5,0	-3,0	-1,3 - -4,9	1,0
78	32,4	26,5 - 36,1	6,1	-3,2	-0,8 - -5,2	1,5
80	30,8	24,8 - 35,4	6,5	-3,1	-0,1 - -5,0	3,5
82	29,0	23,1 - 32,8	5,9	-3,0	-0,5 - -5,1	1,6
84	26,4	21,5 - 29,6	4,3	-3,0	-1,0 - -4,7	1,4
86	24,4	18,3 - 28,0	4,5	-2,7	-1,0 - -4,5	1,1
88	22,4	17,2 - 26,0	5,2	-2,3	-0,7 - -3,8	0,7
90	19,9	14,5 - 23,6	5,8	-2,3	-1,0 - -3,5	0,9
92	16,8	12,0 - 20,0	6,0	-2,1	-0,8 - -3,2	0,9
94	13,4	9,2 - 18,4	7,5	-1,6	-0,7 - -2,7	0,7
96	9,5	7,0 - 14,0	5,0	-1,3	-0,1 - -1,9	0,5
98	5,0	3,8 - 10,5	2,3	-1,1	-0,3 - -2,0	0,6
99	2,8	1,1 - 7,5	1,3	-1,0	-0,6 - -1,6	0,4

Table 4.3 S.macrostigma 130 - 190 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	36,9	29,0 - 43,9	10,8	-2,0	-0,3 - -4,0	1,3
48	39,8	31,8 - 47,0	10,3	-2,6	-0,6 - -4,8	1,5
50	41,5	33,4 - 49,0	9,9	-3,1	-0,6 - -5,3	1,9
52	44,1	35,6 - 53,3	9,6	-3,6	-1,3 - -5,9	1,6
54	45,7	37,6 - 57,4	8,9	-0,5	-1,9 - -6,3	1,7
56	47,4	40,3 - 57,8	9,7	-4,2	-1,9 - -7,0	1,7
58	48,3	42,0 - 57,8	10,9	-4,4	-2,1 - -7,0	1,8
60	48,4	42,2 - 56,9	9,5	-4,5	-2,5 - -7,0	1,6
62	47,7	41,8 - 54,1	9,1	-4,9	-2,3 - -7,4	1,9
64	46,8	41,2 - 52,5	9,2	-5,0	-2,3 - -7,3	1,9
66	45,2	40,0 - 51,5	9,5	-5,2	-2,7 - -7,8	1,6
68	44,0	38,8 - 49,9	9,0	-5,3	-2,5 - -7,9	1,7
70	42,5	37,5 - 47,4	7,0	-5,3	-2,8 - -7,8	1,8
72	41,2	36,0 - 45,8	5,3	-5,1	-2,8 - -8,0	1,8
74	39,5	34,5 - 43,8	5,8	-5,2	-2,6 - -7,5	1,5
76	37,8	32,8 - 42,0	5,0	-5,0	-2,3 - -7,5	1,5
78	35,7	31,0 - 39,9	5,9	-4,9	-3,4 - -7,3	1,5
80	33,9	28,9 - 38,5	5,8	-4,6	-2,2 - -7,2	1,8
82	32,1	26,9 - 36,7	5,8	-4,7	-1,6 - -7,3	1,9
84	29,9	24,1 - 34,4	5,0	-4,5	-1,2 - -7,9	1,9
86	27,5	21,8 - 31,7	4,8	-4,0	-1,3 - -7,8	1,9
88	25,1	39,0 - 29,7	6,0	-3,9	-1,4 - -7,4	1,7
90	22,9	15,6 - 28,6	6,4	-3,8	-1,5 - -7,1	1,5
92	20,3	12,5 - 23,5	4,9	-3,7	-1,9 - -6,4	1,2
94	17,1	9,3 - 20,3	5,3	-3,4	-1,8 - -5,9	1,1
96	10,2	5,5 - 15,5	6,0	-2,5	-0,9 - -4,4	1,1
98	3,8	1,7 - 9,8	3,5	-1,6	-1,1 - -2,8	0,8
99	2,3	0,8 - 6,1	1,5	-1,1	-0,4 - -2,0	0,6

Table 4.4 S.woosnami < 70 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	30,4	26,0 - 34,8	3,5	-1,3	-0,1 - -2,2	0,7
48	31,7	28,0 - 36,5	3,1	-1,6	-0,3 - -2,8	0,8
50	32,7	29,4 - 37,5	2,8	-1,7	-0,5 - -30	0,8
52	33,3	29,8 - 37,2	2,5	-2,1	-0,6 - -3,5	0,8
54	33,0	29,5 - 37,0	2,3	-2,3	-1,0 - -4,4	1,8
56	32,4	28,9 - 36,4	2,2	-2,5	-1,0 - -4,6	1,0
58	31,4	27,9 - 35,4	2,2	-2,8	-1,0 - -4,6	1,0
60	30,1	26,4 - 34,1	2,4	-3,0	-1,5 - -4,6	1,1
62	28,3	24,9 - 33,0	2,6	-3,3	-1,7 - -4,8	1,1
64	27,2	23,7 - 32,0	2,8	-3,4	-1,9 - -5,0	1,0
66	26,3	22,7 - 31,6	2,9	-3,4	-1,9 - -4,9	1,0
68	24,8	21,0 - 30,5	3,2	-3,3	-1,8 - -5,0	1,1
70	24,4	20,0 - 30,0	3,4	-3,2	-1,5 - -5,0	0,9
72	23,5	19,7 - 28,3	3,0	-3,1	-1,9 - -4,8	1,0
74	22,6	19,0 - 27,5	3,0	-3,3	-1,6 - -4,8	1,2
76	22,0	18,1 - 25,9	2,6	-3,2	-1,5 - -4,7	1,3
78	20,6	16,6 - 24,5	2,9	-3,1	-1,0 - -5,0	1,4
80	19,5	15,3 - 23,9	2,5	-2,8	-1,0 - -5,0	1,2
82	18,2	14,3 - 22,3	2,3	-2,8	-0,7 - -4,6	1,3
84	16,7	13,6 - 20,6	2,2	-2,7	-0,8 - -4,4	1,4
86	15,3	12,5 - 19,5	2,0	-2,7	-1,0 - -4,4	1,2
88	13,3	10,8 - 18,4	2,0	-2,8	-1,1 - -4,2	1,2
90	12,0	9,4 - 16,2	1,6	-2,7	-1,0 - -4,1	1,1
92	10,0	7,8 - 14,8	1,4	-2,5	-0,9 - -4,0	1,1
94	8,2	6,3 - 13,0	1,2	-2,6	-1,2 - -3,8	0,9
96	6,3	4,5 - 11,1	1,4	-2,3	-1,0 - -3,1	0,7
98	4,1	2,6 - 8,5	1,4	-2,0	-1,0 - -3,1	0,6
99	2,5	1,3 - 6,3	1,0	-1,5	-0,8 - -2,2	0,5

Table 4.6 S.woosnami 70 - 130 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	30,2	26,2 - 36,0	3,7	-0,4	-0,0 - -3,3	0,4
48	33,4	28,0 - 38,3	3,7	-1,0	-0,0 - -3,4	0,8
50	34,7	30,2 - 39,4	3,3	-1,5	-0,5 - -4,3	0,8
52	36,3	31,7 - 41,0	3,1	-1,9	-1,0 - -4,8	0,8
54	38,1	34,5 - 42,0	3,1	-2,1	-1,1 - -5,0	0,9
56	38,9	34,7 - 42,3	2,5	-2,3	-1,1 - -5,2	1,0
58	38,3	34,9 - 42,0	2,5	-2,7	-1,6 - -5,5	1,0
60	37,5	34,8 - 40,9	2,5	-3,2	-2,1 - -5,6	1,2
62	36,5	33,8 - 39,9	2,4	-3,3	-2,2 - -5,6	0,8
64	35,6	33,1 - 38,9	2,3	-3,5	-2,7 - -5,9	0,7
66	34,7	32,0 - 37,7	2,1	-3,8	-2,7 - -6,1	0,9
68	33,5	31,0 - 36,0	2,1	-3,5	-2,5 - -6,1	0,9
70	32,5	30,0 - 35,0	2,1	-3,7	-2,4 - -6,2	1,1
72	31,0	28,6 - 33,5	2,0	-3,6	-2,2 - -6,4	1,2
74	29,7	27,0 - 32,2	2,1	-3,7	-2,0 - -6,6	1,4
76	28,2	25,3 - 31,3	2,0	-3,7	-1,8 - -6,8	1,4
78	26,6	24,0 - 29,5	2,0	-3,7	-1,7 - -6,6	1,4
80	25,3	22,8 - 28,3	2,0	-3,5	-1,7 - -7,5	1,4
82	23,9	21,0 - 26,5	2,0	-3,2	-1,3 - -6,4	1,4
84	22,0	18,9 - 24,8	2,4	-2,9	-0,9 - -5,8	1,4
86	20,3	17,5 - 23,4	2,3	-2,8	-0,8 - -5,7	1,5
88	18,2	15,2 - 21,0	2,4	-2,7	-1,1 - -5,3	1,4
90	16,4	13,0 - 19,7	2,4	-2,6	-1,0 - -4,4	1,2
92	14,4	10,8 - 17,8	2,6	-2,5	-0,8 - -4,0	1,2
94	12,3	8,3 - 16,3	2,6	-2,3	-0,6 - -3,7	1,1
96	10,2	6,2 - 13,5	2,7	-2,4	-0,8 - -3,7	1,1
98	6,6	3,5 - 9,4	2,3	-1,9	-1,0 - -3,3	0,9
99	5,1	2,5 - 7,5	1,7	-1,5	-0,7 - -2,3	0,6

Table 4.6 S.woosnami 130 - 190 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	35,5	23,5 - 41,0	3,9	-1,9	-0,7 - -3,8	0,7
48	38,3	26,0 - 44,0	3,9	-2,4	-0,8 - -4,7	0,8
50	41,0	30,5 - 45,9	3,9	-2,8	-1,3 - -5,1	0,9
52	43,4	33,6 - 47,5	3,6	-3,2	-1,5 - -5,5	1,0
54	45,0	36,9 - 49,5	4,0	-3,4	-1,5 - -6,2	1,0
56	46,4	40,0 - 50,0	3,3	-3,5	-1,7 - -6,9	1,0
58	46,2	39,7 - 49,0	2,4	-4,0	-2,0 - -7,4	1,1
60	46,0	40,1 - 49,0	2,5	-4,1	-2,3 - -7,0	1,0
62	45,3	40,5 - 48,8	2,9	-4,1	-2,6 - -7,4	1,0
64	44,3	40,3 - 47,3	2,9	-4,4	-2,6 - -7,7	0,9
66	43,4	39,4 - 46,3	2,7	-4,7	-2,9 - -7,9	1,1
68	41,8	38,7 - 45,0	2,5	-4,8	-2,9 - -7,5	1,0
70	40,6	36,8 - 43,3	2,4	-4,9	-3,1 - -8,0	0,9
72	39,2	35,0 - 43,0	3,3	-4,8	-3,1 - -7,8	0,9
74	37,5	33,5 - 41,5	2,6	-4,8	-2,4 - -7,4	1,1
76	36,2	32,0 - 40,5	3,2	-4,8	-2,6 - -7,1	1,4
78	34,3	31,4 - 39,0	2,6	-4,6	-2,5 - -7,0	1,3
80	32,9	30,0 - 37,3	2,6	-4,1	-2,6 - -6,8	1,1
82	31,2	28,0 - 35,8	2,5	-3,9	-2,3 - -5,9	1,1
84	29,9	26,7 - 34,1	2,5	-3,9	-2,3 - -6,0	1,3
86	28,3	25,0 - 32,4	2,6	-3,8	-1,2 - -5,8	1,2
88	26,1	22,5 - 31,0	3,1	-3,5	-1,9 - -5,6	0,9
90	23,4	19,6 - 29,0	2,3	-3,1	-1,7 - -5,0	1,1
92	21,2	16,4 - 26,5	2,8	-2,9	-1,6 - -4,9	0,8
94	16,7	11,3 - 23,5	3,4	-2,7	-1,6 - -4,4	0,7
96	10,0	4,0 - 19,9	4,1	-2,2	-1,2 - -3,4	0,6
98	3,7	1,6 - 12,0	2,0	-1,6	-1,0 - -2,6	0,5
99	2,3	1,0 - 5,0	1,2	-1,1	-0,6 - -1,8	0,4

Table 4.7 <u>S.nebulosus</u> 13 - 19 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	26,1	22,9 - 29,3	2,3	-1,0	-0,1 - -1,0	2,3
48	27,9	24,5 - 31,6	2,6	-1,7	-0,9 - -1,5	2,6
5	29,7	26,4 - 34,4	2,7	-2,1	-0,6 - -1,8	2,7
52	31,5	27,8 - 36,0	2,5	-2,5	-1,0 - -2,1	2,5
54	32,8	29,1 - 37,9	2,1	-2,9	-1,1 - -2,5	2,1
56	34,1	30,2 - 38,7	1,5	-3,5	-1,4 - -3,0	1,5
58	34,3	30,5 - 38,4	1,7	-3,8	-2,0 - -3,1	1,7
6	34,0	30,2 - 38,0	1,8	-3,9	-2,3 - -3,1	1,8
62	33,3	29,0 - 38,0	1,8	-4,1	-2,3 - -3,3	1,9
64	32,8	27,0 - 36,8	1,9	-4,5	-1,4 - -3,3	1,9
66	31,2	25,5 - 35,6	2,1	-4,5	-2,3 - -3,2	2,2
68	29,2	24,3 - 34,5	2,1	-4,4	-3,0 - -3,3	2,1
7	27,4	22,5 - 32,5	2,3	-4,6	-2,6 - -3,5	2,3
72	26,5	21,5 - 30,4	2,1	-4,6	-2,6 - -3,1	2,1
74	25,2	2 ,5 - 29,0	2,0	-4,2	-2,8 - -3,1	2,0
76	23,7	19,4 - 28,0	1,8	-4,4	-2,9 - -3,1	1,8
78	22,4	18,0 - 26,0	1,9	-3,9	-2,5 - -2,8	1,9
8	20,7	17,0 - 24,0	1,7	-3,9	-2,0 - -2,6	1,7
82	19,4	16,2 - 22,9	2,0	-3,7	-1,6 - -2,5	2,0
84	17,9	14,1 - 22,1	1,9	-2,8	-2,0 - -2,5	1,9
86	16,2	13,0 - 20,7	1,8	-3,5	-1,4 - -2,5	1,8
88	14,5	11,7 - 19,3	2,0	-3,1	-1,1 - -2,5	2,0
9	12,4	9,7 - 17,1	1,8	-2,9	-1,4 - -2,1	1,8
92	10,1	7,8 - 13,5	1,8	-2,5	-1,0 - -2,2	1,8
94	8,0	5,5 - 11,2	2,1	-2,5	-1,0 - -2,0	2,1
96	5,0	3,8 - 8,1	1,0	-2,2	-0,6 - -1,6	1,0
98	2,8	1,8 - 6,0	0,8	-1,9	-0,6 - -1,2	0,8
99	2,2	1,4 - 4,9	0,6	-1,1	-0,5 - -1,0	0,6

Table 4.8 S.macrostoma sp.n. 70 - 130 mm SL

% HPL	Dorsal margin			Ventral margin		
	Mean	Range	S.D.	Mean	Range	S.D.
46	25,3	19,3 - 29,8	3,7	-1,2	-0,1 - -2,3	0,9
48	26,9	20,9 - 31,5	3,6	-1,4	-0,3 - -3,2	1,0
50	28,6	22,3 - 32,8	3,4	-1,9	-0,5 - -3,3	1,0
52	29,8	23,5 - 34,5	2,9	-2,3	-0,7 - -3,8	0,9
54	31,3	25,4 - 36,0	3,0	-2,6	-1,1 - -4,1	0,8
56	32,3	27,5 - 37,0	3,0	-3,0	-1,8 - -4,2	0,9
58	32,9	28,8 - 38,8	2,3	-3,2	-2,0 - -4,4	0,9
60	33,7	29,2 - 38,2	2,4	-3,5	-2,1 - -4,5	0,8
62	32,7	29,3 - 37,4	2,4	-3,5	-2,3 - -4,8	0,8
64	31,8	28,3 - 36,7	2,2	-3,7	-2,2 - -5,0	0,9
66	31,1	27,1 - 35,9	2,5	-3,9	-2,5 - -5,0	0,6
68	29,9	25,6 - 34,5	2,3	-3,9	-2,3 - -5,8	0,8
70	28,6	24,7 - 33,4	2,2	-3,9	-2,5 - -5,4	0,8
72	27,4	23,0 - 31,5	2,1	-4,0	-2,7 - -5,4	0,9
74	25,9	22,0 - 30,4	2,2	-4,1	-2,8 - -5,4	0,9
76	24,7	20,5 - 29,0	2,1	-4,0	-2,5 - -5,5	0,9
78	22,9	19,5 - 27,4	2,0	-4,1	-2,6 - -5,6	1,0
80	21,3	18,4 - 24,0	2,0	-3,9	-2,6 - -5,2	0,9
82	19,8	17,0 - 22,5	1,8	-3,9	-2,2 - -5,0	0,9
84	18,5	15,5 - 21,0	1,7	-3,9	-2,3 - -5,0	0,8
86	16,9	13,5 - 19,3	1,8	-3,8	-2,2 - -2,9	1,1
88	14,8	12,0 - 17,0	1,5	-3,1	-1,1 - -5,2	1,5
90	13,3	10,0 - 15,4	1,4	-3,0	-1,3 - -5,0	1,3
92	11,3	8,5 - 13,5	1,5	-2,8	-1,2 - -4,2	1,2
94	9,0	6,5 - 11,0	1,3	-2,9	-1,5 - -4,1	0,8
96	5,9	4,1 - 8,5	1,2	-2,4	-1,0 - -3,3	0,6
98	4,0	3,9 - 5,7	0,9	-1,8	-1,0 - -3,3	0,6
99	3,1	1,7 - 4,2	0,9	-1,2	-0,5 - -1,8	0,4

Table 4.9 S.leopardinus 70 - 130 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	24,7	20,3 - 28,5	3,1	-1,3	-0,1 - -2,5	0,9
48	27,0	22,0 - 31,8	3,6	-1,8	-0,5 - -3,3	0,9
50	29,2	23,9 - 34,5	4,2	-2,3	-0,7 - -4,0	1,3
52	31,7	26,3 - 37,5	4,1	-2,8	-0,8 - -4,8	1,4
54	33,8	27,7 - 39,3	3,5	-3,3	-1,0 - -5,2	1,4
56	35,2	30,2 - 41,1	3,6	-3,5	-1,2 - -5,6	1,6
58	36,6	32,3 - 41,5	3,3	-3,8	-1,5 - -5,9	1,5
60	37,5	33,2 - 42,6	3,2	-4,1	-1,7 - -6,1	1,3
62	37,4	34,0 - 42,0	2,5	-4,8	-1,5 - -6,8	1,4
64	37,6	34,4 - 41,5	2,5	-4,1	-1,5 - -6,4	1,1
66	37,2	34,5 - 40,9	2,4	-4,2	-2,0 - -6,0	1,4
68	36,2	33,5 - 39,3	2,2	-4,1	-1,8 - -6,4	1,2
70	37,6	32,2 - 38,3	2,1	-4,0	-2,1 - -6,1	1,3
72	34,2	31,3 - 37,2	1,9	-4,3	-2,0 - -6,0	1,1
74	32,1	29,5 - 35,8	1,9	-3,8	-1,8 - -6,3	1,3
76	31,6	28,0 - 34,3	2,1	-4,0	-1,8 - -5,4	1,2
78	29,9	26,8 - 33,0	2,1	-3,7	-1,5 - -5,3	1,4
80	28,2	25,1 - 31,7	2,4	-3,6	-1,0 - -5,0	1,1
82	27,0	23,6 - 30,3	2,3	-3,6	-0,8 - -5,2	1,3
84	25,5	21,7 - 28,6	2,1	-3,5	-1,0 - -5,3	1,0
86	23,2	19,6 - 27,3	2,7	-3,4	-0,5 - -5,4	1,1
88	21,3	17,2 - 25,0	2,5	-2,9	-0,3 - -4,9	1,0
90	18,7	14,8 - 23,1	2,6	-2,3	-0,3 - -3,7	1,1
92	15,7	12,2 - 19,9	2,6	-2,3	-0,5 - -5,9	0,8
94	12,3	9,2 - 16,3	2,5	-2,3	-0,1 - -3,3	0,7
96	8,5	6,3 - 12,4	2,4	-2,1	-0,6 - -3,1	0,7
98	4,1	3,3 - 6,8	1,8	-2,0	-0,4 - -2,7	0,6
99	2,0	1,5 - 3,0	0,5	-1,6	-0,6 - -2,3	0,5

Table 4.10 S.thamalakanensis 70 - 130 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	36,5	28,9 - 48,6	4,6	-1,8	-0,8 - -3,2	6,5
48	38,8	29,8 - 49,0	8,0	-2,1	-1,0 - -4,1	5,9
50	40,3	31,8 - 49,4	6,5	-2,8	-1,1 - -5,0	5,2
52	42,1	33,3 - 49,0	5,9	-3,2	-1,4 - -5,4	6,0
54	43,3	34,8 - 50,1	5,2	-3,7	-1,4 - -5,8	6,0
56	43,5	36,0 - 50,3	6,0	-3,5	-1,1 - -5,4	5,8
58	42,8	36,0 - 50,0	5,5	-3,5	-1,0 - -5,7	5,5
60	42,0	36,3 - 47,4	4,8	-4,0	-1,7 - -5,9	4,7
62	41,1	35,8 - 46,0	4,2	-4,2	-2,6 - -5,8	4,1
64	40,0	34,9 - 45,1	4,1	-4,2	-2,5 - -6,2	4,1
66	38,8	33,5 - 44,6	4,2	-4,1	-2,4 - -6,1	4,2
68	37,6	32,4 - 43,5	4,1	-4,2	-2,4 - -6,2	4,1
70	36,2	31,2 - 41,9	3,5	-4,1	-2,3 - -6,2	3,5
72	35,2	30,0 - 40,4	3,6	-4,2	-2,3 - -6,2	3,6
74	33,8	29,0 - 38,6	3,6	-4,3	-2,1 - -6,9	3,6
76	32,3	27,8 - 36,9	3,9	-4,0	-2,1 - -7,3	3,8
78	31,3	26,5 - 35,8	3,6	-3,8	-2,0 - -6,5	3,6
80	29,6	25,1 - 33,8	3,5	-3,5	-1,5 - -6,1	3,4
82	28,4	23,2 - 32,4	3,3	-3,6	-1,3 - -6,1	3,3
84	26,2	20,0 - 30,9	4,1	-3,5	-1,6 - -6,3	4,2
86	24,1	18,2 - 29,4	4,8	-3,2	-1,3 - -5,8	4,8
88	22,2	16,2 - 28,3	4,9	-2,8	-1,0 - -5,1	4,9
90	20,3	13,7 - 27,1	5,0	-2,3	-1,0 - -4,3	5,0
92	17,4	11,2 - 24,4	5,0	-2,1	-1,0 - -3,5	5,0
94	14,3	7,8 - 22,5	4,7	-1,8	-0,7 - -3,4	4,7
96	7,8	3,8 - 16,9	3,0	-1,6	-0,5 - -3,0	3,1
98	4,2	2,3 - 11,5	8,0	-1,3	-0,3 - -2,3	1,5
99	2,8	1,1 - 4,2	0,9	-0,9	-0,1 - -1,5	0,9

Table 4.11 S.vanderwaali sp.n. 70 - 130 mm SL

	Dorsal margin			Ventral margin		
% HPL	Mean	Range	S.D.	Mean	Range	S.D.
46	35,5	26,3 - 44,5	6,6	-2,6	-1,0 - -4,0	0,7
48	37,1	28,5 - 46,3	6,5	-3,1	-1,6 - -4,9	0,9
50	39,8	29,7 - 47,5	5,6	-3,5	-2,0 - -5,1	0,9
52	42,2	31,1 - 49,0	5,5	-3,8	-2,1 - -6,2	0,8
54	43,8	33,0 - 50,5	5,3	-4,1	-2,6 - -6,3	1,1
56	45,3	34,8 - 51,8	3,6	-4,4	-2,7 - -6,5	1,2
58	46,7	36,5 - 52,0	4,8	-4,6	-3,0 - -6,2	1,1
60	46,9	38,4 - 52,5	4,4	-4,9	-3,0 - -7,0	1,1
62	46,0	38,5 - 51,0	4,6	-4,8	-3,5 - -7,1	1,1
64	46,2	37,7 - 51,5	5,2	-4,8	-3,2 - -7,5	1,2
66	44,7	36,3 - 52,5	5,9	-4,7	-3,0 - -7,3	1,1
68	42,5	34,1 - 51,3	6,4	-4,9	-3,2 - -7,6	1,2
70	40,6	32,0 - 50,2	5,9	-5,0	-3,0 - -7,4	1,3
72	39,9	30,9 - 49,9	5,1	-4,8	-2,8 - -7,3	1,2
74	38,0	29,4 - 47,1	5,8	-5,2	-3,5 - -7,5	1,2
76	36,0	28,4 - 44,7	5,8	-4,9	-3,5 - -7,8	1,1
78	35,3	26,6 - 43,0	5,0	-5,0	-3,7 - -8,3	1,1
80	33,3	25,3 - 41,0	4,5	-5,0	-3,5 - -8,2	1,2
82	30,4	23,6 - 38,0	4,8	-5,0	-3,6 - -7,9	1,2
84	29,0	21,5 - 36,9	4,5	-4,8	-2,5 - -6,8	1,0
86	27,2	18,7 - 33,5	4,0	-4,4	-2,0 - -7,1	1,1
88	25,2	15,3 - 31,5	3,7	-3,9	-2,0 - -8,1	1,1
90	22,4	13,3 - 29,0	3,9	-3,9	-2,0 - -8,0	1,2
92	19,2	11,1 - 23,5	3,9	-3,1	-1,1 - -6,8	1,0
94	12,3	8,0 - 19,3	3,4	-2,5	-1,0 - -6,4	0,9
96	6,7	4,6 - 13,6	1,5	-2,2	-1,0 - -5,0	1,0
98	3,7	2,1 - 7,1	1,2	-1,7	-0,5 - -3,4	0,8
99	2,1	1,4 - 3,2	0,6	-1,2	-0,4 - -2,0	0,5