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MONOGRAPH OF THE NEW WORLD NOSODENDRIDAE AND NOTES ON THE OLD WORLD FORMS (COLEOPTERA)

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ABSTRACT

The 12 species of Neotropical Nosodendridae are revised and placed in two groups, the angelum *and the* testudinum *species groups.* Nosodendron leechi *(type-locality, Ecuador,* Pichincha: *6 mi W of Santo Domingo de los Colorados),* N. thompsoni *(type-locality, Peru,* Huanuco: *Tingo Maria) and* N. dybasi *(type-locality, Brazil,* Santa Catarina: *Nova Teutônia), are described as new.* Nesodendron championi *Sharp, 1902 and* N. chiriquense *Sharp, 1902 are synonymized with* N. testudinum *Waterhouse, 1876, and* N. cribratum *of Fleutiaux & Sallé, 1889 and of Sharp, 1902, with* N. punctatostriatum *Chevrolat, 1864.*

The two Nearctic species, Nosodendron unicolor *Say, 1824 and* N. californicum *Horn, 1874 are also reviewed. Comments are made on the possible synonymy of the latter with the European* N. fasciculare *(Olivier, 1790), as suggested by Oehme-Leonhardt (1954).*

A checklist of the Old World species is presented; the zoogeography of the family is discussed. It is concluded that Dendrodipnis *Wollaston, 1873 (described for a Japanese species and subsequently considered a synonym or a subgenus of* Nosodendron*) is a junior synonym of* Nosodendron *Latreille, 1804; and also that the Neotropical species form a homogeneous, independent lineage of glabrous forms.*

INTRODUCTION

My interest in this small family was first aroused when I discovered an undescribed species of *Nosodendron* from Brazil (Reichardt, 1973). After publication of its description I received a fairly large collection of Peruvian and Ecuadorian species from Hugh B. Leech (CASC). I soon discovered that it would be impossible to determine the species without the study of Sharp's Central American species. Fortunately enough the "Biologia Centrali-Americana" types (BMNH) were received for study through the kindness of R. T. Thompson. With this material and other specimens from other collections as well, I was able to

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complete a revision of the Neotropical representatives of the family. Finally I thought it would be useful to include the only two North American species in the study, although I have not seen enough material of them, and have not checked the complete literature for the species. They are essential, however, to the zoogeographical argument.

The literature on Nosodendridae is not extensive. Sharp (1902) was the first author who tentatively grouped his Central American species; Champion (1923) reviewed the "eastern" species (all species, excluding the New World fauna) in a relatively short and mainly taxonomic paper. Otherwise, there have only been individual and isolated descriptions of new taxa.

At the generic level Nosodendridae are homogeneous. Two extraneous elements have already been eliminated. *Pseudonosoderma* Heyden, 1885, included by Dalla Torre (1911: 4) in the family, is actually a tenebrionid (Champion, 1923: 578, footnote). *Orychonotus* Brèthes, 1922, a monotypic genus, does not belong into the family (Reichardt, 1973: 194); it possibly belongs to the Limnichidae.

A total of 48 species is known at present, all ascribed to *Nosodendron*. Wollaston (1873) described a second genus for a Japanese species, *Dendrodipnis*, at the time of description apparently the first "non-fasciculate" (but minutely scaled) species. After the original description only Sharp (1902: 670) and Champion (1923: 579) dealt directly with *Dendrodipnis*. Both reached the conclusion that "... the clothing of the surface does not divide the genus satisfactorily" (Sharp, *l.c.*), but in spite of this conclusion they considered *Dendrodipnis* a subgenus of *Nosodendron*.

It will be seen below that *Dendrodipnis* is a synonym of *Nosodendron*. It is evident that the original description has not been carefully studied, and that most other authors have based their conclusions on the first (mis)interpretation of Wollaston's genus (probably Sharp, 1902, perhaps based on Rye, 1875).

More recently Crowson (1959), describing a larva attributed to the New Zealand *Nosodendron ovatum*, suggested that it might represent a distinct genus, which he did not name because "the basis for a generic separation of *N. ovatum* on imaginal characters is not immediately obvious, and it cannot be taken as certain that the above-mentioned larva belongs to the species" (Crowson, *l.c.*: 85).

The original and main purpose of this paper is a revision of the Neotropical species of Nosodendridae, but during its preparation it became necessary to look into other faunas as well. This led to the examination of representative material from the United States and from Europe.

The results are interesting: the Neotropical fauna appears to be very homogeneous, and not directly related to the Nearctic fauna, which seems most closely related to the Old World species. Unfortunately it is impossible at present to reach a decision on the worldwide relationships. From the description it is apparent that the Old World species are heterogeneous, representing at least two distinct lineages, the minutely scaled species (some of which are also fasciculate) and

the glabrous species. The latter are perhaps related to the Neotropical forms.

These conclusions are also supported by the male and female genitalia, organs which had not been studied before in Nosodrendridae.

Due to insufficient material and knowledge, I will not study the relationships of the family in this paper. In the past they have usually been placed near (or within) the Byrrhidae; Crowson's placement of the family in the Dermestoidea (1959) seems to be more realistic, and is accepted here.

Material

As mentioned before, Nosodendridae are rare in collections, and this seems to be especially true for the Neotropical species. I have tried most collections known to have Neotropical Coleoptera, but the result was not too satisfactory. Only a total of about 120 specimens, representing 12 Neotropical species, has been assembled.

Material was received from the following collections:

BMNH British Museum (Natural History), London (R. T. Thompson);
CASC California Academy of Sciences, San Francisco, California (Hugh B. Leech);
CNCI Canadian National Collection of Insects, Ottawa, Canada (J. M. Campbell);
FMNH Field Museum of Natural History, Chicago, Illinois (Henry Dybas);
MCZC Museum of Comparative Zoology, Cambridge, Massachusetts (J. F. Lawrence);
MNHN Museum National d'Histoire Naturelle, Paris (Mlle H. Perrin);
MZSP Museu de Zoologia, Universidade de São Paulo, São Paulo;
OSUC Ohio State University, Columbus, Ohio (D. S. Chandler);
USNM National Museum of Natural History, Washington, D.C. (T. L. Erwin).

Acknowledgments

Throughout this study I became indebted to numerous colleagues, who were kind enough to try to locate specimens in the collections under their care (see Material). Besides those whose help was acknowledged above, I wish to express my gratitude especially to R. T. Thompson, British Museum (Natural History), who made the arrangements for the indispensable loan of Sharp's types, as well as to Mlle Hélène Perrin, Museum National d'Histoire Naturelle, Paris, who made available the original specimens of Chevrolat and Fleutiaux & Sallé.

To Professors George E. Ball and Roy A. Crowson I am very much indebted for their criticisms of an early version of the manuscript. I am also trankful to P. E. Vanzolini and U. R. Martins for their useful comments.

Nosodendron Latreille, 1804

Nosodendron Latreille, 1804: 146 (Type-species, by monotypy, *Sphaeridium fasciculare* Olivier, 1790); 1810: 188, 428; Lacordaire, 1854: 478; Gemminger & Harold, 1868: 922 (Catalog); Sharp, 1902: 670; Dalla Torre, 1911: 3 (Catalog); Champion, 1923: 578; Blackwelder, 1944: 270 (Catalog).

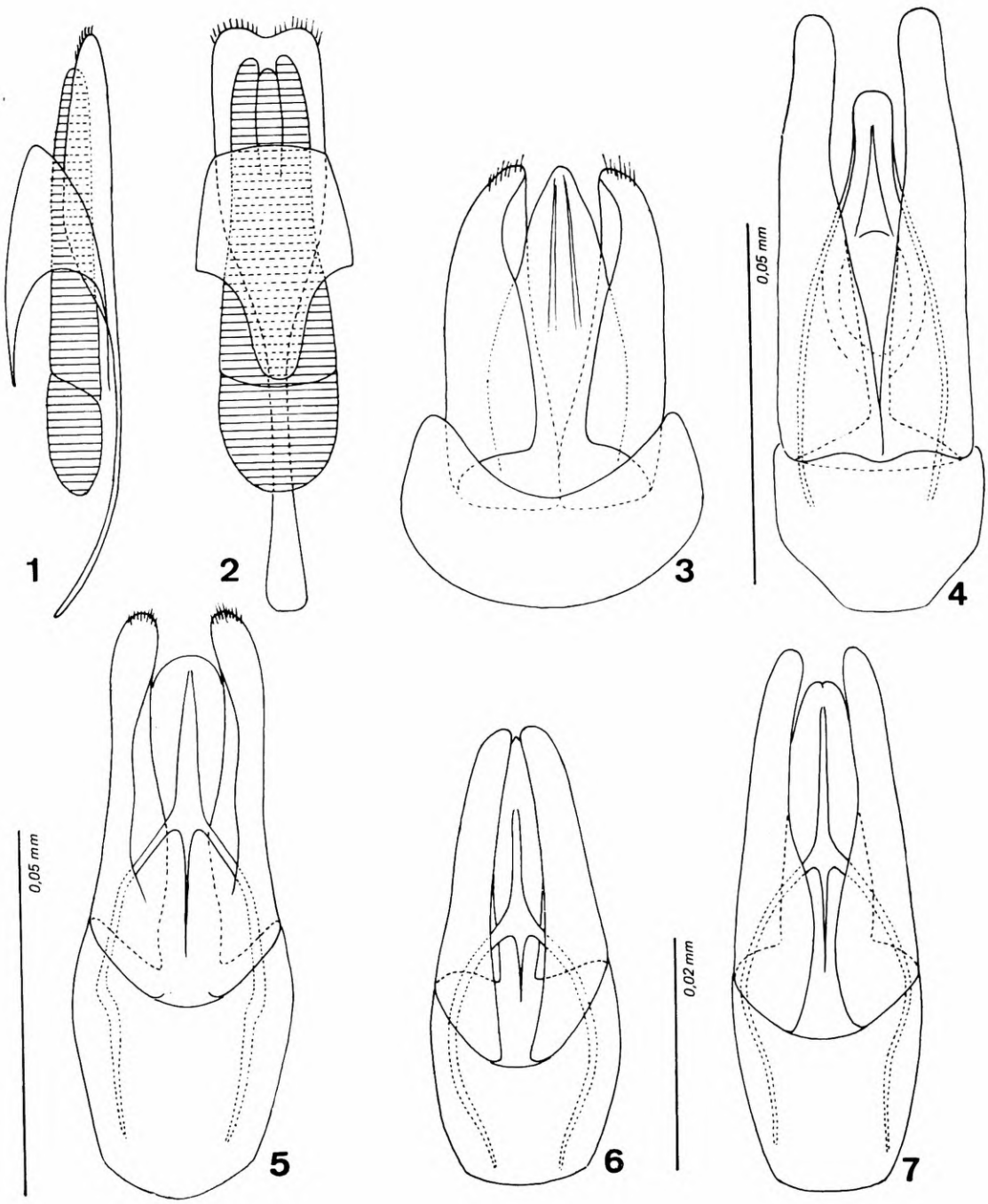
Dendrodipnis Wollaston, 1873: 33 (Type-species, by monotypy, *Dendrodipnis coenosus* Wollaston, 1873); Sharp, 1902: 670 (As subgenus); Dalla Torre, 1911: 3 (As synonym); Champion, 1923: 579 (As subgenus); Blackwelder, 1944: 270 (As synonym).

Discussion. Even though Wollaston was not quite sure about the validity of his *Dendrodipnis,* his description is clear in reference to the dorsal vestiture: "... in its body *not* being fasciculated (but merely clothed, and even that in *unrubbed* examples only, with a short, minute, remote, cinereous pubescence) it recedes from *Nosodendron...*" (Wollaston, 1873: 34). In the Zoological Record for the year 1873 (published 1875, with comments by E. C. Rye), on page 267, *Dendrodipnis* is stated to be "doubtfully distinct from *Nosodendron;* body not fasciculated...", and it seems that later authors (*e.g.,* Sharp, 1902; Champion, 1923), followed the latter statement without a careful examination of the species. Sharp, for example (1902: 670), says *"Dendrodipnis* was founded by Wollaston for an insect destitute of fascicles, and our [Neotropical] species therefore all belong to it...". It is obvious that Sharp did not realize that *Dendrodipnis* was described for a species minutely clothed, but destitute of fascicles, since he would not have made the mistake of considering the completely glabrous Neotropical species as belonging to what he considered subgenus *Dendrodipnis.* The fact that the "fasciculate" species of *Nosodendron,* that is, the species with small tufts of setae on elytra, also bear a dorsal vestiture of very small scale-like setae (Fig. 20), similar to that of the "non-fasciculate" species, is indicative that both types of vestiture are closely related. I have no doubt in considering *Dendrodipnis* a synonym of *Nosodendron.*

All Neotropical species (12) studied in this paper are completely glabrous, but some of the 36 species occurring outside the Neotropical Region are also glabrous (see *e.g.* Champion, 1923, who described or cited the following species as glabrous: *glabratum, madagascariense, calvum* and *celebense*). For this reason, in spite of the Neotropical species apparently forming a distinct and homogeneous lineage, it is premature to segregate any group from *Nosodendron.* The taxonomic picture of the family will certainly change very much when the whole fauna is carefully revised.

The genitalia of *Nosodendron*

Nosodendridae have no external sexual dimorphism, and their genitalia have never been properly studied. The only reference I found in the literature (Jeannel, 1955: 55) simply describes the genitalia of the group Nosodendridae are placed in, "Section des Byrrharia" (Including Byrrhidae, Dryopidae, Georyssidae and Nosodendridae), as follows: "Quant à l'édéage, il est de mode trilobé, mais avec une grande lame basale occupant la face sternale".



Male genitalia. 1, 2, schematic, lateral and dorsal views. 3, *californicum,* Tulare Co. 4, *unicolor,* Belmont Co. 5, *leechi,* paratype. 6, *thompsoni,* paratype. 7, *testudinum,* Santo Domingo de los Colorados.

I dissected a few species, but unfortunately, due to the lack of dimorphism and insufficient material I had to restrict myself to only a few. Nonetheless the results were rewarding, and it seems to me that future studies will have to be based more heavily on these organs.

Male genitalia (Figs. 1-7). Studied in the two North American species (*californicum* and *unicolor*) and three Neotropical ones (*leechi, thompsoni* and *testudinum*). Genitalia of the trilobed type, lateral and median lobes usually more or less equally well developed, the latter with well developed apophyses. Basal piece relatively short.

The three Neotropical species have very similar genitalia, with characteristic posteriorly trifurcate apophyses of median lobe. The North American species, on the other hand, have their genitalia different from those of the Neotropical species and different from each other. The studied male genitalia thus corroborate my findings, (1) that the Neotropical species form a homogeneous and distinct lineage, and (2) that the Neartic species are representatives of one (or more) distinct lineage whose relatives will be found in the Old World. Unfortunately no males of Old World species were available for dissection.

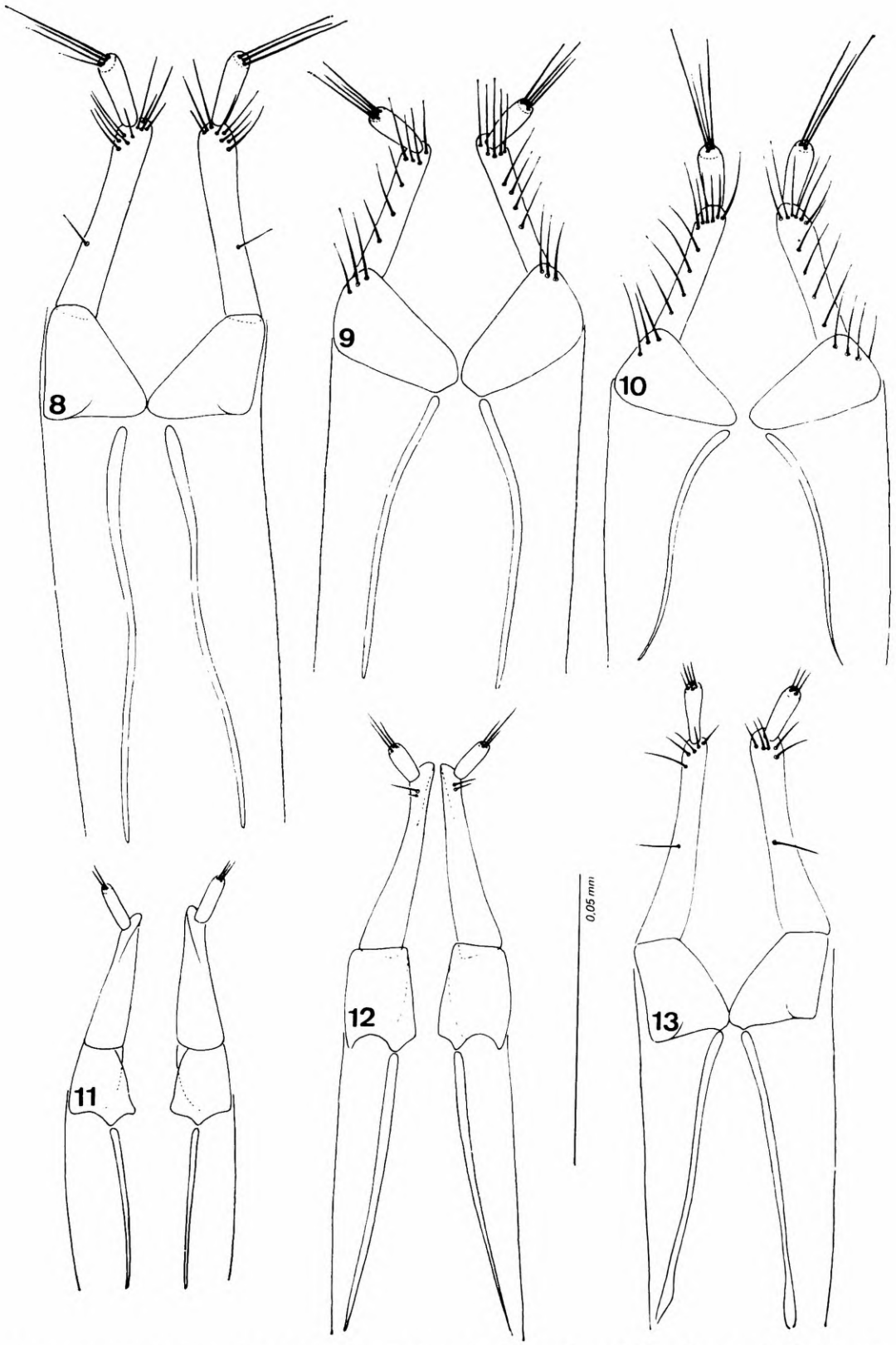
Female genitalia (Figs. 8-13). Also studied in the two North American species (*californicum* and *unicolor*), in *fasciculare* (Europe), and in three Neotropical species, *leechi, angelum* and *testudinum.* Valvifer, coxites and styles always well developed, but variable; bacculi always long and chitinized.

It is interesting that the female genitalia are more homogeneous (variation was noted especially in the presence or absence of setae on coxites and valvifer, and length of setae on styles), but again those of the Neotropical species seem to be more similar to each other than to the other species.

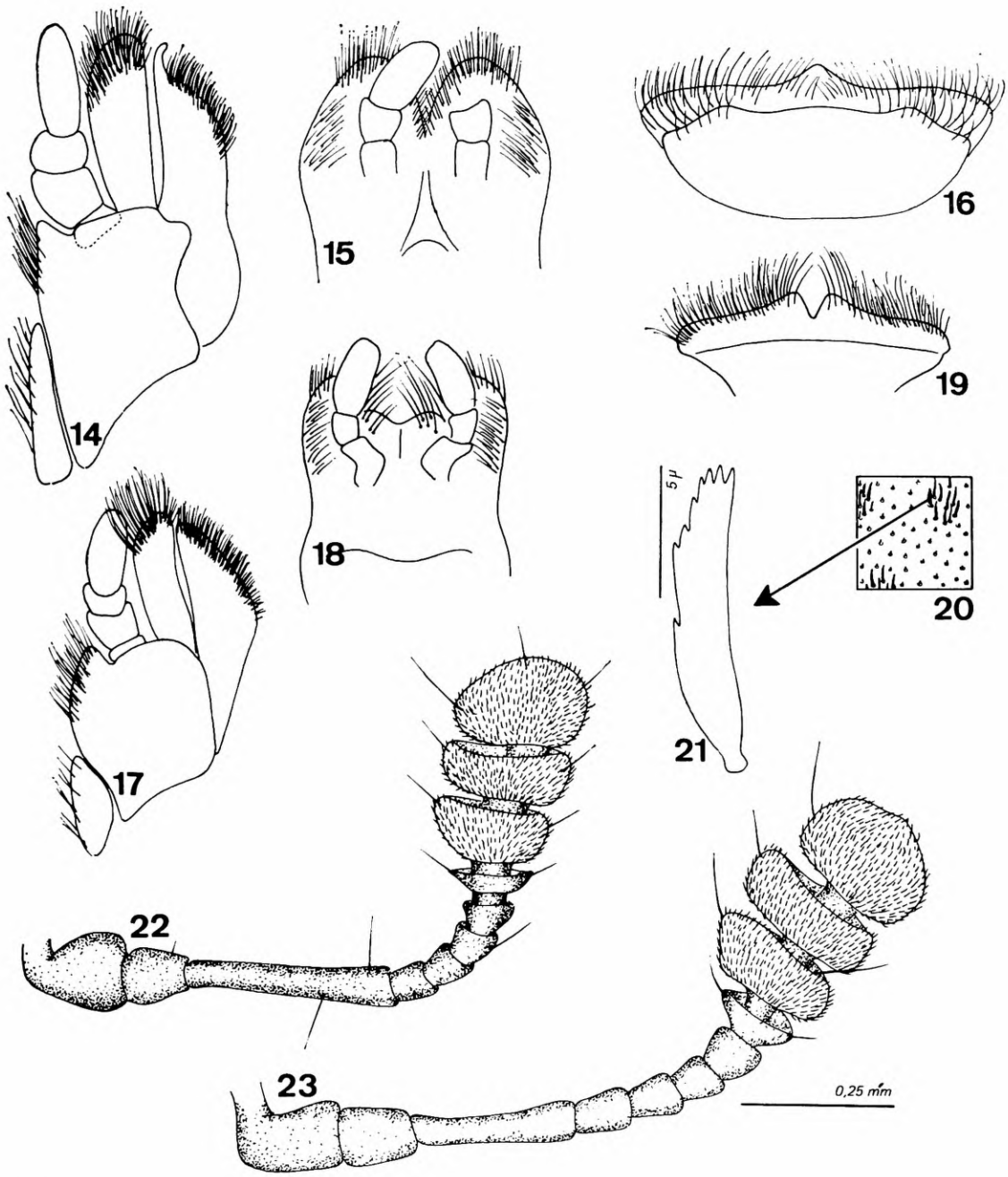
Also important is the comparison of the female genitalia of the Nearctic *californicum* (Fig. 9) with the European *fasciculare* (Fig. 10). I am sure that the female genitalia of both "species" support Oehme-Leonhardt's (1954) findings on the synonymy of the two forms. Unfortunately no males of *fasciculare* were available for dissection.

Mouthparts (Figs. 14-19). The mouthparts of *Nosodendron angelum* were illustrated in Reichardt, 1973 (Figs. 1-5); for comparison I dissected *N. californicum* (Figs. 14-16). The mouthparts of the two (unrelated) species agree in all respects, except that the lacinia of *N. californicum* (Fig. 14) ends in a hooked tooth, while it is untoothed in *N. angelum* (Fig. 17). It is interesting that Reitter (1911, pl. 104, Fig. 10b) illustrates a hook-like structure for *N. fasciculare* as well.

The material at hand is obviously not representative enough for any conclusions, but the study of mouthparts of other species may turn out to be rewarding.



Female genitalia. 8, *unicolor,* Belmont Co. 9, *californicum,* Tulare Co. 10, *fasciculare,* Primorje. 11, *testudinum,* Cachabé. 12, *leechi,* paratype. 13, *angelum,* paratype.



Mouthparts. 14, maxilla; 15, labium; 16, labrum; of *californicum*. 17, maxilla; 18, labium; 19, labrum; of *angelum*. 20, 21, details of elytral pubescence in *fasciculare*. Antennae. 22, *angelum*. 23, *californicum*.

The Old World species

The distribution of the 36 species occurring outside the Neotropical Region is rather curious: five are Holarctic (three Palaearctic, two Nearctic, one of the latter possibly synonymous with one of the Palaearctic species), 30 Oriental, reaching into Australia, New Zealand, Solomon Islands and New Caledonia, and a single species has been described from Madagascar (thus far no species is known from the African mainland).

As catalogs are much outdated, it seems fit to include here a checklist of the Old World species of *Nosodendron,* according to their distribution. As the two Nearctic species are closely related to the Palaearctic species, they will be listed below, in spite of the fact that they will be treated more thoroughly elsewhere.

1. Holarctic species

asiaticum Lewis, 1889	Japan
coenosum Wollaston, 1873	Japan
fasciculare (Olivier, 1790)	Europe
californicum Horn, 1874	United States
unicolor Say, 1824	United States

2. Oriental species (including the Malay Archipelago)

disjectum Champion, 1923	India
hispidum Champion, 1923	India, Burma, Vietnam, Malaysia
indicum Pic, 1923	India
nitidum Champion, 1923	India
irregulare Pic, 1928	Vietnam
tonkineum Pic, 1923	Vietnam
punctulatum Reitter, 1886	Sikkim, Sumatra, Perak Island, Java, Borneo
sikkimense Champion, 1923	Sikkim
ceylanicum Motschulsky, 1863 ...	Sri Lanka
marginatum Reitter, 1886	Malaysia, Sumatra, Java, Sarawak, Borneo, Batjan (Moluccas)
var. *rugiferum* Champion, 1923	Perak Island, Sikkim
var. *siamense* Champion, 1923	Siam
oblongum Champion, 1923	Burma
agaboides Champion, 1923	Penang Island
strigiferum Champion, 1923	Perak Island
batchianum Champion, 1923	Batjan (Moluccas)
celebense Champion, 1923	Celebes
grande Reitter, 1881	Sumatra, Sarawak, Borneo
hageni Reitter, 1886	Sumatra
ritsemae Reitter, 1886	Sumatra, Penang Island, Java
lentum Oehme-Leonhardt, 1954 ...	Philipines

3. New Guinean, Australian and Pacific species

calvum Tryon, 1892	New Guinea
mediobasale Lea, 1931	New Guinea

vestitum Tryon, 1892	New Guinea
australicum Lea, 1931	Australia (Queensland)
interruptum Lea, 1931	Australia (Queensland)
ovatum Broun, 1880	New Zealand
seriatum Broun, 1921	New Zealand
zealandicum Sharp, 1892	New Zealand
australe Fauvel, 1903	New Caledonia
fijiense Lea, 1931	Fidji
glabratum Champion, 1923	Solomon Islands

4. Madagascan species

madagascariense Alluaud, 1896 ..	Madagascar

As there has been no recent revision of these species, I am sure that many changes will occur. Pic, for example, described two species (from India and "Tonkin") in the same year Champion published his paper with the description of species from the same area. Pic's species are most certainly synonyms, but any action in that direction will have to be based on the study of types; it will also be difficult to settle the priority problem.

The Nearctic species

The two North American species, *unicolor* and *californicum,* are more closely related to the Old World species than to the Neotropical species. They have a dorsal vestiture of very small, scale-like setae in each dorsal puncture. These setae slightly increase in size towards the apex, where they are best visible. *Nosodendron californicum* also bears tufts of longer setae (about 10 forming one cluster) irregularly placed on the whole surface of elytra. It seems that setae and clusters are relatively easily rubbed-off, so that this character must be very carefully checked.

The mentum of the two North American species is simply punctate, as in most Old World species of *Nosodendron* (and similar to that of a few Neotropical species, *e.g. angelum*). They also have a large and well developed head, with large and incompletely covered eyes.

Key to Nearctic species

1. Elytra, especially posteriorly, with sparse tufts of short, ferrugineous scale-like setae (as in Fig. 20); remainder of dorsal surface, including head and pronotum, with small scale-like setae, each arising from one puncture. Southwestern Canada (British Columbia) to Southwestern United States (Washington, Oregon, Idaho and California) *californicum* Horn, 1874

   Elytra only with small scale-like setae, without tufts. United States (Michigan, Illinois, Indiana, Ohio, Kansas, Maryland and Alabama) ..... *unicolor* Say, 1824

Nosodendron unicolor Say, 1824
(Figs. 4, 8)

Nosodendron unicolor Say, 1824: 274; Gemminger & Harold, 1868: 922 (Catalog); Dalla Torre, 1911: 4 (Catalog); Casey, 1912: 3 (Redescription in key); Hayes & Chu, 1946: 70-77, figs. 1, 2, 4-9, 12-14, 16-18, 21-23 (Description of larva).

Surface shiny and completely, densely punctate on dorsal surface, each dorsal puncture bearing an extremely small, ferrugineous scale; scales slightly increasing in size towards apex, being best visible near apex of elytra. Head with large, partially exposed eyes; mentum simple, only punctate, its punctures coarser than those of dorsal surface. Scutellum apparently less punctate towards apex. Ventral face completely punctate, punctures without scales. Longitudinal striation at base of abdominal sternites very clearly marked. *Genitalia:* of male (Fig. 4); of female (Fig. 8). *Measurements* (in mm): total length, 4.6-5.5; pronotal length, 0.8-1.0; elytral length, 3.5-4.0; pronotal width (base), 2.4-2.6; pronotal width (anteriorly), 1.4-1.6; elytral width (maximum), 2.9-3.3.

Material examined. UNITED STATES. *Ohio:* Belmont Co. (1♂, 1♀, MZSP; 2 exs., OSUC). *Kansas:* Douglas Co. (1 ex., CNCI). *Alabama:* Mobile (4 exs., CASC, MZSP).

Distribution. Nosodendron unicolor is known from the central states of the United States. It has already been recorded from Illinois and Kansas (Casey, 1912: 3), Indiana (Blatchley, 1910: 672), Michigan (Hayes & Chu, 1946: 69) and Maryland (Sokoloff, 1959). The recorded hosts of *Nosodendron unicolor* are discussed elsewhere.

Discussion. Nosodendron unicolor is easily distinguished from *N. californicum* by the complete absence of tufts of elytral setae. If, as discussed under that species, *Nosodendron californicum* is a synonym of the European *Nosodendron fasciculare, N. unicolor* is the only species endemic to North America.

Nosodendron californicum Horn, 1874
(Figs. 3, 9, 14-16, 23)

Nosodendron californicum Horn, 1874: 22; Dalla Torre, 1911: 3 (Catalog); Casey, 1912: 3-4 (Redescription in key); Hayes & Chu, 1946: 79, figs. 3, 10-11, 15, 19-20 (Description of larva); Oehme-Leonhardt, 1954: 253 (proposed synonymy with *N. fasciculare*); Hatch, 1961: 294, pl. 57, fig. 4 (Characterization); Osborne & Kulhavy, 1975: 71, figs. 1-4 (Habits of larvae and adults).

Extermely similar to *Nosodendron unicolor,* with more or less equally dense dorsal punctures, but these coarser and less foveolate, and thus dorsal surface as if more densely punctate. Dorsal punctures, as in *unicolor,* with extremely small, ferrugireous scales; on elytra, especially in posterior half, with cluster of about 10 scale-like setae each (each seta arising from a single puncture), which are longer, and thus more clearly visible (as in Figs. 20, 21). Tufts of setae, which apparently are easily rubbed-off, separated from each other by about

one eyes diameter. Lacinia with apical, curved and strong tooth (Fig. 14). Antenna (Fig. 23). *Genitalia:* of male (Fig. 3); of female (Fig. 9). *Measurements* (in mm): total length, 4.5-4.7; pronotal length, 0.8-0.9; elytral length, 3.4; pronotal width (base), 2.2-2.4; pronotal width (anteriorly), 1.4; elytral width (maximum), 2.7-2.9.

Material examined. UNITED STATES. *California:* Carrville, Trinity Co. (1 ex., MZSP). Round M'D'W Giant Forest, Tulare Co. (1♂, 1♀, MZSP). North Fork (1 ex., MZSP). Tuolumme Co. (1 ex., MZSP). Chester (4 exs., OSUC, MZSP).

Distribution. Described from California, where the species has been found in a great many localities, *Nosodendron californicum* has also been recorded from CANADA (Southwestern British Columbia, Hatch, 1961: 294) and from the UNITED STATES, *Washington* (Hatch, 1961: 294), *Oregon* (Hayes & Chu, 1946: 69) and *Idaho* (Osborne & Kulhavy, 1975).

Discussion. The larva of *Nosodendron californicum* was described by Hayes & Chu (1946), together with the larva of *N. unicolor,* and was compared to that of the Europen *N. fasciculare.* In a paper on the Philippine *Nosodendron lentum,* Oehme-Leonhardt (1954) pointed out that Hayes & Chu based their comparisons on old, incomplete and unreliable literature descriptions of the larva of *fasciculare,* and concluded that "... *hence, they were unable to detect that the European* Nosodendron fasciculare *Olivier and the later described American* Nosodendron californicum *Horn were one and the same species and thus the latter has to be reduced to synonym*" (my italics). This synonymy has apparently been overlooked by North American writers, and should be considered as provisory until confirmed.

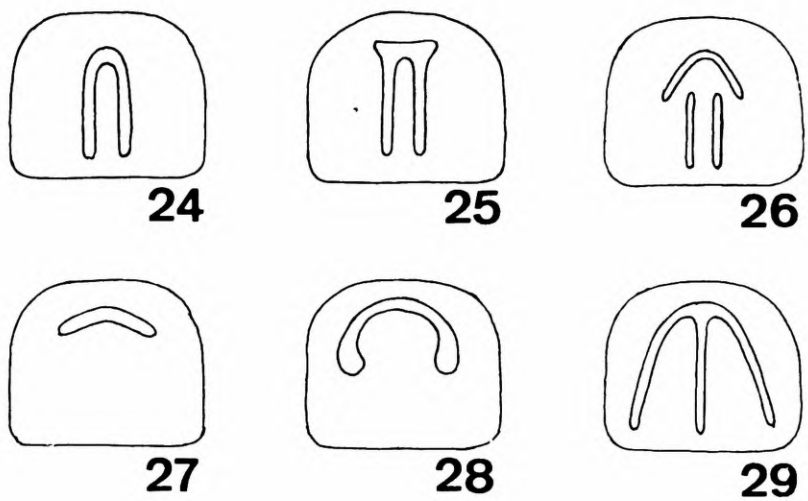
As seen above, the female genitalia (Figs. 9, 10) apparently confirms the synonymy, but unfortunately I am in no position to study this problem more carefully because of lack of material. I should say, however, that the geographic distribution of the two forms is rather strange for a single species. *Nosodendron californicum* is known from the Western United States, while *Nosodendron fasciculare* is only known from Western Europe (apparently a rare species, already known from France, Switzerland, Austria, Germany, western Poland and Scandinavia). It is possible that *fasciculare* occurs in eastern Europe and Asia (perhaps having been described as a distinct species). The material I have seen of *Nosodendron fasciculare* (Figs. 10, 20, 21) are 3 exs., from Primorje (formerly Warnicken), in western Poland.

Nosodendron californicum is easily distinguished from *Nosodendron unicolor* by the elytral tufts of setae, as seen in the key. The two species are allopatric, *N. californicum* living west of the Rocky Mountains, and *N. unicolor* in the Central United States.

The Neotropical species of *Nosodendron*

Description. Dorsal surface black and shiny, punctate, but completely glabrous. Head, as in Old World species, usually retracted under the pronotum, completely or incompletely hiding the eyes; the latter very weakly and almost imperceptibly faceted. Antennae (Fig.

22), 11-segmented, scape globose, III very long (about as long as club), IV-VII small, about equally developed, VIII lenticular, wider than preceding segments, and IX-XI forming the club; only the club finely and shortly pubescent; other segments glabrous, except for a few, irregularly placed, long setae. Mouthparts completely hidden by the large mentum; maxillae (Fig. 17) with lacinia apically untoothed. Mentum simply punctate or with differently shaped impressions (Figs. 24-29). Pronotum convex, much wider than long. Scutellum triangular. Elytra convex, sculpture of dorsal surface variable, always punctate, sometimes forming a regular pattern of quadrangles-hexagons. Ventrally as in Old World species. Abdomen sometimes with transverse impressions along basal margin of sternites.



Impression of mentum (schematic). 24, *leechi, testudinum* and *dybasi.* 25, *mexicanum.* 26, *punctatostriatum.* 27, *subtile* and *derasum.* 28, *thompsoni.* 29, *politum.*

Historical review. Very little has been written on the Neotropical fauna. Gemminger & Harold's catalog (1868: 922) listed a single species; Dalla Torre (1911: 3-4) catalogued 10, and Blackwelder (1944: 270) 12.

The first Neotropical species, *punctatostriatum,* was described by Chevrolat (1864) from Guadeloupe. Fleutiaux & Sallé (1889) later referred to this species under the name *cribratum* (Castelnau, 1840), a species from Guadeloupe, originally described as *Cercyon* (Hydrophilidae; where it is still listed in Blackwelder, 1944: 174). In a footnote Sharp (1902: 671) characterized a species of *Nosodendron* from Guadeloupe, which "... may be the form referred to as *Nosodendron cribratum,* Fleutiaux & Sallé (Ann. Soc. Ent. Fr. 1889, p. 392), but is certainly not *Cercyon cribratus,* Cast., as they supposed, ... The species may be called *N. cribratum,* though it cannot be referred to Castelnau" (Sharp, *l.c.*). Obviously Chevrolat's *punctatostriatum* has priority over Fleutiaux & Sallé's and Sharp's names, as will be seen under that species.

The second Neotropical species, *testudinum,* was described by Waterhouse (1876) from Brazil, Pará. Sharp (1902) added seven Central American species.

Orychonotus excavatus Brèthes, 1922 and *Nosodendron apicale* Pic, 1923 are not Nosodendridae (Reichardt, 1973).

Reichardt (1973) described a new species from southern Brazil and Argentina; Jorge (1973) described another one from Rio de Janeiro. Costa Lima (1953: 77) illustrated an undetermined *Nosodendron,* which might be either *angelum* Reichardt, 1973 or *bucki* Jorge, 1973. This material was not located.

In the present revision the Neotropical species of *Nosodendron* are placed in two species groups; three species are described as new, three are synonymized, so that the total number of Neotropical species is 12, as follows:

1. *angelum* group

angelum Reichardt, 1973	Brazil, Paraguay and Argentina
bucki Jorge, 1973	Brazil
leechi, sp. n.	Ecuador

2. *testudinum* group

derasum Sharp, 1902	Panama
subtile Sharp, 1902	Panama
thompsoni, sp. n.	Peru
politum Sharp, 1902	Panama, Ecuador
dybasi, sp. n.	Brazil
punctatostriatum Chevrolat, 1864	Venezuela, St. Vincent, Guadeloupe
= *cribratum* Fleutiaux & Sallé, 1889	
testudinum Waterhouse, 1876 ...	Guatemala, Costa Rica, Panama,
= *championi* Sharp, 1902	Colombia, Ecuador, Peru and
= *chiriquense* Sharp, 1902	Brazil
latifrons Sharp, 1902	Panama and Colombia
mexicanum Sharp, 1902	Mexico

Taxonomic discussion. The Neotropical species of *Nosodendron* are representatives of a lineage distinct from the Old World/Nearctic species, being especially well characterized by the completely glabrous dorsal surface (as opposed to the minutely scaled dorsal surface of most Old World/Nearctic species). Other differences between the two lineages are less evident, and depend on further evidence, especially from the Old World fauna. There seem to be differences in the male and female genitalia, as discussed above; the mouthparts are very similar in the two groups, but *Nosodendron unicolor* has the lacinia (Fig. 14) with a strong, curved tooth at apex. In *Nosodendron angelum* the lacinia is untoothed (Fig. 17); confirmation of the presence of the tooth in the Old World species would be an additional and important character.

As will be seen below, the hypothetical history of the Nosodendridae supports that the Neotropical species represent a distinct lineage (see also Fig. 46).

Key to species

1. Large species (more than 4 mm total length). Eyes large, when head retracted, still exposed in part. Elytral punctures not forming a clear and regular quadrangular-hexagonal meshwork ..... *angelum* group 2

   Small species (less than 4 mm total length). Eyes small, when head retracted, completely hidden. Elytral punctures frequently arranged in quadrangular-hexagonal pattern .... *testudinum* group 4

2. Mentum with two deep, parallel grooves and dense pubescence (as in Fig. 24). Elytra finely and densely punctate. Ecuador ..... *leechi,* sp. n.

   Mentum not impressed, coarsely punctate and glabrous 3

3. Elytra with 11 striae of large punctures and finely punctate interstices. Brazil (São Paulo, Paraná, Santa Catarina), Argentina (Misiones) and Paraguay (Cordillera) (Fig. 45) ... . *angelum* Reichardt, 1973

   Elytra finely and densely punctate, all punctures of same size. Brazil (Rio de Janeiro)..... *bucki* Jorge, 1973

4. Mentum only punctate, without impressions, and completely glabrous. Panama and Colombia ..... *latifrons* Sharp, 1902

   Mentum often pubescent, and always impressed 5

5. Mentum with a transverse, curved impression along front margin (as in Fig. 27) 6

   Impression of mentum not as above 8

6. Impression of mentum more or less horseshoe-shaped (Fig. 28). Peru ..... *thompsoni,* sp. n.

   Impression of mentum curved along front margin, but not continued backwards, as above (Fig. 27) 7

7. Elytra with quadrangular pattern on whole surface (more or less hexagonal towards apex), except around scutellum (Fig. 36, 37). Panama ..... *derasum* Sharp, 1902

   Quadrangular pattern of elytra restricted to three-fourths, apical fourth finely and densely punctate (Figs. 32-35). Panama ..... *subtile* Sharp, 1902

8. Mentum with anterior U-shaped impression and two posterior, longitudinal impressions (Fig. 26). Venezuela and Lesser Antilles (St. Vincent and Guadeloupe) .... *punctatostriatum* Chevrolat, 1864

   Mentum with two or three longitudinal impressions 9

9. Mentum with three longitudinal grooves which are fused anteriorly (Fig. 29). Panama and Ecuador *politum* Sharp, 1902

Mentum with two longitudinal grooves which are fused anteriorly (Figs. 24, 25) 10

10. Elytral punctures not forming a clear quadrangular-hexagonal meshwork, but with 11 striae of large punctures and finely punctate interstices (Figs. 42, 43). Brazil (Santa Catarina) ..... *dybasi,* sp. n.

Elytral punctures forming a clear quadrangular-hexagonal pattern 11

11. Quadrangular-hexagonal pattern of elytral punctures restricted to anterior two-thirds; at apex elytra densely and irregularly punctate. Mexico (Veracruz) .... *mexicanum* Sharp, 1902

Quadrangular-hexagonal pattern of elytral punctures on whole surface, including apex; sometimes slightly more erased near scutellum. Brazil (Pará and Amazonas), Peru, Ecuador, Colombia, Panama, Costa Rica and Guatemala .... *testudinum* Waterhouse, 1876

The *angelum* group

A small group of species characterized by the relatively large size (the known species average about 4.5 mm total length), the more or less shiny dorsal integument (usually not microrugose), and by the elytral punctures, which do not form a very clear quadrangular-hexagonal pattern (even though in some cases it is possible to see an indication of this pattern at higher magnification and only in certain areas). The most typical character of the group, however, are the relatively large eyes which are partially exposed from under pronotum when the head is in the normal position (as in Old World species of *Nosodendron*).

Two of the species share the same type of mentum, without impression, glabrous and heavily, coarsely punctate: *angelum* Reichardt, 1973 and *bucki* Jorge, 1973, while the third species, *leechi,* sp. n., has two longitudinal grooves on the pubescent mentum.

As will be seen elsewhere, the simple, unimpressed mentum, as found in *angelum* and *bucki,* is also typical of *latifrons* (a species of the *testudinum* group), the two Nearctic species and most Old World species. It is considered as a primitive character.

As has been seen in the key, the three species of the *angelum* group are easily distinguished by the pattern of the elytral punctures. *Nosodendron angelum* seems to be very closely related to *N. bucki,* whereas *N. leechi* is quite distinct, especially in type of mentum.

Nosodendron angelum and *N. bucki* are known from the southern extreme of the distribution of the family, southeastern Brazil, northern Argentina and Paraguay (Fig. 30); *N. leechi* is only known from Ecuador (Fig. 31).

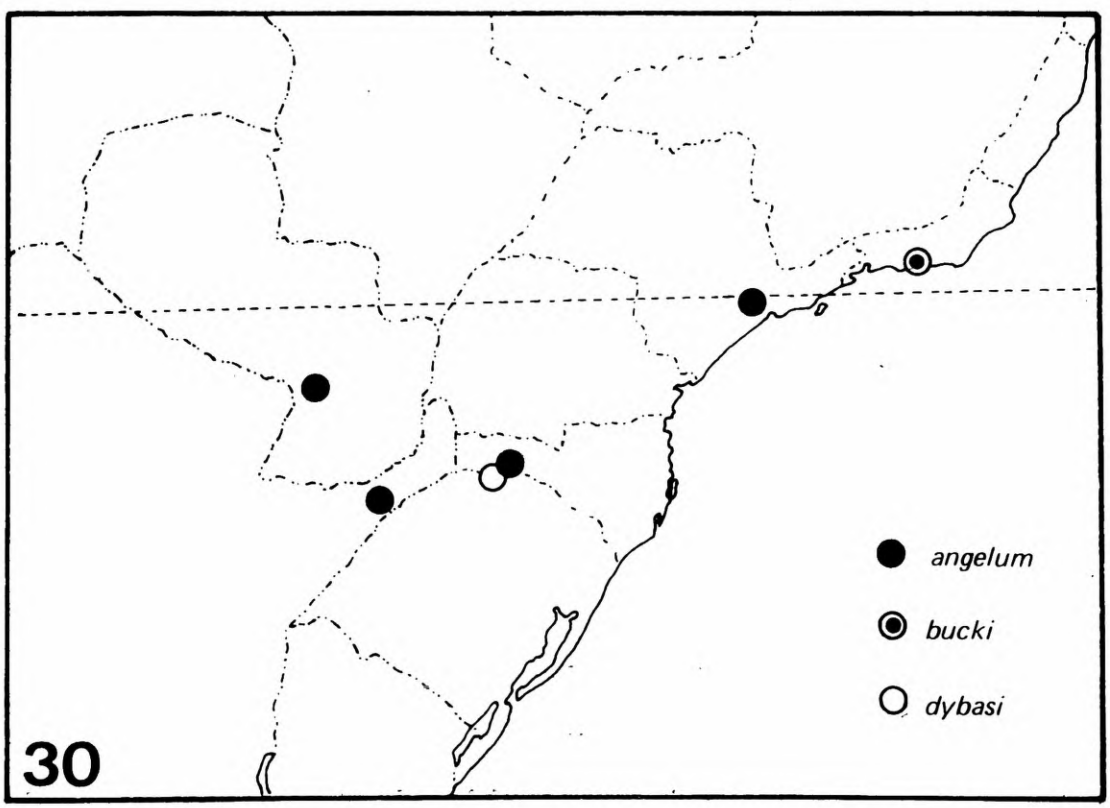
Nosodendron angelum Reichardt, 1973
(Figs. 13, 17-19, 22, 30, 45)

Nosodendron angelum Reichardt, 1973: 194-198, figs. 1-13 (Holotype, BRAZIL, *São Paulo:* Barueri; MZSP*); Jorge, 1973: 76, figs. 1-2 (In key; comments).

Surface shiny. *Head* clearly punctate on whole surface. Eyes large, in part exposed. Mentum large, coarsely punctate, without impression. *Pronotum* very finely punctate, more coarsely so on sides (where punctures are of about the same size as those of head). *Scutellum* microrugose. *Elytra* finely punctate on whole surface and with 11 longitudinal striae of large punctures; at apex these striae become confused with the remaining punctures. Prosternum and mesosternum finely punctate; metasternum coarsely punctate on sides. Longitudinal striation of abdominal sternites well developed. *Genitalia:* of female (Fig. 13). *Measurements* (in mm): total length, 4.1-5.4; pronotal length, 0.7-0.9; elytral length, 3.3-4.0; pronotal width (base), 2.2-2.7; pronotal width (anteriorly), 1.4-1.7; elytral width (maximum), 3.0-3.3.

Material examined. Besides the type-specimens, from Brazil (São Paulo and Santa Catarina) and Argentina (Misiones), I have seen the following specimens:

BRAZIL. "Paraná" (2 exs., BMNH). PARAGUAY. *Cordillera:* San Bernardino (1 ex., "in gallery of Nectandra sp."; USNM).



30. Geographic distribution of *angelum, bucki* and *dybasi.*

Discussion. As seen in the key, *Nosodendron angelum* is easily distinguished from *N. bucki* by the different elytral punctures. Even though *N. bucki* is only known from the type-locality, the two species are most probably sympatric in southeastern Brazil (Fig. 30). From *N. leechi,* the third species of the group, both *N. angelum* and *N. bucki* are distinguished by the unimpressed mentum.

Nosodendron bucki Jorge, 1973
(Fig. 30)

Nosodendron bucki Jorge, 1973: 73-75, figs. 3-5 (Holotype, BRAZIL, *Rio de Janeiro:* Rio de Janeiro; MZSP*).

Very shiny. *Head* finely but clearly punctate. Eyes partially exposed, large. *Pronotum* slightly more finely punctate than head, but punctate on whole surface. *Scutellum* very finely punctate. Elytra as finely and irregularly punctate as pronotum, only in certain places, and at high magnification, with slight indication of meshwork, but central puncture as small as others. Ventrally very finely microrugose; longitudinal striation of base of abdominal sternites well developed, especially on sides. *Measurements* (in mm): total length, 4.2; pronotal length, 0.7; elytral length, 3.4; pronotal width (base), 2.2; pronotal width (anteriorly), 1.4; elytral width (maximum), 2.5.

Notes. Only the holotype of *Nosodendron bucki* is known. It is closely related to *N. angelum* (see above).

Nosodendron leechi, sp. n.
(Figs. 5, 12, 31)

Types. Holotype and 15 paratypes from ECUADOR. *Pichincha:* 6 mi W of Santo Domingo de los Colorados, 23.II.1955 (E. I. Schlinger & E. S. Ross) (Holotype ♂ and 10 paratypes, CASC; 5 paratypes, MZSP). *Imbabura:* Paramba, 3,500 ft., V. 1897 (Rosenberg, "dry season") (1 paratype, BMNH).

Head very finely, but clearly punctate; pronotum and elytra more finely punctate than head; dorsal surface microrugose. Eyes large, partially visible from above. Mentum with two deep, parallel grooves and dense pubescence, especially near lateral margins. *Pronotum* about three times as wide at base as long. *Scutellum* triangular, finely punctate as pronotum. *Elytra* regularly and very finely punctate (punctures about same size as pronotal punctures), and with very faint indication of hexagonal meshwork (longitudinal margins of hexagons very obtusely angulate, frequently almost quadrangular), and an equally faint median and large puncture (this pattern only visible at high magnification and at certain angles). Meso- and metasternum only finely and regularly punctate as dorsal surface. Longitudinal striation of base of abdominal sternites weakly impressed. *Genitalia:* of male (Fig. 5); of female (Fig. 12). *Measurements* (in mm): total length, 4.2-4.5; pronotal length, 0.6-0.7; elytral length, 3.3-3.5; pronotal width (base), 2.0-2.2; pronotal width (anteriorly), 1.2-1.4; elytral width (maximum), 2.5-2.7.

Discussion. Nosodendron leechi, as seen above, is easily distinguished from the other two species of the group by the impression on mentum. From the species of the *testudinum* group with two parallel impressions on mentum (*testudinum, mexicanum* and *dybasi*), *N. leechi* is easily distinguished by its larger size, as well as by details of the dorsal punctuation pattern.

Nosodendron leechi is the only species of the group not to occur in southeastern Brazil: it is known from two localitites in Ecuador (Fig. 31).

It gives me pleasure to name this species after my friend Hugh B. Leech.

The *testudinum* group

A group including the remaining Neotropical species of *Nosodendron,* characterized by the relatively small size of the species (averaging about 3 mm total length), the usually more or less opaque dorsal surface, due to the microrugose integument, and by the elytral punctures, which usually (but not always) form a typical quadrangular-hexagonal meshwork pattern. In the resting position the head is retracted into the pronotum, completely covering the small eyes.

The species of this group have developed five different types of impression on mentum, besides the simple type, without impression, found in a single species, *Nosodendron latifrons* (from Northwestern South America).

In three species the mentum has a curved, transverse impression, which runs more or less parallel to front margin (Fig. 27). In *Nosodendron derasum* and *N. subtile,* two very closely related species (only known from the type-locality, Volcán de Chiriqui, Panama), the mentum has a simple impression, not continued backwards. In the third species, *N. thompsoni,* from Peru, the impression is more or less horseshoe-shaped, continued backwards (Fig. 28).

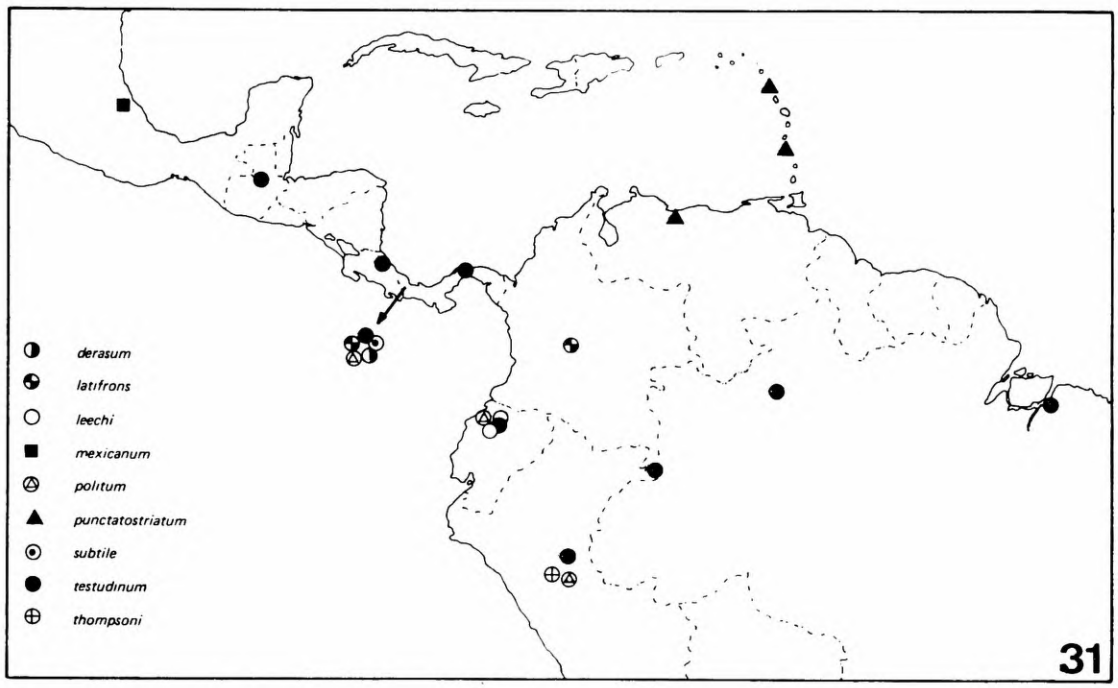
In the other species of the *testudinum* group, the mentum is longitudinally impressed. *Nosodendron politum,* a species also only known from Volcán de Chiriqui, has three longitudinal, anteriorly connected grooves, of which the two outer arms diverge backwards, since they run more or less parallel to the lateral margins of the mentum (Fig. 29).

A mentum with two parallel grooves, also connected anteriorly (Figs. 24, 25), is found in the widespread *N. testudinum,* in the single known Mexican species, *N. mexicanum,* and in a new species from southern Brazil, *N. dybasi.*

Nosodendron punctatostriatum, the only species known from the Lesser Antilles (and Venezuela), has a small anterior U-shaped impression and two short, deep, longitudinal impressions posteriorly (Fig. 26).

The species of the *testudinum* group are all very closely related, but are easily distinguished by the characters used in the key.

The geographic distribution of the group is quite interesting (Figs. 30, 31). There are two completely allopatric species, *N. dybasi* (southern Brazil) and *N. mexicanum* (Mexico). *Nosodendron testudinum* is widespread, occurring in the whole Amazonian Basin (Brazil, Peru, Ecuador and Colombia) and in Central America (as far north as Guatemala). The other species, known from scant material, occur in Panama (*N. derasum, N. subtile* and *N. politum,* the latter also in Ecuador), Peru (*N. thompsoni*) and Venezuela, St. Vincent and Guadeloupe (*N. punctatostriatum*). Their zoogeography and phylogeny are discussed elsewhere.



31. Geographic distribution of the *testudinum* group and *leechi.*

Nosodendron latifrons Sharp, 1902
(Fig. 31)

Nosodendron latifrons Sharp, 1902: 673 (Holotype, Panama, *Chiriqui:* Bugaba; BMNH*); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog).

Head finely and sparsely punctate; part of eyes clearly visible from above and sides; mentum glabrous and sparsely but more coarsely punctate than head. *Pronotum* and *scutellum* more finely punctate than head. *Elytra* with two kinds of punctures: large and coarse punctures forming 8-10 more or less incomplete and irregular striae (the first striae are erased around scutellum, and most are erased at apex), and very fine, irregular punctures which only in certain

areas form a very irregular, hexagonal-quadrangular pattern. Prosternal process and mesosternum very finely microrugose; metasternum sparsely punctate. Longitudinal striation of base of abdominal sternites not very clear. *Measurements* (in mm; of holotype in parenthesis): total length, (4.0) 4.4; pronotal length, (0.7) 0.8; elytral length, (3.0) 3.2; pronotal width (base), (2.0) 2.2; pronotal width (anteriorly), (1.2) 1.3; elytral width (maximum), (2.8) 2.8.

Material examined. PANAMA. *Chiriqui:* Bugaba, 800-1,500 ft., Champion (BMNH, holotype). COLOMBIA. *Cundinamarca:* Puerto Salgar (3 exs., FMNH, MZSP).

Discussion. Sharp's original description of this species says "thorax impunctate", an incorrect statement. Both the holotype and the Colombian specimens examined have the pronotum clearly punctate, even though more finely than the head.

Nosodendron latifrons is the only species of the *testudinum* group with simple mentum, but it is easily distinguished from the species of the *angelum* group with simple mentum (*angelum* and *bucki*) by the characters used in the key.

Nosodendron subtile Sharp, 1902
(Figs. 27, 31-35)

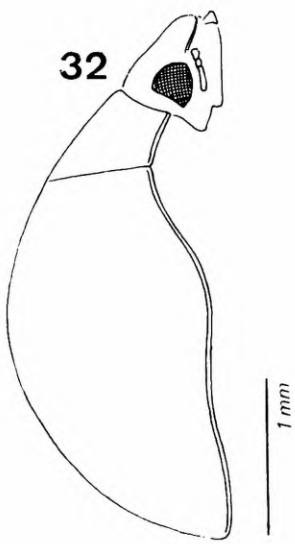
Nosodendron subtile Sharp, 1902: 671 (Holotype, Panama, *Chiriqui:* Volcán de Chiriqui; BMNH*); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog).

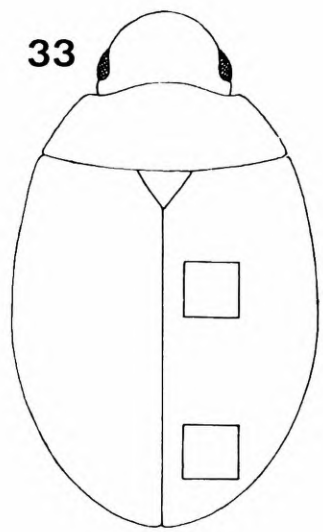
Head finely microrugose and very finely, closely punctate. Eyes completely hidden under pronotum (when head in normal position). Mentum very coarsely punctate, with a curved, transverse impression near front and parallel to front margin (Fig. 27); with sparse but well developed pubescence, especially near front margin. *Pronotum* as microrugose as head, but only very indistinctly punctate. *Scutellum* sculptured as pronotum. *Elytra* punctate, punctures of three different sizes: very fine ones, irregularly placed on whole surface; intermediate-sized, but still fine punctures, forming longitudinal as well as transverse striae, forming a pattern of more or less irregular shaped quadrangules; in the middle of each quadrangle a large and coarser puncture (Fig. 34). In the apical third or fourth of elytra, and in the first two interstices near scutellum, the quadrangular pattern is lost, because only the fine punctures exist (Fig. 35), near the apex they seem to be more densely punctate than elsewhere. Prosternal process and mesosternum microrugose and punctate; metasternum microrugose and only punctate on sides. Longitudinal striation of base of abdominal sternites not very clear. *Measurements* (in mm): total length, 3.0; pronotal length, 0.45; elytral length, 2.2; pronotal width (base), 1.5; pronotal width (anteriorly), 0.9; elytral width (maximum), 2.0.

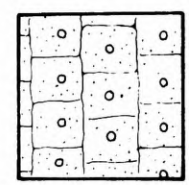
Distribution. The only known specimen of *Nosodendron subtile* is the type, from Volcán de Chiriqui, Panama.

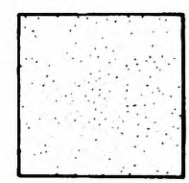
Discussion. *Nosodendron subtile* is most closely related to *N. derasum,* but easily distinguished by the different pattern of elytral punctures: in *subtile* the hexagonal-quadrangular meshwork disappears posteriorly, where the sculpture is reduced to fine and uniform punctures (Fig. 35), while in *derasum* the hexagonal-quadrangular meshwork is clearly developed from front to posterior parts of elytra. In elytral sculpture *N. subtile* is similar to *N. mexicanum,* but the latter has a different mentum.

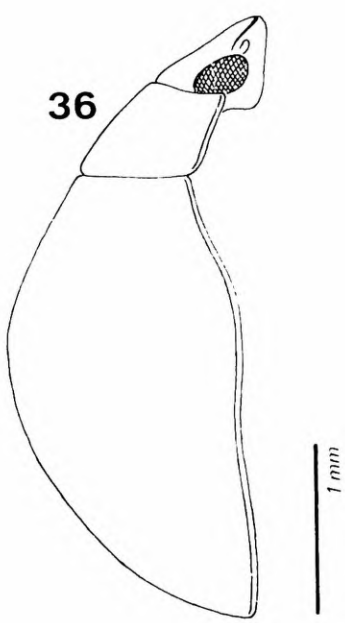
Nosodendron subtile and *N. derasum* have both only been collected at Volcán de Chiriqui: *subtile* at 2,500-4,000 ft. and *derasum* at 3,000-4,000 ft.

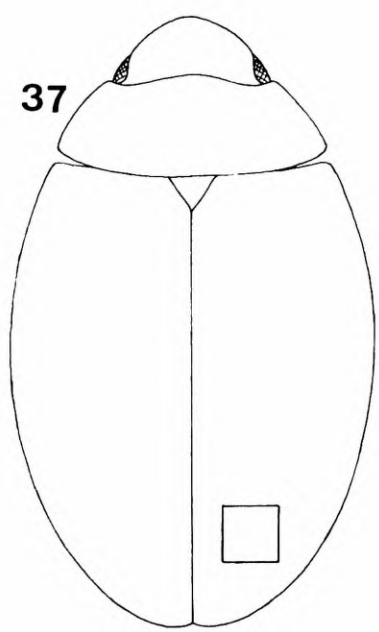


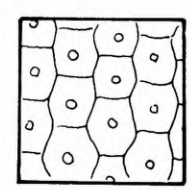












32-35, *subtile,* holotype. 36-38, *derasum,* holotype.

Nosodendron derasum Sharp, 1902
(Figs. 27, 31, 36-38)

Nosodendron derasum Sharp, 1902: 672 (Holotype, Panama, *Chiriqui:* Volcán de Chiriqui; BMNH*); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog).

Head finely microrugose, and less finely punctate than in *subtile.* Eyes as in *subtile.* Mentum as in *subtile,* with the typical curved, transverse impression along front margin (Fig. 27). *Pronotum* microrugose as head, very indistinctly punctate. *Scutellum* sculptured as pronotum. *Elytra* punctate, with punctures forming a pattern of more or less irregular quadrangles, which towards apex tend to be more hexagonal; inside each quadrangle (or hexagon) a larger and coarser puncture (Fig. 38); otherwise quadrangles about impunctate; quadrangular-hexagonal pattern present on whole surface, but slightly erased near scutellum and along first third of suture. Ventral surface as in *subtile. Measurements* (in mm): total length, 3.1; pronotal length, 0.5; elytral length, 2.35; pronotal width (base), 1.5; pronotal width (anteriorly), 1.0; elytral width (maximum), 1.95.

Distribution. Only the holotype of *Nosodendron derasum,* collected at 3-4,000 ft. by Champion, at Volcán de Chiriqui, Panama, is known at present. At this locality it is sympatric with the closely related *N. subtile,* as well as with *N. politum* and *N. testudinum.*

Discussion. As seen above, *N. subtile* is the species most closely related to *N. derasum,* but the two are easily distinguished by the different elytral sculpture.

Nosodendron thompsoni, sp. n.
(Figs. 6, 28, 31)

Types. Holotype ♂ and 9 paratypes from PERU. *Huanuco:* Tingo Maria, Monson Valley, 20.XI.1954 (E. I. Schlinger & E. S. Ross) (Holotype and 5 paratypes, CASC; 3 paratypes, MZSP; 1 paratype, BMNH).

Head microrugose, finely and sparsely punctate. Eyes completely hidden under pronotum. Mentum pubescent, with deep, horseshoe-shaped impression along front margin. *Pronotum* microrugose; impunctate on disc; on sides punctate as head. *Scutellum* microrugose. *Elytra* punctate, punctures fine and forming the typical quadrangular-hexagonal pattern; quadrangles (or hexagons) with very sparse and fine punctures, plus a large, central puncture. Near scutellum and along suture the quadrangle pattern is slightly less evident, but present. Prosternal process and mesosternum finely microrugose; metasternum punctate on sides, impunctate on disc. Longitudinal striation of base of abdominal sternites not clearly marked. *Genitalia:* of male (Fig. 6). *Measurements* (in mm): total length, 3-3.1; pronotal length, 0.4; elytral length, 2.3-2.4; pronotal width (base), 1.5; pronotal width (anteriorly), 0.8; elytral width (maximum), 2.0.

Discussion. Nosodendron thompsoni is well characterized by the impression of mentum (Fig. 28), which is more or less horseshoe-shaped. This type of mentum, as seen above, is similar to that of *N. derasum* and *N. subtile,* but quite distinct.

In general shape *N. thompsoni* is similar to *N. testudinum,* but the shape of the impression of mentum easily distinguishes the two species.

I take pleasure in naming this species in honor of R. T. Thompson, in acknowledgment of his help throughout this study.

Nosodendron politum Sharp, 1902
(Figs. 29, 31, 39-41)

Nosodendron politum Sharp, 1902: 672 (Lectotype and 2 paralectotypes, Panama, *Chiriqui:* Volcán de Chiriqui; BMNH*); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog).

Head finely microrugose and sparsely but clearly punctate. Eyes hidden under pronotum. Mentum coarsely punctate and pubescent along lateral margin; longitudinally trisulcate, with two lateral sulci curved, converging anteriorly to meet median sulcus (Fig. 29). *Pronotum* microrugose as head, impunctate on disc, and as coarsely punctate as head near lateral margins. *Scutellum* microrugose. *Elytra* very shiny, very finely and quite densely punctate; quadrangular-hexagonal pattern formed by equally fine punctures; a large puncture inside each quadrangle (or hexagon) (Fig 41). Meshwork developed on whole surface, except near scutellum and along first half or suture. Pro-, meso- and metasternum (sides) heavily punctate, as also external face of trochanters and femora; first abdominal sternite punctate; logitudinal striation of base of abdominal sternites short, but visible. *Measurements* (in mm): total length, 3.4-3.5; pronotal length, 0.6; elytral length, 2.5-2.6; pronotal width (base), 1.8-1.9; pronotal width (anteriorly), 1.2; elytral width (maximum), 2.6-2.8.

Material examined. PANAMA. *Chiriqui:* Volcán de Chiriqui (lectotype and 2 paralectotypes, BMNH). ECUADOR. *Esmeraldas:* Cachabé (1 ex., MZSP). PERU. *Huanuco:* Tingo Maria, Monson Valley (1 ex., CASC).

Distribution (Fig. 31). Besides the type-locality, where *N. politum* is sympatric with several other species, as dicussed elsewhere, I have seen two specimens from Ecuador and Peru, suggesting that the species occurs in northwestern South America, entering Central America as far north as Panama.

Notes on the types. The type-specimens are all from the same locality, Volcán de Chiriqui, having been collected by Champion between 3,000 and 4,000 ft. Sharp (1902: 672) mentioned "seven specimens" in the original description. I have seen all specimens kept in the British Museum, the three here mentioned. Of these one is selected lectotype, while the others become paralectotypes. The remaining specimens, if located, are to be considered paralectotypes.

Discussion. Besides the very typical impression of the mentum (Fig. 29), *Nosodendron politum* is easily characterized by the very shiny dorsal surface, especially on elytra, near scutellum, by the pattern of elytral punctures, and the very evident convexity of the elytra.

Nosodendron mexicanum Sharp, 1902
(Figs. 25, 31)

Nosodendron mexicanum Sharp, 1902: 670-671 (Lectotype and 2 paralectotypes, Mexico, *Veracruz:* Jalapa; BMNH*); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog).

Head and *pronotum* microrugose, both with sparse and fine punctures, except on disc of pronotum, which is more finely and more indistinctly punctate. Eyes hidden under pronotum. Mentum coarsely and deeply punctate, and with two longitudinal impresions, which are parallel and fused anteriorly by a small transverse impression which is expanded slightly beyond the longitudinal impressions (Fig. 25); pubescence not apparent on mentum. *Scutellum* sculptured as disc of pronotum. *Elytra* with longitudinal striae of widely spaced, large punctures, which are surrounded by a fine, irregular punctuation, and only in certain places gives indications of quadrangular pattern; the large punctures are less well impressed near scutellum, and in apical third they become weaker towards apex, and in that area the punctuation is much denser and irregular (similar to that of *subtile,* fig. 35). Ventrally microrugose and punctate, except on disc of metasternum. Abdomen with sternites punctate, without longitudinal striae at base. *Measurements* (in mm, of lectotype): total length, 3.9; pronotal length, 0.6; elytral length, 2.8; pronotal width (base), 1.8; pronotal width (anteriorly), 1.0; elytral width (maximum), 2.4.

Notes on the types. In the original description three is no mention of the number of specimens. I received three syntypes from the British Museum, a single specimen on one pin (here designated lectotype) and two on another pin (paralectotypes).

Distribution. Only known from the type-locality, Jalapa, in the Mexican state of Veracruz.

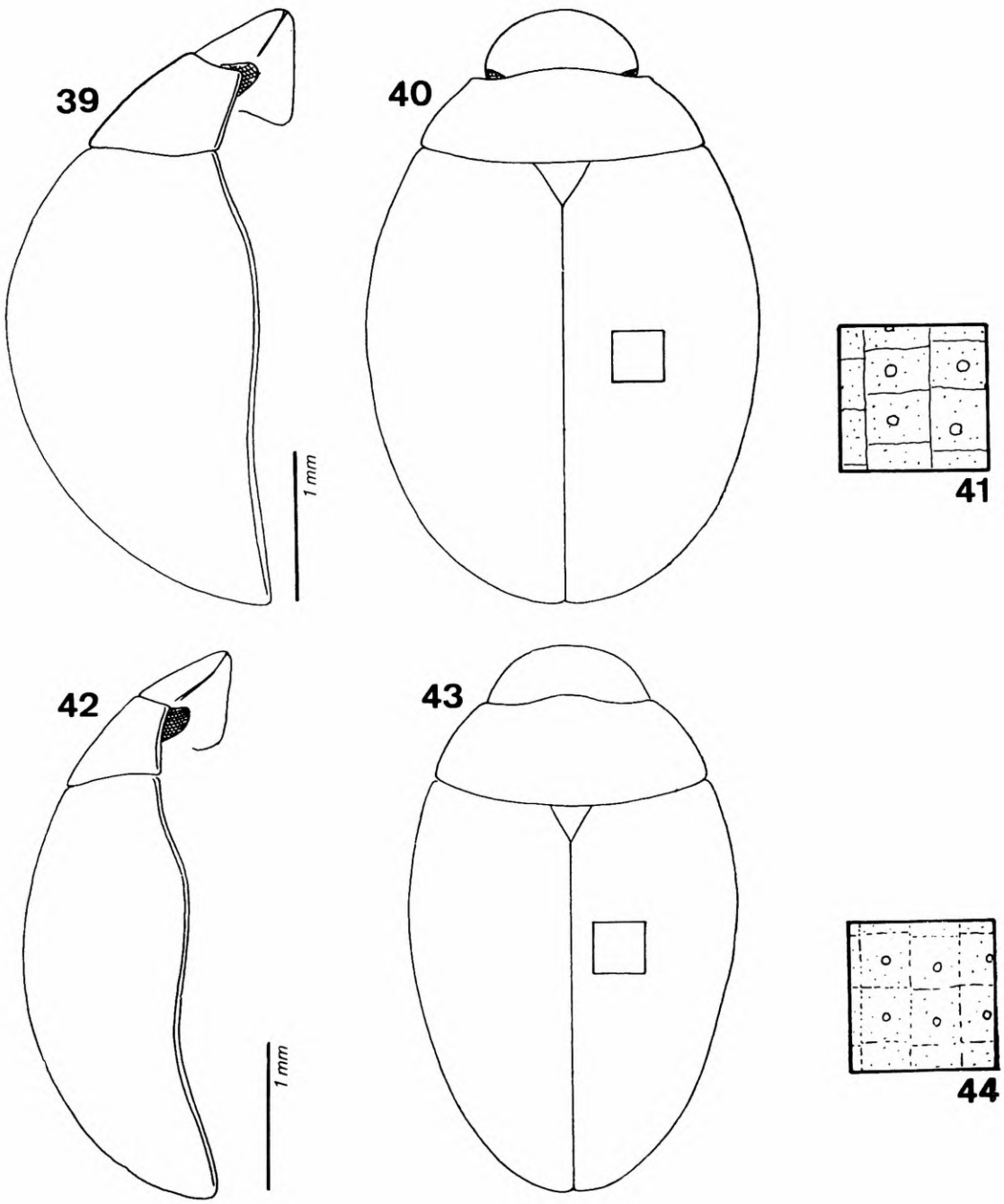
Discussion. Nosodendron mexicanum, the northernmost of the Neotropical species of the genus, is most closely related to *N. subtile* (in both the quadrangular-hexagonal meshwork is substituted posteriorly by a fine and dense, regular punctation), but is easily distinguished by the different impression of mentum.

The specimens were collected by Flohr in "muddy places".

Nosodendron dybasi, sp. n.
(Figs. 24, 30, 42-44)

Types. Holotype from BRAZIL. *Santa Catarina:* Nova Teutônia, X.1940 (F. Plaumann) (CNHM). Paratype, same state, Chapecó, XII.1957 (F. Paumann) (MCZC).

Head microrugose and finely, densely punctate. Eyes completely hidden under pronotum. Mentum punctate, pubescent, with two longitudinal grooves (Fig. 24). *Pronotum* finely microrugose, impuctate on disc, with punctures as those of head on sides. *Scutellum* microrugose. *Elytra* with 11 striae of large punctures each, and finely punctate in interstices; these punctures, in some areas, suggest a loose



39-41, *politum*, lectotype. 42-44, *dybasi*, holotype.

quadrangular meshwork. Pro- and mesoternum finely microrugose, and with fine and sparse punctures; metasternum punctate on sides; longitudinal striation of base of abdominal sternites not well developed. *Measurements* (in mm; of holotype): total length, 3.3; pronotal length, 0.6; elytral length, 2.3; pronotal width (base), 1.8; pronotal width (anteriorly), 1.2; elytral width (maximum), 2.3.

Discussion. Nosodendron dybasi is most closely related to *N. testudinum,* with which it shares the same type of mentum and size. The different elytral sculpture (in *N. testudinum* the quadrangular-hexagonal pattern is very clearly developed), however, easily distinguish the two species. The distribution of *N. dybasi* (state of Santa Catarina, in southern Brazil; Fig. 30), is completely separated from the Amazonian distribution of *N. testudinum.*

The new species is named in honor of my friend Henry Dybas.

Nosodendron testudinum Waterhouse, 1876
(Figs. 7, 11, 24, 31)

Nosodendron testudinum Waterhouse, 1876: 14-15 (Holotype, Brazil, "Pará"; BMNH*); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog); Reichardt, 1973: 198, figs. 14-16 (Redescription; record from Amazonas, Tapuruquara); Jorge, 1973: 75 (in key).

Nosodendron championi Sharp, 1902: 671, pl. 19, figs. 26, 26a (Lectotype and 6 paralectotypes, Guatemala, *Alta Verapaz:* Chiacam; BMNH*); Dalla Torre, 1911: 3 (Catalog); Blackwelder, 1944: 270 (Catalog); Reichardt, 1973: 198 (Notes). *Syn. n.*.

Nosodendron chiriquense Sharp, 1902: 672 (Lectotype and 3 paralectotypes, Panama, *Chiriqui:* Volcán de Chiriqui; BMNH*); Dalla Torre, 1911: 3 (Catalog); Blackwelder, 1944: 270 (Catalog); Reichardt, 1973: 198 (Notes). *Syn. n.*

Head, pronotum and *scutellum* microrugose and very finely punctate. Eyes normally hidden under pronotum. Mentum with a deep U-shaped impression (Fig. 24), its base turned towards the mouth opening, and the arms very close to each other, parallel; front margin pubescent. *Elytra* with very clearly impresesd quadrangular-hexagonal pattern of fine punctures; each quadrangle (or hexagon) with a few sparse and fine punctures, and a large, central one (see fig. 16 in Reichardt, 1973). This elytral pattern is less clearly visible in the first row, near scutellum, in basal third. Thorax punctate ventrally, except on disc of metasternum. Abdominal sternites also punctate along base; longitudinal striae not clearly impressed. *Genitalia:* of male (Fig. 7); of female (Fig. 11). *Measurements* (of holotype of *testudinum;* in mm): total length, 3.3; elytral length, 2.5; elytral width (maximum). 2.1.

Notes on the types. Nosodendron championi: even though Sharp mentions 14 specimens in the original description, only seven have been received from the British Museum; of these one is designated lectotype, and the others become paralectotypes

Nosodendron chiriquense: Sharp mentions 17 specimens from Chiriqui and Bugaba, without specifying the number of specimens from each locality. The British Museum collection houses four from Chiriqui and four from Bugaba. I select the lectotype from the Chiriqui series; the remaining specimens are paralectotypes.

Notes on the synonymy. Judging from the series of specimens examined (including the types of the three described forms), I am inclined to consider the whole complex as a single, variable species. In the original description of *chiriquense* Sharp mentioned the impuctate pronotum as the main character of the species. Sometimes the punctures of certain areas are difficult to see, and when they are very fine, they may even be confused with the microrugosity. I have checked the type-series of *chiriquense* (see above), and reached the conclusion that the pronotum is punctate. This character is also variable in the specimens I have seen. *N. chiriquense* is also characterized by its author as having the "two inner series of punctures on the elytra ... obliterated at the base...". This character is also variable in the specimens seen, and I think it is impossible to distinguish the species, and propose to consider them synonyms.

Material examined. Besides the type-specimens of the three species, I have seen several specimens from the following localities:

COSTA RICA. *Limón:* Reventazón, Hamburgfarm (2 exs., one with the following note by Nevermann: "Nest Trigona amalthea"; USNM); Zent (1 ex., "from banana stumps"; USNM). Not located, Golfito (2 exs., CASC). PANAMA. *Canal Zone:* Barro Colorado Island (1 ex., USNM); Cabima (1 ex., USNM). COLOMBIA. *Amazonas:* Leticia (6 exs., CNCI, MZSP). ECUADOR. *Pichincha:* 6 mi W of Santo Domingo de los Colorados (4 exs., CASC, MZSP). *Esmeraldas:* Cachabé (2 exs., BMNH, MZSP). PERU. *Loreto:* 20 mi W of Pucallpa (4 exs., CASC, MZSP). BRAZIL. *Amazonas:* Rio Negro, Tapuruquara (2 exs., MZSP). *Pará:* no locality (possibly Belém) (Holotype of *testudinum* and 1 ex., BMNH).

Distribution (Fig. 31). *Nosodendron testudinum,* a species described from eastern Amazonia ("Para" — in the past century the capital of the state of Pará was frequently only known as "Para"); it is now recorded from the whole Amazonian Basin, and also extends into Central America, as far north as Guatemala.

Discussion. Nosodendron testudinum is the Neotropical species with the widest distribution. and of which I studied the largest series. *N. testudinum* has the same type of mentum impression as *N. mexicanum* (being distinguished by the different elytral sculpture) and *N. dybasi* (see description of the latter for distinguishing characters).

Nosodendron punctatostriatum Chevrolat, 1864
(Figs. 26, 31)

Nosodendron punctatostriatum Chevrolat, 1864: 618 (Holotype, "Guadeloupe"; MNHN*); Gemminger & Harold, 1868: 922 (Catalog); Dalla Torre, 1911: 4 (Catalog); Blackwelder, 1944: 270 (Catalog).

Nosodendron cribratum (*nec Cercyon cribratum* Castelnau, 1840: 62); Fleutiaux & Sallé, 1889: 392-393; Sharp, 1902: 671; Dalla Torre, 1911: 3 (Catalog); Blackwelder, 1944: 270 (Catalog). *Syn. n.*.

Head and *pronotum* microrugose. Head finely but clearly punctate on whole surface. Mentum pubescent, with a short, anterior U-shaped impression, with the two arms turned backwards, and posteriorly two short, longitudinal impressions (Fig. 26). *Pronotum* only punctate on sides, and less clearly than head; disc only microrugose. *Scutellum* microrugose. *Elytra* with 11 longitudinal striae of large punctures, which in apical third become very shallow and confused; remaining areas finely punctate; a quadrangular pattern barely visible in some specimens. Prosternal process punctate, mesosternum and metasternum microrugose, the latter also punctate on sides. Abdominal sternites punctate; longitudinal striation of base of abdominal sternites not very clearly marked. *Measurements* (in mm): total length, 3.4-3.9; pronotal length, 0.55-0.7; elytral length, 2.6-2.9; pronotal width (base), 1.7-1.9; pronotal width (anteriorly), 1.05-1.2; elytral width (maximum), 2.3-2.5.

Notes on the types. Nosodendron punctatostriatum: the holotype, somewhat poorly preserved, is not labeled as type, but I have no doubts that it is Chevrolat's original specimen. It bears a printed label "Museum Paris Chevrolat 1856", to which Guadeloupe is added in handwriting. A second label, in Chevrolat's handwriting reads "Nosodendron punctato-striatum Chev. Guadeloupe". A third label (printed) reads "Muséum Paris E. Fleutiaux". I have added a holotype label to this specimen.

Nosodendron cribratum. One specimen in the British Museum, glued on a card, has the following information written on the card on which the specimen is fixed: "N. cribratum Type mihi D. S. Guadeloupe"; a green, printed label reads "Guadeloupe", and a white, also printed label reads "Sharp Coll. 1905-313". I consider this specimen as the holotype of Sharp's species.

Notes on the nomenclature. The nomenclature of this first Neotropical species of the family was relatively confused, especially because Fleutiaux & Sallé (1889) considered Chevrolat's species identical to Castelnau's *Cercyon cribratum.* Sharp (1902) also contributed to this confusion by describing a Guadeloupean specimen of *Nosodendron* in a footnote, and considering it as identical to the one studied by Fleutiaux & Sallé (who actually based their conclusions on Chevrolat's specimen), but distinct from Castelnau's species. Ignoring Chevrolat's species, Sharp named the species *cribratum* (and designated a type — see above). There is no doubt that a single species is involved here, and that Chevrolat's name has priority over the other name.

Due to this confusion the Guadeloupean species has been carried along in catalogs under two distinct and valid names, *punctatostriatum* Chevrolat and *cribratum* Fleutiaux & Sallé.

Material examined. VENEZUELA. *Aragua*: Rancho Grande, 1.100 m (1 ex., CNCI). ST. VINCENT (8 exs., BMNH, MZSP). GUADELOUPE. (Holotype of Sharp's *cribratum,* BMNM; holotype of *punctatostriatum* MNHN, and 12 exs., MNHN).

Discussion. *Nosodendron punctatostriatum* is a unique species in the type of mentum structure (Fig. 26), and cannot be confused with any other species of the group. Its elytral sculpture is also unique, and typical, being simply striate-punctate in the anterior two-thirds, its surface finely punctate. A quadrangular pattern of punctures is only visible in certain areas and in some specimens.

Nosodendron punctatostriatum is the only species known from the Lesser Antilles, and is now also recorded from the Venezuelan mainland.

Biology of the New World species

As it is the case with some Old World species, the habitat of the two North American *Nosodendron* is slime fluxes (infected sap exudations from tree wounds). Larvae and adults live in the same habitat, but pupae are unknown (Hayes & Chu, 1946: 69), suggesting pupation in other places, probably in "the decomposed litter and clayish surface soil at the base of the host tree..." (Osborne & Kulhavy, 1975: 73).

Both North American species have been recorded from sap exudations from tree wounds, as follows:

Nosodendron californicum. *Abies concolor* (white fir), Yosemite Region, California (Sokoloff, 1959) and Ashland, Oregon (Hayes & Chu, 1946: 69); *Abies grandis* (grand fir), California (Sokoloff, 1959) and northern Idaho (Osborne & Kuhavy, 1975); *Quercus kelloggii* (California black oak), California (Sokoloff, 1959).

Nosodendron unicolor. *Ulmus americana* (elm), Chicago, Illinois; *Acer saccharum* (sugar maple), La Porte Co., Indiana; *Quercus alba* (white oak), Maryland (Sokoloff, 1959); Hayes & Chu (*l.c.*) cited the same species as follows: "larvae ... were collected in fungi on a dying elm tree" in Urbana, Illinois; "in old *Cossus* boring in Silver Leafed Poplar" (*Populus* sp.) in Chicago, Illinois; and in "sap oozing from wilow [*Salix* sp.] in Victoria Jx"; and in "sap of elm" in Detroit, Michigan.

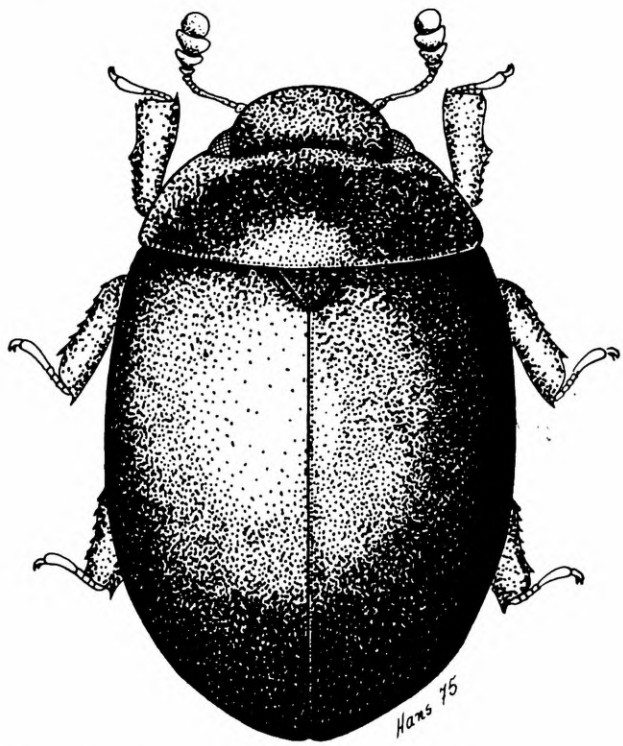
Hayes & Chu (*l.c.*) described the larvae of the two species for the first time, and compared them to that of the European *Nosodendron fasciculare*.

Practically nothing has been recorded on the habitat and habits of the Neotropical species. Sharp (1902: 670) says that *Nosodendron mexicanum* "... was found by Flohr in muddy places". Most specimens of *Nosodendron angelum* were colected at light. A few other specimens studied in this paper bear the following data: *Nosodendron angelum* from San Bernardino, Paraguay, "in gallery of *Nectandra* sp." (Lauraceae); *Nosodendron testudinum*, two specimens collected in Costa Rica, Hamburgfarm, by Nevermann, are from "banana stumps" and "Nest Trigona amalthea".

Zoogeography of Nosodendridae

The present-day distribution of the species of Nosodendridae could tentatively be explained as follows:

The group is of Gondwanian origin. A very early ancestral stock could have remained in Australia, and from there reached New Zealand, New Guinea and the Pacific Islands. This first lineage of Nosodrendridae probably represents the more primitive group, and it is interesting that one of these forms, from the North Island of New Zealand (see discussion of *Nosodendron ovatum* above, and Crowson, 1959), could represent a different lineage, perhaps a distinct genus (actually, there are other forms in the same situation, but they have not been critically examined in recent years).



45. *Nosodendron angelum* Reichardt, 1973.

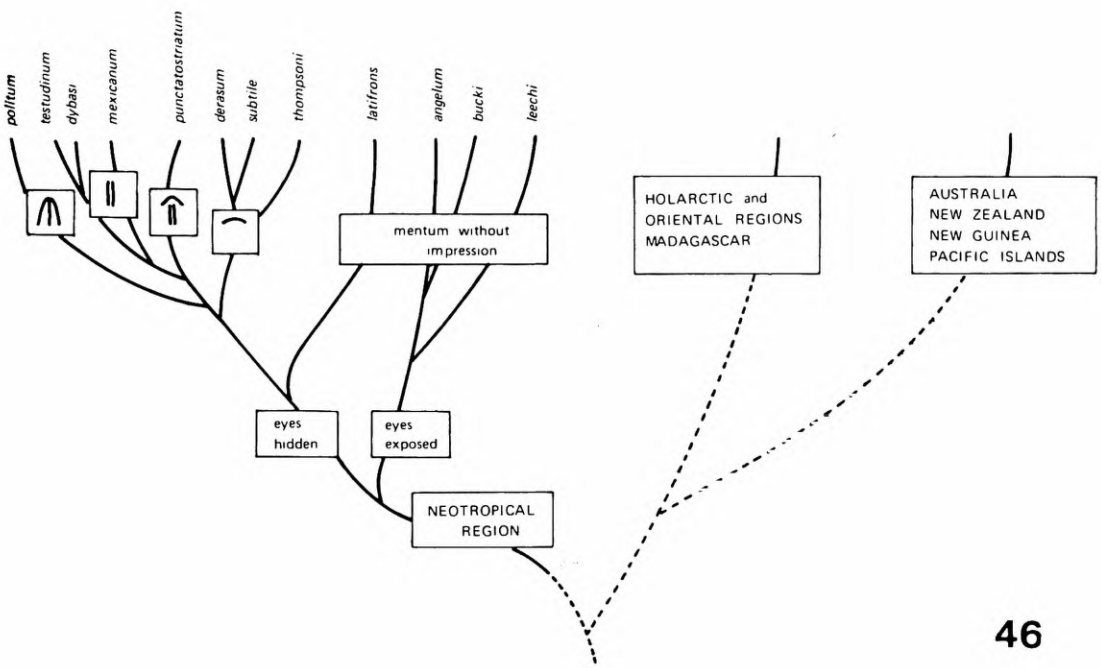
A second ancestral stock could have spread from Africa towards the Oriental and Palaearctic Regions. From the Oriental Region this stock would have reached the islands between Indochina and New Guinea, reaching only slightly beyond Wallace's line. However, the possibility of a secondary invasion of Australia *via* the Oriental Region should not be completely discarded. Some of these species are widespread in Southeast Asia and adjacent islands. The Palaearctic stock would have spread over Europe and Asia (including Japan), and could also have colonized North America, where the group is still represented by two species (one of which possibly the same as the only species thus far recorded from Europe). As a final step in this second radiation, extinction in Africa, where the family has not yet been recorded, would have to be postulated, with survival of a single species in Madagascar.

During separation of South America and Africa a third and last stock of ancestral Nosodendridae, represented by completely glabrous species, would have spread and evolved independently in the Neotropical Region.

Phylogeny of the Neotropical species

In the Neotropical Region the *angelum* group represents the more primitive forms, which still resemble Old World forms in size, type of head and development of eyes. This group did not expand northwards into Central America, being at present restricted to South America (Figs. 30, 31).

The other and larger Neotropical group, the *testudinum* group, is concentrated in the Northern part of South America (Fig. 31), with a single species in southern Brazil (Fig. 30). This group managed to invade Central America, probably after the Tertiary connection was established, reaching as far north as Veracruz in Mexico (in a typically Neotropical locality, according to Halffter, 1965). One of the northern South American species, *punctatostriatum,* penetrated into the Lesser Antilles, but did not reach very far north (Guadeloupe).



46. Phylogeny of Nosodendridae.

Nosodendron testudinum is widespread and common, and most other species have quite restricted, more or less perypheral distributions (Fig. 31), probably the result of expansions and retractions of the area of distribution of the ancestral form(s), following cycles of humid and dry periods, with the consequent isolation in selected refugia around the Amazonian Basin and Central America (Haffer, 1969; Vanzolini & Williams, 1970).

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INDEX TO NEW WORLD TAXA

(Synonyms in italics)