

Research paper

A new *Neocalamites* (Sphenophyta) with prickles and attached cones from the Upper Triassic of China

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Abstract

Remains of the extinct sphenophyte (horsetail) *Neocalamites* are most widespread in the Middle–Upper Triassic and are typically represented by stem and leaf fragments. Here we report on spectacular new finds of *Neocalamites* from the Late Triassic Yangcaogou Formation in Liaoning Province, China that include bedding surfaces dominated by nearly complete aerial stems with attached leaf whorls and rare bractless cones. They reveal a monopodial growth habit for the stems, which are covered with downward projecting prickles that probably provided protection against herbivores. These features provide the basis for a new proposed species, *Neocalamites horridus*. The nodes bear whorls of very long leaves mainly free to their bases, and one specimen bears an attached cone on a long peduncle. Identical dispersed cones have also been recovered. The leaves of adjacent monopodial stems most likely interlocked to support growth in large stands akin to the role now played by branches in large modern *Equisetum* species. The new Chinese *Neocalamites* is among the most confidently reconstructed species, and indicates a greater diversity of sphenophyte morphology during the Mesozoic than previously realized.

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1. Introduction

Large sphenophytes assigned to *Neocalamites* range from the Upper Permian through the Jurassic, but are particularly common in Middle–Upper Triassic assemblages in many parts of the world. Despite this, few of these plants have been confidently reconstructed and, therefore, their role in the evolutionary history of the sphenophytes is debated (Escapa and Cúneo, 2006). Unusually complete specimens from the Upper Triassic Yangcaogou Formation in northern China are described here, which provide new morphological details that verify some previous concepts, and also document features never before reported for *Neocalamites*.

The original report on the rich flora of the Yangcaogou Formation by Zhou (1981) included *Annulariopsis*, *Cycadocarpidium*, *Dictyophyllum*, *Glossophyllum*, *Neocalamites*, *Pterophyllum*, and many other taxa. More recently described taxa include new species of *Leptostrobus* (Liu et al., 2006), *Sorosacculus* (Liu et al., 2005), *Umkomasia* (Zan et al., 2008), and *Leptocycas* (Zhang et al., 2010). Zhou's (1981) original identification of *Neocalamites rugosus*, which is considered conspecific with *N. asperimus* by Shen (1990), was based on stem sections with supposed characteristic wrinkled surfaces. However, it has been suggested that the wrinkled texture of this species could be an artifact of preservation (desiccation), and that affinity with *Equisetites* cannot yet be ruled out (Kustatscher and VanKonijnenburg-van Cittert, 2008). Our recent collections include many essentially complete aerial stems of the Yangcaogou sphenophyte with well-preserved leaf whorls clearly indicating affinity with *Neocalamites*. The new specimens also

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have recurved prickles on the stem surfaces and cannot, therefore, be assigned to *N. asperrimus* regardless of its actual generic affinities. Furthermore, the unbranched architecture of these specimens is different from most other known fossil sphenophytes. Based on these features, we refer the Yangcaogou *Neocalamites* to a new proposed species. This material is also significant for including a specimen with an attached cone, which is very rare for any *Neocalamites*.

2. Geological setting

The fossils described here were all collected from the Yangcaogou Formation outcrops in Yangcaogou Village, Liaoning Province, China. We consider the Late Triassic age estimate, which is based mainly on the composition of the fossil flora, most likely (Zhou, 1981; Liu et al., 2005; Zhang et al., 2010); however, an Early Jurassic age cannot be entirely ruled out based on the conchostracan fauna (Liu, 1987). The best-preserved fossil plants, including the *Neocalamites* described here, come from an 18 m thick interval of bedded yellow-green sandstones and siltstones interbedded with mudstones and carbonaceous shales. These layers are interpreted as a shallow lake and swamp facies (Zan et al., 2008; Zhang et al., 2010). Some layers contain many specimens of the new *Neocalamites* and little else other than occasional *Podozamites* and *Annulariopsis* branches.

3. Materials and methods

Due to their large size, the shale and siltstone slabs bearing the *Neocalamites* axes must be removed from the outcrop in sections and reassembled in the lab. This is significant to note, as specimens from this locality are commonly seen in fossil markets and in some cases appear to be composites enhanced with paint rather than singular specimens. Therefore, the descriptions here are based on specimens observed by the authors in the field, and from previously collected specimens for which authenticity could be verified by detailed matching of part and counterpart slabs. The part and counterpart slabs of the holotype specimen are both illustrated here to demonstrate this point (Fig. 1A).

The specimens are typically preserved as tan to reddish stained impressions on fine-grained, gray shale with occasional coaly material adhering. They can be observed and studied directly on the matrix surfaces. All the specimens observed to date are laterally compressed; therefore, no stem cross-sections, nodal diaphragms, or pith casts are known. No cuticles or spores could be recovered, probably due to the thermal maturity of the sediments.

4. Systematic paleontology

Phylum Sphenophyta

Genus *Neocalamites* (Halle) Vladimirovicz, 1958

Neocalamites horridus Zan, Axsmith, Escapa, Fraser, Liu et Xing n. sp.

(Figs. 1A, B and 2A–E)

Holotype: Specimen no. GMC P1513 is here designated as the holotype (Fig. 1A).

Additional studied materials: Specimen no. GMC P1512 (Fig. 1B); specimen no. GMC P1514 (Fig. 2A); specimen no. GMC P1515 (Fig. 2B); specimen no. GMC P1516 (Fig. 2C); specimen no. GMC P1511 (Fig. 2D); specimen no. GMC P1517 (Fig. 2E).

Repository: The Geological Museum of China (GMC), Beijing, China.

Locality: Yangcaogou Village, Beipiao County, Liaoning Province, China.

Horizon: Yangcaogou Formation, Upper Triassic.

Etymology: The specific epithet *horridus* refers to the prickly aerial stem surfaces, which would have been unpleasant to the touch.

Diagnosis: Aerial stems tall, unbranched except for rare attached cones at the nodes; stem surfaces covered with downwardly projecting prickles; nodes with whorls of long leaves; cones born singly at nodes on long, unbranched peduncles, cone axis bearing whorls of closely spaced, peltate sporangiophores, bracts lacking.

Description: *Neocalamites horridus* is represented by many largely to partially intact aerial stems with whorls of attached leaves (Fig. 1A and B). The largest stems were at least 2.7 m tall based on field observations, and 8.5 cm wide at the base. The nodes are up to at least 12 cm long near the stem base, becoming shorter toward the apex (Fig. 2A). None of the observed specimens show any lateral branches (other than rare cones), buds, or branch scars. The stem surfaces show faint longitudinal striations, especially on the most distal internodes, and are also covered by prickles that are randomly arranged (about 35 per cm²). The prickles are each up to 5 mm long and typically recurved (Fig. 2B and C). Small pit-like structures correspond to the attachment points of the prickles when viewed perpendicular to the bedding plane (Fig. 2B–D). The nodes bear whorls of about thirty mostly free leaves (Figs. 1A, B and 2A, B). Individual leaves are typically 1.5 mm wide at the base and up to at least 30 cm long with a single, central vascular strand. There is occasional fusion of some leaves, especially in the most distal leaf whorls (Fig. 1A). Rare attached cones occur singly at the nodes of the upper third of the stems on long (about 6.6 mm) peduncles (Fig. 2D). The peduncles superficially resemble the bases of leaves but can be distinguished by being slightly more raised from the matrix, the lack of a midvein, and very fine longitudinal striations. The cone axes are up to about 35 mm long and bear about thirty whorls of sporangiophores. Individual sporangiophores consist of basal stalks about 1.4 mm long, and distal, polygonal heads about 0.8 mm in diameter. The cones lack bracts (Fig. 2D and E). Details of the arrangement of sporangia on the sporangiophore heads could not be determined due to preservational limitations. Associated cones of this kind also rarely occur scattered among the aerial stems (Fig. 2E).

5. Discussion

The genus *Neocalamites* was introduced by Halle (1908) to separate three species previously included by Schimper (1869) in the genus *Schizoneura*. The main criterion Halle (1908)

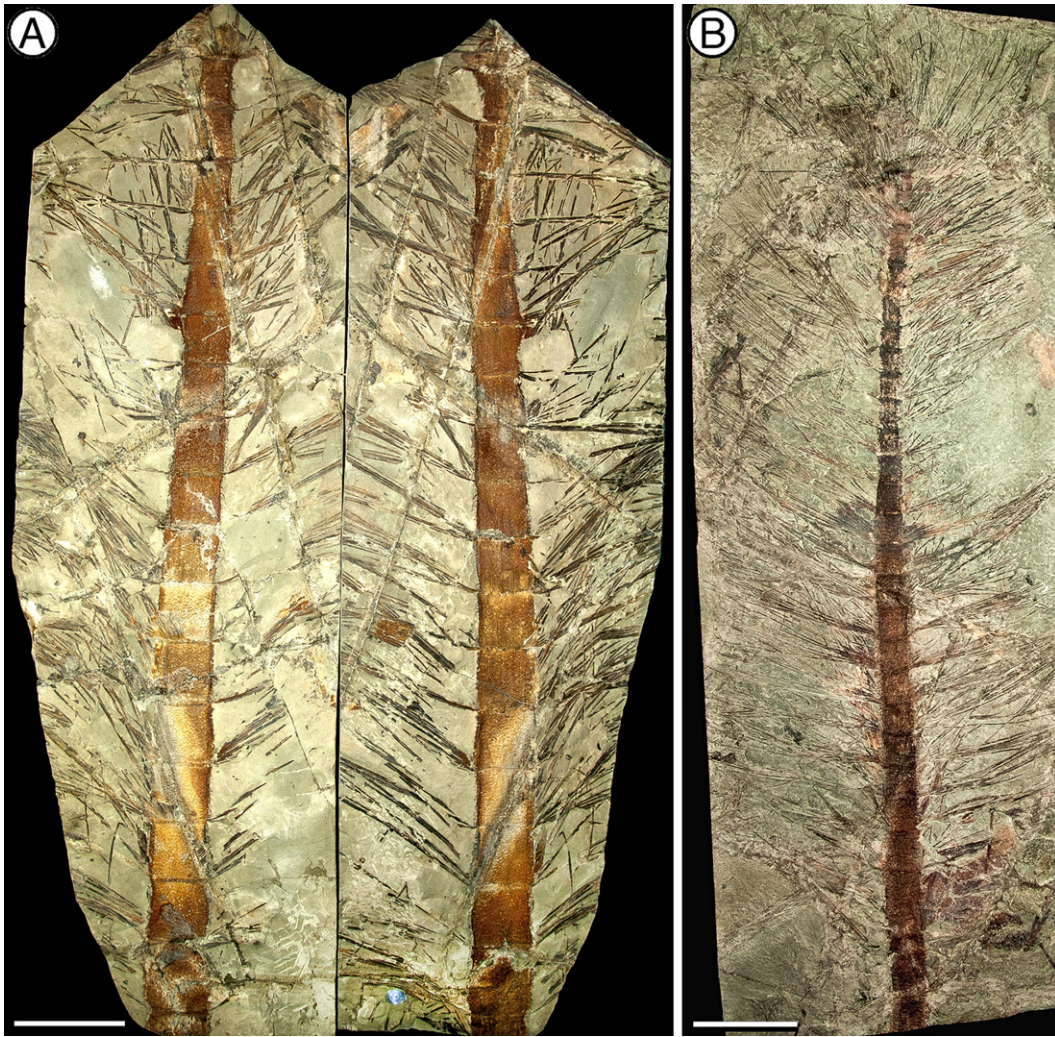


Fig. 1. *Neocalamites horridus* n. sp. stems with attached leaves from the Yangcaogou Formation of China. (A) Holotype specimen showing part and counterpart slabs (specimen no. GMC P1513), scale bar = 10 cm; (B) nearly complete aerial stem with attached leaves (specimen no. GMC P1512), scale bar = 10 cm.

proposed for delimiting *Neocalamites* from other Mesozoic and recent sphenophytes is the presence of free leaves that are longer than the longest internodes; however, the late Paleozoic and Mesozoic sphenophytes in general exhibit considerable variation in the degree of leaf fusion. For example, Harris (1931) documented specimens of *N. carcinoides* from the Triassic of Greenland with fused leaves similar to those more typical of the morphogenus *Schizoneura*. This, along with other examples of vague morphogenus boundaries, led Harris (1931) to recommend that the intermediates should be placed in the genus they resemble most closely. Therefore, the occasional presence of fused leaves reported here (Fig. 2A) in no way negates the attribution of the Chinese fossils to *Neocalamites*.

The new *Neocalamites* remains are densely distributed on some bedding planes. The figured specimens are relatively rare isolated stems chosen for clarity (Fig. 1A and B). Although the stems are sometimes randomly oriented, they are rarely bent. This, and the common presence of attached narrow leaves, indicates that the plants were not transported, or were transported only a short distance before burial. Furthermore, there is no evidence on any of the numerous specimens of any lateral branches

(other than a single attached cone at a node), branch scars, or lateral buds. This supports our interpretation of the growth of large, closely packed stands of plants consisting of completely monopodial aerial stems. No rhizomes have been observed. The long leaves of adjacent stems would have provided an interlocking support similar to that of modern-day stands of large *Equisetum* species or bamboo. However, the lateral structures in large modern sphenophytes, such as *E. giganteum*, are branches rather than leaves as in the Chinese fossils.

One of the most remarkable and diagnostic features of *Neocalamites horridus* is the presence of abundant recurved prickles on the stem surfaces (Figs. 1A, B and 2B–D). We employ the term prickles here instead of spine or thorn as they most likely represent epidermal and perhaps some subepidermal tissue rather than a modification of lateral organs such as leaves, branches, or sporangiophores. This is based on the essentially random orientation of these structures on the internode surfaces. All lateral organs of the sphenophytes throughout their entire long history have a whorled arrangement or are derived clearly from this condition and are, therefore, unlikely homologs for the structures considered here to be prickles. These structures probably did

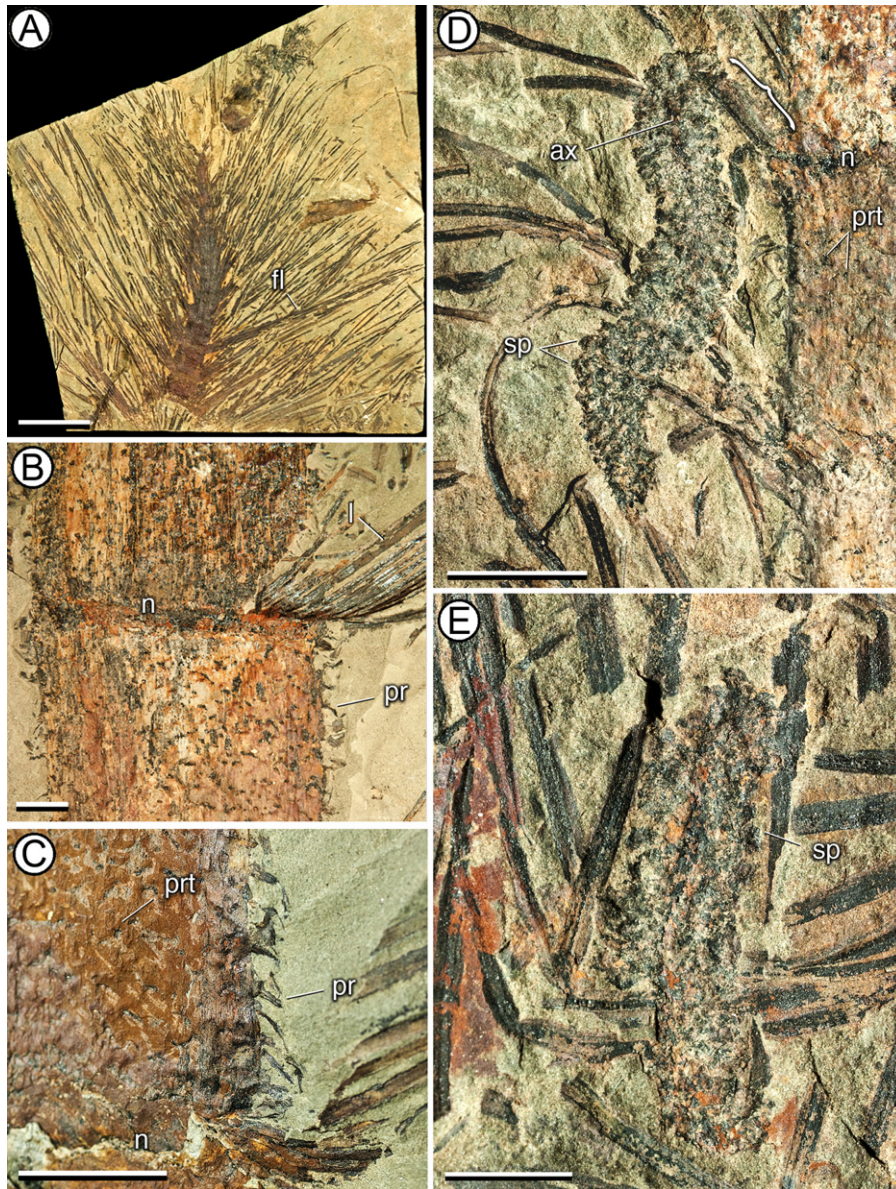


Fig. 2. Stem details and cones of *Neocalamites horridus* n. sp. (A) Stem apex showing short internodes and attached leaves, some in fused groups (fl) (specimen no. GMC P1514), scale bar = 2 cm; (B) detail of nodal region (n) showing attached leaves (l) and prickles (pr) (specimen no. GMC P1515), scale bar = 5 mm; (C) close-up of stem surface showing prickles (pr) in lateral view, prickle attachment points (prt) in plan view (specimen no. GMC P1516), scale bar = 1 cm; (D) complete cone attached at node (n) showing cone peduncle (bracket), cone axis (ax), sporangiophores (sp), and the adjacent axis showing prickle attachment points (prt) (specimen no. GMC P1511), scale bar = 5 mm; (E) dispersed cone among leaves showing sporangiophores (sp) (specimen no. GMC P1517), scale bar = 5 mm.

not play a significant role in interlocking the stems, as the leaves probably filled this function. It is more likely that they served to discourage herbivory by vertebrates or insects, as there is a growing body of evidence for herbivory defense mechanisms in Triassic floras (e.g., Grauvogel-Stamm and Kelber, 1996; Pott et al., 2012).

This is the first report of prickles, or any other form of external armament, in a fossil sphenophyte. Small spine-like projections were reported emerging from epidermal cells of the Late Jurassic species *Equisetum thermale* (Channing et al., 2011), but these do not extend beyond the cuticle layer and could not have functioned as armament. Small, pointed epidermal outgrowths referred to as “tubercles” have been reported in some extant sphenophytes, such as *Equisetum pratense* and *E. sylvaticum*

(Van Cotthem, 1970). These structures occur in rows along the ridges, and are probably not strictly homologous with the scattered structures in *Neocalamites horridus*. The function of the tubercles in extant *Equisetum* has not been discussed to our knowledge, but based on their small size they may be involved in mutual support as in the superficially similar angiosperm *Galium*. In any event, the prickles in *Neocalamites horridus* are the first account in this genus and perhaps the only true example of armament in any fossil or extant sphenophyte.

Cones associated with *Neocalamites* — which are usually referred to the organ genus *Neocalamostachys* when found isolated — have been infrequently reported, and attached cones are especially rare (Dobruskina, 1995). The cones of the new *N. horridus* specimens agree with all other accounts of *Neocalamites*

cones in being composed of whorls of small sporangiophores with no intercalated whorls of bracts (Fig. 2D and E). They are very close in overall dimensions and morphology, including the long peduncle, to the dispersed cone *Neocalamostachys pedunculatus* from the Upper Triassic of Japan, which is closely associated with vegetative remains assigned to *Neocalamites hoerensis* (Kon'no, 1962). Essentially similar cones or cone fragments are also associated with vegetative material assigned to *Neocalamites merianii* from Triassic of Lunz (Pott et al., 2008), *N. hoerensis* from the Triassic of Madygen in middle Asia (Dobruskina, 1995), and specimens from the Upper Permian of Argentina (Escapa and Cúneo, 2006). *Neocalamostachys arrondoii* from the Triassic of Argentina, which is associated with shoots assigned to *Neocalamites carrerei*, is also similar, but has only six to eight larger sporangiophores per whorl (Brea and Artabe, 1999). Other than the new Chinese material, the only attached cone from the Triassic is a specimen attributed to *Neocalamites* aff. *carrerei* from Russia (Vladimirovich, 1958). This specimen agrees with the new Chinese species in having the cones attached singly on long peduncles at the nodes. The only other report of an attached cone is that of *Neocalamites tabulatus* from the Upper Permian of Russia, which differs significantly from all other known forms in having sessile cones attached terminally as well as laterally. However, we suggest that attribution of this species to *Neocalamites* is questionable based on its leaves, which are much shorter than the internodes. The rarity of attached or associated cones in all *Neocalamites* species, including the new species described here, probably indicates that these sphenophytes reproduced primarily asexually.

Comparison of the growth habit of the new Chinese *Neocalamites* with that of other species is difficult. Despite the common reports of *Neocalamites* in many floras, most of the material is fragmentary and the overall growth habit is difficult to determine conclusively, which makes comparisons of any kind challenging (Boureau, 1964). Comparisons are also hindered by descriptions that are often based on overlapping characteristics of uncertain systematic significance, compounded by the confusing nomenclature history of the numerous described species. For example, Pott and McLoughlin (2011) have called attention to the work of Weber (1968), who convincingly argued that the type species, which is usually reported as *N. hoerensis*, should actually be called *N. lehmannianus*. Weber (1968) also suggested that the commonly reported species *N. merianii* and *N. carrerei* are not clearly distinguishable from the type species, and seem to differ only in stratigraphic and geographic ranges. Unfortunately, these findings were overlooked by subsequent workers, and indicate the need for a major systematic and taxonomic revision of the genus (Pott and McLoughlin, 2011).

With the above caveats in mind, the most well reconstructed *Neocalamites* species described to date were apparently composed of at least two orders of aerial branches. For example, Pott et al. (2008) verified the profusely branched growth habit of fossils historically assigned to *N. merianii* from the Lunz flora of Austria based on the occurrence of discrete size classes of shoots, and a portion of shoot apex with attached lateral branches. Harris (1931) reconstructed *N. carcinoides* from the Greenland Triassic as a tall gregarious plant with two types of lateral branches,

and *N. hoerensis* has lateral branches not usually borne in regular whorls. The Korean Triassic species *N. koraiensis* is also known from axes bearing 10–16 narrow branches at each node (Kon'no, 1962). *Neocalamites* has been reported from several North American sites and includes very large, upright trunk specimens from the Chinle Formation that rival the Paleozoic *Calamites* in size (Holt, 1947); however the overall branching pattern of these specimens is unknown. *N. knowltoni* from the Triassic of Virginia had at least one order of small lateral branches (Berry, 1912) bearing *Annularia*-like leaves. The first *Neocalamites* from the Permian of Gondwana also bore lateral branches (Escapa and Cúneo, 2006). With the large number of specimens available for examination, it is clear that the aerial stems of the new Chinese species *N. horridus* described here, by contrast, were completely monopodial except for very rare cones at the nodes (Fig. 1A and B). There is also no evidence for branch scars or dormant lateral buds. Although it is not known for sure if some other *Neocalamites* species were monopodial, the monopodial nature of *N. horridus* is unequivocal and this growth habit appears to be rare, if not unique, in *Neocalamites*. This feature, and the unique presence of the recurved prickles, provides ample justification for recognizing the Chinese fossils as a new species.

6. Conclusions

Due to the presence of the abundant, well-articulated specimens, *Neocalamites horridus* is now among the most completely reconstructed Mesozoic sphenophytes. As such, it agrees with several previously established concepts of the genus including the presence of large stems with whorls of elongate leaves usually free to the base, and cones lacking whorls of bracts. However, it differs from the other well-reconstructed species in having completely monopodial aerial stems. The presence of abundant prickles on the stem surfaces is the most remarkable feature and is otherwise completely unknown in any other fossil sphenophyte.

Although *Neocalamites horridus* is relatively well reconstructed, nothing is known regarding several critical features including the rhizomes, pith structure, sporangia, or spores. As the fossils are all impression/compressions, the internal anatomy is also unknown. These features are also unknown for many other *Neocalamites* species, and this is a likely factor in the diversity of opinion regarding the phylogenetic significance of the genus. In fact, it is not even certain if the currently included species collectively constitute a natural group. With these limitations in mind, we note that *Neocalamites* has classically been considered as intermediate between the extinct, arborescent Calamitaceae and the extant Equisetaceae (Good, 1975). This hypothesis is supported by the bractless cones (as in the Equisetaceae) in combination with the arborescent habit and unfused leaves (as in the Calamitaceae). In addition, permineralized stems from the Triassic of Germany attributed to *N. merianii* are similar to those of extant *Equisetum*, including the arrangement of the carinal and vallecular canals, and the lack of secondary xylem (Brunner and Kelber, 1988). However, new fossil evidence from different Permian localities has inspired alternative scenarios. For

example, Naugolnykh (2009) has recently proposed that *N. tubulatus* represents an intermediate form between the family Tchernoviaceae and the *Equisetites–Equisetum* lineage (see also Cúneo and Escapa, 2006). It is also possible that *Neocalamites* could represent a totally extinct group, probably derived from the Paleozoic Calamitaceae, in which the loss of bracts in the cones and secondary xylem in the stems occurred independently from the Equisetaceae. Testing of these and other proposed hypotheses will require future detailed phylogenetic analyses, and should be based on well-reconstructed terminal species rather than synthetic concepts based on fossils of uncertain relationship. In any case, the new *N. horridus* fossils described here increase our knowledge of the structural diversity of sphenophytes, and provide yet another example of an unexpected taxon from the remarkable Mesozoic deposits of northeastern China.

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