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FUNCTIONAL MORPHOLOGY AND EVOLUTION OF A CARPENTER'S PLANE-LIKE TOOL IN THE MANDIBLES OF TERMITE WORKERS (INSECTA ISOPTERA)

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Abstract. The left mandible of termite workers possesses just in front of the molar plate a characteristic « premolar tooth » that, in most species, is partly or wholly hidden under the mandible. The position, structure and size of this tooth were observed and compared from a functional point of view in 46 wood-feeder species belonging to all termite families and in 33 soil-feeder species belonging to 4 different clades of Termitidae.

In all wood- and other plant matter-feeder species observed the premolar tooth resembles the chisel of a carpenter's plane-like device. It is suited to cut superficial fragments out of the wood before ingestion.

In all soil-feeder species observed the premolar tooth has lost one or several functional features that characterise wood feeders. It assists the other teeth in the gathering of soil particles towards the mouth before ingestion.

In the left mandible of termite workers, the premolar tooth thus shows clear morphological adaptations to the species' diet.

Key words : functional morphology, adaptation, mandibles, termites, diet, food processing.

INTRODUCTION

This work comes into the general scope of functional and comparative morphology of insects.

In chewing insects, mandibles are the most voluminous mouthparts, the hardest ones and those that are moved by the most powerful muscles. They play a key role in the taking and in the first mechanical processing of the food. From one group of insects to another, the morphology of mandibles may vary, particularly as regards their inner margins, which come into direct contact with food. Besides the marked differences between the mandibles of carnivorous and plant-feeder insects, very precise morphological adaptations to different plant matter-diets have been shown in some groups, notably grasshoppers (CHAPMAN, 1964). Such observations inspired the present work.

In termites, the soldier and worker mandibles play crucial roles in defence and feeding. Their morphology may vary from one genus or even from one species to another and is therefore commonly used for the systematic description of termite species. Furthermore, since the beginning of the century, they have proved to be of great interest in the study of phylogenetic relations between termite taxa, as illustrated by the works of HOLMGREN (1911 ; 1912), HARE (1937), AHMAD (1950) and KRISHNA (1970).

Several functional morphological adaptations to diet have been observed in the mandibles of termite workers, notably in the molar plate (or *mola*), i.e. the proximal masticatory part of their inner margin. This *mola* has flattened ridges for grinding in the workers of xylophagous species but becomes smooth and hollow like a spoon in soil-feeder species, as shown by SANDS (1965) for Nasutitermitinae and by DELIGNE (1966) for other families and subfamilies.

Despite the interest in mandibles for systematic and phylogenetic purposes, and their functional importance, only the external outlines of their upper sides have generally been described and represented in taxonomic papers, with a few notable exceptions (*e.g.* SANDS 1972 ; 1992 ; 1998).

The external outline of the mesal margin always shows an « apical tooth », a few « marginal teeth » and the « molar plate » (Fig. 2). During the course of an earlier work (DELIGNE 1970) my attention was drawn to a tooth situated in front of the molar plate and partly or wholly hidden under the left mandible. Due to its position we called it a « premolar tooth » (DELIGNE & PASTEELS 1969) while KRISHNA (1968), SANDS (1972 ; 1992) and MATHEWS (1977) gave it other names as discussed below.

As the premolar tooth of termite workers has not been studied so far from a functional point of view, I compared the position, structure and size of this tooth in wood-feeder and soil-feeder species, in order to detect possible adaptations to diet.

MATERIAL AND METHODS

The study is based on alcohol preserved termites belonging to 79 species and 62 genera, representing all 6 families and most of the subfamilies of termites. The list of examined species is given below.

For each species, from 2 to 5 workers were observed. The mandibles were first handled *in situ* under a stereomicroscope to enable analysis of their relative movements. The adductor apodemes were first cut with micro-scissors. The mandibles were then dissected and observed along different orientations with a stereomicroscope ; to facilitate this multidirectional observation, they were secured on a bed of thin sand covered with alcohol. Some were mounted whole on slides in Canada balsam *with the ventral side upwards* for observation with a light microscope. To observe the mesal cutting edge at right angels to the optic axis, the slide was slightly tilted, as much as necessary, under a stereomicroscope. For most species, mandibles were also prepared for the scanning electron microscope *with their denticulate inner margin upwards*. The mandibles were not cleaned before observation because the distribution of food parcels in different parts might be indicative of the role of these parts.

As a complement to morphological descriptions, the maximal length of the premolar tooth was measured in surface view using an ocular micrometer, and expressed as percentage of the total mandible length (TML, measured from the point of the apical tooth to the most proximal point of the molar plate). Although the proportions of mandible parts generally show very little variability among the workers of a given species, I consider that too few specimens have been measured to calculate a mean value. The values given are therefore rough estimations (*e.g.* >20%, >30% etc). More complete data will be published in a later paper.

The diet is established by examining the workers' intestinal contents with the help of a polarizing microscope, which improves the observation of mineral elements and plant fibres (DELIGNE, 1966). These data were checked and supplemented with other published data (notably NOIROT & NOIROT-THIMOTHÉE, 1969, GRASSÉ, 1986 and SANDS, 1998). The main diet of the major taxa is summarised in the list of examined species. As generally recognised, a wood- and other plant tissue-diet characterises all termite families, except a part of Termitidae among which a soil-diet appeared at least 4 times in the course of evolution.

List of examined species

– [W] means « mainly wood and other plant tissue feeders »
– [S] means « mainly soil feeders »
– The reference of the sample is put in quotation marks
– All cited collecting sites in Gabon are located within a radius of 80 km around Makokou

Mastotermitidae [W]

– *Mastotermes darwiniensis* Frogatt 1896, « TD 31 », North Queensland, Australia

Kalotermitidae [W]

– *Kalotermes flavicollis* (Fabricius 1793), « TD 32 », Banyuls, France
– *Neotermes desneuxi* (Sjöstedt 1904), « Mad 4 », Mandraka forest, Madagascar
– *Cryptotermes havilandi* (Sjöstedt 1900), « TN 541 », Ivory Coast
– *Glyptotermes parvulus* (Sjöstedt 1907), « TD 33 », Banco forest, Ivory Coast
– *Postelectrotermes amplus* (Sjöstedt 1925), « TD 34 », Mandraka forest, Madagascar

Termopsidae [W]

Termopsinae

– *Zootermopsis angusticollis* (Hagen 1858), « TD 35 », Philipsville, California, USA

Stolotermitinae

– *Stolotermes africanus* Emerson 1942, « N 23 », South Africa

Porotermitinae

– *Porotermes planiceps* (Sjöstedt 1904), « N 14 », South Africa

Hodotermitidae [W] (1)

– *Microhodotermes viator* (Latreille 1804), « SAf 5 », South Africa
– *Anacanthotermes ochraceus* (Burmeister 1839), « T 500A », Beni Abbès (Algeria)

(1) Termopsidae and Hodotermitidae are considered as separate families according to GRASSÉ (1986).

Rhinotermitidae [W]

Psammotermitinae

– *Psammotermes allocerus* Silvestri 1908, « SAf 50 », South Africa
– *P. hybostoma* Desneux 1902, « T 205 », Tamanrasset, Algeria

Heterotermitinae

– *Heterotermes sp.* Frogatt 1896, « TC 49 », Santa Cruz Island, Galapagos
– *Reticulitermes lucifugus* (Rossi 1792), « TD 38 », Banyuls, France

Coptotermitinae

– *Coptotermes silvaticus* Harris 1968, « 1145 », Belinga, Gabon

Rhinotermitinae

– *Schedorhinotermes putorius,* (Sjöstedt 1896) « TD 17 », Mayela, Gabon
– *S. lamanianus* (Sjöstedt 1926), « T 617 », Bossembele, Centr. Afr. Rep.

Termitidae [W] or [S]

Macrotermitinae [W]

– *Pseudacanthotermes militaris* (Hagen 1858), « 1056 », Makokou, Gabon
– *P. spiniger* Sjöstedt 1900, « TC 7 », Kisangani, D. R. Congo
– *Acanthotermes acanthothorax* (Sjöstedt 1898), « 1929 », Ekowong, Gabon
– *Protermes prorepens* (Sjöstedt 1907), « 1099 », Madjime, Gabon
– *Sphaerotermes sphaerothorax* (Sjöstedt 1911), 1134-3, Madjime, Gabon
– *Macrotermes nobilis* (Sjöstedt 1911), « 1160 B », Belinga, Gabon
– *Macrotermes natalensis* (Haviland 1898), « TC 55 », Kinshasa, D. R. Congo
– *Odontotermes simplicidens* (Sjöstedt 1899), « 1108 », Madjime, Gabon
– *O. terricola* (Sjöstedt 1902), « 1183 », Makokou, Gabon
– *Microtermes sp.* Wasmann 1902, « 1027 », Mayela, Gabon

Apicotermitinae [S]

– *Eburnitermes grassei* Noirot 1966, « TN 261bis », Anguédedou forest
– *Labidotermes celisi* Deligne &Pasteels 1969, « TC 89 », Lubero Territory, Kivu, D. R. Congo
– *Ateuchotermes ctenopher* Sands 1972, « 1003/2 », Edzamangen, Gabon
– *Speculitermes cyclops* Wasmann 1902, « TD 39 », Ohaver, Mysore, India
– *Allognathotermes hypogeus* Silvestri 1914, « TD 25 », Dabou, Ivory Coast
– *Apicotermes gurgulifex* Emerson 1956, « TC 58 », Kinshasa, D. R. Congo
– *Jugositermes tuberculatus* Emerson 1928, « 1107 », Madjime, Gabon
– *Rostrotermes cornutus* Grassé 1943, « TN 1017 », Dakpadou, Ivory Coast

Termitinae A (genera with biting soldiers) [W] or [S]

1° mainly wood and other plant matter feeders [W]

– *Amitermes evuncifer* Silvestri 1914, Ndili River, D. R. Congo
– *Cephalotermes rectangularis* (Sjöstedt 1899), « 1089 », Belinga, Gabon
– *Microcerotermes fuscotibialis* (Sjöstedt 1896), « 1006 », Madjime, Gabon
– *Microcerotermes progrediens* Silvestri 1914, « 1002 », Endoumavion, Gabon

2° soil feeders [S]

– *Foraminitermes tubifrons* Holmgren 1912, « TN1018 », Dakpadou, Ivory Coast
– *Thoracotermes macrothorax* (Sjöstedt 1899), « 1162 B », Belinga, Gabon
– *Crenetermes albotarsalis* (Sjöstedt 1897), « 1003 », Edzamangen, Gabon
– *Ophiotermes grandilabius* (Emerson 1928), « 1070 », Mekob, Gabon

– *Ophiotermes sp.* Sjöstedt, « 1102 », Madjime Gabon
– *Furculitermes winifredi* Emerson 1960, « 1166 », , Amyéré, Gabon
– *Cubitermes gaigei* (Emerson 1928), « 1132 », Madjime, Gabon
– *Cubitermes heghi* Sjöstedt 1924, « 1017 », Madjime, Gabon
– *Noditermes indoensis* Sjöstedt 1926, « 1120bis » , M'Vadhi, Gabon
– *Proboscitermes tubuliferus* (Sjöstedt1907), « TD 15bis », Mayale, Gabon
– *Basidentitermes malelaensis* (Emerson 1928), « 1153 B 2 », Belinga, Gabon
– *Orthotermes mansuetus* (Sjöstedt 1911), « 1134/2 », Madjime, Gabon
– *O. depressifrons* Silvestri 1914, « 1003/3 », Edzamangen, Gabon

Termitinae B (« *Termes* » group : genera with snapping soldiers) [W] or [S]

1° mainly wood and other plant matter feeders [W]

– *Neocapritermes sp.* Holmgren 1912, « TC5/2 », Rio de Janeiro, Brazil
– *Termes langi* (Emerson 1928), « 1020 », Ngote, Gabon

2° soil feeders [S]

– *Tuberculitermes bycanistes* (Sjöstedt 1926), « 1077 », Mekob, Gabon (2)
– *Cavitermes sp.* Emerson 1925, « 41C », Guajara Mirim, Brazil
– *Pericapritermes magnificus* Silvestri 1912, « 1103 », Madjime, Gabon
– *Discupiditermes incola* (Wasmann 1893), « TD 40 », Dhorwar, Mysore, India

Nasutitermitinae [W] or [S]

1° mainly wood and other plant matter feeders [W]

– *Syntermes dirus* (Burmeister 1839), « TC4, TC10 & TC16 », Rio de Janeiro, Brazil
– *Procornitermes triacifer* (Silvestri 1901), « TC 39 », Alto Araguaia, Mato Grosso, Brazil
– *P. araujoi* Emerson 1952, « TC 62 », Ribeirão Prêto, Sao Paulo, Brazil
– *Cornitermes cumulans* (Kollar 1832), « TC 22 », Panloc Dumont, Mato Grosso, Brazil
– *Rhynchotermes nasutissimus* (Silvestri 1901), « TC 24 », Felixlandia, M. Grosso, Brazil
– *Nasutitermes diabolus* (Sjöstedt 1907), « 1066 », Badi Gabon
– *N. elegantulus* (Sjöstedt 1911), « Be 1149 », Belinga, Gabon
– *N. fulleri* Emerson 1928, « 1048 », Abor, Gabon
– *N. latifrons* (Sjöstedt 1896), « 1093 », Belinga, Gabon
– *Nasutitermes schoutedeni*, (Sjöstedt 1924), « 1021 », Ngota, Gabon
– *Constrictotermes cyphergaster* (Silvestri 1901), « TC 33 », Tres Marias, Mato Grosso, Brazil
– *Leptomyxotermes doriae* (Silvestri 1912), « Be 1129 », Belinga, Gabon

2° soil feeders[W]

– *Labiotermes labralis* (Holmgren 1906), « TC 41 A », Guajara Mirim, Brazil
– *L. pelliceus* Emerson & Banks 1965, « TC 47 », Guajara Mirim, Brazil
– *Armitermes* sp. Wasmann, « TC 34bis », Belo Horizonte, Mato Grosso, Brazil
– *Eutermellus convergens* Silvestri 1912, « 1158 B », Belinga, Gabon
– *Subulitermes sp.* Holmgren 1910, « TC 47bis », Guajara Mirim, Brazil
– *Postsubulitermes parviconstrictus* Emerson 1960, « 1098 », Belinga, Gabon
– *Verrucositermes tuberosus* Emerson 1960, « 1165 », Belinga, Gabon
– *Verrucositermes hirtus* Deligne 1983, « TC 242 », Lome forest, near Kribi, Cameroon (3)

(2) *Tuberculitermes* has been placed in the *Termes* group according to DELIGNE (1971).

(3) *Verrucositermes* is considered here not as a monotypic genus (SANDS, 1998) but as including at least 2 species (DELIGNE, 1983).

RESULTS

The results are presented in the following way. (1) The position and structure of the premolar tooth as well as observations related to its actions are presented for a species chosen as an example of wood feeder and (2) the other wood feeders are then compared to this species. (3) The same data are given for a species chosen as an example of soil feeder and (4) the other soil feeders are similarly presented in a comparative way.

An example of a wood feeder : *Zootermopsis angusticollis*

The premolar tooth is situated at the ventral side of the left mandible.

In a ventral surface view (Fig. 2), it appears as a narrow blade that overlaps the posterior half of the 3d marginal as well as the front part of the molar plate. Its length amounts to more than 20% of the TML (total mandible length). It is completely situated behind an imaginary line (A-M3) passing through the point of the apical tooth and that of the 3d marginal. With very slight differences in the lateral tilt of the specimen, it is entirely seen on the ventral surface of the mandible or as slightly intersecting the indentation separating the 3d marginal from the molar plate. Its mesal edge is long and straight. Its apical edge is rounded and fused with the ventral surface of the mandible, while its ventral proximal edge forms a more angular outline with the long mesal one.

In tangential view (Fig. 21), it appears as a straight and sharp blade which is clearly out of alignment with the marginal teeth and the dorsal edge of the molar plate. Along the dorsal side of the premolar tooth there is thus an elongated « premolar hollow » partially edged frontwards by the 3d marginal tooth and rearward by the edge of the molar plate.

When the mandibles are manipulated under the stereomicroscope and flexed along their natural articulation axis, one can observe how they work during the chewing movements. The two mandibles cross each other, with the left sliding above the right one. Any bit of wood brought into contact with them is thus necessarily held tightly between the ventral surface of the left mandible and the dorsal surface of the right one.

Due to its position and structure the premolar tooth then slightly juts out between the two surfaces (Fig. 1). While moving, it must thus exert shearing forces on the wood bits that are in its way and is perfectly suited for cutting superficial slices or fragments out of them.

This working is analogous with that of a carpenter's plane as discussed below.

Other wood and plant matter feeders

In the termite families that are entirely wood-feeder or phytophagous all the observed species show a premolar tooth with the same general features as those described above for *Zootermopsis angusticollis*. This point is illustrated in the plates for Mastotermitidae (Fig. 20), Kalotermitidae (Figs 5, 22), Termopsidae (Figs 2, 3, 4, 21), Hodotermitidae (Fig. 6), and Rhinotermitidae (Figs 7, 23).

The premolar tooth is always either straight or slightly convex and always long, its length amounting to more than 20% of the TML. It even exceeds 30% of the TML in most Kalotermitidae and Rhinotermitidae observed.

It the case of Termitidae, the 28 wood-feeder or other plant matter-feeder species observed (belonging to 19 genera), all present a similar «plane device», with some differences from one group to the other.

1° In the 10 observed species of Macrotermitinae (belonging to 7 genera), the following features were noted. In surface view, the cutting edge of the premolar tooth shows a nearly straight or slightly convex edge, as illustrated for *Macrotermes nobilis* (Fig. 8). When a concavity is also present in this edge, it is very faint and restricted to the most proximal part of its length (Fig. 9). The tooth always lies behind the line A-M3 as defined above. It generally intersects the indentation separating the 3d marginal tooth from the molar plate. In some species it is at a distance from the inner margin of the mandible and is therefore totally situated under the ventral surface of the mandible. This back position is particularly pronounced in Macrotermes (Fig. 9) and Odontotermes species.

In tangential view the premolar tooth appears as a straight sharp blade (Fig. 24). It is always clearly out of alignment with the edge of the marginal and molar teeth.

The length of the premolar tooth amounts to about 20-25% of the TML, except in Odontotermes (~16%) and *Protermes prorepens* (only 13%).

2° In the group of Termitinae with biting soldiers, the 4 wood-feeder species observed belong to the genera *Amitermes*, *Cephalotermes* and *Microcerotermes*. In these 4 species the premolar tooth presents, either in surface view or in tangential view, the same general features described above for the other wood-feeder species. These features are illustrated for *Microcerotermes* (Figs 12, 25). The premolar tooth amounts to about 20-25% of the TML, except in *Amitermes evuncifer* (~17%).

3° In the group of Termitinae with snapping soldiers, the 2 wood-feeder species observed, i.e. *Termes langi* and *Neocapritermes sp.* (Figs 18-19) also exhibit the same features. In both species, the premolar tooth intersects the indentation between the 3d marginal and the molar plate and its length amounts to about 20% of the TML.

4° The observed wood-feeder Nasutitermitinae belong to 12 species and 7 genera. These species are either Neotropical or African but they all show a premolar tooth with the general morphology described in the previous wood-feeder groups. This point is illustrated for *Procornitermes* (Figs 15, 26) and for *Nasutitermes* (Fig. 27). The premolar tooth however has a more variable position, since it either crosses the A-M3 line (in Neotropical genera *Syntermes*, *Procornitermes*, *Cornitermes* and *Rhynchotermes*), or stays behind this line (in *Constrictotermes*, *Nasutitermes* and *Leptomyxotermes*) and intersects to a variable extent the marginal-molar indentation. Its length amounts to 20-30% of the TML.

An example of a soil feeder : *Thoracotermes macrothorax*

In surface view (Fig. 11), the premolar tooth is no longer situated at the ventral side of the mandible : it reaches the same mesal level as the marginal teeth and its mesal edge crosses the A-M3 line. It is quite short, its length amounting to only about 15% of the TML.

and its apical part hardly overlaps the 3rd marginal tooth. Its mesal edge shows a distinct concave outline, its point is rounded and its proximal edge is a continuation of the apical slope of the molar depression. In surface view this proximal edge overlaps the large dorsal molar prominence.

In tangential view (Fig. 28), the premolar tooth appears with a curved and blunt edge, in the same general alignment as the marginal teeth. Its dorsal side is still adjacent to a «premolar hollow» and its proximal end is enlarged, thus flanking the apical part of the molar depression.

When the mandibles are manipulated under the stereomicroscope and flexed along their natural axis, the left mandible slides over the right one and the premolar tooth matches the opposite dorsal part of the right mandible. Due to its blunt edge it does not appear to be suited for cutting hard plant tissue but rather for pushing soft material with its rounded dorsal side.

Other soil-feeder species

The 33 soil-feeder species observed belong to 4 groups. They include 8 species (from 8 different genera) of Apicotermitinae, 13 species (10 genera) of Termitinae with biting soldiers, 4 species (4 genera) of Termitinae with snapping soldiers and 8 species (6 genera) of Nasutitermitinae. With the exception of some Nasutitermitinae they all present most of the features described above for *Thoracotermes macrothorax*.

The case of Nasutitermitinae is presented separately.

In the three first groups, the observed species all share the following characteristics. In ventral surface view (Figs 10, 11, 13, 14), the premolar tooth reaches the same mesal level as the marginal teeth, or nearly so, and crosses the A-M3 line. Its length amounts to less than 20% of the TML. In tangential view (Figs 28-30), its edge is blunt and lies in continuity with that of the 3d marginal tooth.

Besides these common features the following particularities can be noted.

1° In the observed species of soil-feeder Apicotermitinae, the premolar tooth is very short, amounting to 5 to 15 % of the TML, except in *Eburnitermes* (15-19%). The mesal edge of the premolar tooth is straight in the cases of *Eburnitermes* (Fig. 10), *Allognathotermes*, *Apicotermes* (Fig. 30) and *Jugositermes*. It shows a distinct concave outline in *Labidotermes* and *Ateuchotermes*.

2° Among the observed species of soil-feeder Termitinae with biting soldiers, the premolar tooth has a concave outline in most of the cases. It is straight in *Ophiotermes* and *Furculitermes*.

3° Among the observed soil-feeder species of Termitinae with snapping soldiers, the premolar tooth is straight in *Tuberculitermes bycanistes* and concave in *Cavitermes*, *Pericapritermes* and *Discupiditermes*.

As for soil-feeder Nasutitermitinae, in the observed Neotropical species of *Labiotermes* (Figs 16, 17, 31) and *Armitermes* the premolar tooth does show the same general features as in *Thoracotermes*. In the small African species belonging to 4 close genera (*Verrucositermes*, *Postsubulitermes*, *Subulitermes* and *Eutermellus*), the premolar

tooth is short (~ 15% of the TML) and blunt but it differs from that of *Thoracotermes* in being straight and out of alignment with the 3d marginal tooth.

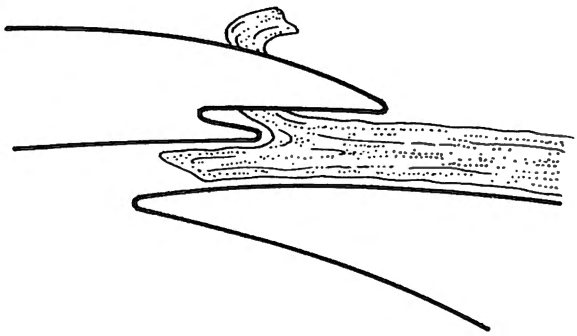
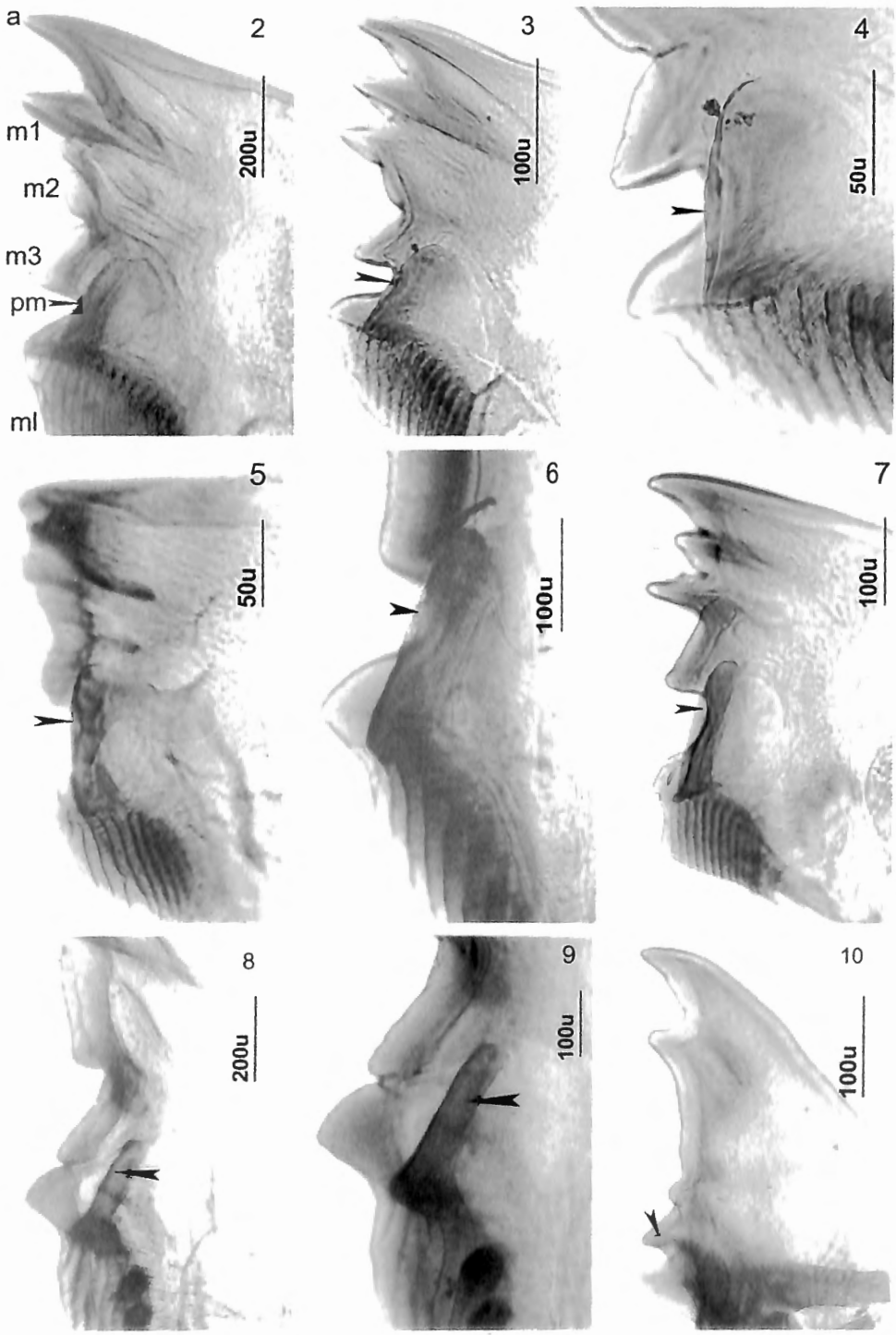


Fig. 1. – Schematic functioning of the premolar tooth of the left mandible of a wood-feeder worker of termite. Left and right mandibles are seen in cross section from their proximal part. The left mandible slides above the right one and ingested bits of wood are held tight between the two mandibles. The premolar tooth slightly juts out between the two mandibles; while moving it exerts shearing forces on the wood bits which are in its way and can cut superficial fragments out of them.

Legend to the figures (see pages 210-214)

Figs 2-17. – Microphotographs of the left mandible of termite worker seen in ventral surface view to show the position and form of the premolar tooth (arrow). – Fig. 2. *Zootermopsis angusticollis.* a : apical tooth ; m1, m2, m3 : first, 2d, 3d marginal tooth ; ml : molar plate ; pm : premolar tooth.- Fig. 3. *Stolotermes africanus*. Fig. 4. *Stolotermes africanus* (detail). Fig. 5. *Kalotermes flavicollis*. Fig. 6. *Microhodotermes viator*. Fig. 7. *Heterotermes sp*. Fig. 8. *Macrotermes nobilis*. Fig. 9. *Macrotermes nobilis* (detail). Fig. 10. *Eburnitermes grassei*. Fig. 11. *Thoracotermes macrothorax*. Fig. 12. *Microcerotermes fuscotibialis*. Fig. 13. *Pericapritermes magnificus*. Fig. 14. *Pericapritermes magnificus* (detail). Fig. 15. *Procornitermes striatus*. Fig. 16. *Labiotermes labralis*. Fig. 17. *Labiotermes labralis* (detail).

Figs 18-31. – SEM micrographs of the left mandibles of worker termites seen in tangential view from the inner side to show the position and form of the premolar tooth (arrow). – Fig. 18. *Neocapritermes sp.* Fig. 19. *Neocapritermes sp.*(detail). Fig. 20. *Mastotermes darwiniensis.* Fig. 21. *Zootermopsis angusticollis*. Fig. 22. *Kalotermes flavicollis.* Fig. 23. *Reticulitermes lucifugus*. Fig. 24. *Acanthotermes acanthothorax*. Fig. 25. *Microcerotermes fuscotibialis* (detail). Fig. 26. *Procornitermes araujoi*. Fig. 27. *Nasutitermes lujae*. Fig. 28. *Thoracotermes macrothorax*. Fig. 29. *Pericapritermes magnificus*. Fig. 30. *Apicotermes gurgulifex*. Fig. 31. *Labiotermes labralis* (detail).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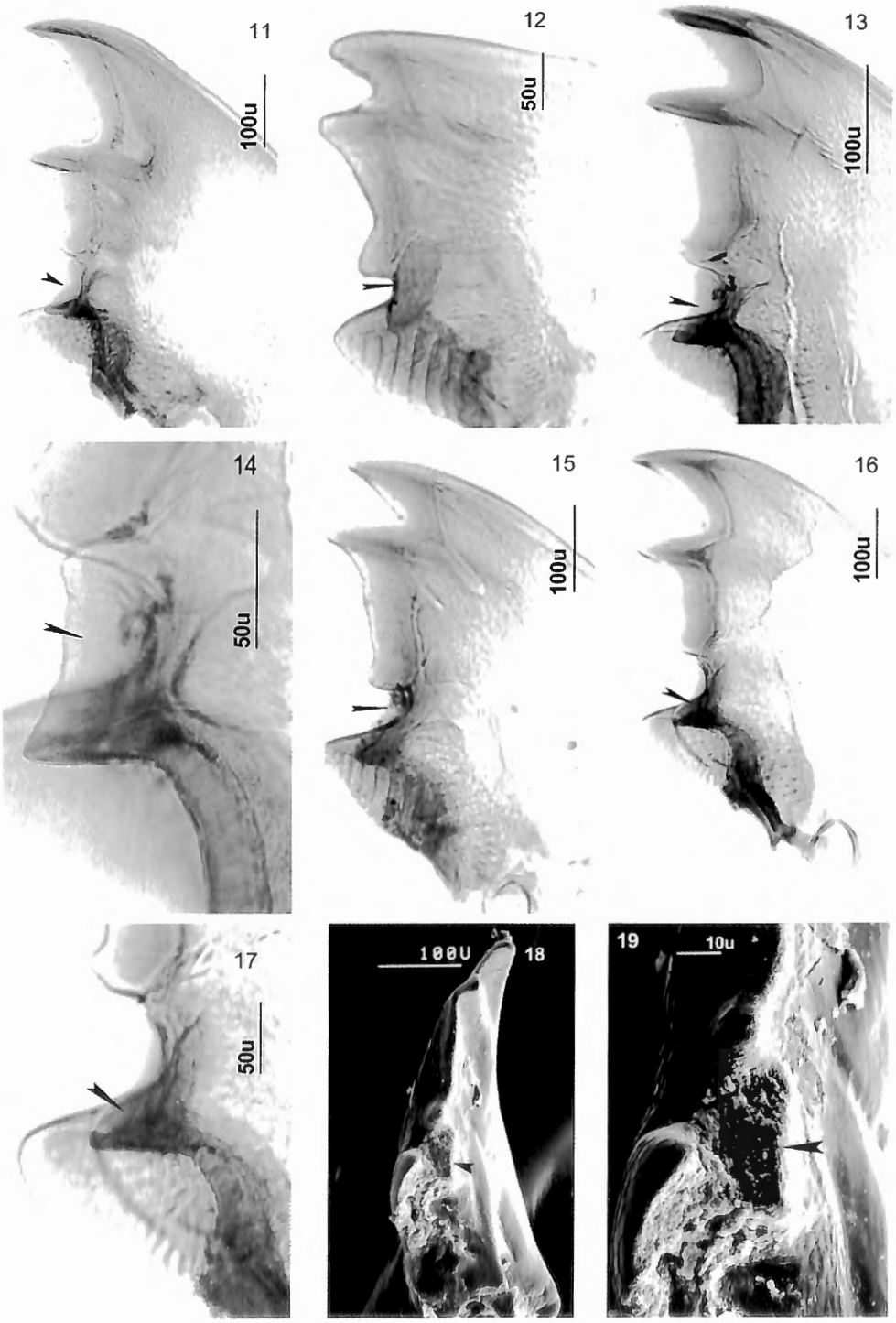
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DISCUSSION

The premolar tooth is an asymmetrical structure only present in the *left* mandible of termite workers. It has escaped the notice of earlier morphologists, probably because it is generally more or less hidden *under* the mandible. Since the late '60s, it has been described under the names of « molar tooth » (KRISHNA, 1968), « premolar tooth » (DELIGNE & PASTEELS, 1969; DELIGNE, 1970), « subsidiary marginal tooth » (SANDS, 1972), « submolar tooth » (MATHEWS, 1977) and « 4th marginal tooth » (SANDS, 1992). Among these names, I consider both adjectives « molar » and « subsidiary marginal » to be ambiguous, the former because it may induce a confusion with the molar plate and the latter because the same terms designate a different tooth in the right mandible. The adjective « submolar » may also be ambiguous or inexact. The tooth under discussion is actually often situated under the dorsal molar prominence but never under the molar plate itself. Furthermore in many Termitidae genera the tooth is wholly situated in front of the molar region and not under any part of this region. Similarly the name « 4th marginal » does not seem appropriate because, in most families and subfamilies, the tooth is *not* situated at the inner margin of the mandible but lies instead more or less far from that margin. The name « premolar tooth » seems better because the tooth is always in front of the molar plate and in close connection with it. Furthermore its sensillae are innervated by the same nerve branch as the molar plate and not by a marginal branch (DELIGNE & PASTEELS, 1969). Finally as it differs in structure and position both from molar plate and from marginal teeth in most families and subfamilies, it seems preferable to also give it a specific name. For all these reasons I retain the name of « premolar tooth ».

Until recently the morphology of the premolar tooth had only been described in a few groups of termites. SANDS (1998) published an outstanding systematic synthesis on the termite genera from soils of Africa and the Middle East, in which the « 4th marginal » (i.e. the premolar tooth) was described for many African species. Even though the information given in the present work is partly based on the same material as Sands', it is not redundant because of the use of different observation techniques. Indeed the observation in ventral view of the mandible, as proposed here in Figs 2-17, allows a more accurate description of the premolar tooth than the dorsal observation used for systematic purposes. The observation in tangential view, as depicted here in SEM Figs 18-31, is necessary in order to observe the precise form and connections of the premolar tooth. I have also observed termites belonging to families (Mastotermitidae, Kalotermitidae), to subfamilies (Termopsinae, Stolotermitinae, Porotermitinae) and to non-African genera or species, which are not included in Sands' material. Furthermore the scope of this work is rather functional morphology than systematics.

Concerning functional morphology, the premolar tooth of wood-feeder species always shows a similar position and structure, as described for *Zootermopsis*. It is suited for exerting shearing forces on bits of wood held tightly between the two mandibles and for cutting superficial slices or fragments out of them (Fig. 1). As briefly mentioned above this function is similar to that of a carpenter's plane. The analogy is as follows. With the plane (*or* with the premolar region of the mandible), wood is held tight between the sole of the plane (*or* the ventral surface of the left mandible) and the workbench (*or* the dorsal sur-

face of the right mandible), while the slightly jutting chisel of the plane (*or* the premolar tooth) cuts superficial shavings out of the wood.

In a very schematic way, Fig. 32 suggests how the resulting fragments may be moved. Under the pressure of newly cut fragments, the first fragments are pushed into the premolar hollow and, from there, towards the molar region (dotted arrow), where they are further rasped. The connection between the premolar hollow and the molar rasp can be clearly observed on Figs 20-27 and the movement of fragments from one part to the other is suggested by Figs 18-19. In the species where the premolar tooth is near the inner margin of the mandible or even intersects the indentation between the 3d marginal tooth and the mola, the cut fragments of wood can also be pushed at the level of this indentation towards the dorsal surface of the left mandible (continuous arrow).

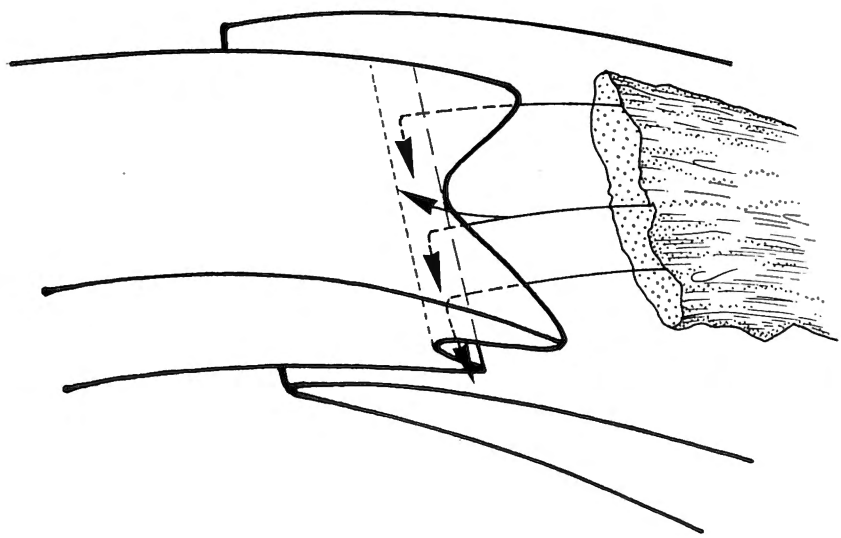

Fig. 32. – Schematic cross section and stereo-diagram of the premolar region of the left mandible and opposite part of the right mandible. The fragments of wood cut by the premolar tooth are pushed into the premolar hollow and, from there towards the molar region (dotted arrow), where they are further rasped. They can also be pushed between the 3d marginal tooth and the molar prominence towards the dorsal surface of the left mandible (continuous arrow) and, from there be moved back towards the molar region and the mouth by the movements of the labrum.

In most of the soil-feeder species that we observed, belonging to at least 4 phyletic clades, the premolar tooth has lost one or several functional features that characterise wood feeders. In particular it reaches more or less the same level as the marginal teeth, comes in alignment with them and becomes blunt. It becomes more similar to the marginal teeth and presumably plays a similar role. During the movements of the mandibles, together with the marginal teeth, it is suited to gather soil particles towards the midline and the rear part of the oral cavity where they are compressed between the mola of both mandibles before being ingested. These adaptive trends appeared at least four times in different groups of soil-feeder Termitidae.

In all cases the other mouthparts, especially the labrum and the hypopharynx, assist the mandibles in moving food items towards the mouth. Besides their key role in the processing of food the mandible teeth, including the premolar tooth, also certainly play a role in the processing of wood and soil material used by workers for building the nest.

CONCLUSIONS

In the left mandible of termite workers, the premolar tooth shows clear morphological adaptations to the species' diet.

In wood- and other plant matter-feeder species, the structure, position and functioning of the premolar tooth are analogous to those of the chisel of a carpenter's plane. It is suited for cutting superficial fragments out from the wood.

In many soil-feeder species, belonging to at least 4 clades, the premolar tooth has lost in a polyphyletic way one or several functional features that characterise wood feeders. Due to its structure and position it is suited to assist the marginal teeth in the gathering of soil particles towards the mouth before ingestion.

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