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Phylogeny of some Devonian trilobites and consequences for the systematics of *Austerops* (Phacopidae)

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A comprehensive phylogenetic hypothesis for Devonian phacopid trilobites of the genus *Austerops* has not previously been proposed. We carried out a cladistic analysis of the 13 species and subspecies assigned to *Austerops*, based on a data matrix of 63 characters. Two species of the morphologically very similar genus *Chotecops*, *C. auspex* and *C. hoseri*, and seven other close relatives (*Reedops cephalotes hamlagdadianus*, *Boeckops stelcki*, *Morocops granulops*, *Paciphacops logani*, *Phacops latifrons*, *Phacops araw* and *Pedinopariops (Hypsipariops) vagabundus*) were also included in the analysis in order to test their relationship with species of *Austerops*. Parsimony analyses using a heuristic method, with *Calypptaulax callirachis* and *C. glabella* as outgroup taxa, produced two most parsimonious trees of 341 steps. These trees are partly consistent with trees obtained from additional analyses performed with modified data sets (deletion of homoplastic characters, multistate characters, continuous characters carved into 5% increments, thoracic and pygidial characters, or taxa with numerous unknown characters). Results suggest that *Austerops* sp. B and A.? sp. D are close to *Chotecops hoseri* and *C. auspex*, and that these species constitute a monophyletic group. *Austerops* *Austerops menchikoffi*, *A. speculator* and *A. punctatus* are also a monophyletic group and reasonably constitute a sister group of that formed by the rest of *Austerops* and *Chotecops* sensu lato, while *A. hottonensis* seems phylogenetically distant from other representatives of *Austerops*. *Chotecops* including *C. hoseri* and *C. auspex* together with *Austerops* sp. B and A.? sp. D seem derived from *A. legrandi*. The relationship between *Austerops* and *Chotecops* remains partly unresolved but it seems likely that their recognition as separate taxa results in paraphyletic groups. The phylogenetic analysis suggests that the currently poorly known *Austerops* sp. B and A.? sp. D should be reassigned to *Chotecops*.

Keywords: Arthropoda; Lower and Middle Devonian; cladistic relationships; North Africa

Introduction

Significant biological events took place during the Phanerozoic (Walliser 2012). The explanation for the disappearance of some species over geological time has become a major scientific and societal concern: biologists try to figure out current extinctions and their potential consequences, whereas palaeontologists contribute to this effort by analysing the loss of biodiversity on a deep-time scale. These two approaches, despite using different scales and data, converge by both using phylogeny. This convergence has already revealed that past extinctions are phylogenetically non-random: taxa in some lineages are more extinction-prone than others (Purvis 2008; Hardy *et al.* 2012). Reconstructing phylogeny is thus a major scientific issue and a prerequisite to evolutionary studies in order to identify factors that profile biodiversity at a broad scale and how species respond (Neige *et al.* 2013). In addition, this phylogenetic framework could help to identify heterochronic processes (Crônier *et al.* 2004, 2005, 2011) and modalities of evolution of ancient species (Eldredge 1972; Vrba 1980; Congreve 2013). It is well known that trilobites have been used as support for the concept of punctuated equilibria (Eldredge & Gould 1972), and interesting to note that the foundation of this model is based on a trilobite phylogeny (cf. Eldredge 1972). Trilobites represent an important part of the Devonian macrobenthic fauna. They experienced great diversification during the eustatic sea level rise of the Basal Pragian Event (House 2002) and the related climate warming (Vacek 2011). This event probably contributed to the widening of shallow marine carbonate realms favourable for the development of trilobite communities (Chlupac 1994; Crônier & Van Vierssen 2007; Khaldi *et al.* 2016), leading to the maintenance of family-level diversity, which lasted with some minor changes until the early Eifelian. The subsequent general decline of trilobites was strongly

accelerated by the Kacak and Taghanic events, in the late Eifelian and middle Givetian, respectively. These events were associated with major rises in sea level and led to more widespread extinctions (Chlupac 1994; Crônier & Van Vierssen 2007; McKellar & Chatterton 2009).

Devonian trilobites are especially well represented and diverse in North Africa. Originally part of a regionally continuous Gondwana passive margin, the North African platform experienced an increase of epeirogenic activity during Devonian times, reflecting the initial collision between Gondwana and Euramerica and the progressive creation of Pangaea (Boote *et al.* 1998). During this episode, intracratonic basins were created, such as the Tindouf, Ma'ader and Tafilalt basins of Morocco, and the Ougarta Basin of Algeria. In these basins, carbonate production led to carbonate-dominated facies and brought favourable conditions for the development of trilobites (McKellar & Chatterton 2009).

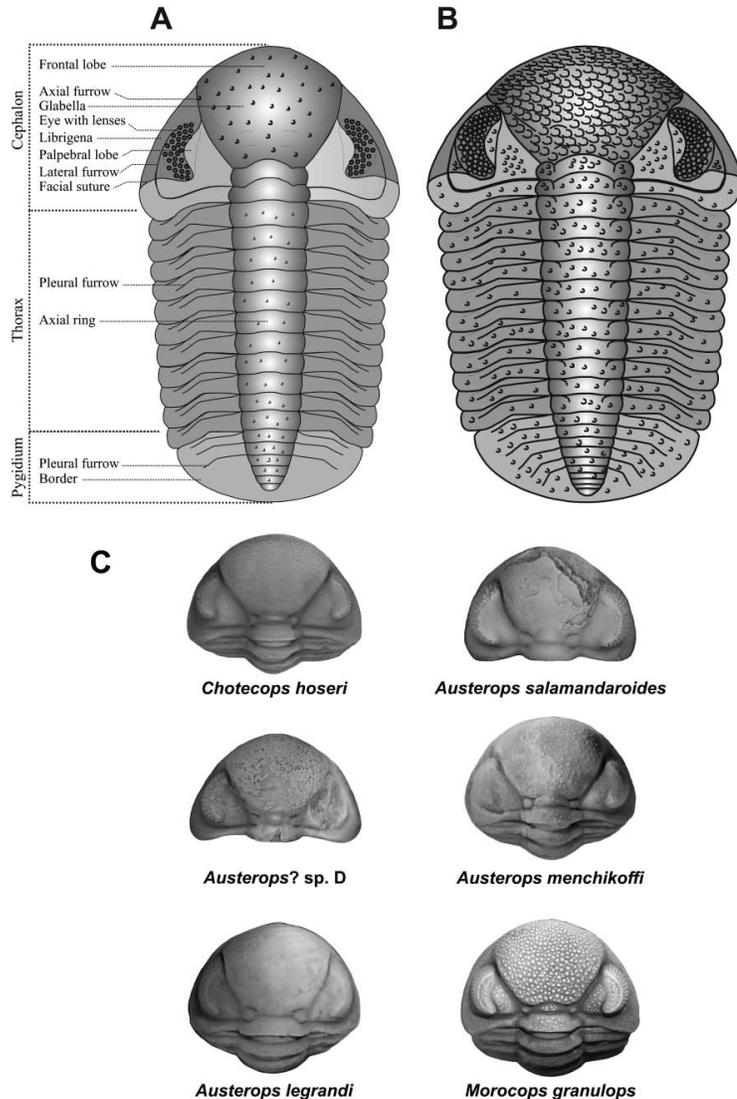


Figure 1. Phacopid trilobite exoskeleton showing major anatomical features. A, reconstructed exoskeleton showing a glabella with sparse and fine tubercles, and subangular anterolateral angles; preoccipital lobes with subquadrate lateral nodes not differentiated from median part; glabellar furrows (S2 and S3) poorly defined; eye with 14 vertical lens files and a thick interlensar sclera; pygidium with six well-defined rings and shallow pleural furrows. B, reconstructed exoskeleton showing a glabella with dense and coarse tubercles which are modified anteriorly into scale-like tubercles, and with 'drawn out' anterolateral angles; preoccipital lobes with subcircular lateral nodes separated from median part by a strong exsagittal furrow; glabellar furrows (S2 and S3) relatively well developed; eye with 19 vertical lens files and a thin interlensar sclera; pygidium with 10 well-defined rings, deep pleural furrows, and tubercles moderately developed on pleural ribs, border and axis. C, some of the studied taxa.

Among Devonian trilobites, phacopids are widespread in Lower and Middle Devonian strata, particularly in Morocco and Algeria where outcrops provide incredibly well-preserved material with an outstanding diversity of form in the family Phacopidae (McKellar & Chatterton 2009; Khaldi *et al.* 2016; Crônier *et al.* *in press*). McKellar & Chatterton (2009) explored the phylogenetic relationships between some phacopid genera using a cladistic analysis. They took into consideration many of the genera recognized in the family, including *Austerops* McKellar & Chatterton, 2009, with all four species they assigned to the genus. *Austerops* appears to be monophyletic and close to *Chotecops* (Chlupae 1971). However, McKellar & Chatterton erected *Austerops* for a small group of Moroccan phacopids sharing a small number of synapomorphies (i.e. subdued and sparse tubercles, faint palpebral furrow, prominent and continuous terrace lines upon the cephalic doublure; see McKellar & Chatterton 2009; Khaldi *et al.* 2016) (Fig. 1). Although McKellar & Chatterton (2009) noted that, at first sight, the species of *Austerops* might be placed in *Phacops* or other existing genera, they stated that doing so would render these genera polyphyletic if their phylogenetic tree is correct.

As *Chotecops* and *Austerops* appear stratigraphically close to each other in the fossil record, and because McKellar & Chatterton assumed a similarity between the two genera, it seems appropriate to perform a new cladistic analysis taking into account the four species added to *Austerops* since 2009 (described by Khaldi *et al.* 2016 and Crônier *et al.* *in press*), as well as the species used by McKellar & Chatterton (2009). Additionally, two newly reported occurrences of *Austerops* from the Eifelian of the Ardennes area (south-eastern Belgium), outside North Africa (van Viersen *et al.* 2017), have been included. Not all of the species now included in *Austerops* appear to share all of the synapomorphies previously defined, and thus clearly challenge the claimed monophyly of the genus.

Additionally, as the species of *Austerops* may be placed in *Phacops* or other existing genera (McKellar & Chatterton 2009), seven other close relatives assigned to *Reedops* Richter & Richter, 1925, *Boeckops* Chlupae, 1972, *Morocops* Basse, 2006, *Paciphacops* (*Paciphacops*) Maksimova, 1972, *Phacops* Emmrich, 1839, and *Pedinopariops* Struve, 1972 have been included in order to test the monophyly of *Austerops*.

In the present study we perform a cladistic analysis on 24 species assigned to 11 genera. The aims of the study are to: (1) test the monophyly of the genus *Austerops*; (2) identify the diagnostic characters – if any – of the genus; and (3) provide a preliminary test of relationships between species assigned to *Austerops* and also between *Austerops* and close relatives.

Data set

Ingroup selection

Austerops is known from 11 well-preserved species, most of them from Morocco and Algeria but two from Belgium (Fig. 2). The Moroccan specimens used in our analysis, from the El Oufal Formation in the Tindouf, Ma'ader and Tafilalt basins, were well described by McKellar & Chatterton (2009) and belong to *Austerops punctatus* from the Emsian (see van Viersen *et al.* 2017, p. 58), and to *A. kermi* and *A. salamandar* from the Eifelian. Algerian specimens from the Ougarta Basin were collected by Algerian co-workers (Y. Khaldi of Oran University and A. Abbache of Mascara University). Species represented are *Austerops legrandi* Khaldi *et al.*, 2016, *A. menchikoffi* (Le Maître, 1952) (*Phacops smoothops* Chatterton *et al.*, 2006; see Khaldi *et al.* 2016) and *A. speculator* (Alberti, 1970), all described by Khaldi *et al.* (2016) from the upper Emsian Chefar el Ahmar Formation in the Erg el Djemel section; and *A. salamandaroides*, *A. sp. B* and *A. sp. D*, newly described by Crônier in Crônier *et al.* (*in press*) from the lower Eifelian Chefar el Ahmar Formation in the Ouarourout I section. Ardennes specimens, from the Eifelian of the southern margin of the Dinant Synclinorium, were well described by van Viersen *et al.* (2017) and belong to *Austerops couvinensis* and *A. hottonensis*.

Anatomical elements of most of these species were described and coded from examination of specimens, completed by literature data (McKellar & Chatterton 2009); the Belgian species were coded exclusively from van Viersen *et al.* (2017). As the relationship between *Austerops* and *Chotecops* is quite ambiguous, two species of *Chotecops*, *C. auspex* (Chlupae, 1971) and *C. hoseri* (Hawle & Corda, 1847), were included.

Furthermore, as species of *Austerops* may be placed in *Phacops* or other existing genera (see McKellar & Chatterton 2009 for a previous cladistic analysis), seven other close relatives, including four well-preserved Moroccan species, have been included in order to test the monophyly of *Austerops*. These species are: *Reedops cephalotes hamlagdadianus* Alberti, 1983 from the Pragian of Morocco (Hamar Laghdad, near Erfoud); *Boeckops stelcki* McKellar & Chatterton, 2009 from the Emsian of Morocco (Taharajat d'Oufatene, near Alnif); *Morocops granulops* (Chatterton *et al.*, 2006) from the Emsian of Morocco (Jbel Gara el Zguilma, near Fom

Zgaid); *Paciphacops* (*Paciphacops*) *logani* (Hall, 1861) from the Emsian of the USA (Helderberg of New York); *Phacops latifrons* (Emmrich, 1839) from the Eifelian of Germany (Gerolstein); *Phacops araw* McKellar & Chatterton, 2009 from the Eifelian of Morocco (Jbel Oufatene near Lahfira); and *Pedinopariops* (*Hypsipariops*) *vagabundus* Struve, 1990 from the Givetian of Morocco (Jbel Issoumour, near Alnif).

Like McKellar & Chatterton (2009), we decided also to include *Acernaspis orestes* (Billings, 1860) and *Ananaspis fecunda* (Barrande, 1846), two well-documented species belonging to genera erected by Campbell (1967) and commonly viewed as the closest ‘ancestors’ to *Phacops* and its relatives (e.g. *Austerops*, *Chotecops*).

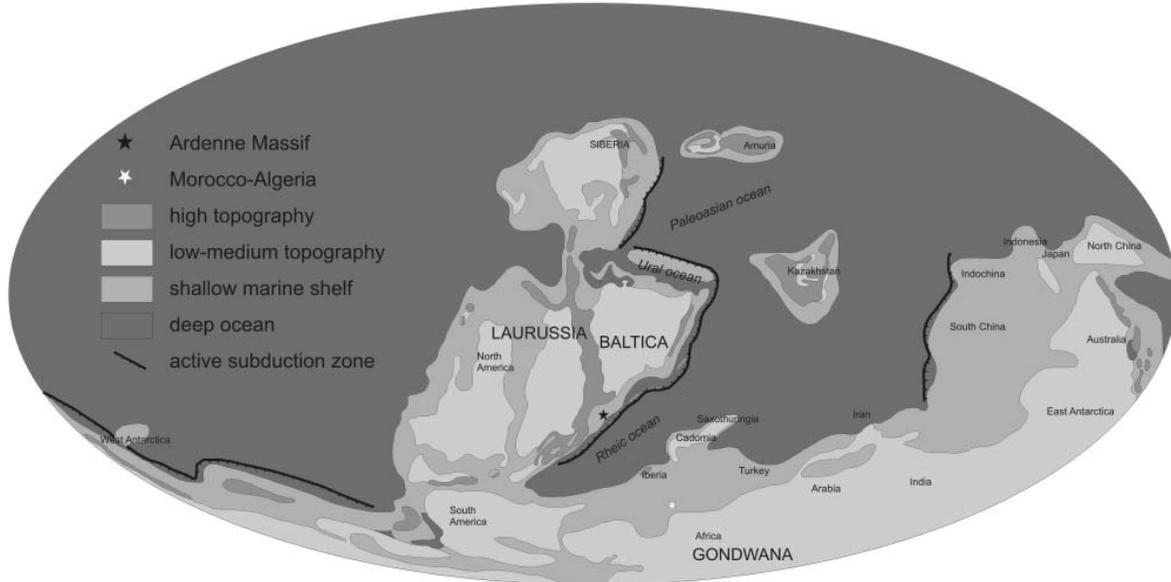


Figure 2. Palaeogeographical map of the Early Devonian (401 Ma) with the location of the Ardenne Massif area (black star) and Morocco/Algeria (white star). Modified from Golonka & Gaweda (2012).

Characters utilized

Sixty-three characters were selected for the data matrix (Supplemental Table 1), 47 characters from the cephalon, 15 from the pygidium and one from the thorax. The thorax is unknown in some species, particularly *Austerops salamandaroides*, *A.* sp. B, and *A.?* sp. D, which are represented only by disarticulated sclerites. The pygidium is not known for the latter two species, and for other species was coded without overweighting it with an excessive number of characters. Figure 1 shows some morphological characters for some studied phacopid taxa in the present analysis.

Characters and character states

Morphological terminology mainly follows Crônier *et al.* (2011). We used some characters and characters states defined by McKellar & Chatterton (2009). All characters and their different states are described in Supplemental Table 2. The following abbreviations have been used: exsag., exsagittal; sag., sagittal; tr., transverse; L0–L1, occipital and preoccipital lobes; S0–S3, for glabellar furrows; abax., abaxially; adax., adaxially.

Outgroup selection

As Phacopidae is considered by some workers to be the sister group of Pterygomtopidae (see McKellar & Chatterton 2009 among others), two Late Ordovician members of the latter family were chosen as the outgroup: *Calyptaulax glabella* G. A. Cooper, 1930 and *C. callirachis* (B. N. Cooper, 1953). Unlike McKellar & Chatterton (2009), we decided to include *C. callirachis* in the analysis, as well as *C. glabella* because it is more completely known. Two species were thus used as outgroups.

Methods

Analytical protocols

We submitted our data matrix (Supplemental Table 1) to a parsimony analysis and used a heuristic search (tree bisection and reconnection, TBR) with simple addition sequence replicates, using the software PAUP*4.0a152 (Swofford 2002) to obtain the most parsimonious trees. As branch length is not used as subsequent information, synapomorphies are optimized under delayed transformation assumption (DELTRAN) in order to reduce ambiguous synapomorphies on internal nodes (Bignon & Crônier 2014). In this cladistic analysis, the weight of all characters is equal. Character states are neither oriented nor ordered. When we were not able to choose only one state for a given character, we decided to use multistate character coding. As these multistate characters imply uncertainties in the coding scheme, they were treated as unordered and uncertain. Node robustness was tested using Bremer support (Bremer 1988) and bootstrap support (Felsenstein 1985) from 100 replicates. We define *Calyptaulax glabella* and *C. callirachis*, the putative ‘ancestor’ of Phacopidae, as a paraphyletic outgroup and leave the rest of the non-*Austerops* genera free in order to see how they will be placed into the phylogenetic tree.

Results

Phylogenetic analysis

The parsimony analysis of our data matrix (Supplemental Table 1) produced two most parsimonious trees (MPTs) (Fig. 3) of 341 steps with a consistency index (CI) of 0.44, a consistency index excluding uninformative characters of 0.43, a rescaled consistency index (RC) of 0.21 and a retention index (RI) of 0.48. Apomorphic (without autapomorphic) character states at nodes are indicated in Figure 3. Of 63 characters, three are parsimony-uninformative and 60 are informative. These trees show no great differences: only the relationships between two basal taxa (i.e. *Acernaspis orestes* and *Calyptaulax glabella*) are modified and they constitute either a monophyletic group or a paraphyletic group, but the phylogenetic location of the youngest taxa (i.e. *Ananaspis*, *Reedops*, *Chotecops*, *Austerops* *Boeckops*, *Morocops* and *Phacops*) remains unchanged.

In these MPTs (Fig. 3, values indicated at nodes refer to their Bremer support), the relationships between *Chotecops* and *Austerops* are unresolved: the two species of *Chotecops* (*C. hoseri* and *C. auspex*) are dispersed among the species of *Austerops*. It seems that these two genera are phylogenetically close to each other. According to these trees, some relationships among species of *Austerops* are resolved (exclusive synapomorphies are underlined): (1) *A. hottonensis* appears basal within the group comprising *Chotecops* sensu lato and other *Austerops*; (2) *A. menchikoffi*, *A. speculator* and *A. punctatus* are close to each other, constitute a group sustained by a weak Bremer support of 1 and by two apomorphies (characters 12₁ and 62₀: ‘pygidial sculpture with subdued tubercles developed on pleural ribs and axis’), and appear as sister group to the group formed by the rest of *Austerops* and *Chotecops*, excluding *A. hottonensis*; (3) *A. kermiti*, *A. salamandar* and *A. salamandaroides* are close to each other, constitute a group sustained by a Bremer support of 2 and by four apomorphies (characters 5₁, 7₁, 50₂, and 62₂: ‘pygidial sculpture with subdued tubercles restricted to axis’, and appear as sister group to the group formed by *A. legrandi*, *A. sp. B*, *A.? sp. D*, *C. auspex* and *C. hoseri*; (4) *A. legrandi* appears basal, with the sister group comprising *C. auspex*, *C. hoseri*, *A. sp. B*, *A.? sp. D*; and (5) the clade composed of *C. auspex*, *h. hoseri*, *A. sp. B*, and *A.? sp. D* is sustained by a Bremer support of 2 and by five apomorphies (characters 1₃, 17₁, 43₂, 56₁ and 62₄: ‘pygidial sculpture with granules and pits’); within this clade *Chotecops hoseri* and *Austerops sp. B* are close to each other and constitute a clade supported by a Bremer support of 2 and by three apomorphies (characters 3₃, 16₁ and 40₂) according to these MPTs. As all of these clades have low Bremer support values and homoplastic character states, this result needs to be confirmed.

According to our data matrix, the clade composed of *Austerops* and *Chotecops* is the best supported, with a relatively strong Bremer support of 3 and by eight (for MPT₂) or nine (for MPT₁) apomorphies (characters 1₀, 6₁, 8₂, 12₂, 15₂, 22₂, 24₁, (34₁) and 40₁). The three exclusive synapomorphies are: ‘dense tuberculation/granulation on front of composite lobe, sparse or absent elsewhere’ (character 6₁); ‘subquadrate, not strongly inflated lateral preoccipital node, separated from median part of L1 by weak exsagittal furrow’ (character 12₂) and ‘subocular librigenal field below eye absent at front of eye and narrow toward back’ (character 40₁).

The *Austerops/Chotecops* clade represents the sister group to six close relatives (*Boeckops stelcki*, *Morocops granulops*, *Paciphacops* (*Paciphacops*) *logani*, *Phacops latifrons*, *Phacops araw* and *Pedinopariops* (*Hypsipariops*) *vagabundus*) (Fig. 3). Together, these two sister groups share 11 (for MPT₁) or 12 (for MPT₂) apomorphies (characters 3₂, 19₂, 25₂, 32₂, 33₁, 36₁, 43₁, 46₁, 47₁, (57₀), 59₁ and 63₂). The seven synapomorphies are: ‘maximum glabellar width (tr.) from 61% to 65%’ (character 3₂); ‘length ratio of

L2 relative to L3 50–59%’ (character 19₂); ‘marginulation extending backwards only to about opposite midlength of eye’ (character 33₁); ‘18 vertical lens files’ (character 36₁); ‘short scaly ridges medially and pits on cephalic doublure/ventral portion of anterior border’ (character 46₁); ‘posterior band of the cephalic doublure with anastomosing terrace ridges’ (character 47₁); and ‘height of pygidial axis tip declining but well-defined’ (character 63₂). In these most parsimonious trees, *Reedops cephalotes hamlagdadianus* appears basal to all other Devonian phacopids, as was also assumed by McKellar & Chatterton (2009).

Homoplastic characters

Among the 63 characters coded here, 37 are highly homoplastic, with CI values ranging from 0.200 to 0.455 (characters 1, 3, 7–11, 13–17, 23–26, 28, 29, 31, 33, 34, 36, 40, 41, 43, 48, 50–54, 56–59, 61, 63). A low CI (less than 0.5) tends to indicate that much homoplasy has occurred. To measure the eventual impact of these homoplastic characters in our cladistic analysis, we performed another analysis by removing from the matrix all the characters with a CI lower than 0.500. This new analysis gave 15,139 MPTs of 113 steps. Conflicts between these MPTs are represented in the 50% majority-rule consensus tree (Fig. 4), where values indicated at each node refer to bootstrap support values (only values > 50% are shown). This 50% majority-rule consensus tree shows some changes from the previous trees. *Austerops hottonensis* (which appeared as a basal taxon within *Austerops*) and *Chotecops sensu lato* now appear close to *A. kermiti* and *A. salamandar* (cf. Fig. 3). *Austerops menchikoffi*, *A. speculator* and *A. punctatus* are still close to each other, but constitute with *A. couvinensis* a group sustained by a strong bootstrap support of 100. The group formed by *Austerops legrandi*, *A. sp. B*, *A. ? sp. D*, *C. auspex* and *C. hoseri* is conserved but *A. legrandi*, which appeared as a basal taxon, is now replaced by *C. auspex*. The *Austerops/Chotecops* clade sustained by a strong bootstrap support of 100 is conserved and represents a sister group to five close relatives (*Boeckops stelcki*, *Morocops granulops*, *Phacops latifrons*, *Phacops araw* and *Pedinopariops (Hypsipariops) vagabundus*; cf. Fig. 3). In this MPT, *Reedops cephalotes hamlagdadianus* appears basal to all other Devonian phacopids excluding *Paciphacops (Paciphacops) logani*.

The removal of these characters from our data matrix leads to a partially unresolved phylogenetic hypothesis where four groups of taxa are present within the monophyletic group formed by *Austerops–Chotecops*. Suppressing these characters because of their degree of homoplasy means that we are weighting characters, so we selected optimal characters which may bias our analysis. Thus, the trees obtained by suppressing these characters are not the same as those obtained without excluding the characters, which means that there are not enough non-homoplastic characters to sustain the phylogenetic tree.

According to the 50% majority-rule consensus tree, *Chotecops auspex* appears as the ancestor of the group including three species of *Austerops*, suggesting that *Austerops* is paraphyletic. However, only two species of *Chotecops* were included in our analysis, and it would be relevant to add more species in order to see how this genus is placed in the phylogenetic tree. If *Chotecops* appears paraphyletic, a nomenclatural revision of its species would be required. But if this genus remains monophyletic and derived from *Austerops*, then *Austerops* would be paraphyletic and should be synonymized with *Chotecops*.

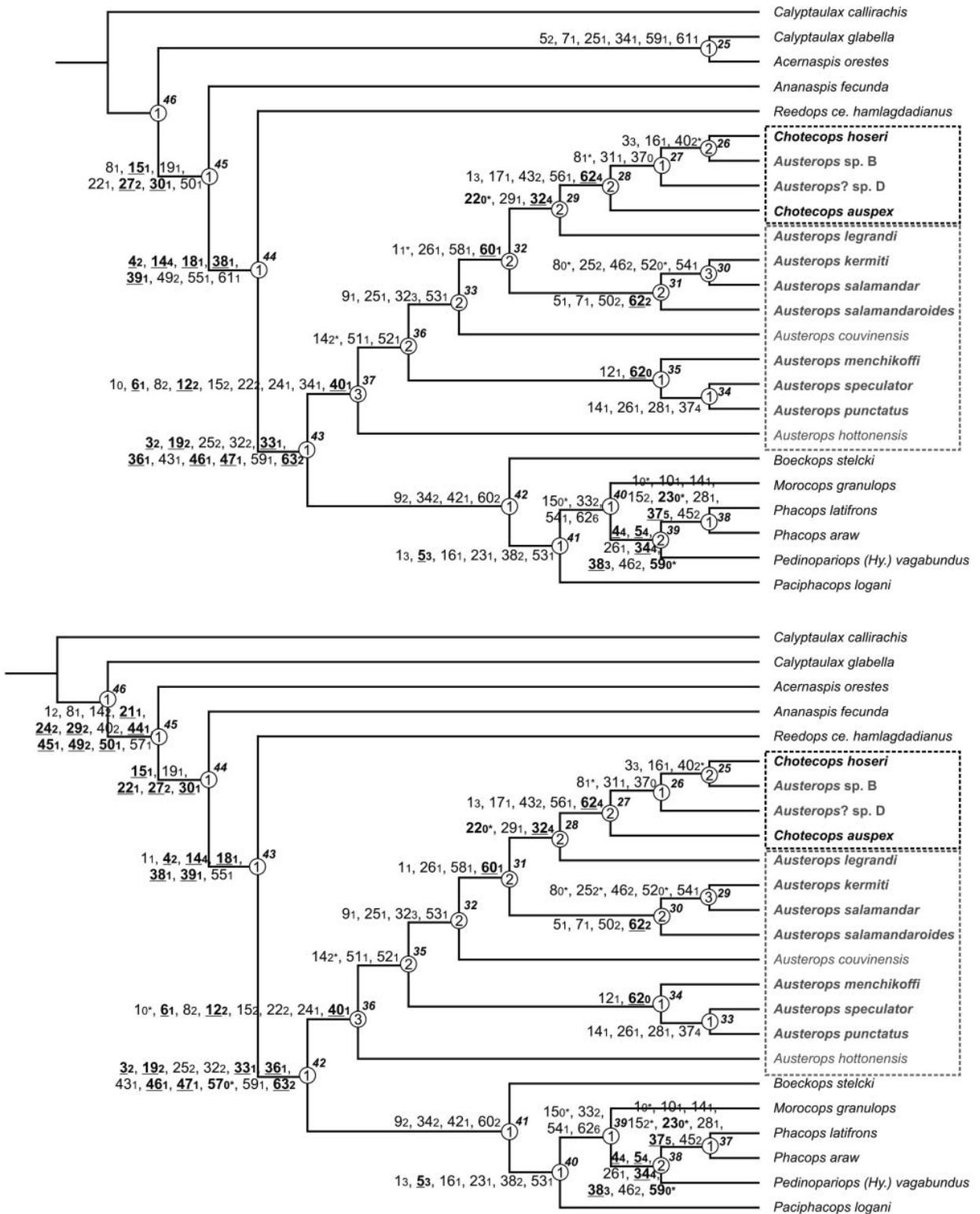


Figure 3. The two most parsimonious trees of 341 steps obtained from cladistic analysis (with the software PAUP^{4.0a159}) using *Calyptaulax callirachis* and *C. glabella* as outgroup taxa, and a heuristic search. Number of nodes (in italics), apomorphic (without autopomorphic) character states (in black), exclusive synapomorphies (underlined), reversed character states (with star), and Bremer support values (in white circles) are indicated. Belgian *Austerops* is in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

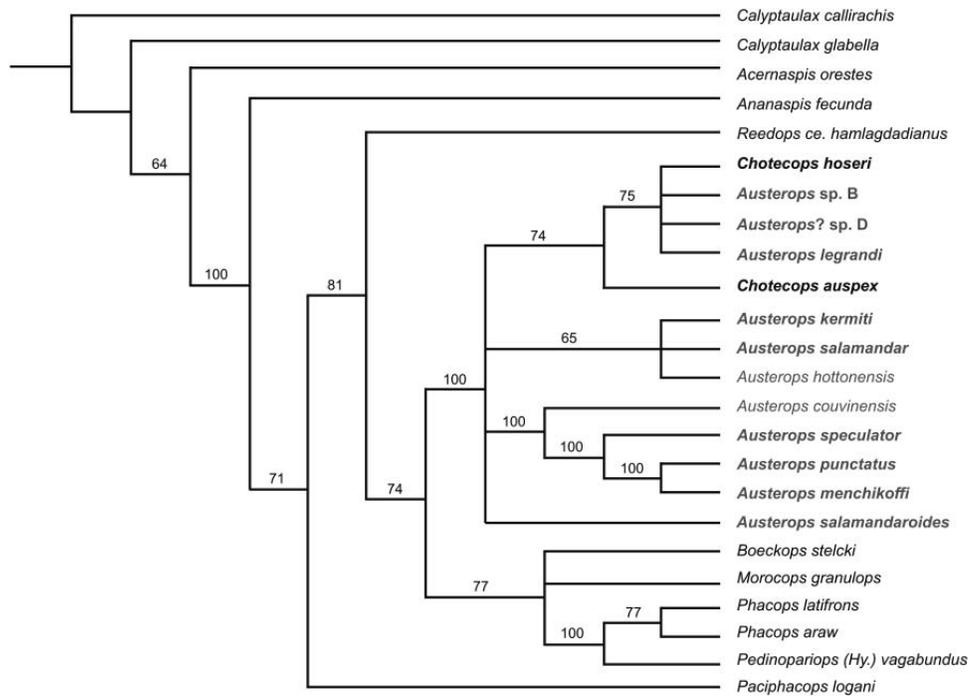


Figure 4. Majority-rule (50%) consensus tree of the 15,139 most parsimonious trees of 113 steps obtained from cladistic analysis by excluding all homoplastic characters with a consistency index lower than 0.500. Bootstrap support values (only values >50% are shown; from 100 replicates) are indicated on each node. Belgian *Austerops* in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

Multistate characters

Of the 63 characters selected in this study, 23 are multistate characters (characters 4, 5, 8, 9, 13, 16, 18, 20, 24, 26–28, 31, 37, 40, 43, 47, 50, 51, 53, 60, 62, 63). In our coding scheme, multistate characters refer to those for which it is not possible to determine the exact state for a given taxon (see Methods). Therefore, multistate characters are treated as unordered and uncertain, and not as polymorphic. As many characters were coded with multistate uncertainties, we considered that this might distort our results. To test this possibility, we excluded all those characters which show more than one state; 17 characters concern the cephalon and six the pygidium. An additional analysis excluding these 23 multistate characters from the data set provided 15 MPTs of 209 steps. Conflicts between these 15 MPTs are represented in the 50% majority-rule consensus tree (Fig. 5), where values indicated at each node refer to bootstrap support values (only values >50% are shown). This 50% majority-rule consensus tree shows several changes from the previous analysis. *Austerops hottonensis* (which appeared as a basal taxon within *Austerops*) and *Chotecops* sensu lato now appear close to *A. kermi* and *A. salamandar* (cf. Fig. 3). *Austerops menchikoffi*, *A. speculator* and *A. punctatus*, which appeared close to each other, now appear to be a paraphyletic group. Nevertheless, the group formed by *Austerops legrandi*, *A. sp. B*, *A.? sp. D*, *C. auspex* and *C. hoseri* is conserved and *A. legrandi* still appears as basal taxa. The *Austerops/Chotecops* clade, supported by a strong bootstrap value of 100, is conserved and represents the sister group to three close relatives (i.e. *Phacops latifrons*, *Phacops araw* and *Pedinopariops (Hypsipariops) vagabundus*) (cf. Fig. 3). *Chotecops* sensu lato still appears derived from *Austerops*.

As different results are obtained with and without excluding these multistate characters, it seems the uncertainties of our coding scheme impact the phylogenetic signal of our data matrix, and the incorrect choice of a character state between two possibilities could lead to incorrect results. The exclusion of these characters yields a topology that modifies the basal nesting structure. This suggests that taxon and character choice play a strong role in the topology that was recovered in this study.

Nevertheless, of the 40 non-multistate characters that remain in the data matrix, 20 are ‘?’ states representing unknown material. Further well-preserved material would allow better coding and may lead to changes within the relationships so far established.

Continuous characters

Among the 63 characters coded here, eight involve ratios that display continuous variation. In order to transform this continuum into discrete classes, we divided them arbitrarily into 5% increments (characters 1, 3, 13, 14, 19, 49, 52, 53). To test the eventual impact of these continuous characters in our cladistic analysis, we performed another analysis by removing from the matrix all the characters divided into 5% increments. This new analysis gave three MPTs of 275 steps. Conflicts between these MPTs are represented in the strict consensus tree (Fig. 6). This strict consensus tree shows few changes from the previous trees. The relationships between *Chotecops* and *Austerops* remain unchanged (cf. Fig. 3). The only significant change is based on the position of *Paciphacops* (*Paciphacops*) *logani*, which had appeared close to other Devonian phacopids (i.e. to the group formed by *Morocops granulops*, *Pedinopariops* (*Hy.*) *vagabundus*, *Phacops latifrons* and *Phacops araw*) but now appears close to *Ananaspis fecunda*, a Silurian phacopid, and these two taxa constitute a sister group of Devonian phacopids. Consequently, this result suggests that our procedure does not play a strong role in the topology recovered in this study.

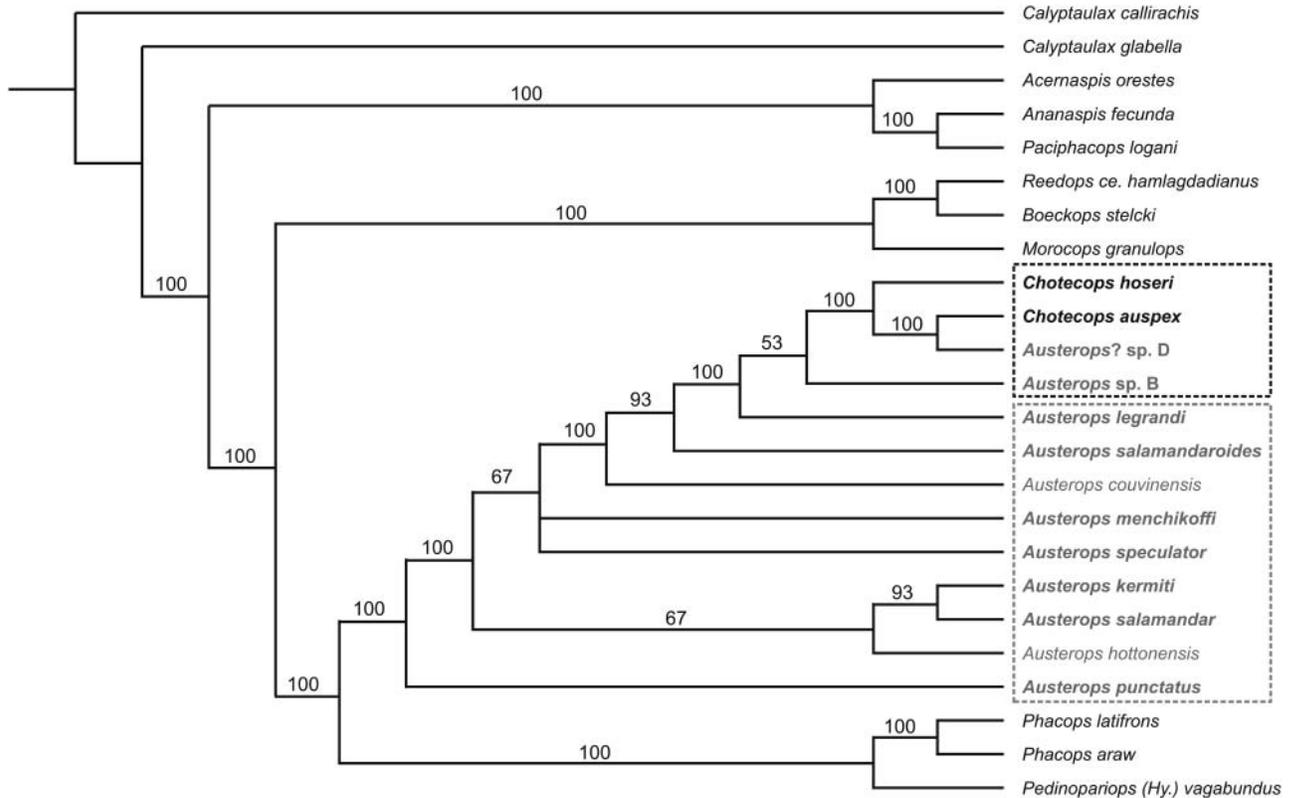


Figure 5. Majority-rule (50%) consensus tree of the 15 most parsimonious trees of 209 steps obtained from cladistic analysis by excluding all characters which present two or more multistate uncertainties. Bootstrap support values (only values >50% are shown; from 100 replicates) are indicated on each node. Belgian *Austerops* in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

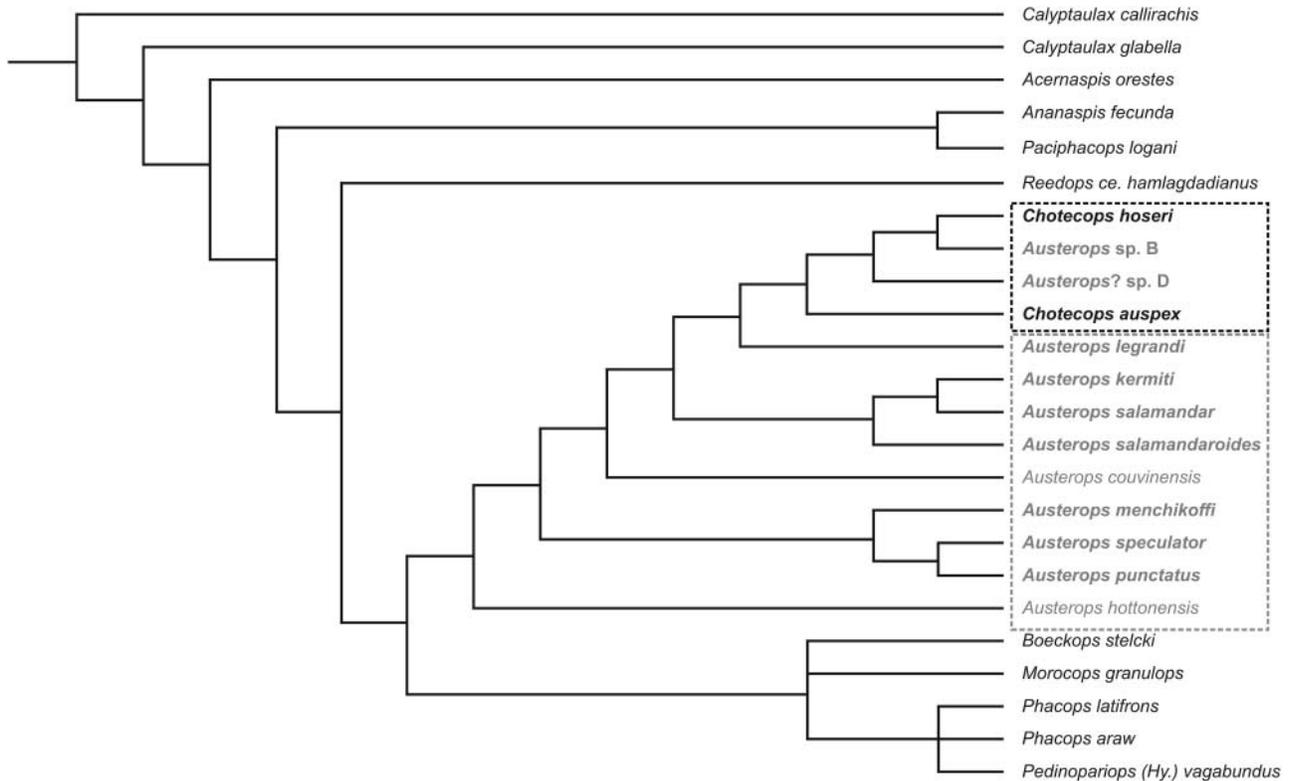


Figure 6. Strict consensus tree of the three most parsimonious trees of 275 steps obtained from cladistic analysis by excluding continuous characters divided into 5% increments. Belgian *Austerops* in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

Pygidial characters

Of the 63 characters coded in this study, 15 are from the pygidium and one is from the thorax. However, the pygidium and thorax remain unknown for *Austerops* sp. B and *A.?* sp. D, and this lack of information may bias our results. Additionally, of the 47 cephalic characters, nine are ‘?’ states. This lack of information, which persists even after removing characters from the pygidium, may bias also our results. In order to test this possibility, we excluded the characters from the thoracopygon from our data matrix and performed an additional cladistic analysis. The analysis recovered three MPTs of 259 steps. The strict consensus tree (Fig. 7) shows one substantial change from previous analyses. If the relationships between *Chotecops* and *Austerops* remain unchanged, those between *Paciphacops* (*Paciphacops*) *logani* and *Morocops granulops* are modified: *Paciphacops* (*Paciphacops*) *logani*, which appeared basal to the group formed by *Morocops granulops*, *Pedinopariops* (*Hy.*) *vagabundus*, *Phacops latifrons* and *Phacops araw*, is now with *Morocops granulops*, a sister group of the group formed by *Pedinopariops* (*Hy.*) *vagabundus*, *Phacops latifrons* and *Phacops araw*. *Morocops granulops* now appears to be basal with *Paciphacops* (*Paciphacops*) *logani*, and all of these taxa constitute a sister group of *Boeckops stelcki*.

Although the relationships between *Chotecops* and *Austerops* remain unchanged, pygidial characters are commonly used to define and differentiate genera. Excluding these characters from our analysis may thus introduce bias, especially to nest the intergeneric relationships. Consequently, results obtained by excluding characters from the pygidium suggest the major role of cephalic characters in the topology recovered in this study.

Missing characters

Of the 17 taxa, five are known from incomplete specimens: data are currently missing for the free cheeks and thorax of *Calyptaulax glabella*, for the pygidium (poorly illustrated) of *Phacops latifrons*, for the pygidium (not preserved) and cephalon (incompletely preserved) of *Austerops* sp. B and *A.?* sp. D, and for the cephalic doublure of *A. hottonensis*. This lack of information may bias our results. Consequently, additional well-preserved material would be necessary to confirm or invalidate these relationships. In order to test the possibility

of bias due to missing data, we excluded these five taxa from our data matrix and performed an additional cladistic analysis. The analysis recovered one MPT of 290 steps (Fig. 8). Of 63 characters, five are parsimony-uninformative and 58 characters are informative. The exclusion of these taxa, and especially one of the two outgroup taxa, yields a topology that modifies the basal relationships from the previous analysis. This suggests that taxon and character choice play a strong role in the topology that was recovered in this study, as previously suggested by deletion of multistate characters. Nevertheless, according to this MPT, relationships among species of *Austerops* seem to be partially resolved and two main groups remain unchanged within *Austerops-Chotecops* (Fig. 8; cf. Fig. 3): (1) *A. menchikoffi*, *A. speculator* and *A. punctatus*, which appeared close to each other, now appear to be a paraphyletic group; (2) *A. kermi*, *A. salamandar* and *A. salamandaroides* constitute a monophyletic group (defined by one exclusive synapomorphy ‘character $\underline{2}_1$, i.e. ‘tubercles weak/subdued on glabella’) with a strong Bremer support of 6, and appear as sister group to the group formed by *A. legrandi* and *Chotecops*; (3) *C. hoseri* and *C. auspex* are close to each other and constitute a monophyletic group that is supported by a strong Bremer value of 6 and one exclusive synapomorphy: ‘granules and pits on pygidium’ (character $\underline{62}_4$); and (4) in this tree, *Chotecops* appears derived from *Austerops legrandi*. The relationships between *Chotecops* and *Austerops* seem to be partly resolved: the two species of *Chotecops* (i.e. *C. hoseri* and *C. auspex*) appear the most derived taxa from *Austerops*. *Austerops* would be paraphyletic and should be synonymized with *Chotecops*.

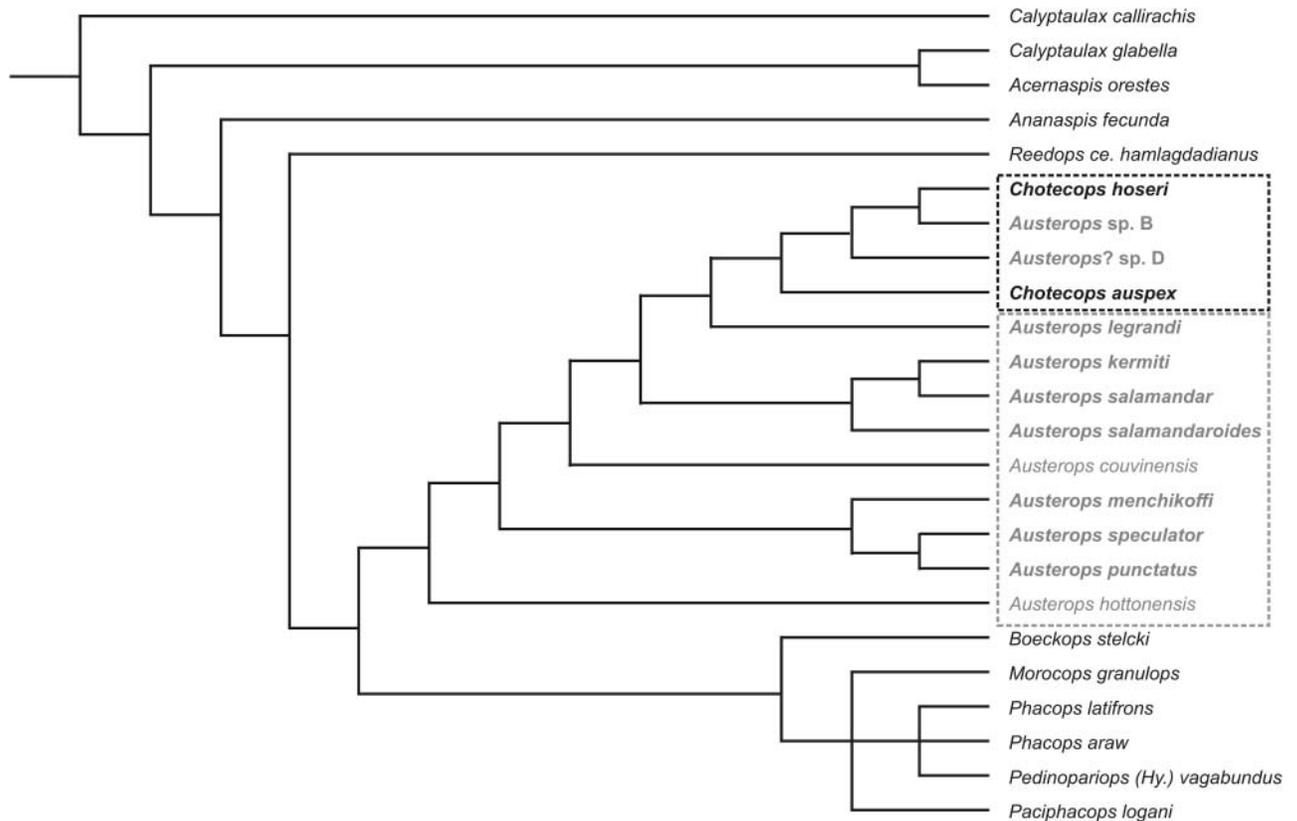


Figure 7. Strict consensus tree of the three most parsimonious trees of 259 steps obtained from cladistic analysis by excluding thoracopygidial characters. Belgian *Austerops* in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

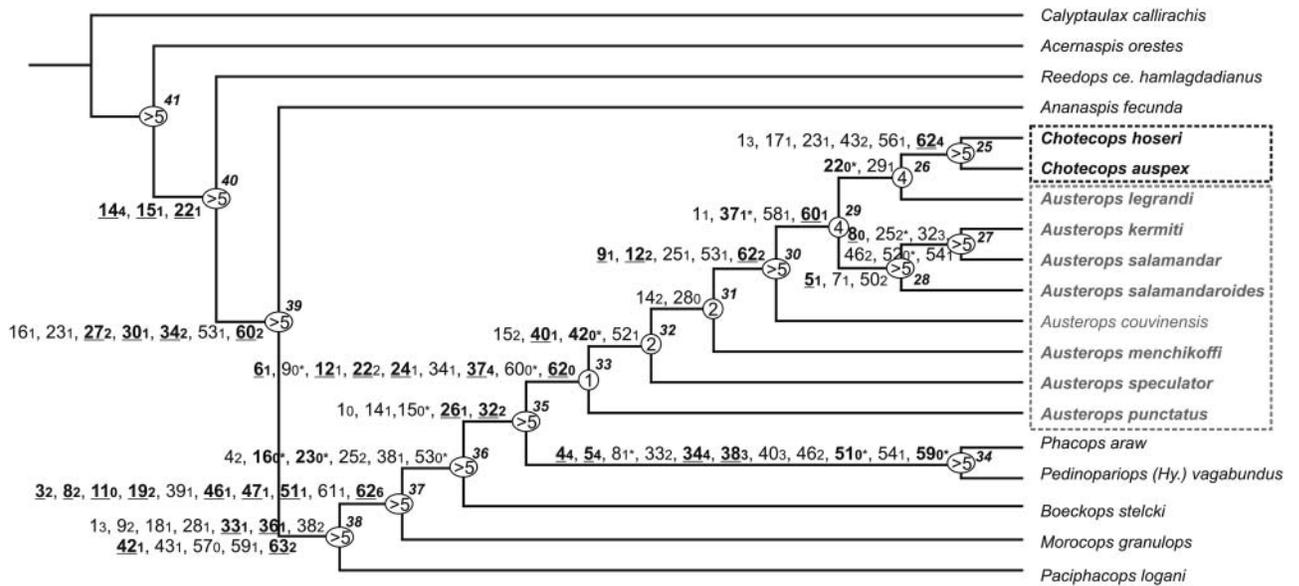


Figure 8. One of the most parsimonious trees of 290 steps obtained from cladistic analysis by excluding five poorly known taxa (*Calyptaulax glabella*, *Phacops latifrons*, *Austerops* sp. B, *A.?* sp. D and *A. hottonensis*). Number of nodes (in italics), apomorphic (without autapomorphic) character states (in black), exclusive synapomorphies (underlined), reversed character states (with star) and Bremer support (in white circles or ovals) are indicated. Belgian *Austerops* in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

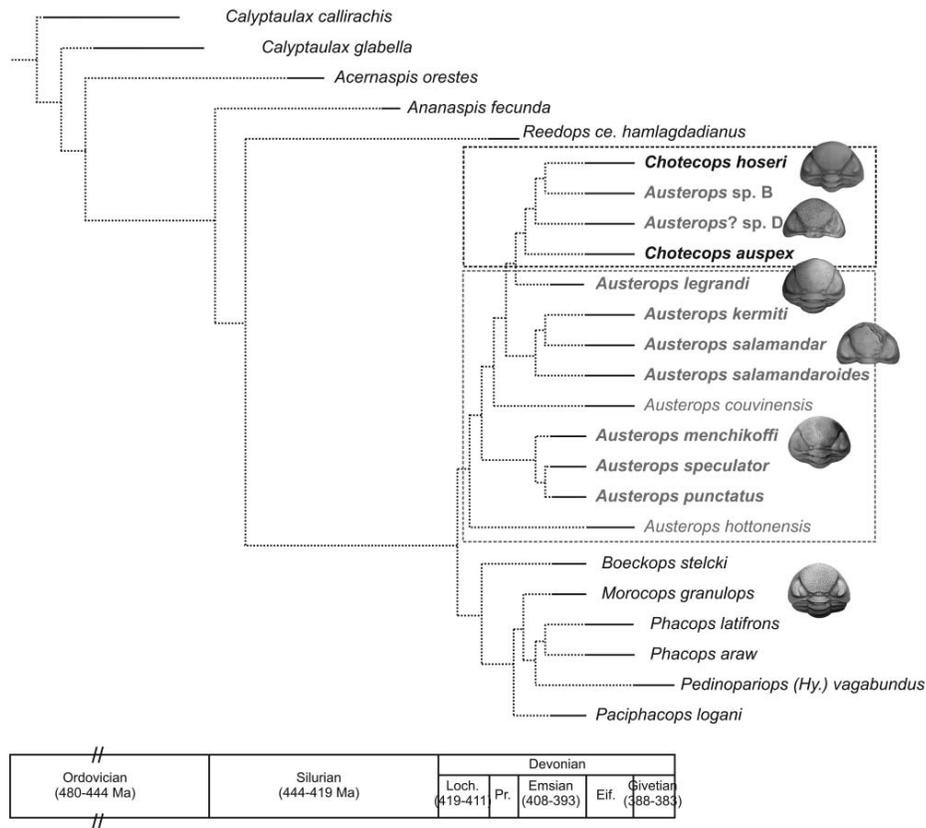


Figure 9. Comparison of stratigraphical data and phylogenetic branching from one of the two most parsimonious trees of 341 steps (cf. Fig. 3) obtained from cladistic analysis using *Calyptaulax glabella* and *C. callirachis* as outgroup taxa. Belgian *Austerops* in grey, North African *Austerops* in bold grey, *Chotecops* in bold black.

Relationships between *Chotecops* and *Austerops*

The MPTs obtained by deleting some characters (Figs 4–8) or not (Fig. 3) reveal partly resolved relationships between *Chotecops* and *Austerops*. These two genera are very similar morphologically, as shown by the features on which they were diagnosed (Supplemental Table 3) and by our data matrix (Supplemental Table 1), and it seems that the differences between the genera are subjective. In our study, every cladistic analysis recovers *Austerops* as a grade within the *Chotecops-Austerops* clade. There appears to be no compelling evidence for *Austerops* being monophyletic. Nevertheless, our analysis did not include enough species of *Chotecops* to test adequately its phylogenetic relationship with *Austerops*. Additionally, *Austerops* sp. B and *A.*? sp. D are less well known, with no information available on the pygidium and the thorax, and it is possible that the inclusion of such morphological information may change the outcome of an analysis.

Stratigraphical consistency

Comparison of stratigraphical occurrences (i.e. Last Appearance Datum (LAD) and First Appearance Datum (FAD)) of taxa with the order of successive phylogenetic branching events (Fig. 9; cf. Fig. 3) shows some congruence between the two sets of data, when all taxa and characters are included in the phylogenetic analysis. The two better defined clades are also the ones most consistent with the stratigraphical data, especially for North African taxa: the group defined by *Austerops menchikoffi*, *A. speculator* and *A. punctatus*, which constitutes a sister group of the one formed by the rest of *Austerops* (excluding *A. hottonensis*), and which appears to be basal, is also older; *Austerops legrandi*, which appears to be basal to the clade defined by *Chotecops* and *A.*? sp. D and *A.* sp. B, is also older. In the case of the two Belgian species *A. couvinensis* and *A. hottonensis*, their stratigraphical occurrences in the Eifelian are not consistent with the phylogenetic results, in which they appear basal and relatively independent. However, the newly discovered *Austerops hottonensis* and *A. couvinensis* are known from few specimens characterized by numerous autapomorphic characters (e.g. ‘median portion of vincular furrow subangular in outline’, character 44₂; ‘pits only on pygidium’, character 62₅) and plesiomorphic characters (e.g. ‘occipital ring ratios of 34–36%’, character 14₄; ‘marginulation extending virtually to genal angle’, character 33₂; ‘hypostomal suture convex forwards medially’, character 45₀) and it is possible that the inclusion of additional, closely related species that have yet to be discovered may change the outcome of our analyses.

Systematic palaeontology

Order Phacopida Salter, 1864

Family Phacopidae Hawle & Corda, 1847

Subfamily Phacopinae Hawle & Corda, 1847

Genus *Austerops* McKellar & Chatterton, 2009

Type species. *Austerops kermi* McKellar & Chatterton, 2009.

Additional species. *Austerops couvinensis* van Viersen *et al.*, 2017; *A. hottonensis* van Viersen *et al.*, 2017; *A. legrandi* Khaldi *et al.*, 2016; *A. menchikoffi* (Le Maître, 1952); *A. punctatus* (McKellar & Chatterton, 2009); *A. salamandar* McKellar & Chatterton, 2009; *A. salamandaroides* Crônier in Crônier *et al.*, in press; *A. speculator* (Alberti, 1970); *Austerops* cf. *couvinensis* van Viersen *et al.*, 2017; *A.* cf. *menchikoffi* of van Viersen *et al.* (2017); *A.* sp. B Crônier in Crônier *et al.*, in press; *A.*? sp. D Crônier in Crônier *et al.*, in press. *Austerops lemaitreae* (see van Viersen *et al.* 2017, p. 58) mentioned in an unpublished student dissertation is not a valid name; it was subsequently published under the name *Austerops legrandi* by Khaldi *et al.* 2016.

Diagnosis. Cephalic sculpture of low, sparse tubercles becoming more dense anteroventrally (coalescing into discontinuous terrace ridges in some species), and fading upon lateral surfaces; cephalic doublure with prominent terrace ridges continuous across most of surface. Eyes large to very large, with 16 to typically 18 dorsoventral files with seven up to 10 lenses per row, and thin interlensar sclera that thickens slightly dorsally; subocular and postocular pads weakly demarcated and form very narrow bands due to size of eye; lateral border furrow effaced. Glabella bulbous or gently sloping, but with minor anterior projection; divergence angle of frontal lobe usually 55–65°. Lobes and furrows effaced; S2 and S3 very faint; S1 fading medially, but deep laterally; L2 and L3 relatively flat; palpebral furrows faint or absent; ventral border non-marginulate; vincular furrow ranging from deeply incised to shallow in some species. Thorax and pygidium with subdued sculpture

isolated to dorsal extremes, and with weakly defined lateral axial lobes and pleural ribs; pygidium with prominent inter-annular rings (from van Viersen *et al.* 2017).

Occurrence. *Austerops* is recorded with certainty from the upper Emsian to the Eifelian in Morocco and Algeria, the upper Emsian of France, and the Eifelian of Belgium.

Remarks. *Austerops* was erected by McKellar & Chatterton (2009) for a group of Moroccan phacopids with subdued and sparse tubercles, a faint palpebral furrow, and prominent and continuous terrace ridges on the cephalic doublure. According to van Viersen *et al.* (2017), *Austerops* shows some variation in eye size and position associated with a trend of increasing eye size. However, as our phylogenetic study provides evidence for considering *Austerops* not a monophyletic group but a grade within the *Chotecops-Austerops* clade, it seems that the diagnostic characters of *Austerops* are actually diagnostic characters of the broader *Austerops-Chotecops* clade. Nevertheless, as our analysis did not include enough species of *Chotecops* to test adequately its phylogenetic relationship with *Austerops*, we decided to keep *Austerops* as it is until more well-preserved *Chotecops* are sampled and included in new maximum parsimony analyses. Most of the species have a northern Gondwanan distribution (i.e. North Africa), except for two Belgian species from the middle Eifelian occurring in Avalonia.

Genus *Chotecops* (Chlupac, 1971)

Type species. *Phacops (Chotecops) auspex* Chlupac, 1971.

Additional species. *Chotecops chlupaci*, Sandford, 2005; *C. despujolsi* (Richter & Richter, 1943); *C. ferdinandi* (Kayser, 1880); *C. glabrens* (Chlupac, 1977); *C. glabrens* spp. of Basse, 1998; *C. hassiacus* (Herrmann, 1911); *C. hoseri* (Hawle & Corda, 1847); *C. koeneni* (Holzapfel, 1895); *C. latissimus* (Holzapfel, 1895); *C. occidomaurus* (Alberti, 1981); *C. opitzi* Struve, 1985; *C. sollei* Struve in Flick & Struve, 1984; *C. spectabilis* (Meischner, 1965); *C. sterzeli* Struve, 1985; *C. successor* (Haas, 1968); *C. zizensis* (Alberti, 1983); *C. zofiae* Chlupac, 1993; *C.? breviceps* Barrande, 1846; *C.? erfoudensis* Richter & Richter, 1943; *C.? hyla* (Holzapfel, 1895); *C.? supradevonicus* (Frech, 1887).

Diagnosis. Glabella moderately inflated, gently overhanging or falling vertically to the anterior border furrow. S2 and S3 not impressed, S1 markedly shallowing or interrupted medially. Preoccipital ring not reduced medially; lateral preoccipital lobes flat. Eyes large to moderate in size; visual surface kidney shaped in outline. Palpebral area broad (tr.), flat; palpebral furrow weak; palpebral lobes flat. Vincular furrow continuous, commonly shallow medially, notched laterally. No coarse tuberculation on glabella. Sculpture on cephalon represented by granulation only, usually unequally distributed and lacking on some parts. Pygidium with narrow axis; pleural furrows narrow and shallow, rapidly weakening posteriorly; ribs flat; interpleural furrows indistinguishable (from Chlupac 1977).

Occurrence. *Chotecops* is recorded in the Pragian of Australia, the Emsian of Germany and Turkey, the Eifelian of the Czech Republic, Morocco and Algeria, and the Givetian of Germany and Poland. Some species tentatively assigned to *Chotecops* occur in the Middle Devonian of France and Upper Devonian of Morocco.

Remarks. *Chotecops* was erected by Chlupac (1971) for a group of phacopids with a glabella of relatively low convexity, subdued glabellar tuberculation, a raised preoccipital ring with flat L1 node, a relatively flat palpebral area and palpebral lobes, and a weakly segmented pygidium with rather shallow pleural furrows and pleural ribs remaining much lower. The concept of *Chotecops* was supplemented by Struve (in Flick & Struve 1984) by additional characters including a broadly rounded cephalic and pygidial outline, a rather long postocular area (length greater than 0.2 eye length), the relative height of the librigenae and visual surface (ratio 0.5–1.0), and generally 18 dorso-ventral files of lenses with a maximum of six lenses per file. Basse (2006, p. 80) followed Struve's (1972, 1995) concept of the genus and confirmed the distinction between *Chotecops* and the closely related *Arduennops* Struve, 1972, the latter characterized by coarser glabellar sculpture and a backwardly shifted visual complex. Otherwise, according to Feist *et al.* (2009), mid-Devonian representatives of *Chotecops* also have strongly vaulted posterior genae with weak palpebral furrows, poorly differentiated lateral occipital lobes, a narrow pygidial axis and sparse tuberculation. Campbell (1977) considered *Chotecops successor* (Haas, 1968) from the Emsian of Turkey as indicating an ancient derivation of *Chotecops* from *Phacops*, and *Chotecops chlupaci* described by Sandford (2005) from the Pragian of Victoria (Australia).

indicates an even older derivation.

Discussion

The phylogenetic relationships between North African species of *Austerops* suggested by our cladistic analyses are quite well supported: *A. menchikoffi*, *A. speculator* and *A. punctatus* are close to each other and reasonably constitute the sister group of a group formed by the rest of *Austerops* and *Chotecops sensu lato*, while the Belgian taxon *A. hottonensis* seems phylogenetically distant from other representative of this genus. The relationships between *Chotecops* and *Austerops* remain partly resolved:

C. hoseri, *C. auspex* and less-known taxa of *Austerops* (i.e. *A.* sp. B and *A.*? sp. D) are close to each other and may be derived from *Austerops legrandi*. In order to clarify this matter and to test the monophyly of *Chotecops* it would be relevant to include additional species of this genus, closely related genera – such as other species assigned to *Reedops* – and a wide range of derived genera in future analyses. Currently, the poorly known *Austerops* sp. B and *A.*? sp. D should, on the basis of this phylogenetic analysis, be reassigned to *Chotecops*. Some results of the present analysis suggest that separating *Chotecops* and *Austerops* creates paraphyletic genera, and if this is confirmed by further analysis with the inclusion of additional species of *Chotecops*, *Austerops* should be merged with *Chotecops* in order to create a monophyletic group.

Our cladistic analyses based on large numbers of morphological characters may have had some biases, but they produced resolved trees and proved capable of resolving phylogenetic relationships at a low taxonomic level in phacopid trilobites, due to the presence of sufficient morphological variability. Such data are further needed to evaluate the phylogenetic affinities of an increasing number of taxa and to establish the phylogenetic relationships at a higher taxonomic level for the family Phacopidae as a whole. The establishment of such phylogenetic relationships is a prerequisite to investigate macroevolutionary patterns in phacopid trilobites, infer their evolutionary processes, and estimate trait-dependent speciation and extinction rates from resolved phylogenies.

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Supplemental material

Supplemental material for this article can be accessed at <https://doi.org/10.1080/14772019.2018.1471105>.

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