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Abdominal characters and status of the cerapachyine ants (Hymenoptera, Formicidae)

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For nearly a century myrmecologists have worried about the cerapachyine ants. Are they worthy of subfamily status, or not? Current work on the abdominal segments of the poneroid subfamilies, the first part of which is discussed in this paper, indicates that the cerapachyines should be treated as a separate subfamily. The history of the cerapachyines is discussed and apomorphies diagnostic of the group are noted. Separation from the Ponerinae is stressed and the possible relationships of the group to other poneroids are mentioned. Full descriptions of the abdominal sclerites are presented for each of the three cerapachyine tribes and a subfamily diagnosis and zoogeographical synopsis are given.

KEYWORDS: Formicidae, Cerapachyinae, Abdominal characters, Status.

Introduction and history

The ants which occupy the poneroid tribes Cerapachyini, Acanthostichini, and Cylindromyrmecini present a century-old puzzle to ant systematists and students of the internal phylogeny of the Formicidae. Many times in the past hundred years authors have worried and debated about whether these three tribes together constitute a separate subfamily (Cerapachyinae), or whether they should be included as three tribes within an expanded subfamily Ponerinae, or whether they should in some way be linked to the subfamily Dorylinae.

The reasons for all this puzzlement lie in the strange habitus of the cerapachyine groups involved. They show a baffling combination of ponerine, doryline and independent characters. Some authors have stressed the importance of one set of characters, others of another set, to support their particular concept of classification, as the following historical overview will illustrate.

The earliest appearance of a cerapachyine group-name in the literature was in Forel (1893). He postulated a 'Ponerinae, tribe Cerapachysii', including in it the currently recognized genera *Cerapachys*, *Simopone*, *Cylindromyrmex*, *Sphinctomyrmex*, and *Acanthostichus*, as well as the now-synonymized names *Parasyscia*, *Lioponera*, *Syscia*, and *Ooceraea*, (for the fate of which see Brown, 1975). Forel (1893) merely defined his Cerapachysii as 'a group of genera with cylindrical bodies, carinate cheeks, (and) aberrant abdominal form'.

Emery (1895) shifted these cerapachyine genera out of the Ponerinae and into the Dorylinae as 'tribus Cerapachyi' of that subfamily. A few years later Emery (1901) formed a supertribal group to hold them. His 'subfamily Dorylinae, Group 2—Cerapachinae', contained the tribes, as he spelled them, Acanthostichii (*Acanthostichus* only), Cylindromyrmii (*Cylindromyrmex* plus *Simopone*), and Cerapachyi (including

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the remainder of Forel's Cerapachysii). His reasons for this shift were based on characters of the male genitalia (cerci absent from dorylines, present in ponerines), and the male subgenital plate (forked apically in dorylines, simple in ponerines). On these criteria the cerapachyine groups fell into his concept of subfamily Dorylinae.

This apparently upset Forel who, later in the same year (Forel, 1901) defended his earlier classification, saying that Emery's male genitalia characters were insufficient to characterize a subfamily, and citing ethological characters in support of his thesis.

The following year Wheeler (1902) succinctly summarized the differing views of Emery and Forel, and introduced the term Cerapachyinae to cover the entire group. He repeated Emery's classification in his text but concluded that he was inclined to 'regard the Cerapachyinae as true Ponerinae'. He also made the interesting remark that in general 'comparatively little value can be attached to the conditions of the pedicel in the taxonomy of ants'; a statement which will be show to be incorrect in this paper.

The next development came a few years later, when Emery (1909) introduced the term Prodorylinae to include the cerapachyines. This division, 'Ponerinae, sectio Prodorylinae' was presented in fuller detail in the Genera Insectorum series (Emery, 1911) and indicates that he had changed his opinion, switching the cerapachyines from Dorylinae back to Ponerinae. He defined this section, which is exactly the same as Wheeler's (1902) earlier Cerapachyinae, as follows. 'Larvae uniformly hairy, without piligerous tubercles. Males with mandibles well developed; genitalia entirely retractile and subgenital plate broadly forked; no cerci.' This 'sectio Prodorylinae' included the tribes Cerapachyini, Acanthostichini, and Cylindromyrmecini.

The production of Genera Insectorum stabilized the situation for a number of years. For instance, the classification was repeated by Forel (1917) in his synopsis of Formicidae. But then Wheeler (1920, 1922) upset the boat again. He rightly pointed out that the names Cerapachyinae and Prodorylinae covered exactly the same groups, and that the former was the correct name. He also (Wheeler, 1920) treated the Cerapachyinae as a separate, distinct, subfamily. Shortly thereafter Wheeler (1922: 636–640) produced a classification which used Cerapachyinae as a subfamily but which transferred the tribe Cylindromyrmecini to subfamily Ponerinae. No reason was given for this strange move, which is odd as *Cylindromyrmex* had been regarded as a cerapachyine since earliest times. Further, Wheeler himself (1922: 51) had said, earlier in the same publication, that the limits of his Cerapachyinae agreed with those of Emery's (1911) Prodorylinae. Nevertheless, the system again appeared stabilized, and it remained much as Wheeler left it for the next thirty years or so. Mention should perhaps be made here of a rather aberrant and idiosyncratic classification proposed by Clark (1951), where a number of poorly characterized and short-lived subfamilies were proposed and quickly rejected (see diagnosis of subfamily Cerapachyinae, below).

The next serious contribution to the debate was by Brown (1954), who said that it was possible 'to support the cerapachyines as a weak subfamily'. As proof of this he pointed out that in all the cerapachyine genera the worker pygidium (tergite of abdominal segment 7) was 'more or less flattened or impressed toward its apex, and is bordered apically, at least on the sides, by serially arranged small to minute spinules'.

The universality of this apomorphic character in the cerapachyine groups allowed Brown (1954) to return the Cylindromyrmecini to the Cerapachyinae, and thus rectify Wheeler's (1922) earlier error of excluding this tribe from the subfamily.

Finally Brown (1975) completed a world revision of the cerapachyine genera and species. His treatment, discarding numerous pointless 'genera' and 'subgenera', constituted a huge advance over all previous systems, and enormously increased our

understanding of the taxa involved. He recognized just seven genera, distributed in three tribes, as follows.

Cerapachyini: *Cerapachys, Simopone, Sphinctomyrmex, Leptanilloides*
Cylindromyrmecini: *Cylindromyrmex.*
Acanthostichini: *Acanthostichus, Ctenopyga.*

Coincidentally, he discarded the idea of a subfamily Cerapachyinae and reverted to the concept of these three tribes being members of the subfamily Ponerinae. He speculated on the possible relationships of Cerapachyini and Cylindromyrmecini to the ectatommine ponerines, but did not reach any solid conclusions. As for the Acanthostichini, Brown (1975) considered 'Amblyoponini, Ectatommini, and Typhlomyrmecini in turn as possible acanthosticine ancestors, but the evidence for each of these origins is as yet insufficient to be convincing'.

An alternative to this three tribe arrangement, Brown said, would be to consider all three to belong to a single phyletic lineage. He cited the specialized worker pygidium, the biaculeate male hypopygium, and the form of the larval mandibles, as support for this hypothesis. Yet he concluded that at present he was 'forced to be sceptical of the monophyletic hypothesis', and correctly considered that a 'polyphyletic taxon would only aggravate confusion and misunderstanding'.

Brown (1975) also referred to Emery's (1901) old idea that the cerapachyines may be close to the Army Ant subfamilies Dorylinae and Ecitoninae. The idea still has much merit and will be investigated in detail in a later paper. For the moment, a number of features displayed by the dorylines and ecitonines appear to exclude them from membership of the same subfamily as the cerapachyines, though the distinctly possible existence of an 'Army Ant group' of subfamilies remains to be investigated in detail. On the side of the alitrunk the propodeal spiracle in the dorylines and ecitonines is usually large, always high on the side and far forward, where it is closely associated with a metathoracic endophragmal pit. In cerapachyines the propodeal spiracle is small, low on the side, at or behind the midlength of the sclerite, and is not associated with an endophragmal pit. The cerapachyine condition is considered apomorphic as, ancestrally, abdominal spiracles are located close to the leading edge of each segment. Metapleural lobes (=inferior propodeal plates) are absent from ecitonines and dorylines, except for *Aenictus*, and pygidium is usually reduced. Among cerapachyines the pygidium is reduced only in *Leptanilloides*, but here it is very specialized and overhung by the sixth tergite, a feature not seen in Army Ant subfamilies. In *Dorylus* the pygidium is bidentate, though the nature of this armament is different from that seen in cerapachyines. The dorylines have also lost the depressed proprioceptor zone on the petiolar sternite, though this is retained in ecitonines. Finally the dorylines and ecitonines have grossly modified and highly characteristic males, and dichthadiiform queens. Although some approach to the latter is made in a very few cerapachyine queens, the grotesque 'sausage-fly' males are not developed, although a few *Sphinctomyrmex* appear to be evolving in this direction. Instead they retain, in general, a remarkably ponerine habitus (Brown, 1975).

During this current survey of the formicid abdomen, to see what light, if any, can be shed on the internal phylogeny of the ants, it became apparent that the cerapachyines were very distinct from the remainder of subfamily Ponerinae. The cerapachyine taxa share several derived characters which are lacking in the Ponerinae, and exhibit the plesiomorphic state of several apomorphies developed by the remaining ponerines. These findings and their application to the classification of the ant subfamilies are discussed below.

Terminology of the abdominal segments

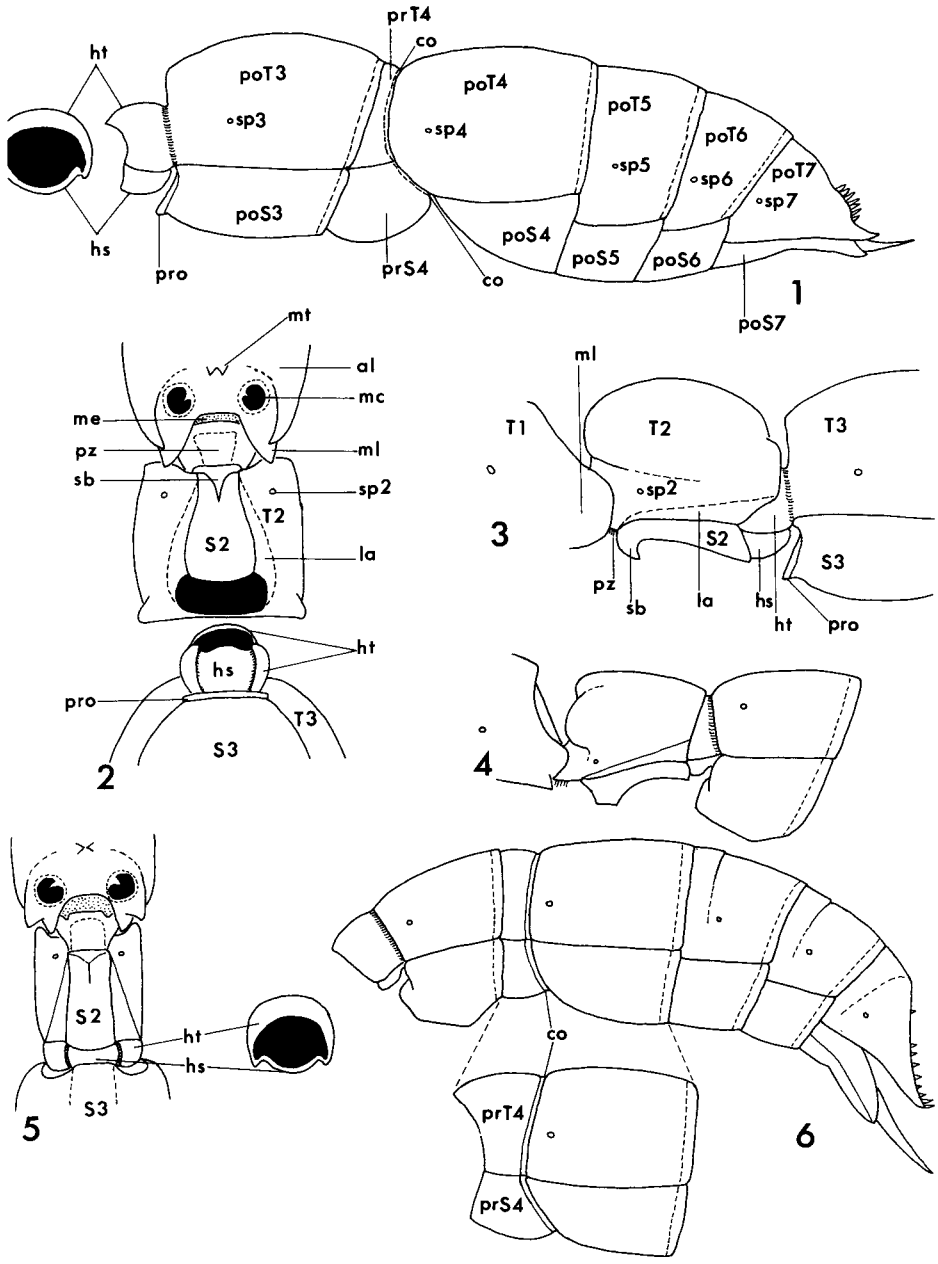
Among the apocritan Hymenoptera a number of specialized terminologies for different abdominal segments have gained currency in different family-level taxa, as summarized in Gauld and Bolton (1988). The ants are no exception and in fact have acquired a more than usually specialized terminology. This is because, superimposed upon the primary set of abdominal modifications common to all Apocrita, they also have a secondary set of modifications which are peculiar to the ants. Thus to avoid confusion between abdominal segment number, gastral segment number, etc., all segments referred to in this paper are those of the true abdomen (see Figs 1, 3); these segments are as follows.

In ants abdominal segment 1 is the propodeum, fused to the thorax proper (Fig. 3) and consisting only of the tergite. Abdominal segments 2 to apex are sometimes collectively called the metasoma. Abdominal segment 2 is the petiole, a reduced and more or less isolated segment in all the ants (e.g. Figs 2–5. 8–10). Abdominal segment 3 is termed the first gastral segment when it is full-sized, but the postpetiole when it is reduced. Confusingly it is sometimes also called the postpetiole when full-sized. Abdominal segment 2, or segments 2+3 when 3 is also reduced, may be termed the waist or pedicel. The remaining abdominal segments, 3 or 4–7 in female castes, and 3 or 4–8 in males, are collectively called the gaster, and together form the enlarged apparent 'abdomen' (e.g. Figs 1, 6, 7, 11, 15, 17–23). Abdominal segment 8 is reduced and internal in female castes, not visible externally, and forms a part of the sting apparatus. Each abdominal segment behind the first otherwise consists of a dorsal tergite (=tergum, tergal plate) and a ventral sternite (=sternum, sternal plate). In females and workers the last visible abdominal tergite, that of segment 7, is termed the pygidium, and the last visible sternite the hypopygium. In males the sternite of abdominal segment 9 is called the subgenital plate.

Abdominal segments 1 (propodeum) and 2 (petiole) (Figs 2–5) have been much used in ant systematics, and no new terminology is required for them or their component parts. However, the remaining segments have seen only very little use as systematic tools and a couple of terms need to be introduced or clarified here.

The anterior sections of abdominal segments 3 to the apex are inserted into the posterior ends of the preceding segments (Figs 1, 6, 7), and are not normally visible unless the waist and gastral segments are artificially distended or dissected. When this is done a distinct division between the normally concealed anterior portion of each segment, and its normally exposed posterior section, can usually be clearly seen (Figs 6, 11, 17). The anterior portion of the segment may narrow at this point, or there may be a transverse impression, groove or constriction, or the sculpture may change or be lost, or pilosity and pubescence may be lost. Frequently more than one of these differences may occur on the anterior section of each segment, to contrast it to the posterior section.

Taylor (1978) has suggested that the concealed anterior sections of the segments may be acrosclerites, but was aware that this was not necessarily so. Considering the definitions of acrosclerites (acrotergite, etc.) given in Snodgrass (1935), it is almost certain that these modified concealed portions of the abdominal sclerites in ants are not genuine acrosclerites but represent a secondary development. Fortunately Brown (1975) had used the term pretergite, in the form 'pretergital belt', for this concealed portion, and a nomenclature derived from this beginning will be used here. Thus, each abdominal tergite from segment 3 to the apex consists of a normally concealed *pretergite* and a normally exposed *posttergite*. Similarly each sternite from segment 3 to the apex consists of a *presternite* and a *poststernite*.



Key to abbreviations

al = alitrunk, co = constriction, la = laterotergite, hs = sternite of helcium, ht = tergite of helcium, mc = metacoxal cavity, me = membrane, ml = metapleural lobe, mt = metasternal process, poS = poststernite, poT = posttergite, pro = process, prS = presternite, prT = pretergite, pz = proprioceptor zone of petiole, S = sternite, sb = subpetiolar process, sp = spiracle, T = tergite.

FIGS 1–6. 1–3, *Simopone grandis*, worker: 1, profile of abdominal segments 3–7 (= gaster), offset shows helcium in front view; 2, ventral view of posterior alitrunk and abdominal segments 2–3, with 2 dissociated from 3; 3, profile of abdominal segments 1–3. 4–6, *Acanthostichus* species, worker: 4, profile of abdominal segments 1–3; 5, ventral view of posterior alitrunk and abdominal segments 2–3; 6, profile of abdominal segments 3–7 (= gaster), offsets show helcium in front view (left) and isolated segment 4 (below).

Another term suggested by Taylor (1978) is 'tubulate', used to indicate a condition shown in many poneroid ants. When the pretergite and presternite of an abdominal segment are broad and are separated from the posttergite and poststernite by a transverse constriction and an incised groove, the segment is said to be tubulate (Figs 1, 6). The term is useful in a general way but it must be borne in mind that, taking the Formicidae as a whole, there are many degrees of development and secondary obliteration of this feature exhibited.

The pretergite and presternite of abdominal segment 3 are usually extremely reduced in size and very specialized, being thickened and collar-like, and fitting tightly into the posterior foramen of the second abdominal segment (petiole) (Figs 1–6. 7, 11, 13, 15). They form part of a complex and very efficient articulation which allows flexion between the second abdominal segment and segments 3 to the apex. I propose a special term for this articulatory collar, the *helcium*, and define it as follows.

> *The helcium is the much-reduced collar-like pretergite and the accompanying presternite of abdominal segment 3, which anteriorly is socketed in, and articulates with, the posterior end of segment 2 (the petiole).*

In taxa such as the Myrmicinae, where abdominal segment 3 is also very reduced in size (postpetiole) the articulatory pretergite plus presternite of segment 4 may also be very small and specialized, and in this condition may be referred to as the second helcium or helcium of abdominal segment 4.

Finally, the tergites and sternites of abdominal segments 2–4 may or may not be fused in ants (segments 5 to apex are always unfused), as was first pointed out by Gotwald (1969). For the purposes of this study 'fused' is defined as the condition in which the tergite and sternite of any given segment either meet edge to edge, or narrowly overlap (tergite over sternite), and are immovably welded together. This may occur throughout the length of the tergosternal junction or may leave a short distance posteriorly where the tergite narrowly overlaps the sternite but fusion is incomplete.

A small to vestigial band of muscle may arise on the poststernite and insert internally on the tergite, but this appears to be functionless. Overlap of the sclerites is minimal and there is no free movement of the sclerites one against the other.

'Unfused' is defined as the condition in which the tergite of any given segment broadly overlaps the sternite and the two are connected only by thin flexible interscleritic membrane and/or dorsoventral bands of muscle arising from the dorsal margin of the poststernite. The two sclerites are free and capable of considerable movement one against the other.

The cerapachyine taxa

The following descriptions of abdominal segments 2–7 are based on the female and worker castes of the cerapachyine taxa. Where males are known they correspond to the females and workers in the characters mentioned, but in general too few are available for study to make any strong contribution to the investigation. The descriptions complement and add to those presented by Brown (1975).

Acanthostichini (*Acanthostichus, Ctenopyga*)
(Figs 4–6)

Abdominal segment 2 (petiole) (Figs 4, 5). In ventral view proprioceptor zone present on sternite anteriorly, in front of subpetiolar process. Laterotergite developed and also visible in profile (Fig. 4), articulating posteriorly with ventral portion of helcial tergite

only. Sternite of petiole overlapping helcial sternite when gaster flexed down, the overlapping portion of the sternite convex and with thinner cuticle than elsewhere. Posterior foramen of petiole, where helcium inserts, very broad and deep, the tergite in profile without a differentiated posterior face. Sternite in ventral view simple at apex, rounded (Fig. 5).

Abdominal segment 3 (Figs 4, 6). Helcium broad and deep, almost as broad as anterior width of posttergite in dorsal view. Helcium located very high on anterior face of segment (Fig. 6), its dorsum almost level with the posttergal dorsum; the latter without an anterior declivity. Helcium sessile; a weak constriction present between it and the posttergite (Fig. 6) but no post-helcial neck developed nor with a sharp rim or margin bounding the articulatory portion of the helcium. Helcial sternite strongly convex in frontal view (Fig. 6), projecting ventrally beyond apices of the tergite; the sternite freely visible in profile, large and convex (can be seen in ordinarily mounted specimens, as in Fig. 4). Tergosternal fusion complete, the suture more or less straight to the base of the helcial tergite. Posttergite and poststernite in profile approximately equal in size or the latter slightly smaller than the former. Spiracle clearly visible on posttergite, close to the helcium. Sternite lacking an anteromedian process but this region convex or bulging and the anterior face separated from the lateral faces by a V-shaped margin. Maximum depth of segment occurring at or close to its posterior margin.

Abdominal segment 4 (Fig. 6). Pretergite and presternite with convex outlines in profile, suture between them visible. A strong girdling constriction separates pre- from postsclerites. Spiracle visible, situated anteriorly on side of posttergite. Posttergite and poststernite about the same size in profile, the postsclerites together larger than those of segment 3. Tergite and sternite not fused.

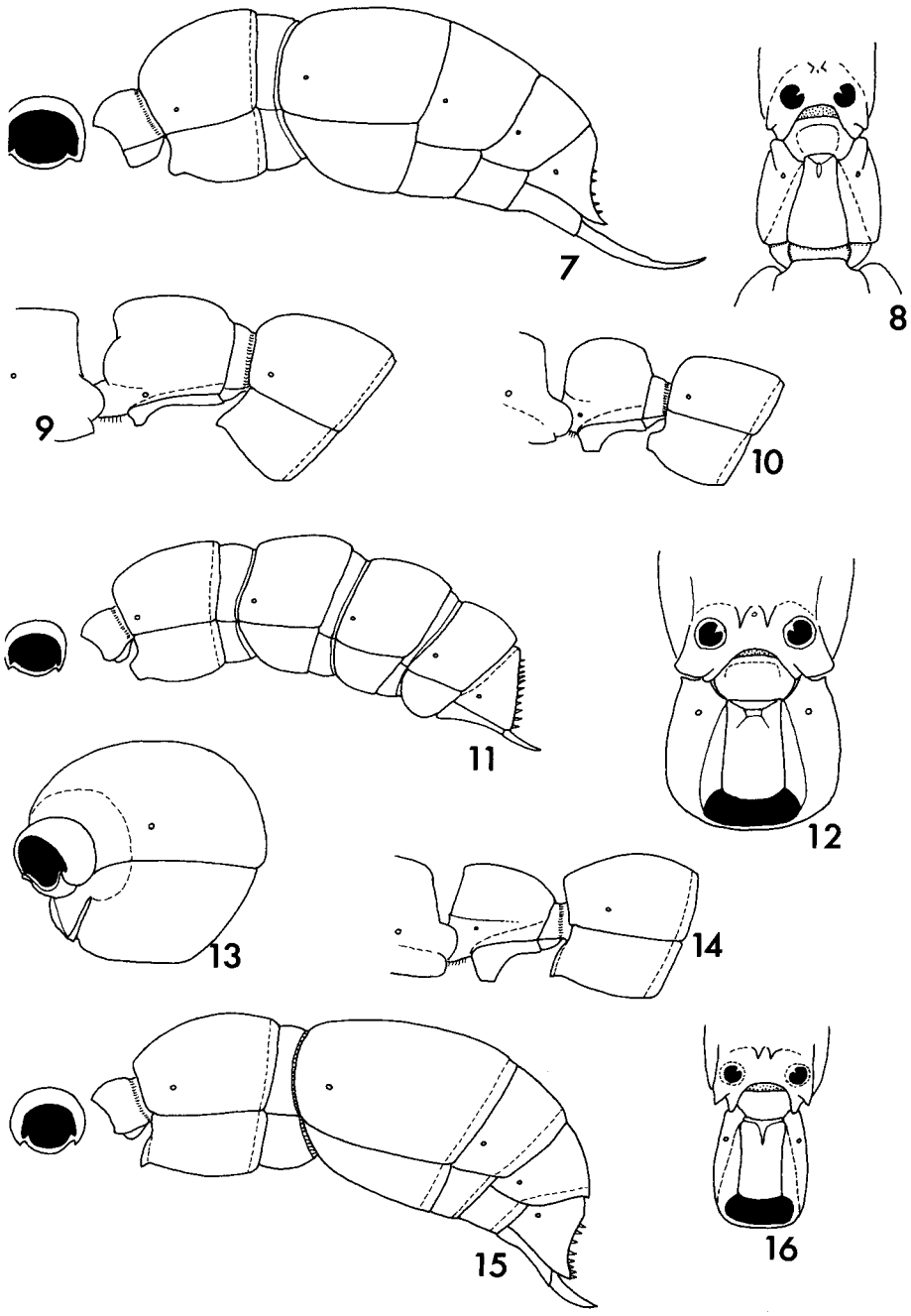
Abdominal segments 5–7 (Fig. 6). Presclerites always differentiated from postsclerites. In some species the tergite with a transverse impression or constriction across the dorsum, which runs down the sides to about the level of the spiracle. In others the sternites with a constriction or impression between pre- and postsclerites (e.g. *Ctenopyga*). These features resemble, in a weak and ill-formed way, the very strong constrictions seen in *Sphinctomyrmex* (Fig. 11) and *Leptanilloides* (Figs 22, 23). All spiracles on posttergites, visible. Tergite 7 (pygidium) large and flattened dorsally, the flattened portion armed laterally with peg-like teeth (Fig. 6). Sternite 7 (hypopygium) downcurved between pre- and poststernite, flattened and much smaller than the tergite.

Acanthostichus: six species examined (two dissected).
Ctenopyga: one species examined.

Cylindromyrmecini (*Cylindromyrmex*)
(Figs 7–9)

Abdominal segment 2 (*petiole*) (Figs 8, 9). Proprioceptor zone present on sternite anteriorly, in front of the subpetiolar process. Laterotergite discernible but fused to tergite proper, convex posteriorly and overlapping helcial sternite. Posterior foramen of segment 2, where helcium inserts, broad and deep, the tergite with a small poorly developed posterior face. Sternite in ventral view simple at apex, rounded (Fig. 8).

Abdominal segment 3 (Figs 7, 9). Helcium broad and deep, almost as broad in dorsal view as the anterior width of the posttergite. Helcium located approximately at midheight on anterior face, or slightly above midheight (Fig. 7). Posttergal dorsum with a short anterior declivity. Helcium distinctly narrowed posteriorly, with a marked deep



FIGS 7–16. 7–9, *Cylindromyrmex striatus*, worker: 7, profile of abdominal segments 3–7; 8, ventral view of posterior alitrunk and abdominal segments 2–3; 9, profile of abdominal segments 1–3. 10–11, *Sphinctomyrmex rufiventris*, worker: 10, profile of abdominal segments 1–3; 11, profile of abdominal segments 3–7. 12–13, *Sphinctomyrmex turneri*, worker: 12, ventral view of posterior alitrunk and segment 2, segment 3 removed; 13, abdominal segment 3 showing helcium and ventral process. 14–16, *Cerapachys sulcinodis*, worker: 14, profile of abdominal segments 1–3; 15, profile of abdominal segments 3–7; 16, ventral view of posterior alitrunk and segment 2, segment 3 removed.

constriction before its junction with the posttergite, but without a sharp rim or margin bounding the articulating portion of the helcium; nor is there a post-helcial neck. Helcial sternite large and strongly convex (Figs 7, 9), clearly visible in profile and bulging strongly ventrad in frontal view (Fig. 7); easily seen in normally mounted specimens. Tergosternal fusion complete, the suture more or less straight to the base of the helcial tergite. Posttergite and sternite approximately equal in size or the former slightly larger than the latter. Spiracle clearly visible on posttergite, close to helcium. Sternite anteriorly concave, with a thickened U- or V-shaped rim below the helcium, which may project as a shallow lip-like process in profile. Maximum depth of segment occurring at or close to its posterior margin.

Abdominal segment 4 (Fig. 7). Pretergite and presternite large, convex in outline, the suture between them visible. A strong girdling constriction separates pre- from postsclerites. Spiracle visible, situated anteriorly on side of posttergite. Posttergite and poststernite about the same size in profile, the postsclerites together larger than those of segment 3. Tergite and sternite not fused.

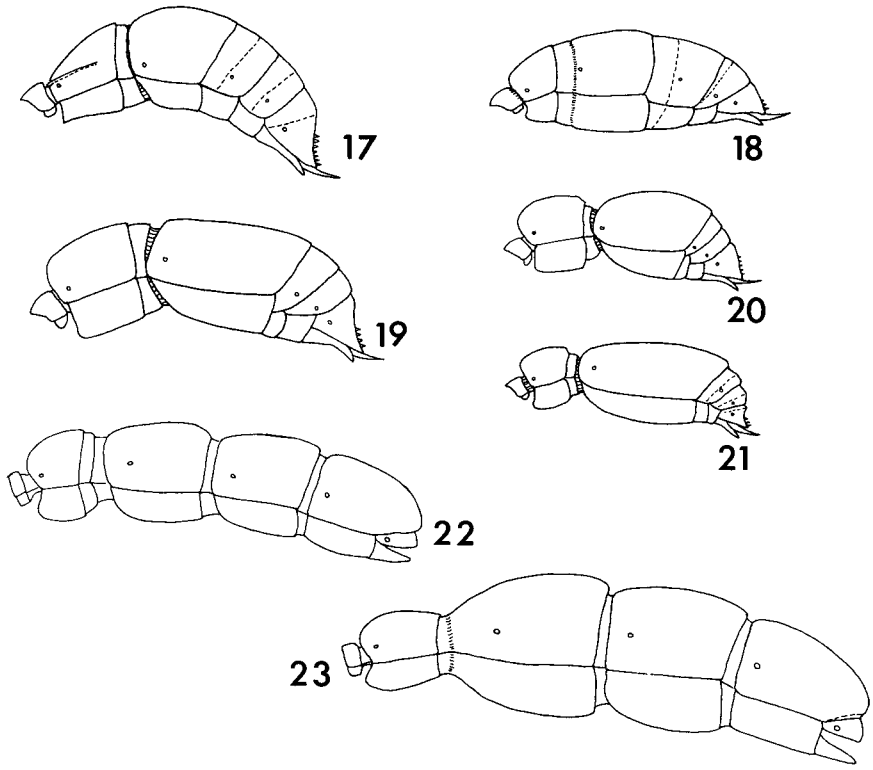
Abdominal segments 5–7 (Fig. 7). Either presclerites not strongly differentiated from postsclerites (i.e. differentiated only by lack of pilosity and weaker sculpture on the former), or pre- and posttergites, pre- and poststernites, or both, separated by weak transverse constrictions or impressions. All spiracles on posttergites, visible. Tergite 7 (pygidium) large and flattened dorsally, the flattened portion armed laterally with weak denticles or teeth. Sternite 7 (hypopygium) downcurved between pre- and poststernite.

Cylindromyrmex: three species examined (one dissected).

Cerapachyini (*Cerapachys, Simopone, Sphinctomyrmex, Leptanilloides*)
(Figs 1–3, 10–23)

Abdominal segment 2 (petiole) (Figs 2, 3, 10, 12, 14, 16). Proprioceptor zone present and usually conspicuous on sternite anteroventrally, in front of the subpetiolar process. Laterotergite sometimes present and discrete, but showing all grades of fusion with the tergite. Posterior foramen of segment 2, where helcium inserts, relatively narrow (Figs 2, 12, 16). Tergite with a short to deep posterior face, most frequently the former (Figs 3, 10, 14). Sternite in ventral view simple at apex and rounded, the sides roughly parallel or converging or diverging slightly posteriorly (Figs 2, 12, 16).

Abdominal segment 3 (Figs 1–3, 10, 11, 13–15, 17–23). Helcium at maximum development broad and deep, almost as broad as anterior width of posttergite in dorsal view; reducing in size from this, in several lines, until its width is less than half that of the anterior posttergal margin. Helcium usually located approximately at midheight on anterior face of segment (Figs 1, 11, 13, 15, 18–23), its dorsum well below the level of the posttergal dorsum and the latter with a short to moderate anterior declivity. Flattening and sloping of the posttergal dorsum may obliterate the anterior declivity in some *Cerapachys*, and bring the helcium, secondarily, to a relatively high point of attachment (Fig. 17). Helcium distinctly narrowed posteriorly, with a deep constriction before its junction with the posttergite. In some species a sharp rim or margin bounds the articulatory portion of the helcium, and a post-helcial neck may be developed in some *Cerapachys* (Figs 15, 20, 21), *Simopone*, *Leptanilloides* (Figs 22, 23) and *Sphinctomyrmex* (Fig. 11). Helcial sternite large and strongly convex, clearly visible in profile and bulging ventrad in frontal view (Figs 1, 11, 13, 15); easily seen in normally mounted specimens. Tergosternal fusion complete, the suture stright or feebly arched. Postsclerites approximately equal in size in profile, or the posttergite slightly larger than the



FIGS 17–23. Profile of abdominal segments 3–7 (= gaster). 17–21, *Cerapachys* species, workers: 17, *C. dumbletoni*; 18, *C.*, undescribed species (in BMNH); 19, *C.*, indeterminate species (in BMNH); 20, *C. nitidulus*; 21, *C. biroi*. 22–23, *Leptanilloides* species, workers: 22, *L. biconstricta* (?); 23, *L.* undescribed species (MCZ).

poststernite. Spiracle clearly visible, on posttergite close to helcium. Segment 3 primitively larger than 2 and smaller than 4, but in *Cerapachys* (Figs 18–21) and *Leptanilloides* (Figs 22, 23) a gradual morphoclinal reduction in the size of segment 3 is exhibited. In its advanced stages this size reduction is extreme, so that segment 3 is scarcely larger than 2 and very much smaller than 4, separating segment 3 as an isolated postpetiole (Figs 21, 23), which may also be very narrow in dorsal view. In species where reduction is marked the posttergite of 3 may develop a small but distinct posterior declivity. Poststernite anteriorly bluntly rounded or bulging forward beneath the helcium. Anterior face of this bulge often with a thickened U- or V-shaped rim separating it from the lateral faces (Figs 13, 15). The edge of this rim may project as a shallow lip-like process when viewed in profile. A morphoclinal modification of this rim can be seen: the V-shape becomes narrower and more centralized until it forms a discrete and solid medioventral process. Maximum depth of segment 3 is usually at about the midlength, but in some the maximum depth occurs at the posterior margin.

Abdominal segment 4 (Figs 1, 11, 15, 17–23). In a couple of undescribed *Cerapachys* (in BMNH) the presclerites are scarcely distinguished from the postsclerites in terms of width (Fig. 18). The diameter of the pretergite plus presternite is hardly less than that of

the posttergite plus poststernite, and a girdling constriction is nonexistent. In general, however, a strong girdling constriction usually separates the pre- and postsclerites. The constriction is frequently more strongly developed ventrally and may be so pronounced that the poststernite is concave anteroventrally (Figs 1, 15). Pretergite and presternite are usually large and convex in outline, the latter often more extensive than the former. Presclerites may be small and narrow in species where segment 3 is much reduced (Figs 20, 21), but even here the presclerites are always much larger than the helcium. Spiracle visible, situated anteriorly on side of posttergite. Posttergite and poststernite about the same size in profile, the postsclerites together larger than those of segment 3 (Figs 1, 15), sometimes enormously larger in species where advanced reduction of 3 has taken place (Figs 19–23). Segment 4 is the largest abdominal segment in all Cerapachyini except in some *Sphinctomymex* where the postsclerites are somewhat reduced and slightly smaller than those of segment 3 (Fig. 11), and in those mentioned below where segments 4–6 or 7 are much the same size. Tergite and sternite not fused.

Abdominal segments 5–7 (Figs 1, 11, 15, 17–23). Either pre- and postsclerites differentiated by lack of pilosity on the former or by a reduction of sculpture, or separated on each segment by strong girdling constrictions (*Sphinctomyrmex*, Fig. 11), or with strong girdling constrictions except preceding segment 7 (*Leptanilloides*, Figs 22, 23). In some *Cerapachys* the postsclerites are set at an angle to the presclerites, and the outline of each segment narrows posteriorly (Fig. 21). In general the segments reduce in size from 4–7, but in *Leptanilloides* and in many *Sphinctomyrmex* segments 4–6 or 4–7 are of much the same size in profile (Figs 11, 22, 23), or segment 6 may even be slightly larger than 5. All spiracles visible. Tergite 7 (pygidium) large and flattened dorsally in *Cerapachys*, *Simopone*, and *Sphinctomyrmex*, the margin of the flattened portion generally armed with denticles, teeth or small spines (Figs 1, 11, 15, 17–21), though these may be reduced in some *Cerapachys* and *Simopone*. In *Leptanilloides* (Figs 22, 23) the pygidium is very specialized, being reduced in size, distinctly displaced ventrally, and partially overhung by the tergite of segment 6; armament of the pygidium has been secondarily lost. Sternite 7 (hypopygium) downcurved posteriorly, usually flattened.

Cerapachys: 94 species examined (14 dissected).
Simopone: eight species examined (three dissected).
Sphinctomyrmex: 10 species examined (four dissected).
Leptanilloides: two species examined (one dissected).

Holophyly of the Cerapachyinae

Analysis of the abdominal characters of cerapachyine ants, and a comparison of the results with ants constituting the remainder of the Ponerinae, shows five critical features. These are discussed below, following which some other characters, both old and new, are mentioned.

(i) *Sternite of segment 2 (petiole)* (Figs 2–5, 8–10, 12, 14, 16)

In ventral view the posterior margin of the sternite in cerapachyines is a simple shallow convexity which projects posteriorly over the helcial sternite (Figs 5, 8). With segments 2 and 3 dissociated (Fig. 2) the posterior foramen of segment 2 is very simple (Figs 2, 12, 16). The tergite forms an arch above and the sternite forms a simple U-shaped floor beneath. The tergite overlaps the sternite laterally and the two are fused

where their margins meet. This arrangement is considered plesiomorphic as it represents the closest approximation to a simple reduced segment, without any superimposed or secondarily derived specialisation.

In contrast the apex of the sternite is complex in ponerines and often highly specialized. It may be truncated, concave, or bilobate; the tergal apex may flare outwards from the sternite; clefts or incisions may be developed on each side between tergite and sternite; complex internal inflections or lobes from the sternite may develop; or combinations of these may occur. Dissociation of segments 2 and 3 in ponerines shows that the posterior foramen of segment 2 is complex and modified away from the simple reduced segment state seen in cerapachyines. All these specializations in ponerines are regarded as apomorphic.

(ii) *Sternite of helcium* (Figs 1–11, 13–15, 17–23)

The cerapachyine helcium, seen in profile, shows a large convex and prominent sternite which is very conspicuous. It is so large that it can be seen in normally mounted specimens, without dissection (Figs 3, 4, 9, 10, 14, 15), and appears to play an important part in the articulation of segments 2 and 3. In front view the helcial sternite is attached (fused) low down on the inner sides of the tergal arch and is strongly convex ventrally (Figs 1, 6, 7, 11, 15). Its lowest point always projects well beyond the lower margins of the helcial tergite.

The ponerines show a much reduced helcial sternite which is not nearly so convex. In profile the sternite is invisible and the helcium appears to consist solely of the tergite. Frontal view reveals that the sternite is small, only weakly convex to flat, and runs transversely between the inner walls of the tergal arch, being attached (fused) well above the lower tergal margins.

The state of the helcium in cerapachyines is regarded as plesiomorphic, that of the ponerines as apomorphic. The cerapachyine condition reflects the closest approximation of the ancestral segment shape, with a simple arched tergite and sternite and with both sclerites visible.

(iii) *Spiracles of segments* 5–7 (Figs 1, 6, 7, 11, 15, 17–23)

The spiracles of segments 5–7 are all visible in cerapachyines without artificial distension or dissection of the gaster. In general they are situated on the posttergite of each segment, just behind the posterior margin of the preceding tergite. In some species the spiracle may be very close to the pre-posttergal boundary. (This condition also occurs in the subfamilies Dorylinae and Ecitoninae.)

In ponerines the spiracles of segments 5–7 are not visible without artificial distension or dissection of the gaster. The spiracle of segment 5 is on the pretergite but very close to the pre-posttergal boundary; it may be revealed with only a slight retraction of the posttergite of segment 4. The spiracles of segments 6–7 are far forward on each pretergite and are fully concealed by the posttergites of the preceding segments.

Examination of 'lower' poneroid groups such as Myrmeciinae and Pseudomyrmecinae, considered primitive on many morphological grounds, and of lower aculeates such as *Tiphia*, indicates that the plesiomorphic condition in poneroid ants is that exhibited by the Ponerinae; and hence the cerapachyines are apomorphic in these characters.

(iv) *Tergosternal fusion of segment 4*

The tergite and sternite of segment 4 are unfused in the cerapachyines, fused in the ponerines. The fused condition is apomorphic and thus the cerapachyines express the plesiomorphic condition.

(v) *Tergite of segment 7 (pygidium)* (Figs 1, 6, 7, 11, 15, 17–23)

Except for the aberrant and derived *Leptanilloides* the cerapachyines show a remarkably uniform pygidial structure, as first pointed out by Brown (1954). Throughout the group the posttergite is flattened dorsally and slopes steeply posteriorly. The edges of the flattened portion are marginate and the margins are equipped with denticles, teeth or peg-like spines. In *Leptanilloides* (Figs 22, 23) specialization is taken further as the pygidium is reduced, displaced ventrally, and partially overhung and concealed by the sixth tergite when seen in dorsal view.

Among the ponerines the pygidium is usually an evenly rounded unmodified sclerite similar to tergites 5 and 6. A number of ponerine species have the dorsal rim of the hypopygium armed with teeth or spines (*Ophthalmopone berthoudi*, *Paraponera clavata*, *Amblyopone* species of the *reclinata*-group), but only a single species of *Pachycondyla*, *P. crassinoda*, out of more than 100 in that genus, shows a flattened pygidium armed with a pair of spines. As this species stands alone and otherwise shows all the many apomorphies of tribe Ponerini (none of which is shared with the cerapachyines; paper in preparation) this development is an autapomorphy in this isolated species. It is probably analogous with the cerapachyine condition but is certainly not homologous with it.

Workers of the genus *Dorylus* have a medially impressed pygidium which may be sharply marginate laterally. Pygidial armament in this genus is, however, restricted to a single pair of posteriorly directed cuticular spines or teeth, and is certainly not homologous with the specializations seen in the cerapachyines.

The highly derived and specialized state of the cerapachyine pygidium is considered apomorphic with respect to the plesiomorphic ponerine condition.

(vi) *Metacoxal cavities* (Figs 2, 5, 8, 12, 16)

Throughout the cerapachyines the metacoxal cavities are completely closed. By this I mean that an unbroken sclerotised annulus surrounds the cavity in which the metacoxa (=hind coxa) articulates. Thus the metacoxal cavities are fully separated from the cavity in which the petiole (abdominal segment 2) articulates.

In lower aculeates the metacoxal cavities are wide open, and confluent with the cavity of the petiolar articulation. The ponerines have metacoxal cavities which are either open, though not as broadly so as in lower aculeates, or an annulus is almost complete but interrupted medioventrally by a mobile suture or break in the annulus.

The only exceptions so far detected in the ponerines occur in a few unrelated small isolated genera which also tend to be very specialized in many other ways. In these the metacoxal cavities are closed. I currently consider this to be autapomorphic in each of the small genera in which it occurs (*Discothyrea*, *Probolomyrmex*, *Harpegnathos*). These genera do not exhibit any other cerapachyine characters.

(vii) *Earlier characters*

A number of characters have earlier been listed as apomorphies of the cerapachyines, principally by Emery (1911) and Brown (1975). These include a biaculeate male subgenital plate (abdominal sternite 9), a lack of cerci on the male genitalia, the shape of the larval mandibles, the form and function of the antennae and their insertions, and the elongate cylindrical body shape in the females and workers (for discussion see Brown, 1975). All of these are accepted as being apomorphic with respect to the ponerines.

Conclusion

The evidence gathered here indicates most strongly that the cerapachyines constitute a holophyletic lineage among the poneroid ants. When viewed across the whole Formicidae the characteristics isolating the cerapachyines are of the same magnitude as those which define taxa at the subfamily level. I therefore propose that the subfamily name Cerapachyinae be reinstated, to include the taxa listed below. The possible relationship of Cerapachyinae with the subfamilies Dorylinae and Ecitoninae remains to be investigated in detail. A real possibility exists that these subfamilies together may form a closely related group. However, the Cerapachyinae alone, or grouped with Dorylinae and Ecitoninae, stand apart from the Ponerinae.

Diagnosis of subfamily

Subfamily CERAPACHYINAE subfam. rev.

Cerapachysii Forel, 1893: 162. (Ponerinae, tribu Cerapachysii.) *Type-genus*: *Cerapachys* Smith, 1857: 74.

Cerapachyinae: Wheeler, 1902: 185. (As a group within Ponerinae.)

Prodorylinae Emery, 1909: 355. (Ponerinae, Hauptgruppe Prodorylinae.) Unavailable name, not based on a genus-level taxon (see Wheeler, 1920: 51).

Cerapachyinae: Wheeler, 1920: 51. (Raised to subfamily status.)

Eusphinctinae Clark, 1951: 15 (diagnosis in key). *Type-genus*: *Eusphinctus* Emery, 1893: cclxxv (= *Sphinctomyrmex* Mayr, 1866: 895; synonymy by Brown, 1975: 31). Syn. n.

Cerapachyinae: Brown, 1975; 14. (As synonym of Ponerinae.)

Diagnosis of workers and females

Heavily sclerotized elongate, parallel-sided and roughly cylindrical poneroid ants which are termitophagous or myrmecophagous. With the following combination of characters.

1 Clypeus short and narrow; antennae inserted close together and close to anterior margin of head.
2 Antennae short and thick, projecting anteriorly in life; frontal lobes frequently much reduced.
3 Mandibles short and thick, subtriangular, closing tightly against the clypeus.
4 Alitrunk in worker generally fusiform and box-like, without promesonotal suture except in 1–2 *Cerapachys* species and in *Leptanilloides*.
5 Metacoxal cavities closed; metapleural lobes present.
6 Propodeal spiracle low on side in profile, small, circular, at or behind the midlength; not associated with an endophragmal pit.
7 Waist generally of a single separated sessile segment (the petiole, (= abdominal segment 2), usually also with a deep constriction between abdominal segments 3 and 4. Rarely abdominal segment 4 reduced to a small postpetiole.
8 Depressed proprioceptor zone present anteroventrally on petiolar sternite.
9 Posterior margin of petiolar sternite simple and rounded in ventral view.
10 Sternite of helcium large and convex, visible in profile; helcium located at about midheight of abdominal segment 3, or higher, when viewed in profile.
11 Tergosternal fusion of abdominal segment 3 complete; segments 4–7 with tergites and sternites unfused.
12 Abdominal segment 4 strongly tubulate anteriorly.
13 All spiracles visible on abdominal segments.
14 Pygidium large, with dorsum flattened; lateral margins of flattened area armed with denticles, small teeth or peg-like spines; or pygidium reduced and overhung posteriorly by sixth tergite (in which case strong girdling constrictions occur between segments 4 and 5, and 5 and 6).
15 Sting large and strongly developed.

Diagnosis of males (provisional)

With ponerine habitus but specialized as follows.

1 Mandibles triangular to falcate, edentate.
2 Subgenital plate (sternite of ninth abdominal segment) biaculeate.
3 Genitalia lacking cerci.

Constituents of subfamily Cerapachyinae

Tribe Acanthostichini. Genus: *Acanthostichus.*
Genus: *Ctenopyga.*
Tribe Cylindromyrmecini. Genus: *Cylindromyrmex* (= *Holcoponera*, = *Hypocylindromyrmex*, = *Metacylindromyrmex.*)
Tribe Cerapachyini. Genus: *Cerapachys* (= *Ceratopachys*, = *Chrysapace*, = *Cysias*, = *Lioponera*, = *Neophyracaces*, = *Ooceraea*, = *Parasyscia*, = *Phyracaces*, = *Procerapachys*, = *Syscia.*)
Genus: *Leptanilloides.*
Genus: *Simopone.*
Genus: *Sphinctomyrmex.* (= *Aethiopopone*, = *Eusphinctus*, = *Nothosphinctus*, = *Zasphinctus.*)

For complete revision of these tribes and genera, and species-level keys, see Brown, 1975.

Zoogeographical synopsis of Cerapachyinae

The table below summarizes the number of described cerapachyine species of the world and indicates their zoogeographical distribution. The Afrotropical and Malagasy are recorded as separate regions; the Indo-Australian region includes New Guinea and the Pacific island systems. Widely distributed species which occur in more than one region are recorded here under the region containing their type-localities. Many new species of cerapachyine ants await description in the major collections of the world.

Abbreviations of the zoogeographical regions are: Ne, Nearctic; No, Neotropical; Pa, Palaearctic; Af, Afrotropical; Ma, Malagasy; Or, Oriental; In, Indo-Australian; Au, Australasian.

	Region								
	Ne	No	Pa	Af	Ma	Or	In	Au	Total
Acanthostichus		9							9
Ctenopyga	1								1
Cylindromyrmex		10							10
Leptanilloides		1							1
Sphinctomyrmex		1		2		2	1	16	22
Simopone				9	3		3		15
Cerapachys	2	4	5	25	4	13	41	45	139
Total	3	25	5	36	7	15	45	61	197

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