THE EXTERNAL STRUCTURE OF THE HEAD OF *STRUTHIOLIPEURUS*

STRUTHIONIS (GERVAIS 1844) WITH PARTICULAR REFERENCE TO THE

CLYPEUS: AN INVESTIGATION OF THE RELATIONSHIP BETWEEN THE

PARASITE AND ITS HOST'S (*STRUTHIO CAMELUS* L.) FEATHER

THESIS

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Jodie Danielle Rappe, B.A.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Introduction to Coevolution

Coevolution is a topic that has been investigated extensively. Coevolution embraces the concept that a trait evolves in one organism in response to a trait in a second organism. The trait in the second organism may also evolve in a response to the trait in the first (Futuyma and Slatkin 1983). Both organisms in a specific interaction may have traits that evolved in response to traits in the other. Three models have been proposed to explain host-parasite coevolution; these are the mutual aggression model, the prudent parasite model, and the incipient mutualism model. In the mutual aggression model, the host and parasite constantly evolve adaptations with the host or the parasite being forced to respond rapidly or be at an ecological disadvantage; this disadvantage could result in extinction for one or both (Van Valen 1973). Holmes (1983) proposed that those parasites and hosts with genetic resistances to each other, such as *Aedes aegypti*, a mosquito, and its host *Brugia pahangi*, a filarial worm, are examples of this model. In the prudent parasite model, damage done by the parasite to the host is not lethal and is minimized, resulting in small detriment to the host. Finally, in the incipient mutualism model, the host and parasite interactions evolve into a cooperative relationship where one benefits the other (Lincicome 1971). An example of this is the protozoan, *Trypanosoma lewisi*, a parasite of the rat (*Rattus rattus*). The parasite, while feeding on the host, produces micronutrients that aid the rodent (Lincicome 1971). A fourth theory incorporates aspects of the previous three. In the game-theory model the host and parasite play

1

against each other and can adopt either a cooperative or an aggressive strategy, the approach adopted will determine fitness and selective costs (Renaud and de Meeus 1991). Eichler (1982) summarized the process of coevolution stating that "because parasites are specific to their hosts, they coevolve; because they coevolve, they must be specific."

Coevolution of host and parasite has been documented in many organisms and can occur in numerous ways. One of the most commonly cited examples of coevolution is the myxoma virus (*Myxoma*) found in rabbits (Nuttall 1997). This association is a classic example of the prudent parasite model. With serial passage of the parasite through several generations of the rabbit, a reduced level of pathogenicity occurs (Nuttall 1997). Species of the oestrid genus *Cuterebra* are additional examples of parasites that are adapted to their hosts. In these flies, the bee-like adult lays eggs on a rat, other rodent, or lagomorph. The hatched larvae migrates under the skin, leaving a "breathing hole" to the surface (Foreyt 1994). Adaptations may also involve the parasite's reproductive strategies. The bot fly, *Gastrophilus* sp., has adapted in behavior and reproductive strategy to its host, *Equus caballus*. The eggs of *Gastrophilus*, laid only in places the horse can reach with its mouth, cause a skin irritation which the equine then licks. The eggs hatch in the moisture of the mouth, and the adapted larva bore through the lips and migrate to the stomach (Foreyt 1994).

The Mallophagan Parasite

Harb (1980) divided the order Phthiraptera into four suborders, Amblycera, Ischnocera, Rhynchophthirina, and Anoplura. Kim and Ludwig (1982) determined that Anoplura should represent a separate order of Psocodea and that Mallophaga was, perhaps, a paraphyletic group including the suborders Amblycera, Ischnocera, and Rhynchophthirina. Clay (1957) recognized Mallophaga as a suborder of Phthiraptera and included the Ischnocera and Amblycera as superfamilies. Ischnocera and Amblycera are very diverse, and as a result are classified by some as suborders (Askew 1971, Marshall 1981).

Avian Mallophaga are chewing lice, feeding typically on the host's feather, yet some species may also feed on blood and tissue fluids (Gill 1990). There is a general correlation between body structure of mallophagans and feather structure of the host bird. Those lice found on the head and neck regions are short, rounded, and possess a large head, while species found on the torso tend to be flattened and elongated (Clay 1957). These different shapes enable efficient movement of lice. In addition, the elongated shape of the mallophagan inhabiting the torso reduces the possibility of displacement during preening behavior of the host (Askew 1971). Generally, lice inhabiting the head and neck region are more secure (Clay 1957). The relationship between the structure of the mallophagan head and the microstructure of the host feather has not been investigated.

Struthiolipeurus spp. are mallophagan parasites of Struthioniformes and Rheiformes, ostriches and rheas, respectively. The ostrich and rhea are closely related phylogenetically (Sibley 1990). The genus *Struthiolipeurus* is found on no other bird orders, suggesting a phylogenetic relationship between the birds where the parasite's hosts shared a common avian ancestor (Rothschild and Clay 1952). The fact that these lice are host-specific indicates a long association between the parasite and its bird hosts and supports the idea that the ostrich and rheas have a close evolutionary relationship (Askew 1971, Sibley 1990).

Initially, four species of *Struthiolipeurus* (*Struthiolipeurus struthionis*, *S. andinus*, *S. renschi*, and *S. rheae*) were reported on the Ostrich (*Struthio camelus* L.) the Lesser Rhea (*Rhea pennata* Chubb.) and the Rhea (*Rhea americana* L.), respectively (Hopkins and Clay 1952). Descriptive research on these lice included examination of cross sections (Keler 1959) and whole and cleared specimens using light microscopy (Carriker 1945, Meister 1958, Keler 1959, Ziegler 1971, Weisbroth and Seelig 1974, and de Tena et al. 1976). Additional work was done on *S. renschi* (Eichler 1943, Meister 1958, Ziegler 1971) a parasite of *Rhea pennata*. In addition, *S. nandu* (Eichler 1950, Meister 1958), a parasite of *Struthio camelus*, and a more recently described parasite, *S. stressmani* (Keler, 1959), a parasite of *Rhea americana*.

The asymmetry of the head of *Struthiolipeurus* spp. has been described (Cummings 1916, Clay 1951, 1957, and Symmons 1952). Species of *Struthiolipeurus* have an asymmetrical ventral premandibular area characterized by an anteromedial groove and a lobular structure to the left clypeal margin. The function of this asymmetrical area may be an adaptation to the microstructure of the host's feathers, possibly allowing for more efficient feeding or reducing chance removal during preening (Keler 1959, Lakshminarayara 1971). Also, the left mandible is more robust, with four large, distinct rugae, than the slender bilobed right mandible with weakly delineated apical rugae. The mandibles are directed downward and may serve as a firm attachment point to host feathers (Blagoveschensky 1959). An asymmetrical head has been documented in other species of Mallophaga, including the genera *Bizarrifrons* (Piaget 1885, Eichler 1938), occurring on the Montezuma, Olive and Chestnut-headed Oropendolas (*Gymnostinops montezuma, G. yuracares,* and *Psarocolius wagerli,* respectively) and the Great-tailed Grackle (*Ostinops decumanus*), and *Dahlemhornia asymmetrica* (Burmeister), occurring on the Lesser Emu, *Dromiceius novaehollandiae.* However, the nature of the asymmetry of these lice is much different from that of *Struthiolipeurus* spp., in which the head itself is symmetrical, and asymmetry exists only in the clypeal and mandibular regions.

Purpose of the Study

There is paucity of information on the fine structure of the head of species of *Struthiolipeurus.* Scanning electron micrographs are lacking, but some line drawings of the head region of this louse do appear in the literature. The general asymmetrical nature of the *Struthiolipeurus* head has been noted (Cummings 1916, Carriker 1945, Symmons 1952, and Clay 1957), but a detailed morphological study of the head has not been done. I investigated the relationship between the head structure of *S. struthionis* and the structure of ostrich contour feathers. Head size and the size of the feather channel were compared to the width of feather barbs. Comparisons to *S. andinus* and *S. rheae* and their respective host contour

feathers were also made. It was hypothesized that the width of the feather channel would demonstrate itself as a coevolutionary adaptation of the parasite to its specific host feather.

MATERIALS AND METHODS

Collection of Specimens

Specimens of *Struthiolipeurus struthionis* were collected from *Struthio camelus* in Navarro County, Texas on 24 January 1983 and preserved in 70% glycerated ethanol. Microscope slides of *Struthiolipeurus struthionis*, *S. andinus*, and *S. rheae* were obtained from the Smithsonian Institution, National Museum of Natural History. Feathers from *Struthio camelus* were obtained at Neighbors Ostrich Farm, Somerset, Texas; from *Rhea pennata* at Caskey Orchards, San Marcos, Texas; and from *Rhea americana* at Wilson's Rhea and Emu Farm, Iola, Texas. Feathers were randomly collected from those that had fallen on the ground. Since *Struthiolipeurus* spp. are not native to the United States, attached lice were not expected on feathers. Though lice have been recovered from imported birds, decontamination procedures (including treatment with decontaminant solutions and visual inspection) are quite thorough (Deason, personal communication). Additionally, importation of these birds is no longer routine, and the majority of breeders obtain livestock from eggs rather than adult birds. Thus, infestation by *Struthiolipelrus* spp. does not occur (Caskey and Neighbors, personal communication).

Microscopic mounts of *Struthiolipeurus struthionis* (from *Struthio camelus*, Tshokwane, South Africa, 23 September 1983 and from an unknown location, 28 November 1938), *S. andinus* (from *Rhea pennata*, Zoo, Vancouver, B.C., 1954), and *S. rheae* (from *Rhea americana*, Matto Grosso, Brazil, date unknown, and from National Zoological Park, Washington, D.C., 16 September 1926) were obtained from the Smithsonian Institution, National Museum of Natural History.

Scanning Electron Microscopy

Whole specimens of alcohol preserved lice were placed in a 2% glutaraldehyde solution in phosphate buffer for 1 h and transferred into phosphate buffer solution for 2 h. Specimens were dehydrated in a 75% buffer solution with acetone. After agitation for 15 minutes, the solution was decanted and specimens were covered with pure acetone. Specimens were dried using the DCP1 Critical Point Drying Apparatus™ (Denton Vacuum, Inc., Moorestown, NJ) and mounted to aluminum stubs with conductive graphite paste. In the final step of preparation, the stubs and specimens were sputter-coated with colloidal gold in the DESK-1™ (Denton Vacuum Inc.).

Specimens were examined using a Cambridge Instruments Steroscan 90™ scanning electron microscope (SEM), and micrographs were taken with Kodak TMAX™ 100 film at varying magnifications and an accelerating voltage of 15. Particular emphasis was placed on mouthparts and the asymmetrical groove on the ventral premandibular region of the head. Measurements of this groove and mouthparts were taken using the SEM. One specimen with feather barbs still held in the groove by the mandibles was photographed, showing the method of attachment.

Five feathers from each host species were attached to stubs with conductive graphite paste, dehydrated in the sputter-coater, coated with colloidal gold, and examined with the scanning electron microscope. The width of the base of each ramus (the large feather barbs projecting from the rachis) was measured (Fig. 1). Four barbs (2 from each side of the rachis) were measured in three regions: distal, medial , and proximal. The average ramus width per feather was then calculated.
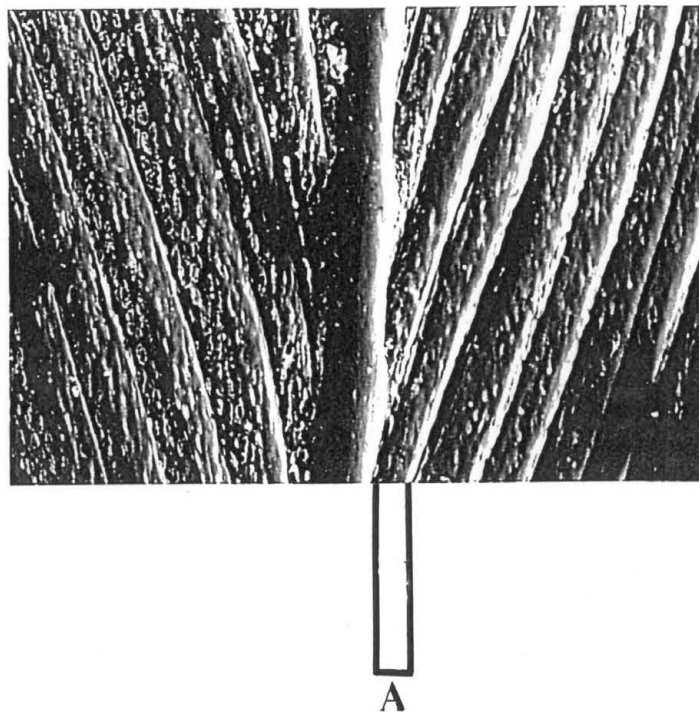
Figure 1.   Area measured on each host feather.   A - ramus width (scanning electron micrograph of *Struthio camelus* feather).

Light Microscopy

With the aid of a light microscope (at 100x) and an ocular micrometer, structures on the louse head were drawn and measured for later comparisons (Fig. 2).

Analyses of Data

All data were entered into a spread sheet (Microsoft Excel™). As specimens of *Struthiolipeurus andinus* (2 specimens) and *Struthiolipeurus rheae* (3 specimens) were limited, only the mean and standard deviation were calculated for each data set. Mean and standard deviation were calculated for feathers of *Struthio camelus*, *Rhea pennata* , and *Rhea americana*. Data were examined for general trends.
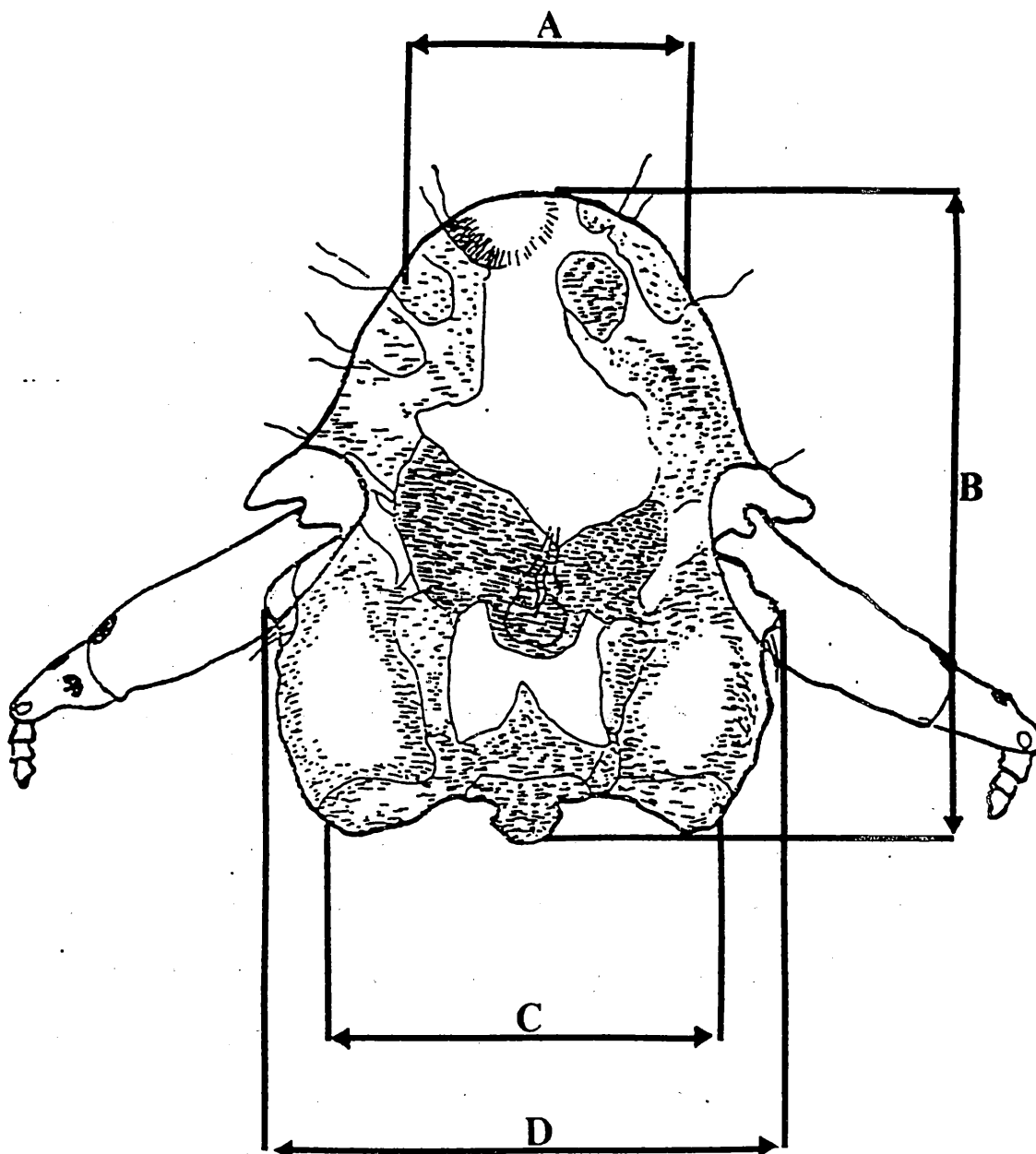
Figure 2. Areas measured on each ostrich louse. A - width of head at anterior margin of clypeus; B - length of head along midline; C - width of head at base of temporal lobe; D - width of head at post-antennal region. (*Struthiolipeurus nandu* - male, from de Tena et al. 1976)

RESULTS AND DISCUSSION

Specialization of a parasite on one host species or a few closely related species is a feature common to many parasites. This seems to be the case in members of the genus *Struthiolipeurus*. Although *S. struthionis* primarily inhabits feathers of *Struthio camelus*, it has been infrequently reported on *Rhea pennata* (Keler 1959). One might assume the two birds are closely related, in fact parasites are commonly used as a method for determining host phylogeny (Askew 1971, Brooks 1981, Page 1994, Ronquist 1995, Page et al. 1996).

Keler (1959) expressed concern that there is a one-sided migration of the lice. In other words, *S. andinus* has not been reported on *Struthio camelus* , while *S. struthionis* has been reported on *Rhea pennata*. He suggested that to understand this migrational tendency, a closer examination of the feathers of the two birds was necessary (Keler 1959). That concern is addressed in this study.

Even a casual observer can see the similarities between members of the genus *Struthiolipeurus*. An initial examination of the lice verifies that *S. struthionis* (Fig. 3) and *S. andinus* (Fig. 4) have a greater resemblance to one another than either has to *S. rheae* (Fig. 5). Head measurements of *S. struthionis* and *S. andinus* were similar (Table 1), but head measurements were different from *S. rheae*, the larger louse. Standard deviations were high in some cases, due to the small sample size. It should also be noted that observed louse size is not a function of age. *Struthiolipeurus* spp. are not native to the United States, but are found primarily in Africa, Australia, New Zealand, and South America. Due to an extensive
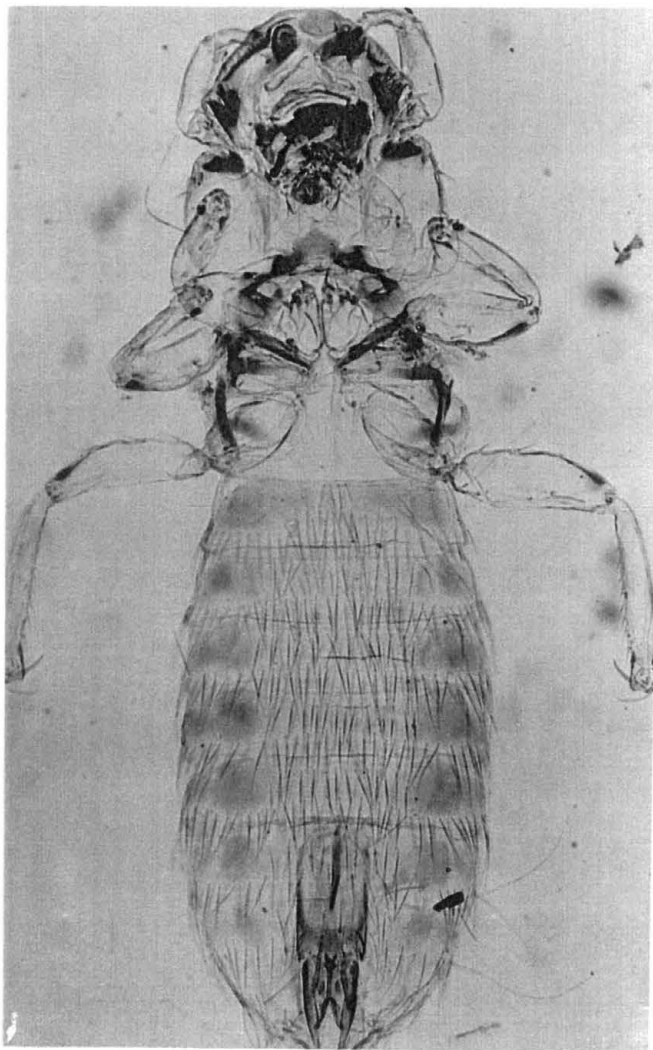
11

Figure 3. Photograph of male *Struthiolipeurus struthionis*, ventral view. (270X)
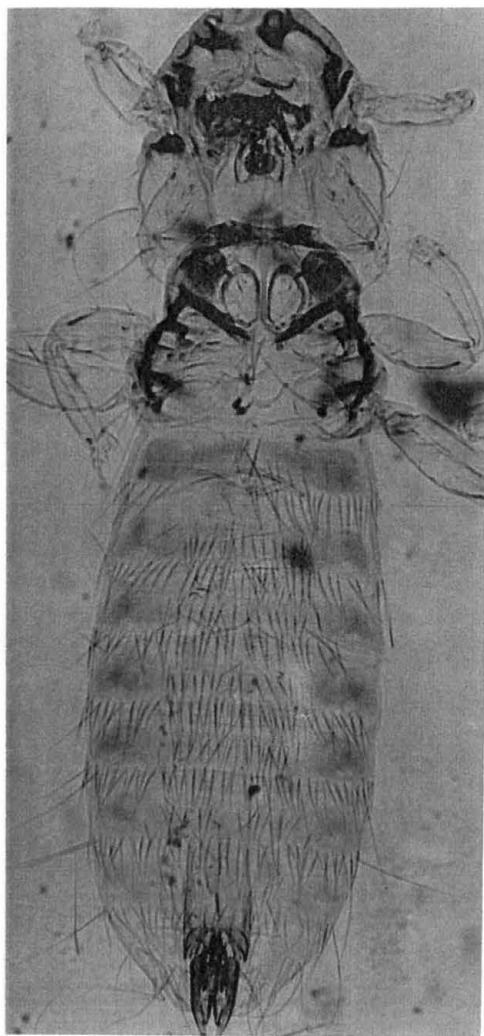
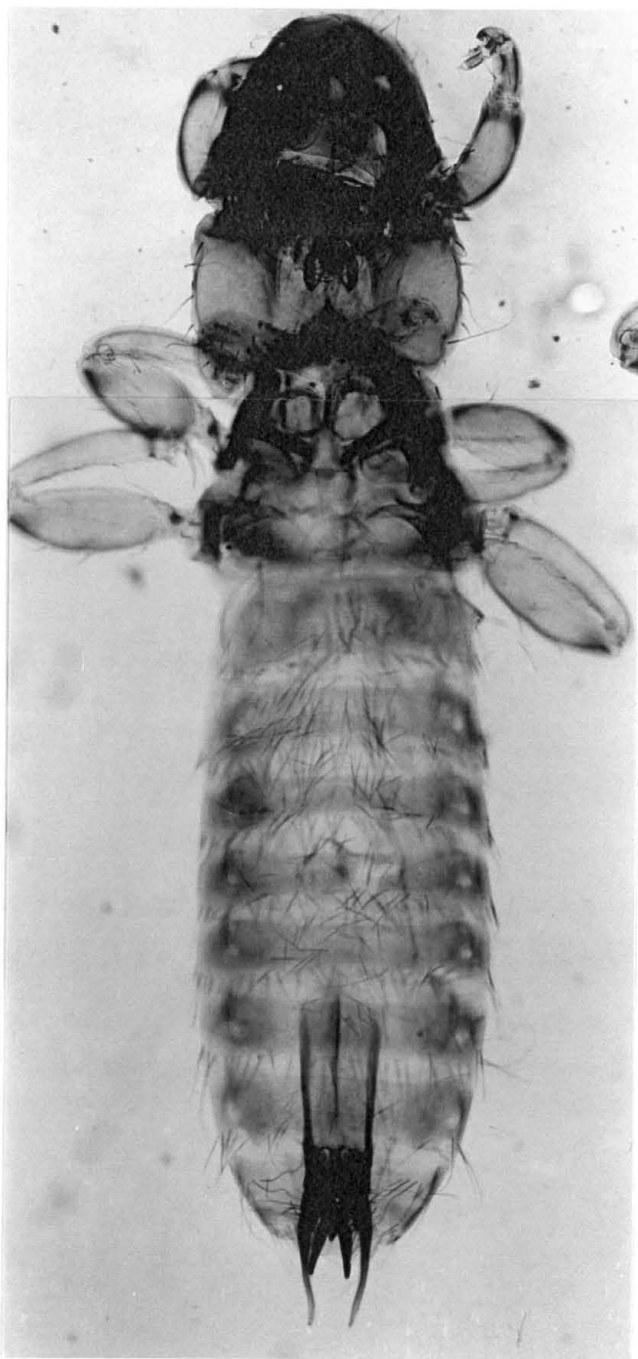Figure 4. Photograph of male *Struthiolipeurus andinus*, ventral view. (265X)

Figure 5. Photograph of male *Struthiolipeurus rheae*, dorsal view. (265X)

Table 1. Mean width and length (mm) of the head of species of *Struthiolipeurus*. Standard deviation shown in parenthesis.

| Species | n | WIDTH | | | LENGTH |
		anterior margin	midline	temporal lobe	midline
S. struthionis	12	0.354 (0.024)	0.702 (0.097)	0.710 (0.104)	0.712 (0.809)
S. andinus	2	0.385 (0.007)	0.640 (0.014)	0.700 (0.014)	0.700 (0.028)
S. rheae	3	0.495 (0.035)	0.845 (0.007)	0.890 (0.042)	1.050 (0.057)

decontamination process during importation, these lice species rarely occur in the United States. At present, adult birds are seldom imported and are usually confined to zoos; most stock comes from birds having been in the United States for 2 or 3 generations (Deason 1997).

A trend of similar size between groove and width of the host feather is indicated (Table 2). However, it is doubtful that this indicates species specificity. Because the channel holds several barbs, a comparison of barb size to channel size would only yield the number of barbs that could be held by the pulvinus and mandibles within the channel. This factor would not hinder lice of *Struthiolipeurus* from attachment to another host species. Overall head width and barb width should have no correlation, but the number of barbs in the channel may vary with respect to channel size; this was not determined in this study. Because species specificity was not seen, this study does not support coevolution of ostrich louse and host. The asymmetrical clypeus does not seem to be a coevolutionary adaptation to the respective host feather.

Over 250 scanning electron micrographs were taken. The asymmetrical groove was elucidated along the ventral premandibular area of *S. struthionis*. This groove, leading to the mouthparts, may act in "channeling" feather barbs into the mouth (Fig. 6, Fig. 7, Fig. 8). This function was confirmed when a louse was found with its mandibles grasping feather barbs located in the grooved channel (Fig. 9). All species of the genus *Struthiolipeurus* examined had a similar groove. Drawings of the head of each species, *S. struthionis* (Fig. 10), *S. andinus* (Fig. 11), and *S. rheae* (Fig. 12), showed the nature of the asymmetry of each species more clearly.

Mallophaga on birds lack specificity because of the gregarious nature of their host birds, such that parasites can transfer from one host to phylogenetically unrelated host species (Kellogg 1896). However, later Rothschild and Clay (1952) and Clay (1957) indicated that Mallophaga were host specific. Given geographic isolation, hosts tend to speciate more extensively than their parasites (Klassen 1992). Harrison (1927) and Clay (1957) disagree

Table 2. Mean width (mm) of the ventral groove on the head of species of *Struthiolipeurus* and the corresponding mean width (μm) of host feather ramus. Standard deviation shown in parentheses.

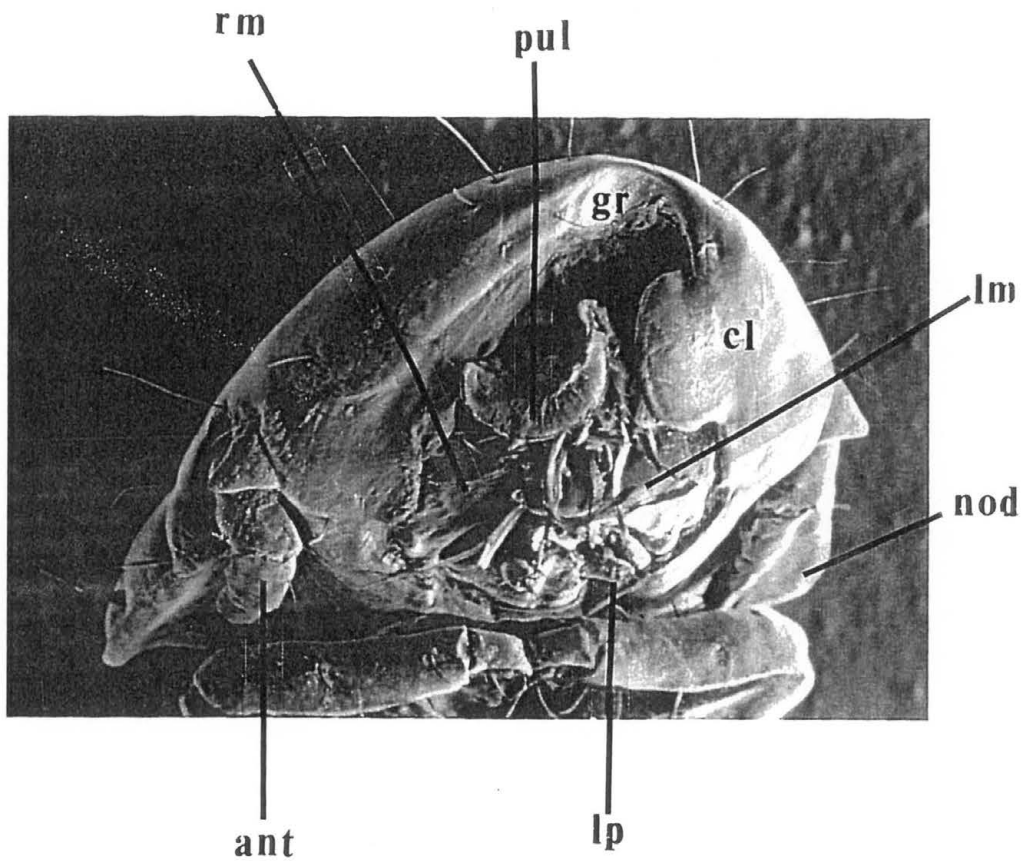| Species	n	Groove	Ramus
S. struthionis	12	0.642 (0.083)	18.40 (4.40)
S. andinus	2	0.595 (0.011)	17.12 (4.539)
S. rheae	3	0.809 (0.013)	26.56 (3.449)

Figure 6.   Scanning electron micrograph of inclined head of female *Struthiolipeurus struthionus*. ant - antenna; cl - thickened rim of clypeus; gr - asymmetrical longitudinal groove; lm - left mandible; lp - labial palp; nod - nodus; pul - pulvinus; rm - right mandible. (403X)
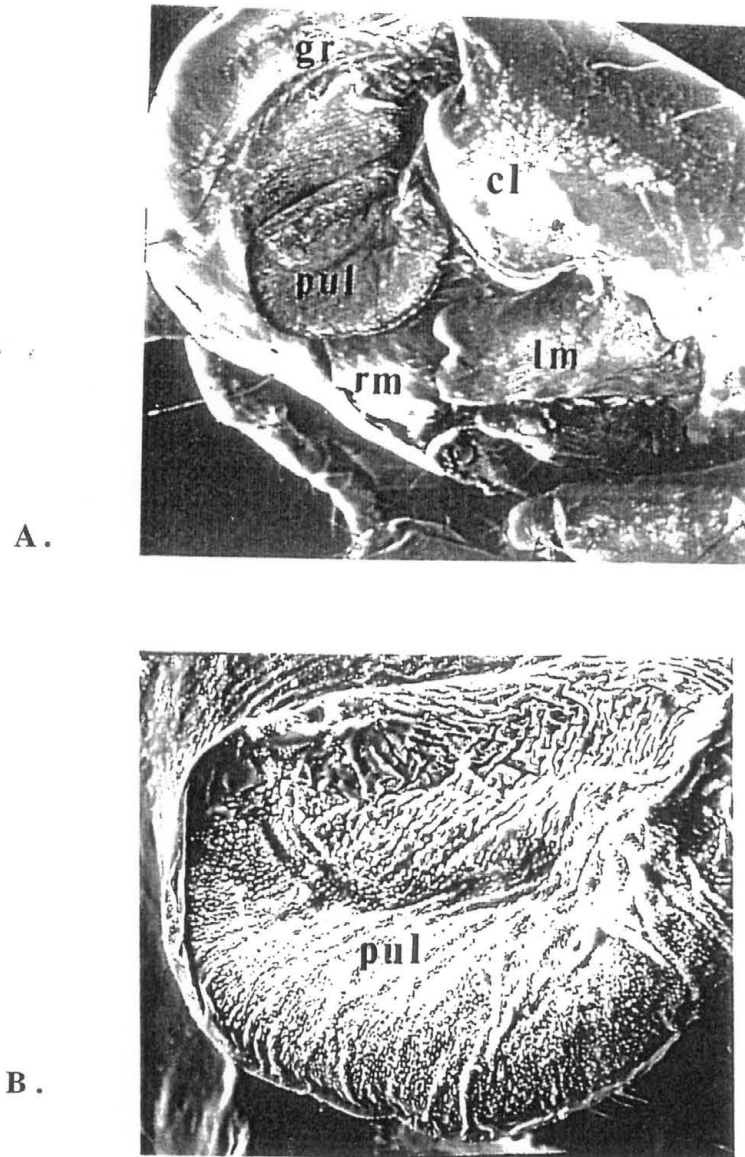
Figure 7.Scanning electron micrograph of male *Struthiolipeurus struthionis*. A) ventral view of head (538X); B) enlarged view of pulvinus (1249X). cl - thickened rim of clypeus; gr - asymmetrical clypeal lobe groove; lm - left mandible; pul - pulvinus; rm - right mandible;
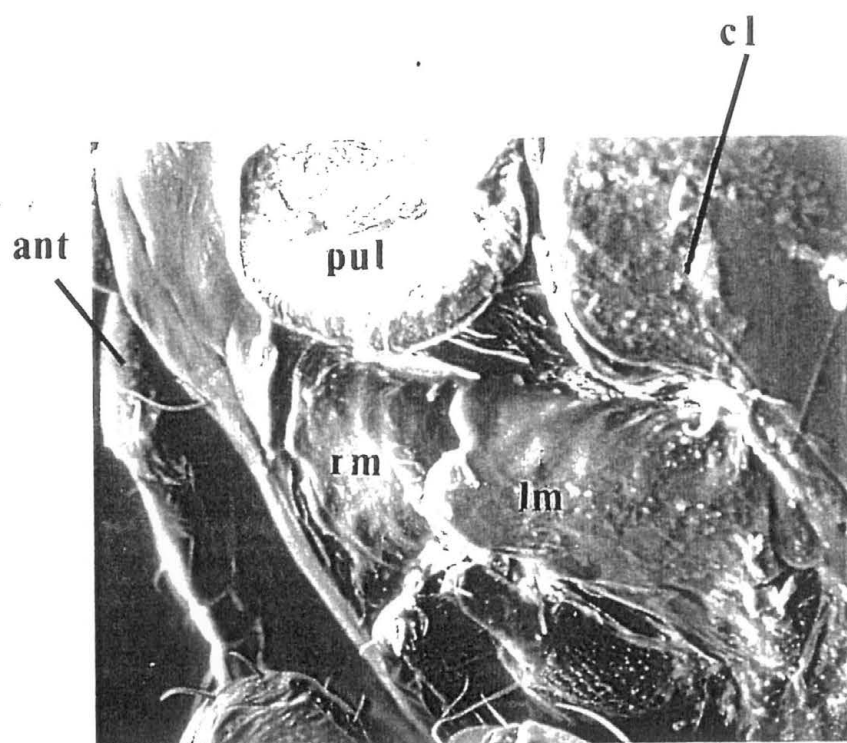
Figure 8. Scanning electron micrograph of anteroventral region of head of female *Struthiolipeurus struthionis*. ant - antenna; cl - clypeal lobe; lm - left mandible; pul – pulvinus; rm - right mandible (717X).
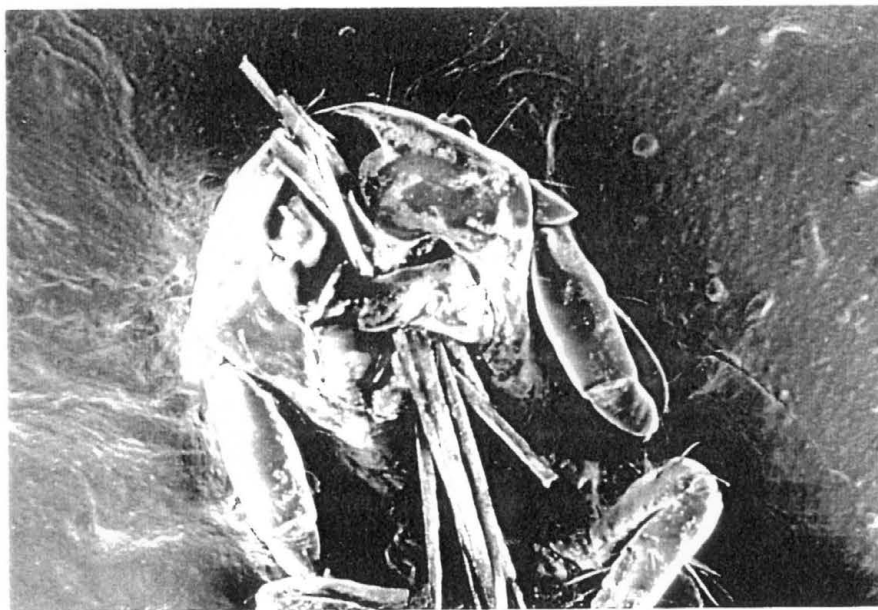
Figure 9. Scanning electron micrograph of male *Struthiolipeurus struthionis* attached to *Struthio camelus* feathers. Feather barbs can be seen running through the asymmetrical groove (268X).
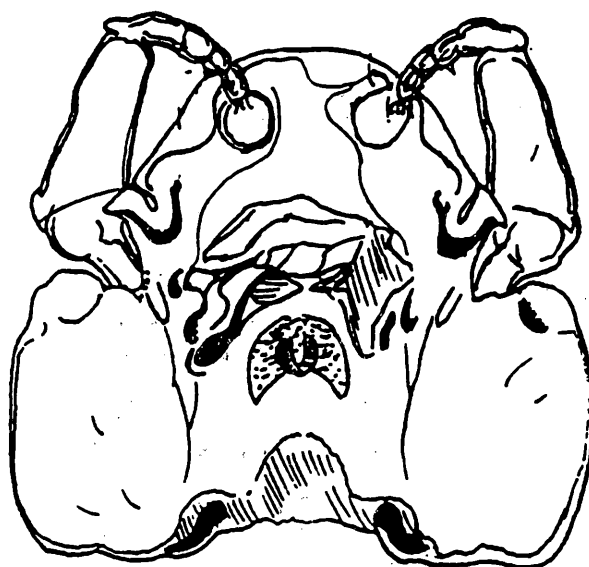
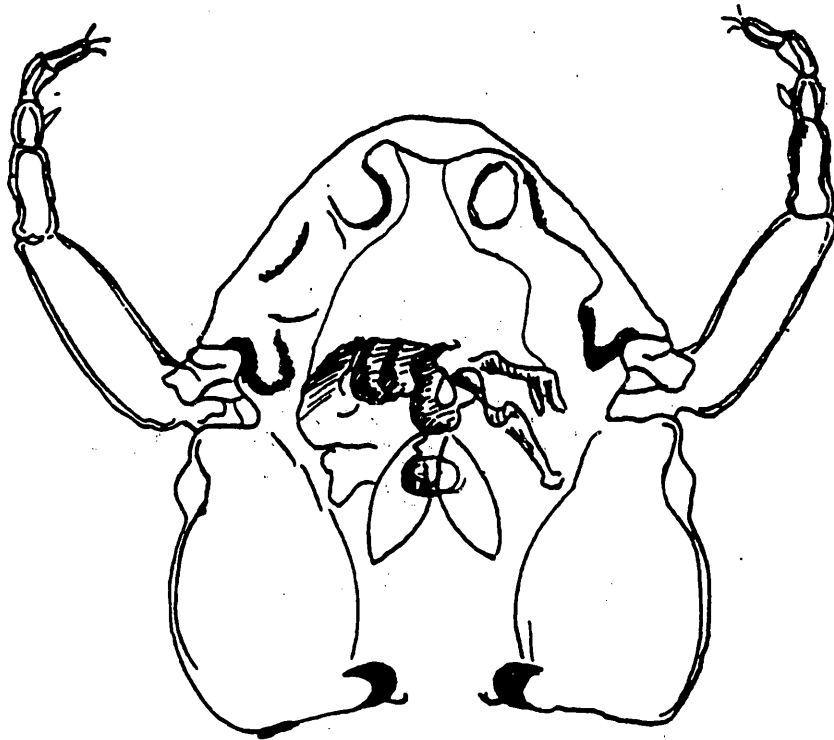Figure 10. Ventral view of male *Struthiolipeurus struthionis* head. (440X)

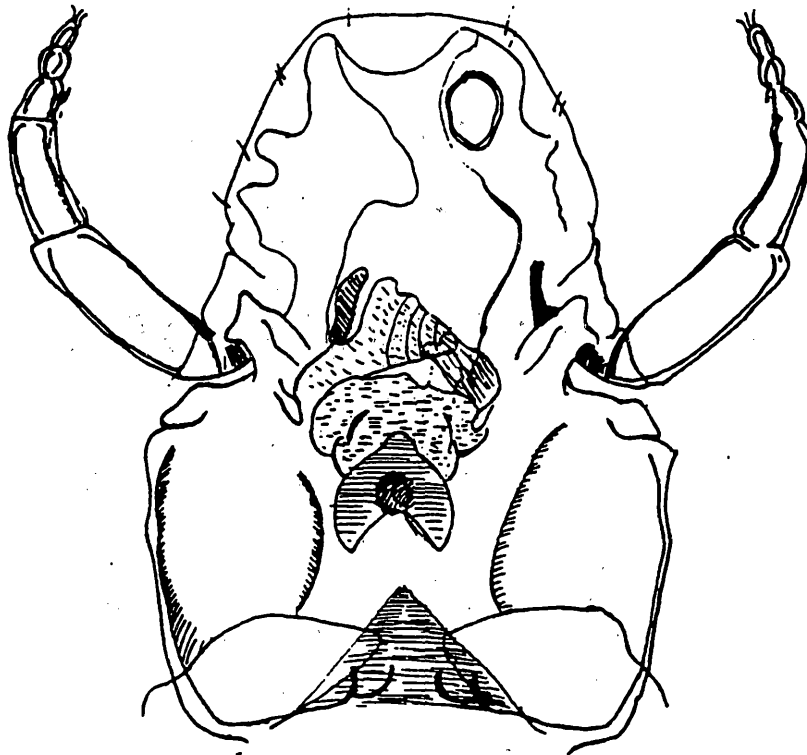Figure 11. Ventral view of male *Struthiolipeurus andinus* head. (450X)

Figure 12. Ventral view of male *Struthiolipeurus rheae* head. (450X)

with Klassen, stating that species of *Struthiolipeurus* are so similar to each other and so different from other bird lice, that the lice must be phylogenetically linked, thus the birds must have had a common ancestor as well. Keler (1959) referred to the migration of lice from *Struthio camelus* to *Rhea pennata* ; it should be noted that these hosts are not sympatric as the former bird is native to Africa, while the latter is native to South America. Therefore, although he did not cite the location of these birds, it is likely that transfer occurred while the birds were housed in a zoo. Factors such as parasite activity and level of infestation could have caused the transfer to one bird and the lack of transfer to the other.

Similarities were seen between *S. andinus* and *S. struthionis*. Head measurements of these species consistently overlap, and no differences in structure were seen between the two, while no areas of overlap were seen in *S. rheae*. This supports earlier work identifying *S. rheae* as a distinct species and raises the possibility that the *S. andinus* and *S. struthionis* may be synonymous.

SUMMARY

The head structure of *Struthiolipeurus struthionis*, *S. andinus*, and *S. rheae* was investigated and measurements of the head and asymmetrical longitudinal groove were taken, the latter being compared to width of the host feather rami. It is thought that the groove acts in a "channeling" fashion, directing the feather barbs to the mouth. Though the asymmetrical nature of the head may be an adaptation to the host feather, the asymmetry of the groove does not prohibit a species from attachment to another host. It was noted that several barbs are held in the groove, between the pulvinus and the mandibles. The number of barbs are likely to be limited by the width of the channel, but this point was not investigated in this study. Correlation analyses of feather width and barb width were not performed as the limiting factor is likely to be number of barbs rather than width of barbs.

In addition, similarities between *Struthiolipeurus struthionis* and *Struthiolipeurus andinus* were noted in the overlap of head measurements. This raises the issue that these species may be synonymous.

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